OPUSCULA ZOOLOGICA

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OPUSCULA ZOOLOGICA

INSTITUTI ZOOSYSTEMATICI ET OECOLOGICI UNIVERSITATIS BUDAPESTINENSIS

Redacta ab

Á. BERCZIK et CS. CSUZDI

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Preface

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Almost one year ago, between August 25-31, 2019, we were glad to organize the 18th International Congress of Myriapodology, at the Hungarian Natural History Museum in Budapest. Ninety two scientific participants (plus 13 accompanying persons) arrived from 32 countries, all around the world. Only now, in the present pandemic situation, do we realize, how lucky we were that we could organize such a great congress.

The meeting was successful not only in the number of participants: During the four scientific days we had 48 lectures (including four invited plenary presentations) and 55 posters, which covered a wide range of the field of myriapodology, from the zoological subjects of morphology, anatomy, taxonomy, systematics, physiology, biogeography and nature conservation. We also had a joyful day excursion to the nearby Buda Hills, where participants could encounter some representatives of the local soil fauna.

In the name of the organizing committee we would like to thank our 16 Hungarian colleagues who helped to make the congress really enjoyable.

From the presentations, 11 scientific papers have already been published in a Special Issue of Zookeys (No. 930), and now we are presenting here another 7 papers. We are grateful to the editors of Opuscula Zoologica, Prof. Csaba Csuzdi and Prof. Árpád Berczik for providing the opportunity to publish this second volume of the cross-section of the 18th International Congress of Myriapodology.

Dr. László Dányi and Dr. Zoltán Korsós

Guest editors

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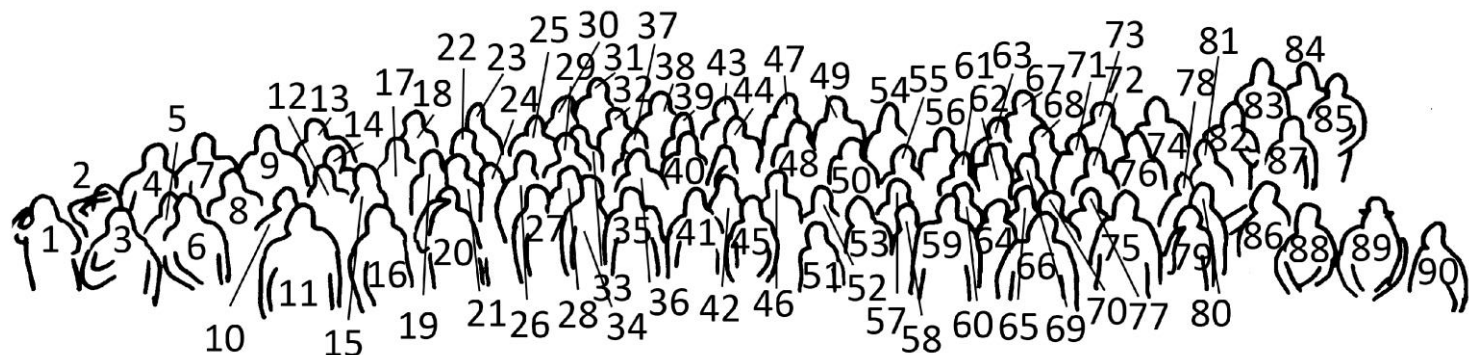
Group photograph of the 18th International Congress of Myriapodology, 25–31 August 2019, Budapest, Hungary

1 – Weixin Liu, 2 – Mengzhen Chen, 3 – Victor Carvalho Calvanese, 4 – Aleksandr Evsyukov, 5 – Fieng–Lan Sun, 6 – Hsueh–Wen Chang,,
7 – Jan Philip Oeyen, 8 – Žan Kuralt, 9 – Ivan Hadrian Tuf, 10 – Drazina Tvrtko, 11 – Andrej Mock, 12 – Ivan Kos, 13 – Sergei I. Golovatch,
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Arthropod segments and segmentation – lessons from myriapods, and open questions

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Abstract. The current understanding of the segmental organization of myriapods is dramatically different from the traditional views, due both to fresh research on a number of myriapod species and to progress in comparative developmental biology at large. In the late eighties, the emerging paradigm of ecdysozoan affinities of arthropods prompted a revisitation of the concept of the segment as an archetypical body unit. Fresh approaches to myriapod comparative morphology and pioneering studies on the developmental genetics of segmentation in *Strigamia maritima*, *Lithobius atkinsoni* and *Glomeris marginata* contributed to the definitive abandonment of the Articulata hypothesis and suggested a reformulation of the segment concept as the product of a functional integration between a number of distinctly repeated serial units, e.g. neuromeres, tergites, sternites. In the light of this refreshed interpretation of myriapod segmental architecture, we must reject the naïve views that (a) segment production is necessarily prior to segment patterning, (b) serial features evolve from polymerous and poorly patterned to oligomerous and strongly patterned series (Williston's law), and (c) the divide between embryonic and post-embryonic development is necessarily a major turning point in morphogenetic processes. Open questions remain, e.g. to which extent the production of serial structures along the main body axis of myriapods is multiplicative rather than sequential.

Keywords. Anamorphosis, developmental genetics, epimorphosis, saltational evolution, Williston's rule.

ARTHROPOD SEGMENTS – THE TRADITIONAL VIEW

Up to the last quarter of the XX century, the segmented nature of the main body axis of the Arthropoda was generally accepted as well understood, except perhaps for specific problems of homology, e.g. the debated nature of the terminal body units, customarily known as the acron and the telson and mostly regarded as nonsegmental.

According to the different perspectives from which it was considered, the segment was regarded as an archetypical module of arthropod body architecture, as a fundamental building block in development and also as an evolutionarily conserved trait shared by all Articulata, i.e. annelids, onychophorans, tardigrades and arthropods.

In this context, myriapods represented a study object of choice, for a number of reasons. First, because of the conspicuous articulation of their long trunk into serial units with numbers often exceeding those of all other extant arthropods (a female specimen of *Illacme plenipes* Cook & Loomis, 1928 with 192 (diplo)segments and 750 legs, thus approaching the target of the thousand legs according to which these animals are named in many languages, was described by Cook & Loomis 1928). Second, because of the modest degree of regional specialization within the trunk, a condition regarded as more primitive than e.g. the more extensive patterning (thorax and abdomen, at least) found in the hexapods. Third, because of the diversity of segmental patterns occurring in this lineage, including features not found in any other arthropod clade (Fusco & Minelli 2013, Minelli & Fusco 2013). An overview of these features follows here; the taxonomic arrangement of the myriapod taxa discussed in this article is given in Table 1.

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Table 1. Taxonomic arrangement of the myriapod taxa discussed in the text.

Chilopoda
 Scutigeromorpha: *Scutigera*
 Lithobiomorpha: *Lithobius atkinsoni* Bollman, 1887
 Craterostigmomorpha
 Scolopendromorpha: *Scolopendropsis bahiensis* (Brandt, 1841), *Sc. duplicata* Chagas-Junior, Edgecombe &
   Minelli, 2008
 Geophilomorpha
  Placodesmata
   Mecistocephalidae: *Mecistocephalus diversisternus* (Silvestri, 1919), *M. japonicus* Meinert, 1886,
    M. microporus Haase, 1887
  Adesmata
   Himantariidae: *Himantarium gabrielis* (Linnaeus, 1767), *Stigmatogaster subterraneus* (Shaw,
    1789)
   Oryidae: *Orphnaeus heteropodus* Lawrence, 1963
   Linotaeniidae: *Strigamia maritima* (Leach, 1817)
   Geophilidae: *Clinopodes flavidus* C.L. Koch, 1847
Diplopoda
 Penicillata
  Polyxenida: *Polyxenus lagurus* (Linnaeus, 1758)
 Chilognatha
  Pentazonia
   Limacomorpha
    Glomeridesmida
   Oniscomorpha
    Sphaerotheriida
    Glomerida: *Glomeris marginata* (Villers, 1789)
  Helminthomorpha
   Colobognatha
    Platydesmida: *Illacme plenipes* Cook & Loomis, 1928
    Siphonocryptida
   Eugnatha
   Merocheta
    Polydesmida: *Devillea, Dobrodesmus mirabilis* Shear, Ferreira & Iniesta, 2016,
     Nannaria conservata Chamberlin, 1940, *Polydesmus angustus* Latzel, 1884, *P.
     complanatus* (Linnaeus, 1761)
   Nematophora
    Chordeumatida
    Callipodida
    Stemmiulida
   Juliformia
    Julida: *Ommatoiulus moreleti* (Lucas, 1860), *Pachyiulus flavipes* (C.L. Koch, 1847)
    Spirostreptida
    Spirobolida
   incertae sedis: Siphoniulida
Pauropoda
Symphyla

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Dorsoventral mismatch. – The units serially repeated along the trunk of myriapods are mostly very different from the textbook idealized segment with dorsal and ventral sclerites (tergites and sternites, respectively) in 1 to 1 relationship, together with one pair of articulated limbs and perhaps one or more additional sclerites (pleurites) in lateral position between tergite and sternite. The most familiar example of departure from this scheme is found in millipedes (Diplopoda), the trunk of which – next to a legless collum and (generally) three units with one pair of legs each – features a more or less numerous series of units with two pairs of legs each. According to the group, the serial units corresponding to sets of two pairs of legs each are either restricted to the dorsal sclerites, or extended to also involve part or all of the lateral and ventral sclerites. In the Pentazonia, tergites and pleurites are not fused and the sternites are very small (Glomeridesmidae) or, more frequently, absent. Within the Helminthomorpha, tergites, pleurites and sternites (to which the stigmatic plates are attached) are generally separate only in the Colobognatha, while in the Eugnatha these units are more or less extensively fused. In the Chordeumatida, Callipodida and Stemmiulida, the trunk is formed by 'rings' in which sterna+stigmatic plates do not fuse with the pleuroterga (tergum+pleura), but in the Juliformia, Polydesmida and Siphoniulida all segmental sclerites are fused to form complete rings. This distinction between ring and 'ring' is in agreement with the recent overview of millipede taxonomy by Enghoff *et al*. (2015).

An extensive mismatch between dorsal and ventral segmentation is observed also in pauropods and in symphylans. Within the Chilopoda, the Scutigeromorpha have 15 leg-bearing segments (LBS), and the corresponding sternites, but only seven tergites, while the Craterostigmomorpha, also with 15 LBS, have 21 tergites.

Forbidden numbers. – In centipedes, specimens with an even number of LBS are limited to some early post-embryonic stages in species belonging to the hemianamorphic clades, e.g. *Lithobius* and *Scutigera*, but only odd number of LBS – between 15 and 191 – are found in adult Chilopoda (e.g., Minelli & Bortoletto 1988, Arthur & Farrow 1999), including those with segmentation defects, except for a 'monster' specimen of *Stigmatogaster subterraneus* (Shaw, 1789) with 80 LBS, described and discussed in Leśniewska *et al*. (2009).

Number fixed in major lineages. – In many myriapod clades, segment number is very strictly fixed, in others however it is more or less extensively variable (see table in Minelli & Fusco 2013). For example, the number of LBS is 15 in all adult centipedes belonging to the Scutigeromorpha, Lithobiomorpha and Craterostigmomorpha, but it varies between 27 and 191 (odd numbers only!) in Geophilomorpha.

Of interest, in exploring the evolvability of segment number as a possible cue to discovering the underlying developmental mechanisms, are the rare exceptions recorded in clades otherwise remarkable for stability in segment number. One example are the scolopendromorph centipedes, with a majority of species having 21 pairs of legs, a sizeable minority 23, the only two exceptions (to which we will return later) being *Scolopendropsis bahiensis* (Brandt, 1841), in which individuals with 21 LBS occur alongside others with 23 (Schileyko 2006), and the closely related *Sc. duplicata* Chagas-Junior, Edgecombe & Minelli, 2008, with individuals of both sexes with either 39 or 43 LBS (Chagas-Júnior *et al.* 2008).

Differences between the sexes. – The number of segments is often the same in both sexes, but with major exceptions. The sex with higher segment number is either the male or the female, according to the group. In glomerid and sphaerotheriid millipedes males have two tergites more than the conspecific females, while in the other myriapod clades with sexually dimorphic segment number, males have less numerous segments than the conspecific females: the difference is two tergites in some species of Polydesmida, two or more tergites in many millipedes and two or more LBS in geophilomorph centipedes except for the Mecistocephalidae. In a number of geophilomorphs belonging to several independent clades in which there is also intraspecific variation affecting both sexes,

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the modal difference is equal or close to a multiple of two, up to 16 segments (Minelli & Bortoletto 1988, Berto *et al.* 1997). In *Orphnaeus heteropodus* Lawrence, 1963 (Oryidae) the females have been described as possessing about twice as many trunk segments as the males (Lawrence 1963), but the original description is inaccurate, as Lawrence (1963) gave the following counts for the specimens on which he described the species: 57, 60 and 65 LBS in the three males, 119 and 120 in the two females; both 60 and 120 are even numbers, thus very unlikely, given the universality of odd number of LBS in the Chilopoda.

Intraspecific variation. – Within the Chilopoda, besides the two species of *Scolopendropsis* cited above, there is within-sex intraspecific variation in the number of trunk segments in most of the Geophilomorpha except for the vast majority of the Mecistocephalidae. Within the latter, however, this condition has evolved at least three times; as expected, variation has been recorded in the mecistocephalid species with the highest total segment number: 57 or 59 LBS in *Mecistocephalus diversisternus* (Silvestri, 1919), 63 or 65 in *M. japonicus* Meinert, 1886, and between 93 and 101 in *M. microporus* Haase, 1887 (Bonato *et al.* 2003, Uliana *et al.* 2007). Within the Adesmata, the clade of geophilomorphs sister to the Mecistocephalidae, the range of variation within a species varies between 2 LBS and more than 80 (*Himantarium gabrielis* (Linnaeus, 1767) (Minelli *et al.* 1984, Minelli & Bortoletto 1988). Within the Diplopoda, intraspecific variation is universal in the euanamorphic clades, but has been additionally recorded in teloanamorphic (several Callipodida) and hemianamorphic species (one species of Glomeridesmida and several Spirostreptida and Spirobolida, in the latter with intraspecific variation in a range up to 10 rings) (Enghoff *et al.* 1993).

Occasional instability in segment number has been occasionally recorded in otherwise segment-invariant species such as *Polydesmus complanatus* (Linnaeus, 1761) and *P. angustus* Latzel, 1884 in which occasional supernumerary

molts have been found to release individuals with one extra leg-bearing ring (Verhoeff 1916, 1928, David & Geoffroy 2011).

Patterns of segment addition during post-embryonic development. – In a pioneering paper on myriapod reproduction and development, Fabre (1855) suggested a 'law of anamorphosis' according to which all apodous rings of a given pre-adult stage will bear two pairs of legs each in the following developmental stage. Fabre documented this regularity in *Polydesmus complanatus*. Subsequent authors demonstrated that this 'law' is not restricted to polydesmidans, but also applies to other clades, but it is not universal for millipedes: indeed, it is limited to two major clades, the Merocheta (Polydesmida) and the Juliformia (Julida + Spirobolida + Spirostreptida) (Enghoff *et al.* 1993). There is no consistent correlation between the kind of anamorphosis (i.e., hemi-, telo- and euanamorphosis) and a segment addition agreeing or not with Fabre's rule.

Lack of segment regeneration. – In myriapods, and in arthropods at large, regeneration is limited to the appendages. The process is well documented in Scutigeromorpha and Lithobiomorpha (both legs and antennae), less so in Scolopendromorpha, where it is possibly limited to the last pair of legs and the antennae; no reliable example of regeneration of appendages is available for the Geophilomorpha (Minelli *et al.* 2000). In millipedes, evidence of regeneration is also restricted to the antennae, where autotomy may occur between articles II and III (*Polydesmus angustus*; Petit 1974) or between III and IV (*Polyxenus lagurus* (Linnaeus, 1758); Nguyen Duy-Jacquemin 1972), and the legs (Petit 1973), but experimental evidence is available for very few species only. One might expect that myriapods (and other arthropods) with anamorphic development would regenerate segments posteriorly, but this is not the case. This shows that the posterior growth zone of anamorphic or hemianamorphic myriapods is not a unpatterned blastema, but rather an irreplaceable organizing region.

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NEW FRAMEWORKS AND NEW EVIDENCE

Current appreciation of the nature and evolution of segmentation in myriapods is largely the result of a renewed intellectual framework involving phylogenetics, macroevolution and developmental biology.

The phylogenetic context

Until the late '80s of the past century, arthropods were generally regarded as closely related to the annelids, the other major phylum of overtly segmented animals. In this context, myriapods, with their worm-like habitus and the modest degree of regional patterning along the trunk, seemed to represent a natural midway step along a morphocline beginning with homonomously segmented and limbless annelids and eventually ending in heteronomous segmented arthropods with body articulated in three tagmata (e.g., the head, thorax and abdomen of insects) and provided with segmental pairs of limbs with specializations parallel to the anatomical and functional differentiation of body regions. To some extent, the old notion of the Articulata, introduced by Cuvier (1816) for this *embranchement* of segmented animals, seemed still acceptable and even suitable as phylogenetic background for a reconstruction of the evolution of the evidence emerging from comparative developmental genetics. But a close relationship between Arthropoda and Annelida is not supported by molecular evidence. Instead, one of the most important results of the earliest efforts in molecular phylogenetics at the level of the relationships among the major clades of metazoans was the demonstration of the close affinities between the arthropods and the other molting animals (Aguinaldo *et al*. 1997). Even earlier, a phylogenetic analysis based on a large dataset of morphological and embryological data (Eernisse *et al*. 1992) had also failed to provide support for the Articulata. The Articulata hypothesis was rapidly abandoned, although with some resistance, in favor of the Ecdysozoa hypothesis (for arthropods) and the Spiralia and Lophotrochozoa hypotheses

(for annelids). The phylogenetic background against which to reconstruct the origin and evolution of segmentation in Arthropoda must therefore accept their closer relationships to the Nematoda etc. rather than to the Annelida.

Interestingly, myriapods and their segments have played a role in stimulating a revisitation of the phylogenetic relationships between the arthropods and other metazoan phyla. In discussing the potential implications of models of segmentation suggested by the distribution of segment numbers in several myriapod clades, Minelli & Bortoletto (1988, p. 340) remarked that arthropod and annelid segments might not be homologous, as generally taken for granted, while "In annelids, segments are primarily mesodermal units arising in serial sequence by steps punctuated by mitotic cycles, whereas in Atelocerata (possibly in all arthropods) they are primarily ectodermal units, not arising in sequence, but by iterative doubling of biochemical markings laid down independently from mitotic cycles." In this sentence, two points have not resisted the progress of knowledge in the following thirty years, namely the Atelocerata (myriapods+hexapods) hypothesis, which has been rejected in favor of a closer alliance between crustaceans and hexapods, and the suggestion that double-segment periodicity might be universal among arthropods, but this does not shake the main point, eventually accepted by most zoologists today.

The general question, how many times segmentation might have emerged among metazoans, is still open to discussion (e.g., Davis & Patel 1999, Seaver 2003, Minelli & Fusco 2004, De Robertis 2008, Tautz 2004, Couso 2009, Chipman 2010, 2019, Hannibal & Patel 2013).

Macroevolutionary scenarios

A naïve approach to evolutionary trends in animal (and plant) clades whose representatives feature serial structures in a diversity of numbers and degrees of specialization may suggest, as a rule, a progressive reduction in the number of units and a corresponding increase in their specialization. In arthropods, and in myriapods

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particularly, this would translate into a trend from a higher to a lower number of segments and from a less patterned to a more extensively patterned trunk. This corresponds to the so-called Williston's rule (e.g., Saunders & Ho 1984). This putative macroevolutionary principle, however, often fails to withstand phylogenetic analysis (Minelli 2003). Opposite trends, in fact, prevail among myriapods. In Enghoff's (1990) reconstruction, there are no more than 21 body segments in the ground-plan of chilognathan millipedes, while among the geophilomorph centipedes there is no consistent trend in either increase of decrease of segment number (Bonato *et al*. 2014) or in complexity (local patterning) of the trunk (Berto *et al*. 1997).

New taxa and phylogenetic analysis

Our current appreciation of ontogeny and evolution of the segmental organization of myriapod body has benefitted from the often revised and eventually stabilized reconstruction of the phylogenetic relationships among the major clades of Chilopoda and Diplopoda (e.g., Shear & Edgecombe 2010, Edgecombe 2011, 2015, Fernández *et al*. 2018) as well as by phylogenetic analyses of smaller clades, e.g. the Mecistocephalidae, within which both decrease and increase in segment number have been revealed, including whole-trunk duplication accompanied by release of intraspecific variation in segment number (Bonato *et al*. 2001, 2003). Moreover, as discussed below, of critical importance has been the discovery of species with segment number very different from the condition in all other species in their clade, namely the scolopendromorph centipede *Scolopendropsis duplicata* (Chagas *et al*. 2008) and the polydesmidan millipede *Dobrodesmus mirabilis* Shear, Ferreira & Iniesta, 2016 (Shear *et al*. 2016).

Segment production, before
and after hatching

The only myriapod with intrapopulation variation in adult segment number for which experimental studies on the possible causes of this variation are available is the geophilomorph centipede *Strigamia maritima* (Leach, 1817). In this species, segment number is slightly influenced by the temperature to which the embryo is exposed (Vedel *et al*. 2008), especially during blastoderm formation and before, or very shortly after the onset of segmentation (Vedel *et al*. 2010). A genetic component, however, seems to be also present (Vedel *et al*. 2009).

Precious efforts, aided by progress in microscopy and imaging technology, have been put into refreshing descriptive embryology. Of this production, which has revealed important gaps and errors in the old literature on this subject, I will briefly summarize here the work of Brena & Akam (2012, 2013) and Brena (2014) on *S. maritima*.

In the embryo of this species, most trunk segments take shape as morphogenetic units marked by the regularly spaced expression of segmentation genes with periodicity equivalent to two future segments (Chipman *et al*. 2004a). However, the most posterior segments are laid down as single segments, rather than as double-segment units, and the process is associated with active cell proliferation, a feature usually characteristic of post-embryonic elongation.

Unexpectedly, a rudimentary leftover of anamorphosis is present in this centipede, as the genital segments are added after hatching, at which time, additionally, the prospective last leg-bearing segment is limbless and in some individuals the external delineation of this segment is only manifest at the beginning of the post-embryonic life. Previous to this study, post-hatching addition of a few segments in some geophilomorph species was suggested by Archey (1936) and Misioch (1978), but this had been discounted (Prunescu & Capuse 1971, Minelli 1985, Horneland & Meidell 1986) as based on unconvincing evidence.

As noted by Brena (2013), these newly discovered features of segment production in *Strigamia* suggest that, in this clade at least, the pre- vs. post-hatching divide is not a clear-cut one, something already questioned by Minelli *et*

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al. (2006). Nor is this divide strictly comparable, even among close relatives: at stage I most millipedes have three pairs of legs, but several exceptions have been recorded, apparently restricted to individual species, e.g. 27 pairs in *Pachyiulus flavipes* (C.L. Koch, 1847) (Dirsh 1937), whereas in all other members of the Julida for which the number of LBS at stage I is known, this number is always three.

Modes of segment production

In his excellent review of myriapod evo-devo, Brena (2015) remarked that no general model is available at this time to explain the spatial and temporal patterns of segment production in myriapods. Basically, segments in myriapod embryos differentiate in antero-posterior sequence from a posterior segment addition zone, but the latter is probably better described as a segmental organizer rather than as a segment generator (Fusco 2005).

A problem with a strictly sequential production of segments from a posterior (subterminal) part of the body is the nearly absolute precision required to generate segmented animals with a total segment number fixed at the level of species and also conserved throughout major clades. Based on the unlikely existence of a 'counting device' of such precision, Maynard Smith (1960) suggested that the constancy in segment number peculiar to many myriapod clades could be tentatively explained as the result of a different process of segment production. Segmentation would thus be obtained in two steps: first, the production (perhaps in the ordinary, progressive way) of a quite small number of primary segments, followed by one or more rounds of duplication, that is, splitting of each primary segment into two secondary (or tertiary etc.) segments. Controlling both steps (the production of a small number of primary segments and their subsequent duplication) and thus escaping variation in segment number would be much easier and thus more likely than an error-free sequential process producing high but also fixed numbers of units, one after the other. According to Minelli & Bortoletto (1988), a multiplicative process of segmentation would also explain several features of the distribution of segment numbers in myriapods other than the frequent stability of high segment numbers, in particular the idiosyncratic lack of centipedes with even number of LBS and some segment number distributions in selected clades of Geophilomorpha, where relative frequency maxima are spaced by intervals of 2^n units. This model has been further developed in subsequent papers by this author (Minelli 2000, 2001). A few years before, spatial patterns of gene expression with 2-segment periodicity were discovered in *Drosophila* (Nüsslein-Volhard & Wieschaus 1980) and both their significance as a possible step in body (or at least trunk) segmentation and their occurrence in different arthropod clades, myriapods included, has been targeted by developmental geneticists.

The multiple-duplication model performs much better than alternative models of arthropod segmentation in respect to two critical predictions.

The first prediction is about the evolvability of segment number in epimorphic centipedes and in millipede clades in which segment number is not fixed. If the binary splitting of primary segments hypothesized under the multiplicative model of segmentation is occasionally repeated one extra time, individuals will be produced with a roughly duplicated number of segments, and no intermediate will be found between specimens with the original number and those expressing the duplication. This would be an example of 'saltational' evolution. This is a sensible explanation for the occurrence, in Scolopendromorpha, of the two closely related species mentioned above, one of which (*Scolopendropsis duplicata*) has a segment number approximately double compared to the other (*Sc. bahiensis*) (Minelli *et al*. 2009). A parallel case of 'whole-trunk duplication' is represented by a recently described representative of the teloanamorphic millipedes. Uniquely among the Polydesmida, in the adult males of *Dobrodesmus mirabilis* there are 39 rings (Shear *et al*. 2016), whereas the number of rings in the vast majority of species in the same order is 19, the remaining ones having between 17 and 21 rings, except for some species in the genus

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Devillea, with up to 28 rings (Enghoff *et al.* 1993, David & Geoffroy 2011).

A second kind of prediction is about multisegmental patterns due to late effects of positional markers expressed much earlier in development. Invoking regularities in the post-embryonic segment addition is arguably sensible as an explanation for the serial color patterns described by Enghoff (2011) in several species belonging to Spirobolida, Spirostreptida, Platydesmida, Siphonocryptida and Chordeumatida, consisting of units, each of which extends over several rings. In the majority of cases, the elements of these patterns correlate with the successive batches of segments added with subsequent molts, as expected in the light of the so-called 'law of anamorphosis' (Fabre 1855) mentioned above. However, rather than agreeing with the pattern of stepwise addition of segments at the posterior end of the trunk, the distribution of other multisegmental patterns may mirror instead an early expression of positional markers. This is likely the case in the julid millipede with ectopic extra pairs of gonopods described by Akkari *et al.* (2014). In this male specimen of *Ommatoiulus moreleti* (Lucas, 1860) there are eight pairs of gonopods: the usual two pairs representing the appendages of ring 7 (positionally homologous to leg-pairs 8 and 9), plus six extra pairs of gonopods replacing the walking legs of rings 8, 15 and 16 (positionally homologous to leg-pairs 10–11, 24–25 and 26–27, respectively). Thus, in this specimen there are two distinct sets of four pairs of gonopods each, the anterior one corresponding to leg-pairs 8–11, the posterior one to leg-pairs 24–27. The fact that the posterior set reiterates the anterior one after exactly 16 leg positions along the main body axis suggests that a body section corresponding to eight rings (16 leg-pairs) might be a structural module deriving from 4 cycles of regular binary splitting of an embryonic 'primary segment'. As to the discontinuous distribution of gonopod pairs in the teratological specimen, let's consider that, very likely, in male helminthomorph millipedes generally, the positions where walking legs will metamorphose into gonopods are marked early, during embryonic development, by the localized expression of a 'position marking gene', perhaps

the Hox gene *Abdominal-B* (Drago *et al.* 2008). This may explain the distribution of the extra gonopods in the homeotic specimen, if the molecular marker 'interpreted' post-embryonically as fixing the position for the walking leg-to-gonopod metamorphosis was present in a primary trunk segment before its eventual splitting into secondary segments (mechanistic details are given in the original paper). But this explanation is only compatible with a multiplicative model of segmentation, whereas the alternative model does not offer any plausible explanation for the observed pattern.

Also in favor of a multiplicative, rather than strictly serial model of segmentation is the segmental anomaly described by Shelley (1975) in a male of *Nannaria conservata* Chamberlin, 1940. This polydesmidan features three pairs of gonopods: the normal ones, corresponding to leg-pair 8, plus two ectopic pairs, in the place of leg-pairs 4 and 12, respectively. In other words, the three gonopod pairs in this specimen are spaced by two intervals of 4 units (leg-pairs) each. This has been interpreted by Akkari *et al.* (2014) as suggesting a degree of segment multiplication lower than in *O. moreletii*, in agreement with a total number of segments much lower in a typical polydesmidan than in an average julid.

Developmental genetics

The single most important field that has opened new vistas in understanding arthropod (and myriapod) segmentation is developmental genetics, despite the fact that up to now these studies have been limited to three species only, the pill millipede *Glomeris marginata* (Villers, 1789) and two centipedes, *Lithobius atkinsoni* Bollman, 1887 and *Strigamia maritima*.

Several sets of genes are involved in the segmentation of the arthropod germ-band, in particular the pair-rule genes, expressed in the embryo in domains often corresponding to two (definitive) segments of the animal, hence the name, and the segment polarity genes, by the expression of which segment boundaries are generated. Most of the genes of these two

classes, first discovered in *Drosophila*, are present in arthropods generally, myriapods included, and are similarly involved in segmentation, although the precise mechanics of the process may differ. Divergence is more extensive in gene expression at the earlier embryonic stages, whereas the involvement of segment polarity genes (especially *engrailed* and *wingless*) in generating segmental boundaries has been found in all arthropods studied thus far (Peel 2004, Peel *et al.* 2005, Chipman 2008).

Pair-rule genes and their expression. – Because of their widespread bisegmental patterns of expression, pair-rule genes have been most closely targeted in the study of myriapod developmental genetics. In *Drosophila*, some of these genes (*even-skipped*, *oddskipped*, *hairy* and *runt*) are initially expressed in a two-segment periodicity, but the large transversal bands in which they are expressed split subsequently to give a pattern with single-segment periodicity on the segmented germ band. The circumstance that only odd numbers of LBS – between 15 and 191 – are found in adult Chilopoda suggests that their germ band also undergoes a stage with double segment periodicity (Chipman *et al.* 2004a). Evidence of such a stage was not been recorded in the earliest studies on developmental genetics of centipedes (Hughes and Kaufman 2002, Kettle *et al.* 2003, Chipman *et al.* 2004b), but was eventually demonstrated for two genes in the embryo of *Strigamia maritima* (Chipman *et al.* 2004a). As recently noted by Clark *et al.* (2019), it is still uncertain where and how many times, in arthropod evolution, the bisegmental pattern of expression of pair-rule genes evolved.

As described in *Drosophila* and insects generally, in myriapods there are both early- and late-activated pair-rule genes, but the relative timing of expression of some genes of the first set is not the same as in insects (Green & Akam 2013). Nevertheless, in both *Strigamia* (Janssen *et al.* 2011b, 2012) and *Glomeris* (Green & Akam 2013), these genes are expressed in stripes preceding discernible morphological segmentation, a pattern suggesting their likely role in segment patterning (Brena 2015).

The stripes of expression of the segment-polarity genes emerge at the anterior margin of the segment addition zone (Clark *et al.* 2019), progressively specified by the regularly periodic waves of expression of the primary pair-rule genes *hairy*, *eve*, *runt* and *odd*. This behavior, observed – among myriapods – both in *Glomeris* (Janssen *et al.* 2011) and in *Strigamia* (Green & Akam 2013), has been described as a segmentation clock (Clark *et al.* 2019). In *Strigamia*, this periodic expression gives rise to stripes corresponding to all segments starting from the mandibular one (Brena & Akam 2013). In myriapods (and in arthropods in general) the anterior part of the body possibly becomes segmented through a different mechanism (Brena 2015).

Segmentation vs. germ-band elongation. – Remarkable is the apparent independence, in *Strigamia* at least (Brena & Akam 2013, Brena 2015, Clark *et al.* 2019), of the early patterning process from germ-band formation and axis elongation, two processes usually considered intrinsically interconnected in arthropods (Sander 1976).

Ectoderm vs. mesoderm. – The early dynamic patterning process of the primary pair-rule genes has been shown in *Strigamia* to be specifically ectodermal (Green & Akam 2013), as long ago tentatively suggested by Minelli & Bortoletto (1988), who first pointed to this property as possibly differentiating arthropod segmentation from segmentation in annelids, where this process is primarily a mesodermal affair.

Pair rule gene expression in (hemi)anamorphic myriapods. – For centipedes other than *Strigamia*, the only available information about the developmental genetics of segmentation is Hughes & Kaufman's (2002) study on the expression patterns of three segmentation genes (*even-skipped*, *engrailed*, and *wingless*) in *Lithobius atkinsoni*. In this centipede, the expression of *even-skipped* is apparently segmental (unlike the seven bisegmental stripes observed in the embryonic germ-band of *Drosophila*) and possibly limited to a part of the

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trunk rather than extending over its total length. It remains to be proved if this behavior specifically correlates with the hemianamorphic, rather than epimorphic, schedule of segment production in *Lithobius*.

Glomeris*: gene expression and dorsoventral mismatch.* – In *Glomeris marginata*, the study of the spatial and temporal patterns of expression of homologues of the genes known to be involved in the segmentation process in *Drosophila* and other arthropods have been targeted to address the developmental origin of the problematic serial units of the millipede trunk. Previous to the advent of developmental genetics, the obvious mismatch between the dorsal and ventral aspects of trunk segmentation in millipedes had been already interpreted as suggestive of independence between the developmental processes producing the dorsal vs. ventral serial units of the millipede body. Some arguments from comparative morphology were offered by Enghoff *et al.* (1993), e.g. the fact that in Glomerida sternites and leg-pairs differentiate at a pace other than the production of new tergites; the addition of leg-pairs in *Glomeridesmus* continuing even after the production of the last tergite, and the lack of correspondence, across the developmental stadia of platydesmids, between the number of tergites and the number of sternites and leg-pairs. In *Glomeris marginata*, several segmentation genes, the segment polarity genes especially, although homologous to those of the other arthropods, are expressed according to divergent patterns. For example, in *G. marginata*, *wingless* is expressed ventrally, but not dorsally; *engrailed*, *hedgehog*, *cubitus-interruptus* and *patched* are expressed both dorsally and ventrally, but the dorsal pattern of expression suggests that it is not involved in segmentation (Janssen *et al.* 2004, Damen *et al.* 2009). Most important, the spatial and temporal patterns of gene expression suggest that in *Glomeris* dorsal and ventral segmentation are uncoupled (Janssen *et al.* 2006a). Moreover, the boundaries between embryonic segments do not correspond to those between neighboring tergites (Janssen *et al.* 2006b). A bisegmental pattern of expression is observed in the blastoderm of *Glomeris* for *pairberry* and other pair rule gene

orthologues (Janssen *et al.* 2012). These stripes split subsequently in two, as observed for the primary expression stripes of pair-rule genes in other arthropods, but this pattern does not correspond to either the ventral or dorsal segmental units of the millipede.

CONCLUSIONS

In the light of the observational and experimental evidence gathered in the last decades and the steadily revised interpretation of the diverse pieces of information, both old and new, available today, the most sensible starting point for an overall evaluation of our current understanding of segmentation in arthropods, and in myriapods specifically, is Hannibal & Patel's (2013, p. 8) statement, that "more than two millennia of studying segmentation in animals have failed to produce a definition of segmentation that is applicable in even a majority of cases. Moreover, discussions on segmentation are often reduced to debates over the definition of segmentation and whether the animal or system described is actually segmented, rather than to debates over the developmental mechanisms and evolutionary processes."

Some provisional conclusions, however, can be offered:

The old notion, that the body of myriapods (and arthropods generally) is made of segments must be replaced with the notion that the body of these animals features a multiplicity of serially repeated units, partly but not necessarily or universally integrated into blocks approximating conventional textbook segments (Budd 2001). The trunk of a myriapod certainly exhibits segmental patterns, but is not made of segments (Fusco 2005, 2008).

Rather than resulting from the regular addition of 'preformed' segmental building blocks, the whole trunk – in centipedes at least – appears to be the 'primary given' eventually subdivided into units of more or less strictly fixed number. For example, in the geophilomorph *Clinopodes flavidus* C.L. Koch, 1847, among the adults of the same sex belonging to

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the same population, total body length is independent from the number of segments, the latter being in inverse relationship to the average length of segments in the individual (Berto *et al*. 1997, Minelli *et al*. 2010; but see Hayden *et al*. 2012 for contrasting evidence in *Strigamia maritima*).

As far as the number and patterning of segments is concerned, the prevailing macroevolutionary trend in myriapods does not follow Williston's rule.

Kind and degree of integration among the different series of periodically arranged units, e.g. tergites, sternites and leg-pairs are not simply to be read in terms of function (locomotion, especially), but also in terms of mechanisms of segment production and patterning and especially of heterochronic shifts among the different processes involved.

The divide separating embryonic from post-embryonic development and, as a consequence, the contrast of anamorphic vs. epimorphic developmental schedules are not necessarily solid, as traditionally accepted.

Bisegmental patterns of gene expression in the early embryo, following by splitting of the corresponding stripes into secondary, one-segment stripes, are likely more widespread, among arthropods in general and myriapods in particular, than accepted some years ago. It is possible that a multiplicative process of segmentation has evolved, in different myriapod lineages, by iteration of this mechanism of primary stripe splitting.

Many open questions remain, e.g. to what extent the production of serial structures along the main body axis of myriapods is multiplicative rather than sequential.

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A new species of penicillate millipede from genus *Mauritixenus* (Diplopoda, Polyxenidae) found in Vietnam

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Abstract. Genus *Mauritixenus* Verhoeff, 1939 comprises a group of penicillate millipedes found only in Mascarene Islands, Madagascar and West Africa. The characteristics of this genus are 13 pairs of legs, 8 ommatidia, labrum with apical granular structure and tarsus 2 with a spine. There are seven described species in this genus. Penicillate millipedes were collected from Vietnam, Ninh Thuan Province, which proved to be a previously undescribed species in the genus *Mauritixenus*. Their distinguishing characteristics include the number of sensilla on gnathochilarium and the anterior lateral process in the claw, as well as the genetic makeup, concluded this is a new species in this genus.

Keywords: Genomic DNA, Mascarene Islands, *Mauritixenus*, penicillate millipedes.

INTRODUCTION

The genus *Mauritixenus* (Polyxenidae) was described by Verhoeff in 1939 based on a species, *Mauritixenus gracilicornis* Verhoeff, 1939, found on Mauritius Island. The description of this genus by Verhoeff included few taxonomic details and this resulted in uncertainty about the identification of this genus. Nguyen Duy-Jacquemin & Condé (1967) defined genus *Mauritixenus* by the presence of eyes with eight ommatidia; antennal article VI with a group of 3–5 bacilliform sensilla, with the anterior one being the shortest; the surface of labrum has granular structures – spine setae or apical papillae in some species; tarsus 2 with a sharp spine. Six species from Mascarene Islands (Mauritius, Rodrigues and Reunion Islands), Madagascar and West Africa, were placed in this genus based on their similarity to *Mauritixenus gracilicornis*: *Mauritixenus betschi* Nguyen Duy-Jacquemin & Condé, 1969; *M. borbonicus* (Condé & Jacquemin, 1962) formerly known as *Monographis borbonicus* Condé & Jacquemin, 1962 from Reunion Island; *M. pauliani* (Condé & Jacquemin, 1962) formerly *Monographis pauliani* Condé & Jacquemin, 1962 from Reunion Island; *M. sakalavus* (Marquet & Condé, 1950) formerly *Monographis sakalavus* Marquet & Condé, 1950 from Madagascar; *M. vachoni* Nguyen Duy-Jacquemin & Condé, 1969 and *M. betschi retusus* Nguyen Duy-Jacquemin & Condé, 1969 (subspecies). *Mauritixenus ninhthuanensis* sp. nov., the first species of *Mauritixenus* from Southeast Asia – Vietnam is described below.

MATERIALS AND METHODS

Penicillate millipedes with the following characteristics: Eight ommatidia, adults with 13 pairs of legs and tarsus 2 with a spine, are expected to belong to genus *Mauritixenus* (Polyxenidae). These millipedes were collected from Vinh Hy Bay (11.710833N, 109.189722E, elevation 100 m, Ninh Hai District), 40 km northwest from Phan Rang City, Ninh Thuan Province. Ninh Thuan Province is located on the South-Central coast of Vietnam (Fig. 1). This region has an arid climate with an annual rainfall of less than 800 millimetres (https://www.ninhthuan.gov.vn, accessed 26 Oct 2019).
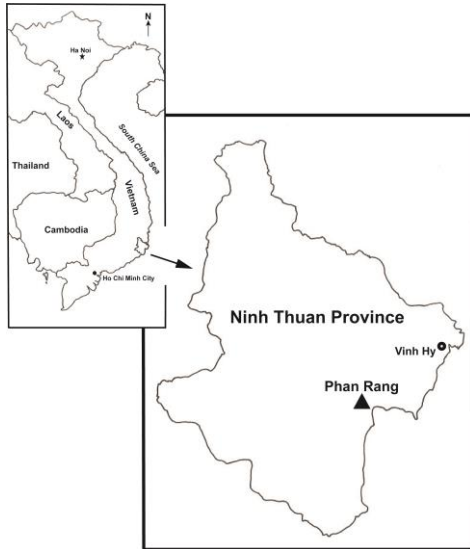
Figure 1. A map of Ninh Thuan Province, where *Mauritixenus ninhthuanensis* sp. nov. was collected, and the inserted map of Vietnam (Not to scale).

Morphometric study

Specimens were examined and measured using light microscopy and prepared for taxonomic illustration following the staining and slide mounting technique of Short & Huynh (2010). This technique was used with modifications (included in the paragraph below) to permit the extraction of DNA for genetic studies. The remaining cuticles of the specimens were mounted on slides for morphometric analysis as described in Huynh & Veenstra (2015). Scanning electron microscopy (SEM) followed the technique of Huynh & Veenstra (2018*a*). Holotype and paratypes were deposited in the Queensland Museum (QMS), Brisbane, Australia.

Genetic studies

The quantity of DNA extracted from six individual *Mauritixenus* specimens from Ninh Thuan Province was determined using a NanoDrop 1000 Spectrophotometer (ND 1000V3.60 software) following the manufacturer's instructions. Two genes were sequenced for this study: The 18S small subunit ribosomal RNA gene (primers 1F and 5R, White *et al*. 1990) and the mitochondrial cytochrome c oxidase subunit I gene, COI (primers dgLCO1490 and dgHCO2198, Meyer 2003). Both primer sets are conserved universal primers for these gene regions and are common molecular markers used for species-level identification. The 18S gene marker has been used to elucidate relationships among arthropod groups including crustaceans, insects and myriapods (Turbeville *et al*. 1991, Luan *et al*. 2005, Wesener *et al*. 2010, 2016). This region has also been used to help separate penicillate millipede species of the genera *Lophoturus*, *Monographis* and *Phryssonotus* in combination with morphological characters (Huynh & Veenstra 2015, 2018*a*, 2018*b*). The COI region was included because it is commonly used in the Barcode of Life (2010–2019) for species identification. The polymerase chain reaction (PCR) protocol followed Huynh & Veenstra (2018*a*).

Representative DNA sequences from *Mauritixenus ninhthuanensis* sp. nov. have been deposited in GenBank (http://www.ncbi.nlm.nih.gov), the following accession numbers for *M. ninhthuanensis* sp. nov.: MN621363 (18S) and MN621892 (COI). The accession numbers for other *Mauritixenus* species also used in this study: *Mauritixenus gracilicornis* (MN621361 for 18S and MN621890 for COI) and *M. pauliani* (MN621362 for 18S and MN621891 for COI). The 18S and COI sequences from the new species were queried in a BLAST search (http://www.ncbi.nlm.nih.gov) to find sequences of closely related species. All sequences from the search were aligned with sequences from the studied species using BioEdit (Hall 1999), MEGA 7 (Kumar *et al*. 2016) was used to generate the bootstrap maximum-likelihood tree for determining phylogenetic relationships. Numbers above branches represent bootstrap values. GenBank accession numbers for the sequences from penicillate millipede species and outgroups are listed in Table 1 (http://www.ncbi.nlm.nih.gov, accessed 8 Aug 2019).

Table 1. GenBank accession numbers of the partial sequences of 18S and COI of *Mauritixenus ninhthuanensis*, other penicillate millipedes and the Outgroups were used in the study of genetic relationship.

Family	Genus	Species	Location	18S rRNA	COI
Synxenidae	*Phryssonotus*	*Phryssonotus australis*	Australia	KY820871	KY820869
		Phryssonotus chilensis	Chile	MF592749	MF592728
		Phryssonotus novaehollandiae	Australia	KY820870	KY820867
		Phryssonotus occidentalis	Australia	KY820872	KY820868
Polyxenidae	*Mauritixenus*	*Mauritixenus gracicolus*	Mauritius	MN621361	MN621890
		Mauritixenus ninhthuanensis	Vietnam	MN621363	MN621892
		Mauritixenus pauliani	Rodrigues	MN621362	MN621891
	Monographis	*Monographis dongnaiensis*	Vietnam	KP255446	–
		Monographis phuquocensis	Vietnam	MG210571	MG279505
		Monographis queenslandica	Australia	KF147166	MG279506
	Polyxenus	*Polyxenus fasciculatatus*	Europe	AF173235	–
		Polyxenus lagurus	Europe	MF592763	–
		Polyxenus pugetensis	Europe	MF592764	–
	Unixenus	*Unixenus corticolus*	Australia	–	MG279507
		Unixenus intragramineus	Vietnam	MG210572	MG279508
		Unixenus karajinensis	Australia	MF592754	–
		Unixenus mjobergi	Australia	MF592755	–
Lophoproctidae	*Lophoturus*	*Lophoturus boondallus*	Australia	MG210573	MG204536
		Lophoturus molloyensis	Australia	MG210574	MG204537
		Lophoturus queenslandicus	Australia	MG210575	MG204535
Outgroups		*Procyliosoma leae*	Australia	FJ409955	FJ409910
		Sphaeromimus musicus	Africa	FJ409961	–
		Glomeridella minima	Europe	–	JN271878

TAXONOMY

Subclass Penicillata Latreille, 1831

Order Polyxenida Verhoeff, 1934

Family Polyxenidae Lucas, 1840

Genus *Mauritixenus* Verhoeff, 1939

Type species. *Mauritixenus gracilicornis* Verhoeff, 1939

Diagnosis. Each eye 8 ommatidia; body 10 tergites, 9 pleural projections; 13 pairs of legs; 8 antennal articles, VI longest, VIII shortest with 4 sensory cones. Antennal article VI with 4 baciliform sensilla, sensilla located in anterior position shortest than posterior ones, arranged in transverse row; surface of the labrum with apical papillae; palps of gnathochilarium well developed, lateral palp of gnathochilarium 2 times longer than the medial palp, with 16 conical sensilla; a spine on tarsus 2; coxal glands on coxae 8th and 9th.

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Mauritixenus ninhthuanensis sp. nov.

(Figure 2)

Material examined. Type specimens. Adult male holotype (Queensland Museum registered number: QMS 110919), 4 adult female paratypes (QMS 110920–110923), 5 adult male paratypes (QMS 110924–110928) from Vietnam, Ninh Thuan Province, Vinh Hy Bay, Ninh Hai District, Phan Rang City, 11.710833 N, 109.189722E, elevation 100 m, 8th November 2018 (Collected by C. Huynh). All mounted slides will be cataloged and lodged in the Queensland Museum, Brisbane, Queensland, Australia.

Figure 2. A live image of *Mauritixenus ninhthuanensis* sp. nov.

Etymology. The species is named *Mauritixenus ninhthuanensis* sp. nov. as this *Mauritixenus* species was first found in Ninh Thuan Province, Vietnam.

Diagnosis. Adults 3.0–3.8 mm in length, 8 ommatidia, 13 pairs of legs. Antennal article VI with a conical sensillum, 3 bacilliform sensilla and a setiform sensillum, arranged transversely; labrum with apical papillae; the telotarsus with anterior lateral process presents, posterior process longer than half the claw and setiform process is longer than the claw.

Description. Specimens are light yellowish-brown, 2 dark lateral bands contrasting with a light-yellow medial band across the body. Eye areas with dark brown and connecting each area with a brown colour band in the vertex region. Pearl white pleural trichomes, and lighter col-oured caudal bundle (Fig. 2). Holotype male body length 3.2 mm (Paratypes: males 3.0–3.5 mm, females 3.4–3.8 mm). Male caudal tri-chome bundle narrower in width, bundle slightly longer (0.6 mm) than female (0.5 mm).

Head: Each side 8 ommatidia: 4 dorsal, 4 lateral (1 anterior, 2 medial and 1 posterior position). Vertex with two posterior trichome groups and a large medial gap. Each trichome group has 2 rows: anterior row, curved slightly, on an oblique angle with larger sized trichome sockets in the middle, and small sockets on both ends; posterior row with 2–6 trichome sockets, commonly 3 sockets on both sides; a narrow medial space between these 2 rows. Holotype's posterior trichome groups has 15 sockets (Left: L) and 14 sockets (Right: R) in the anterior rows; 3 sockets on both sides in the posterior rows (Figs. 3A and 3E) (Paratypes with 14–20 sockets in the anterior rows and 2–6 in the posterior rows (Fig. 6C)).

Trichobothria: Typically thin sensory hairs with narrow cylindrical funicles; trichobothria equal in socket size forming an isosceles trian-gle with equal distance *ab* and *bc* (Figs. 3F and 6C) (trichobothrium *a* located in posterior posi-tion in relation to the head capsule, trichoboth-rium *b* in lateral position, trichobothrium *c* in anterior position).

Antennae: Eight antennal articles, 4 sensory cones, typical characteristics of Polyxenidae. Holotype: Antennal article VI with 3 bacilliform sensilla, different lengths: Shortest, thin bacilli-form sensillum located in anterior position (ta), the intermediate long thick bacilliform sensillum (Ti), and the longest thin bacilliform sensillum (tp) in the posterior position. Setiform sensillum (s) between ta and Ti and conical sensillum (c) in next to tp (Figs. 4A, 4C, 7A and 7C). Anten-nal article VII has 2 thick bacilliform sensilla, equal in length, Ta and Tp, a setiform sensillum (s) between them and a conical sensillum (c) located next to Tp. (Figs. 4A, 4B, 7A and 7B). (This pattern of sensilla on the antennomere VII is commonly seen in all *Mauritixenus* species).

Clypeolabrum: Holotype with 11 setae along labrum's posterior margin, these setae

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being less than half the width of the labrum (Setae in paratypes ranging from 10–16 in both sexes). Labral surface with apical papillae, forming rows of large size setae along the ante-

rior margin and reducing in size on posterior margin. Anterior margin of the labrum with 2+2 lamellae (lateral lamella and lamella) on each side of median cleft (Figs. 3H, 6D and 6E).
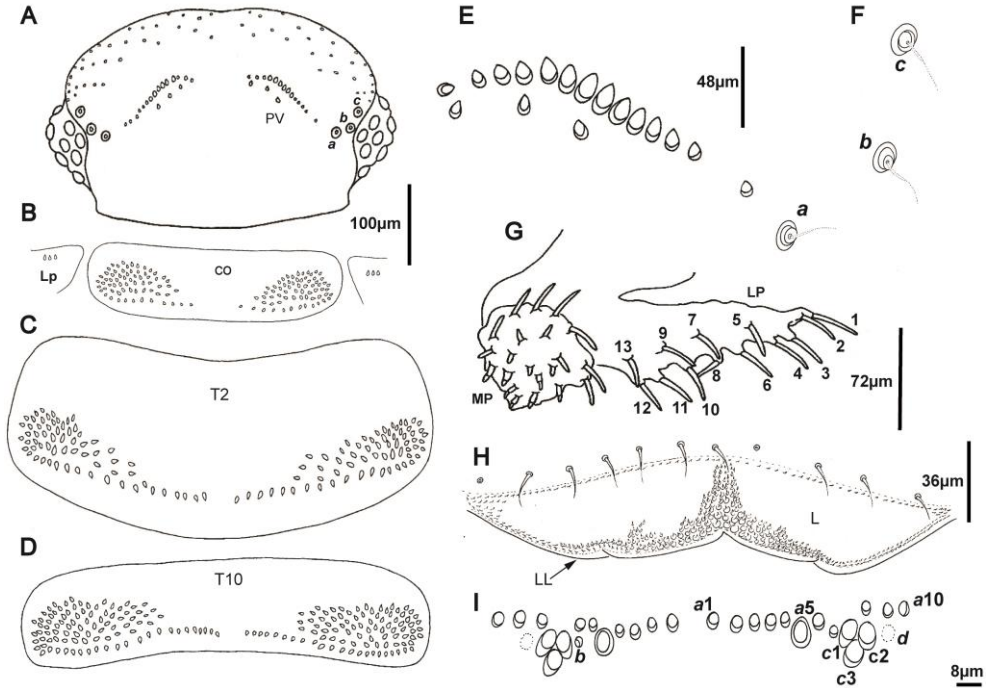

Figure 3. Holotype of *Mauritixenus ninhthuanensis* sp. nov. A = Head capsule, showing eye patterns with 8 ommatidia on each side, 3 trichobothrium sockets (*a*, *b* and *c*) and 2 posterior vertex trichome sockets (pv); B = Collum (co) and the lateral protuberances (Lp) showing pattern of trichome sockets with all trichomes removed; C = Tergite 2 (T2) with trichome sockets arrangement depicted; D = Tergite 10 (T10 – last tergite) with smaller trichome sockets (A, B, C and D drawn to the same scale); E = Posterior vertex trichome sockets (enlarged, right hand side); F = Trichobothria (right hand side): trichobothrium *a* (posterior position to the head capsule), trichobothrium *b* (lateral position next to the eye) and trichobothrium *c* (anterior position to the head capsule); G = Gnathochilarium: Lateral palp (LP) with 13 sensilla and medial palp (MP) with 21 sensilla; H = Clypeo-labrum: labrum with lamella (L) and lateral lamella (LL) on each side of the median cleft, labrum surface showed apical papillae, 11 setae (2 setae missing and only presented with the sockets) along the posterior margine of labrum; I = Dorsal ornamental trichome sockets: 10 trichome *a* sockets, 1 trichome *b* socket, 3 trichome *c* with protruding based sockets and the circular indentation *d*.

Gnathochilarium: Lateral palp twice as long as medial palp. 13 conical sensilla on lateral palp, medial palp with 21, same in holotype and paratypes (Figs. 3G and 6F). *Trunk*: 10 tergites, 9 pleural projections, and telson excluding caudal bundle.13 pairs of legs. Collum (tergite 1) with trichome sockets arranged in 2 oval shapes in the lateral position opposite each other, connected by a posterior row of trichome sockets

forming a line with a gap in the middle. Holotype, trichome sockets in collum with 65 (L) and 67 (R), lateral protuberances with 3 trichome sockets on each side (Fig. 3B) (Trichome sockets on collum varying in paratypes ranging from 64–83 sockets and 3–4 sockets on lateral protuberances). Tergites 2–10, each with pleural projections located in anterolateral positions. Tergal trichome socket arrangements from tergites 2–9

typically with 2 broad oval shapes, slightly enlarged laterally, connected with a posterior row extending toward to the centre with a large gap between these trichome sockets (Figs. 3C and 6C). Tergite 10 is the exception, with trichome sockets being smaller and denser (Fig. 3D). Trichome sockets of tergite 2 in holotype have 67 (L) and 65 (R) (Fig. 3C). Tergite 10 with 93 sockets on both sides (Fig. 3D) (In contrast, trichome sockets on tergite 2 in paratypes 66–70, whereas tergite 10 has between 91–110 trichome sockets). *Legs*: Leg segmentation following Manton (1956). Legs 1 and 2 without trochanter, leg 1 lacking tarsus 1.
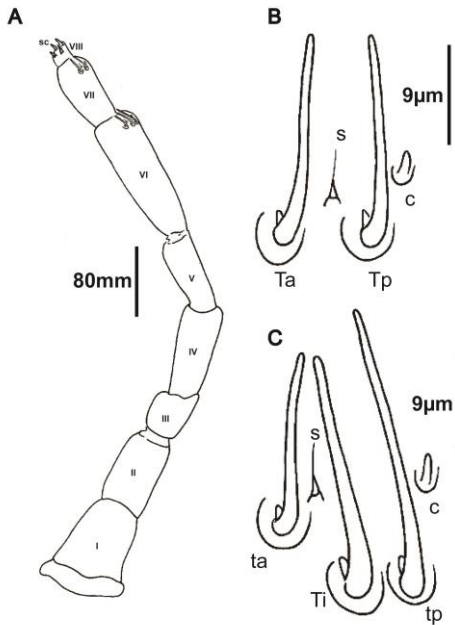

Figure 4. Holotype of *Mauritixenus ninhthuanensis* sp. nov. A = Whole antenna showed 8 article; B = Bacilliform sensilla (T) arrangement on article VII: Ta (Thick bacilliform sensillum located in anterior position in the sensilla arrangement on VII), Tp (posterior), s (setiform sensillum located in between Ta and Tp) followed by c (conical sensillum located in the posterior position in the arrangement structure); C = Bacilliform sensilla (T) arrangement on article VI: ta (thin short bacilliform sensillum located in anterior position), Ti (Thick long bacilliform sesnillum located in the intermediate position in the structure) and tp (thin longest bacilliform sesnillum located in posterior position); s (setiform sensillum located between ta and Ti and c (conical sensillum located in the posterior position).

Chaetotaxy (setae on leg articles): coxa 1: 1 seta, coxa 2: 2 setae, coxae 3–13: 2–4 setae; pre-femur, post-femur and tibia with a seta (sometimes with 2 setae on tibia); femur with 2 setae and tarsus 2 with a long, sharp spine (Figs. 5A and 8A). Setae on coxa, pre-femur, femur distally with the ridged bi-articulated, funicular cylindrical sensilla (Fig. 5D); setae in mid femur and tibia are similar, but smaller (Figs. 5B and 5C), tarsus 1 without seta and tarsus 2 with a long sharp spine (Figs. 5E and 8B). Posterior edge of the last sternite with 2 setae similar those present on coxa (Number of these setae vary from 2–4 in paratypes). Sex organs in male: Pair of penes present on coxa 2; 2 pairs of coxal glands on coxal plates of legs 8th and 9th.

Telotarsus-Claw: A slender structure bearing a posterior lateral process that is longer than half the length of the claw. A small anterior lateral process and a lamella process present, anterior setiform process slightly enlarged at base and longer than the claw (Figs. 5F and 8D).

Telson: Dorsal ornamental trichome sockets arranged symmetrically on both sides of telson with 10 trichome *a* sockets in holotype (Paratypes with 10–17 trichomes *a*), these trichome *a* sockets form 2 rows with small sockets above and larger sockets in a row below, the largest trichome *a* socket is often in position 5 (Figs. 3I). A single trichome *b* socket and 3 trichome *c* with large protruding base sockets: *c*1, *c*2 and *c*3, forming a triangular shape each side of telson. Circular indentation *d* apparent near the exterior side of trichomes *c*.

Caudal bundles: Male, caudal bundle with a single bundle of uniform large trichome sockets of caudal trichomes. Female, two obvious distinguishing structures: A main dorsal structure similar to the male, but with 2 latero-sternal bundles of smaller trichome sockets of nest trichomes (Fig. 8C). Caudal trichomes 2–4 hooks. (These caudal structures are like those observed in *Monographis* (Huynh & Veenstra 2013) which is classified as caudal bundle type I (Condé & Nguyen Duy-Jacquemin 2008)).

Remarks. Mauritixenus ninhthuanensis sp. nov. is the first species from genus *Mauritixenus*

(Polyxenidae) found in Vietnam which is outside the Mascarene Islands and African region. *Mauritixenus ninhthuanensis* characteristics are similar to most species in genus *Mauritixenus* in having a spine on tarsus 2, labrum with apical papillae structures and antennal article VI with three bacilliform sensilla. All these characteristics are found in a group of *Mauritixenus* species: *Mauritixenus pauliani* and *M. sakalavus*. *Mauritixenus ninhthuanensis* sp. nov. differs in body length (3.0–3.6 mm) and the number of sensilla on the gnathochilarium lateral palp (13 sensilla).
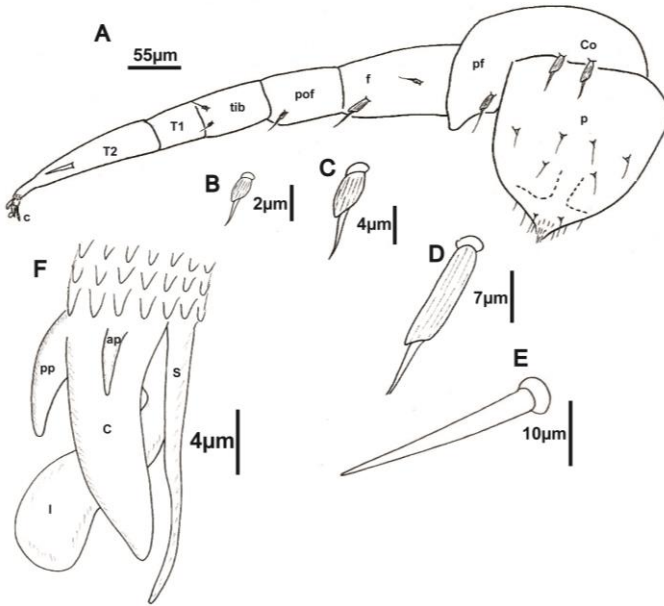
Figure 5. Holotype of *Mauritixenus ninhthuanensis* sp. nov. A = Leg segments and chaetotaxy (Setae on leg segments) of the second leg and penis (Co: coxa, pf: prefemur, f: femur, pof: post femur, tib: tibia, T1: tarsus 1, T2: tarsus 2 and c: claw). Three types of ridged biarticulate funicular cylindrical setae present; B = the smallest seta found in tibia and the mid femur; C = smaller seta found in post femur; D = normal seta found in coxa, prefemur and femur; E = A long sharp spine on Tarsus 2; F = Telotarsus with processes indicated (c: claw, ap: anterior lateral process, pp: posterior lateral process, s: setiform process and l: lamella process).

Key to described species of *Mauritixenus*

(*Mauritixenus betschi retusus* Nguyen Duy-Jacquemin & Condé, 1969 was not included in this key due to inefficient characters as subadult stage).

1. Labrum with apical papillae, lateral gnathochilarium palp with ……………………………………………………..**2**
– Labrum with spine setae, lateral gnathochilarium palp with ………………………………………………………..**3**

2. 12 sensilla, Antennal article VI with 5 sensilla ……………...*Mauritixenus borbonicus*
– 16 sensilla, Antennal article VI with 4 sensilla ……………...…………………......................*Mauritixenus gracilicornis*

– 8 sensilla, Antennal article VI with 3 sensilla ……………...…………………….…...........…....*Mauritixenus sakalavus*
– 12 sensilla, Antennal article VI with 3 sensilla …………….…...…….*Mauritixenus pauliani*
– 13 sensilla, Antennal article VI with 3 sensilla …………….………..................*Mauritixenus ninhthuanensis* sp. nov.

3. 10 sensilla, Antennal article VI with 3 sensilla ……………...…..…….*Mauritixenus vachoni*
– 11 sensilla, Antennal article VI with 3 sensilla ……………...…...............................….……...*Mauritixenus betschi*

Phylogenetic Analysis

Sequences from the new species *Mauritixenus ninhthuanensis* were compared with

other penicillate millipede sequences available from GenBank (Tab. 1). The 18S maximum likelihood tree generated by 1000 bootstrap rep-

lications yielded a strongly supported phylogenetic tree with the bootstrap value (>50, shown on the nodes of the clade). The 18S region of the
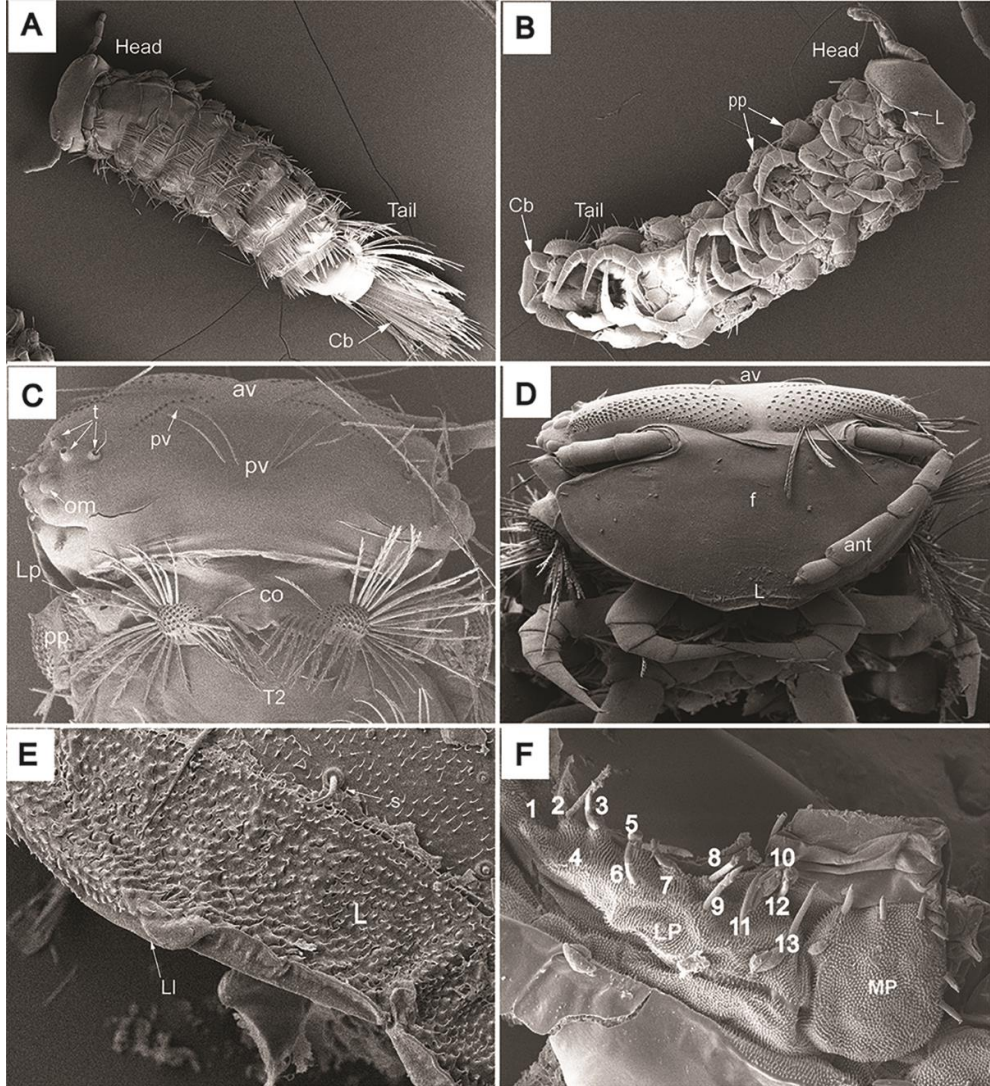
Figure 6. *Mauritixenus ninhthuanensis* sp. nov. A = Dorsal view (Cb: caudal bundle); B = Ventral view (L: labrum, pp: pleural projections); C = Head capsule, collum (co) and T2 (Dorsal view, av: anterior vertex, PV: posterior vertex, pv: posterior vertex trichome group, t: trichobothria, om: ommatidia, Lp: lateral protuberances, pp: pleural projection); D = Head capsule and mouth part (Ventral view, f: frons, L: labrum, ant: antenna); E = Labrum surface with apical papillae (L: labrum, Ll: lateral labrum); F = Gnathochilarium showed lateral palp (LP) with 13 sensilla and medial palp (MP) showed few sensilla and some missing sensilla.
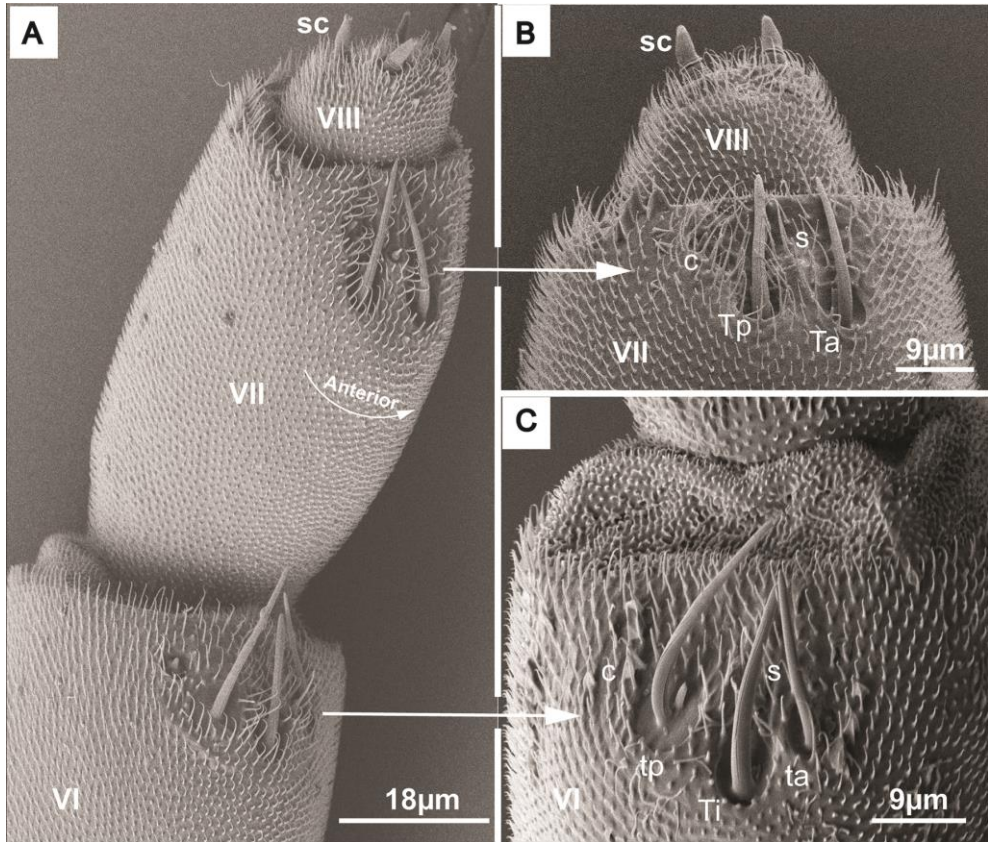
Figure 7. *Mauritixenus ninhthuanensis* sp. nov. A = Antennal articles VI, VII, VIII and sensory cones (sc) and the sensilla arrangements; B = Antennal article VII, VIII, sensory cone (sc) and sensilla on article VII (c: conical cones, Tp: thick bacilliform sensillum (posterior position), Ta: thick bacilliform sensillum (anterior position) and s: setiform sensillum); C = Antennal VI and its sensilla arrangement (ta: Thin short bacilliform sensillum located in anterior position, Ti: Thick long bacilliform sensillum located in the intermediate position in the structure and tp: Thin longest bacilliform sensillum located in posterior position).

3 sequences from studied species of *M. ninhthuanensis* sp. nov., *M. pauliani* and *M. gracilicornis* formed their statistically supported clades with sequences of the genus that they belong (Fig. 9A). Another bootstrap maximum likelihood tree based on a comparison of the COI region of this new species of the genus *Mauritixenus* also yielded a strong supported phylogenetic tree (Fig. 9B). All phylogenetic analysis indicated that this species is a new species from the genus *Mauritixenus* in family Polyxenidae.

DISCUSSION

The discovery of *Mauritixenus ninhthuanensis* in the Southeast Asian region showed that the genus *Mauritixenus* is not restricted to the Mascarene and African regions. *Mauritixenus* species have a wide distribution. In this genus, the species are characterised by a spine on tarsus 2 making it different from other genera in family Polyxenidae: *Monographis* Attems,

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1907 has spines on tarsus 1 and 2, it is distinctively different from *Unixenus* Jones, 1944, *Eudigraphis* Silvestri, 1948 and *Saroxenus* Cook, 1896 species that have a setiform seta on tarsus 2. The Vietnamese *M. ninhthuanensis* sp. nov. has characteristics similar to two *Mauritixenus* species – *M. pauliani* and *M. sakalavus* – all have a labrum with apical papillae, and 3 bacilliform sensilla on the antennal article VI. But they differ in the number of gnathochilarium's sensilla. The minor differences in characteristics within these species indicated little variation among species within this genus. The genetic study of *M. ninhthuanensis* sp. nov., including *M. gracilicornis* and *M. pauliani* which were collected from Mauritius and Rodrigues, showed that this is a new species according to the study of COI genes. The 18S genes indicate that they belong to the genus *Mauritixenus* (Polyxenidae). The description of this new species will enhance the knowledge of penicillate millipedes worldwide.
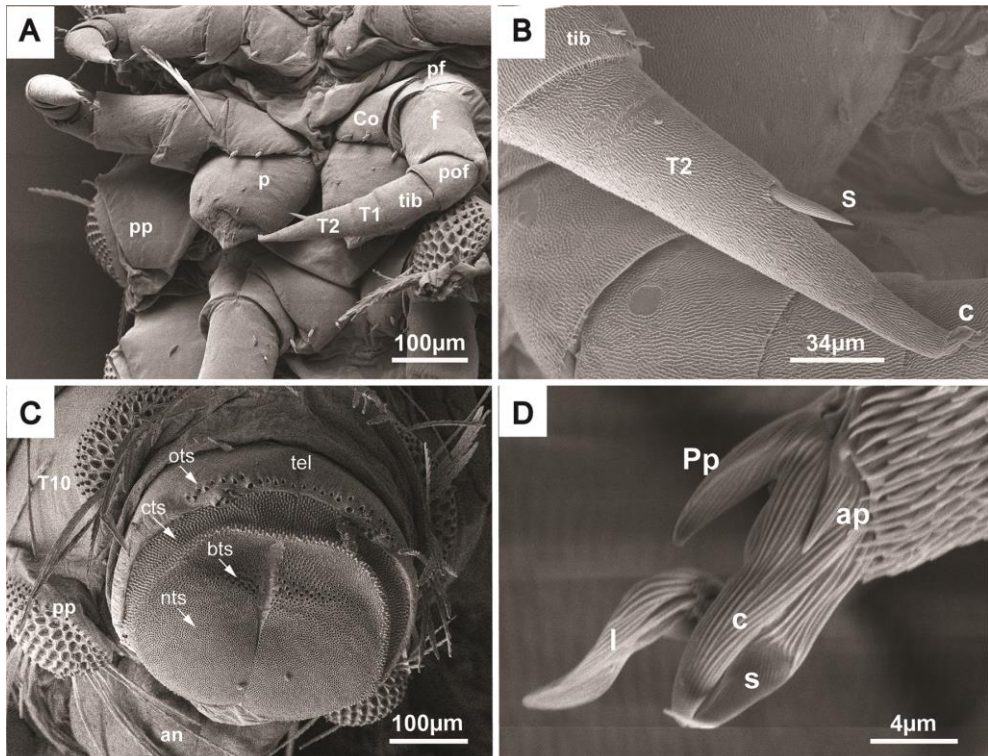
Figure 8. *Mauritixenus ninhthuanensis* sp. nov. A = Leg segments and chaetotaxy (Setae on leg segments) of the second leg and penis (Co: coxa, pf: pre femur, f: femur, pof: post femur, tib: tibia, T1: tarsus 1, T2: tarsus 2 and c: claw; p: penis, pp: pleural projection); B = segment of the 1st leg showed T1 and T2 with a spine (S) and claw (c); C = Caudal bundle structure showed telson (tel), ornamental trichome sockets (ots), caudal bundle trichome sockets (cts), barbate trichome sockets (bts), nest trichome sockets (nts), tergite 10 (T10), pleural projection (pp), anus (an); D = Telotarsus showed the claw (c), lamella process (l), setiform process (s), anterior lateral process (ap), posterior lateral process (Pp).
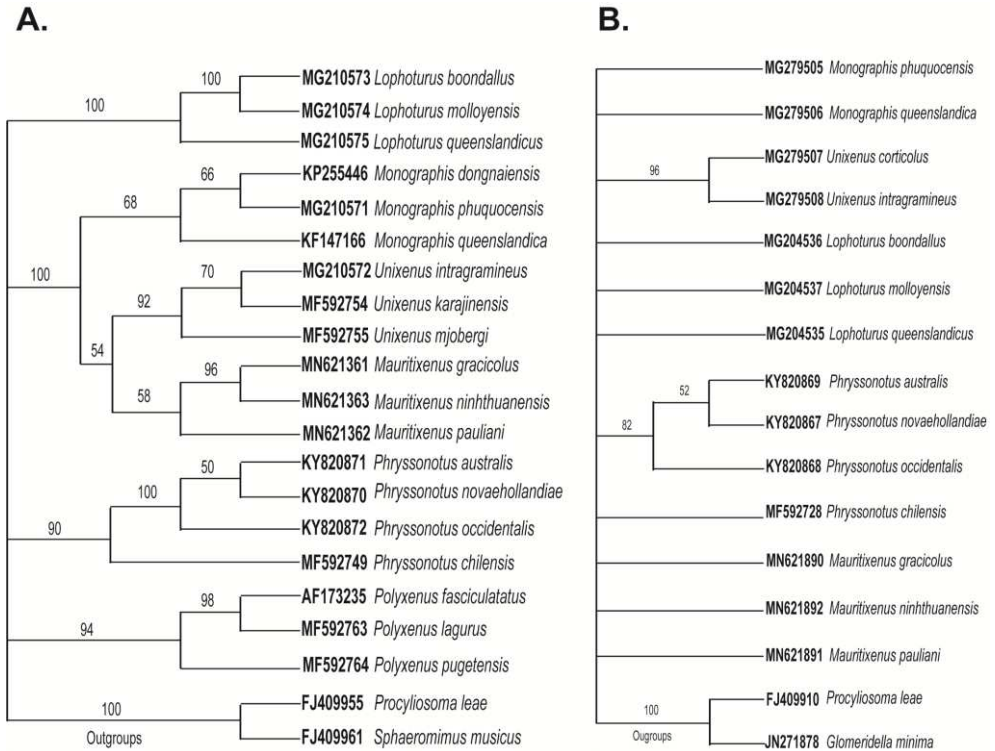
Figure 9. Molecular phylogenetic trees analysis of *Mauritixenus ninhthuanensis* sp. nov. with other penicillate millipedes from the GenBank (Bootstrap values >50) by maximum likelihood method. A = based on 18S genes; B = based on COI gene.

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New species of Polyxenida in Israel (Diplopoda, Penicillata)

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Abstract. The identification of 5 species from a recent collection of 23 specimens from two areas in Israel is given. Two new species of Polyxenida are recorded, including the first species in the family Synxenidae (*Phryssonotus* sp.) and the first species from the family Polyxenidae, subfamily Macroxeninae (*Chilexenus* sp.), from Israel. These species are identified only to genus due to the lack of undamaged adult material. Two species in the family Lophoproctidae are also identified, one previously recorded but not described, is now described as *Lophoproctus israelensis* sp. nov., and *Lophoproctinus chichinii* Condé, 1951is recorded from Israel for the first time. The fifth species is identified as possibly a new species in the genus *Polyxenus* and likely to be synonymous with the specimens identified as *Polyxenus lagurus* Linnaeus, 1758 in a previous study. This is just the second collection from Israel to be identified and brings the total number of Polyxenida species found in Israel to 8. All 3 families of Polyxenida are represented in this list, together with all 3 subfamilies of the most numerous family, Polyxenidae.

Keywords. Bristly millipedes, biodiversity, Mediterranean, millipedes.

INTRODUCTION

In the period 1962–1966, Dr G. Levy of The Hebrew University of Jerusalem (Department of Entomology and Venomous Animals) made the first recorded collection of Polyxenida from Israel, with Condé & Nguyen Duy-Jacquemin (1971) identifying 5 species from this collection, namely *Polyxenus lagurus* Linnaeus, 1758, *Polyxenus chalcidicus* Condé & Nguyen Duy-Jacquemin, 1971, *Propolyxenus trivittatus* Verhoeff, 1941 (now a junior synonym of *P. argentifer* (Verhoeff, 1921), see Short *et al.* (2020)), *Miopxenus mootyi* Condé, 1951, all in the family Polyxenidae, and one species from the family Lophoproctidae, incompletely identified as *Lophoproctus* sp.. Polyxenidans have been identified from just 2 neighbouring countries, namely *Lophoproctinus chichinii* Condé, 1951, from Egypt and Lebanon (Condé 1951, 1954*a*), *Miopxenus mootyi* Condé, 1951 from Egypt, and *Lophoproctus jeanneli* (Brölemann, 1910) from Lebanon (Condé 1954*b*). In this study, recent collections of polyxenidans from Israel are identified, including description of a new species.

MATERIALS AND METHODS

The millipedes examined for this study were collected between 2014–2018 by Amir Weinstein and stored in 75% ethanol. Selected specimens were measured and then cleared and mounted on slides in Hoyer's medium, and examined with an Olympus Vanox compound microscope. One specimen, not collected, was identified to family from a photograph. Photographs were provided by Amir Weinstein.

RESULTS

A total of 23 Polyxenida from collection sites in Israel were examined with one new species being described, 2 new species were identified to genus only, but not described due to lack of material, and 2 further species being identified. The geographic distribution of all known localities of the specimens in this study plus

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those reported in Condé & Nguyen Duy-Jacquemin (1971) were plotted (Fig. 1). Some additional localities outside Israel were also included.

Abbreviations: ZMUC—Zoological Museum, University of Copenhagen; HUJ—National Natural History Collections, Hebrew University, Jerusalem, Israel.
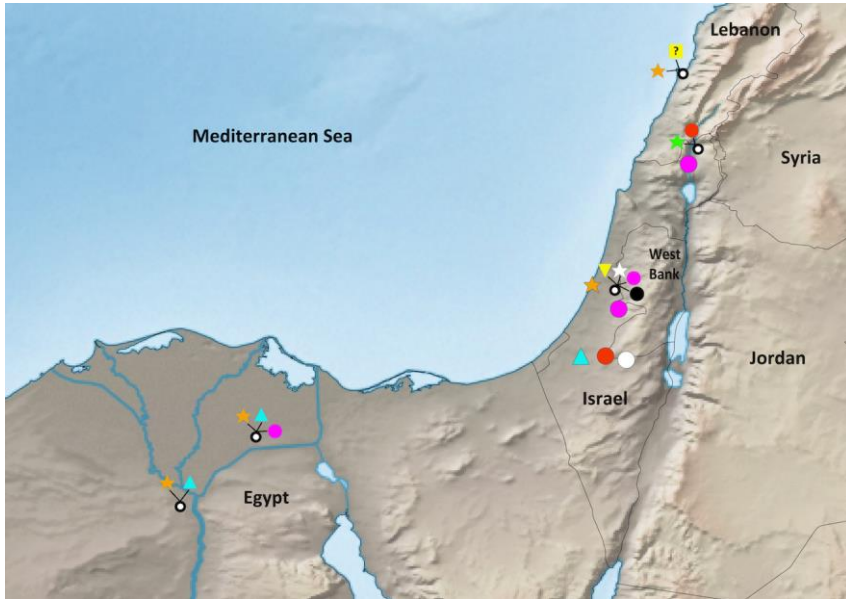
Figure 1. Map showing collection locations of Polyxenida in Israel and neighbouring countries. Legend: purple circle = *Polyxenus* sp.; red circle = *Polyxenus chalcidicus* Condé & Nguyen Duy-Jacquemin, 1971; green star = *Propolyxenus argentifer* (Verhoeff, 1921); aqua triangle = *Miopsxenus mootyi* Condé, 1951; inverted yellow triangle = *Lophoproctus israelensis* sp. nov.; orange star = *Lophoproctinus chichinii* Condé, 1951; yellow square = *Lophoproctus jeanneli*?; white star = *Phryssonotus* sp., black circle = *Chilexenus* sp., white circle = Lophoproctidae sp.

TAXONOMY

Subclass Penicillata Latreille 1831

Order Polyxenida Verhoeff, 1934

Family Lophoproctidae Silvestri, 1897

Genus *Lophoproctus* Pocock, 1894

Type species. *Lophoproctus coecus* Pocock, 1894.

Diagnosis. Distinguished from other genera of Lophoproctidae, in possessing 4 basiconic sensilla on the 6th antennal article and greater than 4 linguiform processes along the entire anterior rim of the labrum.

Lophoproctus israelensis **sp. nov.**

(Figures 1, 2A, 3A–O)

Material examined. Holotype. Adult male (aw-1), Israel, Modi'in area in Judean Hills, near Tel-Hadid, Ben Shemen Forest, N31°57', E34°56', 25 Mar. 2016, leg. A. Weinstein. Specimen mounted on slide. *Paratypes.* One adult male (aw-3), 2 sub-adult females (aw-2, aw-4), same collection as holotype. Specimens mounted on slides. Two adult females (aw-5) same collection as holotype, stored in 80% ethanol. All material deposited in HUJ.

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Figure 2. A = *Lophoproctus israelensis* sp. nov.; B = *Lophoproctinus chichinii* Condé, 1951; C = *Polyxenus* sp.; D = Lophoproctidae sp.. All polyxenidans photographed alive by Amir Weinstein. Used with permission. Scale bars = 1 mm.

Etymology. Adjective, named after the country where it was found.

Diagnosis. Very similar morphology to *Lophoproctus jeanneli* (Brölemann, 1910), differing in the arrangement of sensilla on the 6th antennal article.

Description. Measurements: Body length without caudal bundle after mounting on slides; holotype: 2.0 mm, tarsus length 13th leg, 128 μm; paratype sub-adult female (aw-2): 2.0 mm, caudal bundle 0.4 mm, tarsus length 13th leg: 117 μm.

Head (Fig. 3A): Lacking ommatidia. Vertex with 1 pair of posterior tufts each with a single anterior row of 10–12 trichomes, 1 trichome posteriorly, distance between each tuft twice their length, wide gap to anterior vertex trichomes. All trichomes long, slender and barbate. Three trichobothria arranged in an equilateral triangle with the most anterior smaller than the other 2 and with a clavate funicle (Fig. 3H).

Gnathochilarium typical of Lophoproctidae, with a medial palp only. Male holotype with 30 long and 10 smaller biarticulate sensilla (Fig. 3J), female paratype with 12 long and 8 biarticulate sensilla. Anterior margin of labrum with 11 linguiform processes each side, median pair with pointed apex, rest with parallel sides and a rounded apex. External surface of labrum with folds but lacking any visible ornamentation, 9–11 setae along posterior margin (Fig. 3K).

Antennae: Long antennae with proportions of antennal articles as in Figure 3G. 6th article a third longer than 7th article, while 7th and 8th articles equal in length. Of note is the unusually elongate 4th article. Details of sensilla based on holotype and sub-adult female paratype. Antennal article VI with 4 long basiconic sensilla arranged in diamond pattern, with a conical sensillum posteriorly (Fig. 3F); antennal article VII with 1 basiconic sensillum to posterior of 1 short basiconic sensilla and 1 posterior coeloconic sensillum (Fig. 3E).

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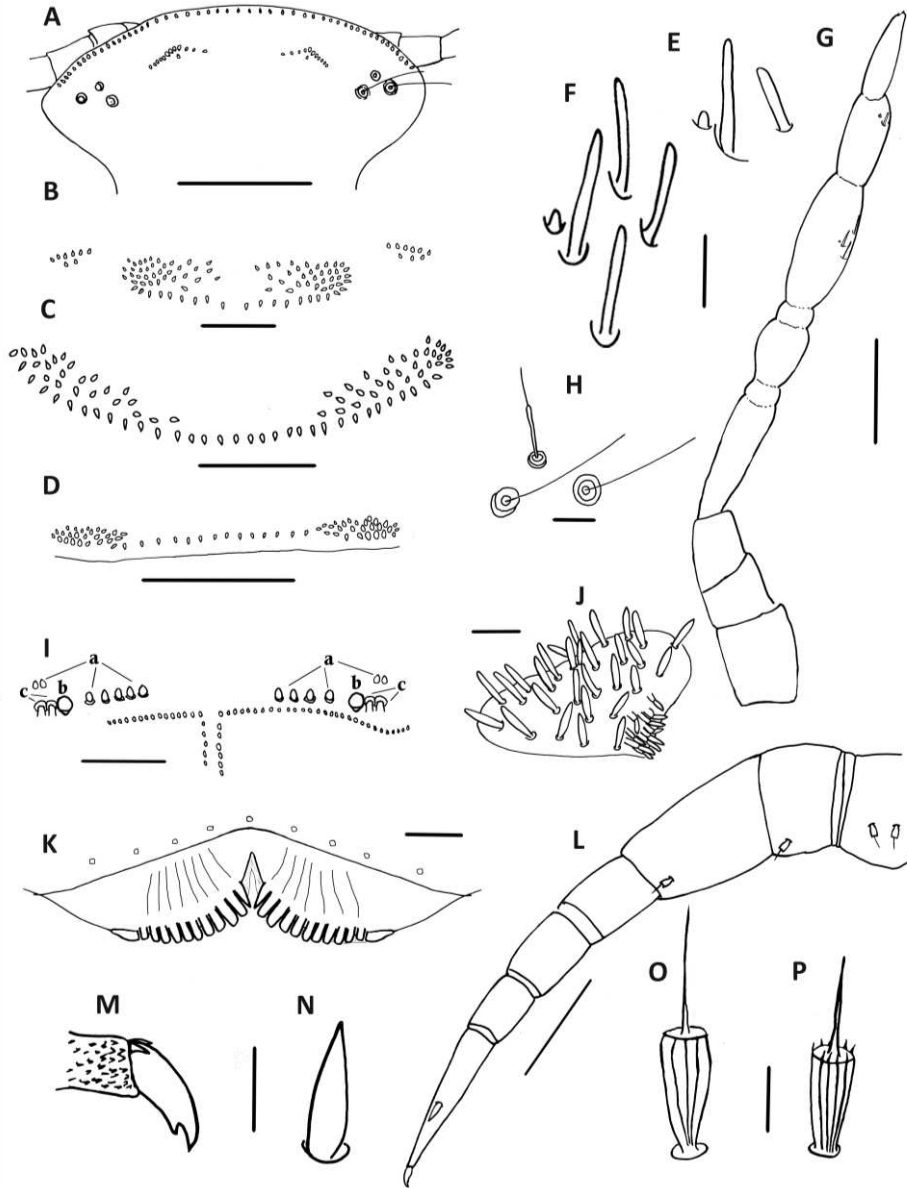
Figure 3. *Lophoproctus israelensis* sp. nov. (A–O) and *Lophoproctinus chichinii* Condé, 1951. (P). A = Head; B = Collum showing pattern of insertions of trichomes; C = Tergite 2 showing pattern of insertions of trichomes; D = Tergite 10 showing pattern of insertions of trichomes; E = Pattern of basiconic sensilla on antennal article VII; F = Pattern of basiconic sensilla on antennal article VI; G = Left antenna; H = Trichobothria; I = Pattern of insertions of dorso-medial trichomes, see text for details of *a*, *b* and *c*; J = Right gnathochilarium, male; K = Labrum; L = Sixth leg, left side; M = Telotarsus; N = Tarsal spine; O = Seta on femora, pre-femora and coxae. P = Seta on femora, pre-femora and coxae in *Lophoproctinus chichinii* Condé, 1951.
Scale bars: A, C, G, L =100 μm; B, D, I = 50 μm; H, K =20 μm; E and F (shared bar), J, M and N (shared bar),
O and P (shared bar) = 10 μm.

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Trunk: Collum with almost symmetrical arrangement of 86 trichomes (holotype), made up of lateral rosettes either side with 31+29 trichomes and a posterior row of 26 trichomes facing posteriorly, a small medial gap (Fig. 3B). Lateral protuberances of collum with 8–9 barbate trichomes arranged in two rows (Fig. 3B). Remaining tergites (Figs. 3C, D) with lateral elongate rosettes linked by a continuous posterior row of trichomes. Holotype tergite 2 with 85 trichomes. Trichomes, barbate with serrations not extending to the base, those of posterior row wider than those of the lateral tufts.

Legs (Fig. 3L): Naming of leg segments is after Manton (1956). Legs 1 and 2 without trochanter, leg 1 also lacking tarsus 1. Trochanter, post-femur and tarsus 1 lacking setae. Prefemora and femora each with 1 seta, coxa 1 with 1 seta, coxae 2–9, 2–3 setae, coxae 10–13, 1 seta, setae biarticulate with 8–10 longitudinal striations along funicle, and a long setiform process distally (Fig. 3O); spine on tarsus 2 slightly longer than claw (Fig. 3N); claw of telotarsus with a denticle and two small processes at base (Fig. 3M).

Telson: Dorso-medial (ornamental) trichomes each side of midline with 4–5 trichomes *a* internally and 2 smaller trichomes *a* externally, 1 trichome *b*, and 2 trichomes *c* in cluster between external and internal trichomes *a* (Fig. 3I); two bundles of caudal trichomes beneath with a very narrow gap, hooked trichomes of caudal bundles most commonly with 4 hooks.

Habitat. In soil and litter under tree canopy, adjacent to large rocks, in pine forest planted in the mid 1960s.

Remarks. Species in the genus *Lophoproctus* share a very similar morphology with species identification being based on small differences. Just two species, *L. jeanneli* and *L. israelensis* have a denticle associated with the claw. It is for this reason that Condé & Nguyen Duy-Jacquemin (1971) identified the specimen from Israel that they examined as *Lophoproctus* "*jeanneli* group". However, they noted the different pattern of sensilla on the 6th antennal article preventing identification as *L. jeanneli*. The speci-

men they examined is now assumed to be *L. israelensis* sp. nov. A further lophoproctid was photographed by collector Amir Weinstein in 2014 (Fig. 2D) under stones in an exposed arid area of the Yatir forest, a planted forest on the southern slopes of Mt Hebron on the edge of the Negrev Desert. Unfortunately, the specimen was not collected but although a photograph suggests it is likely to be *L. israelensis* sp. nov., the species cannot be confirmed until material is examined.

Genus *Lophoproctinus* Silvestri, 1898

Type species. Lophoproctinus inferus (Silvestri, 1903) [= *Lophoproctus inferus* Silvestri, 1903]

Diagnosis. Distinguished from other genera of Lophoproctidae, in possessing 3 basiconic sensilla on the 6th antennal article and greater than 4 linguiform processes along the anterior rim of the labrum.

Lophoproctinus chichinii Condé, 1951

(Figures 1, 2B, 3P)

Diagnosis. Very similar to *Lophoproctinus inferus* var. *maurus* (Marquet et Condé, 1950), but differs in the basiconic sensilla of the 6th antennal article being arranged in a spaced oblique line rather than transversely. Also differs in having a stockier telotarsus.

Material examined. One adult female (aw6), 1 sub-adult female (aw7), whole mounts on slides, 1 sub-adult female in ethanol (aw8), Israel, Bat-Yam, in rotting cypress log in back garden, N32º0', E34º45', 14 Jan. 2017, leg. A. Weinstein. All material is to be deposited in HUJ.

Remarks. This species was described in Condé (1951) from 2 adult female specimens found in the Nile Valley, Egypt. In a footnote in Condé (1954*a*), there is brief mention of identification of a sub-adult male *L. chichinii* from Beirut, Lebanon. It is unfortunate that the figures in Condé (1951) lack an illustration of a typical leg seta, as his written description merely indicates that the setae are biarticulate with a subcylindrical, glabrous funicle. The Israeli specimens examined in this

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study have setae with funicles that are not only sub-cylindrical and glabrous but are also distinguished by longitudinal striations extending distally in a series of thin points that surround the base of the flagellum (Fig. 3P). The absence of any mention of these distinctive details is a concern, however it should be noted that in describing *Anopsxenus indicus* Condé et Jacquemin, 1963, the authors neglected to mention the longitudinal striations that are obviously present in the figure provided in the same paper of a leg seta. In his description, Condé (1954*a*) described the caudal bundles of the Egyptian specimens of live *L. chichinii* as light brown, whereas the Israeli specimens have a distinctly white caudal bundle when alive (Fig. 1B).

Family Polyxenidae

Subfamily Polyxeninae Condé, 2008

Diagnosis. Structure of the telson with two caudal bundles of trichomes widely separated, with a dorso-medial fan of barbate trichomes.

Genus *Polyxenus* Latreille, 1802

Type species. Polyxenus lagurus Linnaeus, 1758

Diagnosis. Tergites with trichomes arranged in rosettes laterally, with 2 evenly spaced transverse rows along posterior edge.

Polyxenus sp.

(Figures 1, 2C)

Material examined. One adult male (aw9), Israel, Modi'in area in Judean Hills, near Tel-Hadid, Ben Shemen Forest, N31°57', E34°56', 25 Mar. 2016, leg. A. Weinstein, slide mounted; 5 specimens from same collection in 80% ethanol (aw10), all deposited HUJ; 1 adult male, Israel (no further details), ex coll. M. Warburg, slide mounted, deposited in ZMUC.

Remarks. Polyxenus sp. specimens have been collected from a number of countries, but although their morphological characters would suggest that they are *P. lagurus*, they can be distinguished by their very small size, sexual mode of reproduction, and their genetic distinctness (Short *et al.* 2020). Only one of these tiny *Polyxenus* has been described to date, *P. lankaranensis* Short *et al.*, 2020 (see Short *et al.* 2020), found in Azerbaijan and Russia. Other genetically distinct small *Polyxenus* have been collected from Spain, Hungary, Italy and Crimea (Short *et al.* 2020).

The specimens examined in this study appear morphologically very close to *P. lankaranensis*, with a small size (body length adult male 1.85 mm). Medial anterior vertex trichomes are similar to *P. lankaranensis*, being shorter, a darker colour, and more bulbous with shorter serrations than those of *P. lagurus* (Short *et al.* 2020). However, it will require collection of specimens suitable for gene sequencing to determine if they are a new or an existing species.

It is unfortunate that Condé & Nguyen Duy-Jacquemin (1971) did not give the size of specimens they identified from Israel as sexually reproducing populations of *Polyxenus lagurus*, as it is possible that these might not be *P. lagurus*. The only description given is of the number of thin sensilla on antennal article VI, the numbers of which are not useful for distinguishing *P. lagurus* from *P. lankaranensis* or other *Polyxenus* species. In Figure 1, both *P. lagurus* and *Polyxenus* sp. have been mapped simply as *Polyxenus* sp..

Family Polyxenidae

Subfamily Macroxeninae Condé, 2008

Diagnosis. Presence of pseudoarticulated sensilla on the palpi of the gnathochilaria. Type II (Condé 1969) telson with two latero-dorsal bundles of hooked trichomes joined closely side by side; dorsal face of telson with a row of barbate trichomes *a* each side of median plate, and a cluster of longer barbate trichomes *c* each side protruding into the bundles of hooked trichomes.

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Genus *Chilexenus* Silvestri, 1948

Diagnosis. Spine on tarsus 2. Short distance between oval lateral tufts of trichomes. Three basiconic sensilla on antennal article VI.

Type species. Chilexenus rosendinus Silvestri, 1948.

Chilexenus **sp.**

(Figures 1, 4)

Material examined. One female adult (aw-11), Israel, Modi'in area in Judean Hills, near Tel-Hadid, Ben Shemen Forest, N31°57', E34°56', 25 Mar. 2016, leg. A. Weinstein, slide mounted.
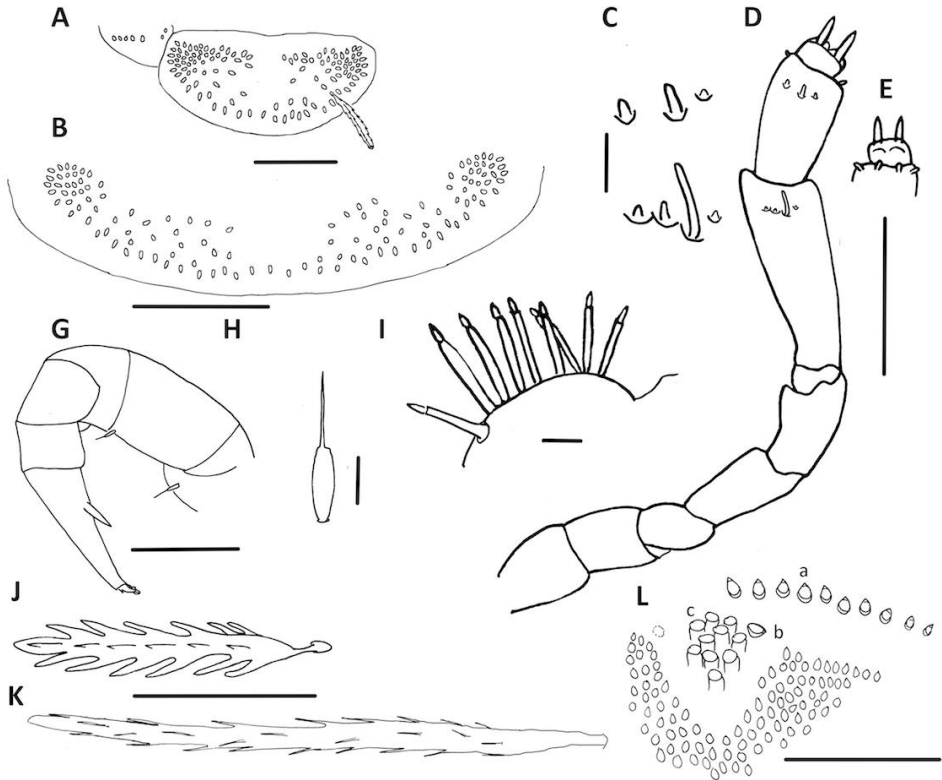
Figure 4. *Chilexenus* sp. A = Collum showing pattern of trichome insertions; B = Tergite 2 showing pattern of trichome insertions; C = Detail of sensilla on 6th and 7th antennal articles; D = Right antenna, dorsal view; E = Right antenna, ventral view of 7th (part) and 8th antennal articles; G = Part of leg 6; H = Seta found on femora and prefemora; I = Portion of medial palp showing pseudoarticulated sensilla; J = Typical shape of tergal trichomes of transverse posterior rows; K = Barbate trichome of the lateral tergal rosettes; L = Pattern of dorso-medial trichome insertions (refer text for details of a, b and c). Scale bars: A, B, D and E (shared bar) = 100 μm; G, J and K (shared bar), L = 50 μm; C, H, I =10 μm.

Remarks. Nguyen Duy-Jacquemin (2009) in her revision of the subfamily Macroxeninae provided a key to the genera within the subfamily. The single adult female from Israel possesses characters consistent with the subfamily, namely,

8 ommatidia, a small gap between bundles of caudal trichomes (giving the appearance of a single bundle), pseudoarticulated sensilla on the gnathochilaria (Fig. 4I), and the pattern of dorso-medial trichomes (Fig. 4L). Classification to the

genus *Chilexenus* can be made based on the presence of a large tarsal spine (Fig. 4G), 3 basiconic sensilla on antennal article VI (Fig. 4C), and the pattern of tergal trichomes (Figs. 4A and 4B). Comparison with descriptions of *C. rosendinus* (Silvestri 1903, 1905, Nguyen Duy-Jacquemin 2009) indicates that the specimen from Israel is a new species. This specimen is smaller with a body length (without caudal bundle) of 1.95 mm in comparison with *C. rosendinus* at 2.70 mm (Nguyen Duy-Jacquemin 2009), and the antennal sensilla are very reduced in size with the exception of the posterior sensillum on article VI. An unusual feature is the presence of 4 distinctive oval structures evenly positioned protruding from the ventro-distal edge of antennal article VI (Fig. 4E). Although these structures are not mentioned in any of the descriptions of *C. rosendinus*, two are shown to be present in Silvestri (1905: plate 36, fig. 38). A further unusual feature of the Israeli specimen is the apparent presence of just two very large apical sensilla on antennal article VIII, when the typical pattern for Polyxenida is four. It will be necessary to collect more specimens of this species in order to determine if the absence of 2 apical sensilla is typical of the species.

It is interesting to note that *Chilexenus* has a similar disjunct geographic distribution (South America and Mediterranean) to *Macroxenus* with *C. rosendinus* found in Chile while the new species is from Israel. In the genus *Macroxenus*, of the two species identified to date, *M. rubromarginatus* (Lucas, 1846), is found in Portugal, Morocco, Algeria and Malta, and *M. caingangensis* (Schubart, 1944) in Brazil. Of the two remaining genera in the subfamily Macroxeninae, *Macroxenodes* Silvestri, 1948 is only found in the Americas while *Afraustraloxenodes* Nguyen Duy-Jacquemin, 2003 has only been identified from southern Africa.

Family Synxenidae

Genus *Phryssonotus*

Diagnosis. This genus is characterised by 17 pairs of legs, 15 normal walking pairs of legs and 2 pairs of pushing legs caudally; 11 tergal plates and a telson; 10 pleural projections; tergites covered medially with scale trichomes

directed caudally, long thin barbate trichomes laterally, 8–11 ommatidia; a long frontal trichome A and short frontal trichomes B adjacent to anterior trichobothrium c. Trichobothrium c smaller than other two trichobothria.

Type species. *Phryssonotus hystrix* (Menge, 1854).

Phryssonotus sp.

(Figures 1, 5B)

Material examined. One immature only (aw-12), Israel, Modi'in area in Judean Hills, near Tel-Hadid, Ben Shemen Forest, N31°57', E34°56', 25 Mar. 2016, leg. A. Weinstein, slide mounted, deposited in the National Natural History Collections in the Hebrew University of Jerusalem, Israel.

Remarks. The single specimen collected is not only an immature stadium, but also damaged, lacking almost all trichomes including the scale-like dorsal trichomes so distinctive of the genus. However, the two characteristics Silvestri (1923) used to distinguish species of *Phryssonotus*: number of ommatidia and number of short frontal trichomes B are visible. In their paper redescribing *P. novaehollandiae* (Silvestri, 1923), Short & Huynh (2006) noted that the number of trichomes B increases with each molt until the adult stadium, whereas the number of ommatidia is unchanged from stadium V1. The immature (stadium VI) *Phryssonotus* sp. in this study has 9 ommatidia and 2 trichomes B (Fig. 5B) indicating that the adult characters are most likely to be 9 ommatidia and > 2 trichomes B. As adult *P. platycephalus* (Lucas, 1846), the only species described to date from the northern hemisphere (Silvestri 1923), has 11 ommatidia and only 1 trichome B (Fig. 5A), it appears that the *Phryssonotus* specimen from Israel is a new species.

P. platycephalus has a Mediterranean distribution, having been collected in Algeria, eastern Libya, Spain, Sicily, and in the Balearic Islands. The first very brief description of the species by Lucas (1846) with figures in Lucas (1849) used uninformative characters, such that the more detailed redescription by Silvestri (1948) from
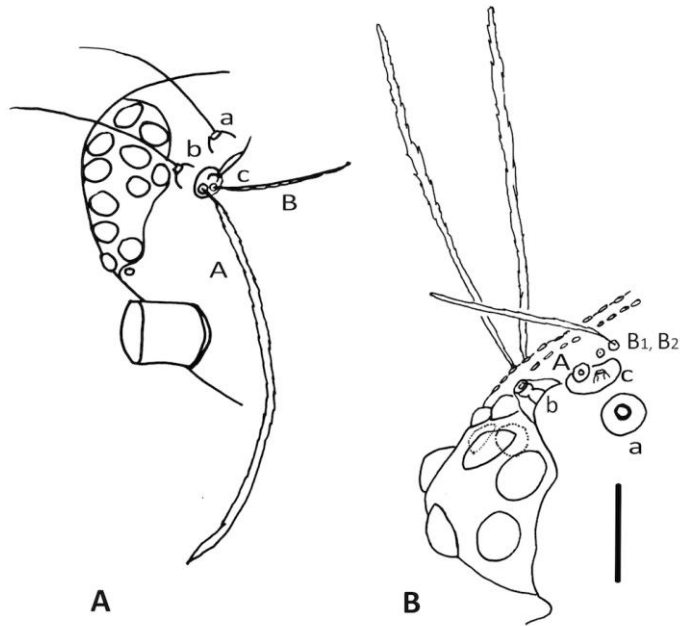
Figure 5. A = *Phryssonotus platycephalus* (Silvestri, 1923), ventral view of the right side of head redrawn from Silvestri (1923) showing characters used in the original description; B = *Phryssonotus* sp., Immature, stadium VI, dorsal view of left side of head showing the same characters. Diagnostic characters illustrated are: trichobothria a, b and c, long frontal trichome A, and short frontal trichomes B, B1, B2. No scale was given in the original drawing, scale bar for Figure 5B = 100 µm.

specimens collected in Spain is now used to identify and define the species. It is possible that the type from Algeria differs from the *Phryssonotus* from Spain, and synxenids from other countries identified from Silvestri's description may in fact not be *P. platycephalus*. This will be a problem until such time as the types from Algeria are found and re-examined, or a new collection is made from the type locality. As well, detailed examination of specimens from other populations needs to be made.

DISCUSSION

Eight species have now been identified, if not all fully described as yet, from Israel (Tab. 1). Quite remarkable is not only the number of species from the northern half of such a tiny country, collected by just two individuals, but also the diversity, with all 3 families of Polyxenida (Polyxenidae, Synxenidae and Lophoproctidae)

represented, as well as all 3 subfamilies of the largest family Polyxenidae. Such a concentrated diversity of Polyxenida has yet to be found elsewhere worldwide. It can only be speculated as to the reasons for this diversity. Is it possibly due to Israel being at the intersection of the African and European continents, with a Mediterranean climate to the north and a drier desert to the south? Polyxenidans have been found in arboreal birds' nests (Nguyen Duy & Condé 1966, Tajovský *et al.* 2001) and in elevated habitats such as tree canopies, so it is possible that they are transported by wind and attached to birds' feathers by their hooked setae. Aerial dispersal is supported by unpublished data from three different investigations in the Harz Mountains National Park, Germany, with *P. lagurus* being found in air traps as well as in color traps (Lindner pers. comm. 2020). So, might the bird migration flight paths or direction of winds across Israel also be factors contributing to polyxenidan diversity?

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Table 1. List of Polyxenida identified from Israel.

Family	Subfamily	Species	Records of presence in Israel
Synxenidae		*Phryssonotus* sp.	Current study
Polyxenidae	Polyxeninae	*Polyxenus* sp. (formerly identified as *Polyxenus lagurus,* Linn., 1758).	Condé & Nguyen Duy-Jacquemin 1971, current study
		Polyxenus chalcidicus Condé & Nguyen Duy-Jacquemin, 1971	Condé & Nguyen Duy-Jacquemin 1971
		Propolyxenus argentifer (Verhoeff, 1921), (= *Propolyxenus trivittatus* Verhoeff, 1941)	Condé & Nguyen Duy-Jacquemin 1971
	Monographinae	*Miopxenus mootyi* Condé, 1951	Condé & Nguyen Duy-Jacquemin 1971
	Macroxeninae	*Chilexenus* sp.	current study
Lophoproctidae		*Lophoproctus israelensis* sp. n.	Condé & Nguyen Duy-Jacquemin 1971, current study
		Lophoproctinus chichinii Condé, 1951	current study

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Two new species of centipedes, *Lithobius keelungensis* sp. nov. and *Lithobius* (*Monotarsobius*) *qingquanensis* sp. nov., from Taiwan (Chilopoda, Lithobiomorpha, Lithobiidae)

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Abstract. Male secondary sexual characters are diverse in Taiwanese *Lithobius*. We describe two new species with their male secondary sexual characters, *Lithobius* (*Ezembius*) *keelungensis* sp. nov. and *Lithobius* (*Monotarsobius*) *qingquanensis* sp. nov.. In *L.* (*E.*) *keelungensis*, male 14–15th femora and tibiae are markedly thick, the femora have a deep furrow on each dorsal surfaces, and the tibiae are oval, with a wide shallow excavation on each dorsal surfaces. In *L.* (*M.*) *qingquanensis*, a small wart-like outgrowth bearing about 15 slightly curved setae is present on the dorsoposterior surface of the male 15th femur.

Keywords. Keelung, male secondary sexual character, taxonomy.

INTRODUCTION

The centipede genus *Lithobius* Leach, 1814 is among the poorly studied taxa of Taiwan. Takakuwa (1939, 1941a, 1941b) described and recorded eight species of *Lithobius* from Taiwan. However, his specimens were destroyed in an air attack during the war in 1945. Wang (1955, 1956, 1957, 1959, 1963) recorded the localities of seven species of *Lithobius* from Taiwan without descriptions, and we could not locate Wang's specimens in any collections. We studied new specimens of *Lithobius* from Taiwan, and deposited them at the National Museum of Natural Science (NMNS). Male secondary sexual characters are important characters in the taxonomy of *Lithobius*: several several longitudinally arranged long setae were present on the ventral surface of male 15th tibia in *Lithobius trichopus* Takakuwa, 1939; a small tunnel at the top of a longitudinal excavation is present on the dorsal surface of 14th tibia in

male *Lithobius ongi* Takakuwa, 1939, and the tunnel and bottom of the excavation bear numerous small pores (Chao *et al.* 2018a); a large ventral swelling on the male 15th femur in *Lithobius* (*Monotarsobius*) *meifengensis* Chao, Lee & Chang, 2018, and the apical region of the swelling bearing numerous small pores (Chao *et al.* 2018b). We here describe two new species from Taiwan, *Lithobius* (*Ezembius*) *keelungensis* sp. nov. and *Lithobius* (*Monotarsobius*) *qingquanensis* sp. nov. using two other types of male secondary sexual characters.

MATERIAL AND METHODS

One and fifteen specimens, respectively, of the two new species treated below were collected from Keelung City and Hsinchu County, Taiwan. The specimens were examined by light microscopy (Leica MZ16) and SEM (Hitachi SU-1510). Type specimens are preserved in 75% alcohol and deposited in the Department of

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Biology, National Museum of Natural Science, Taichung, Taiwan. Terminology of the external anatomy follows Bonato *et al.* (2010). The following abbreviations are used in the text and tables: a—anterior, C—coxa, F—femur, m—median, p—posterior, P—prefemur, S/SS—sternite/sternites; t—trochanter, T/TT—tergite/tergites, Ti—tibia.

TAXONOMY

Order Lithobiomorpha Pocock, 1895

Family Lithobiidae Newport, 1844

Genus *Lithobius* Leach, 1814

Subgenus *L.* (*Ezembius*) Chamberlin, 1919

***Lithobius keelungensis* sp. nov.**

(Figures 1–15)

Material examined. Holotype. ♂ (NMNS8103-001): forest floor, Hepin Island, Keelung City, Taiwan, 25°09.36'N, 121°45.94'E, 13 m in elevation, 12 Jan 2019, leg. Jui-Lung Chao. *Paratypes,* 1♂ (NMNS8103-002): same data as holotype. *Other material,* 2♂♂, 2♀♀ (NMNS7843-019, NMNS7843-020, NMNS7843-021, NMNS7843-022), same locality as holotype, 14 Jan 2018, leg. Jui-Lung Chao; 1♀ (NMNS8103-003), 12 Jan 2019 and 2♂♂, 4♀♀ (NMNS8103-004), 08 Apr 2019, forest floor, Keelung City, 25°07.85'N, 121°43.72'E, 84 m, leg. Jui-Lung Chao; 2♂♂ (NMNS8103-005), forest floor, Keelung City, 25°08.90'N, 121°46.73'E, 33 m, 27 Jan 2018, leg. Jyh-Jong Cherng.

Etymology. Refers to the type locality.

Diagnosis. A *Lithobius* species, antennae with 20 articles; 7–9 ocelli arranged in three irregular rows [1 + 2, 3(4), 2(1)], posterior ocellus largest, two posterosuperior ocelli large, ventral seriate ocelli smallest; Tömösváry's organ larger than adjacent ocelli; 2+2 coxosternal teeth; porodonts posterolateral to outer tooth; all tergites lacking posterior triangular projections; coxal pores 4–6, round; male secondary sexual characters on 14–15th: femora and tibiae mark-

edly thick, 14–15th femora with a furrow on each dorsal surface, male 14–15th tibiae oval, with a wide shallow excavation on each dorsal surfaces; male gonopods with three long setae; female gonopods with 2+2 sharp coniform spurs, point of terminal claw undivided, a small sharp lateral denticle on base of terminal claw.

Description. Body length: 11–13.5 mm. Body colour: dark brown (Figs. 1–2). Antennae with 20 articles; basal article width subequal to length, following articles markedly longer than wide; distal article much longer than wide, up to 3.4 times as long as wide; abundant setae on antennal surface, less so on basal articles, gradual increase in density to around fourth article, then more or less constant in number. Cephalic plate smooth, convex, width subequal to length, posterior marginal ridge moderately broader and weakly concave; setae scattered sparsely over whole surface (Fig. 7). 7–9 ocelli on each side [1 + 2, 3(4), 2(1)], one posterior, two dorsal, three or four middle and one or two ventral, arranged in three irregular rows; posterior ocellus largest, two posterosuperior ocelli large, ventral seriate ocelli smallest; ocelli domed, translucent, usually darkly pigmented (Figs. 3–4). Tömösváry's organ nearly rounded, situated at the anterolateral margin of the cephalic plate, larger than adjoining ocelli (Fig. 4). Forcipular coxosternite sub-trapezoidal, anterior margin narrow, external side slightly longer than internal side; median longitudinal cleft moderately deep; anterior border with 2+2 large triangular coxosternal teeth, inner tooth slightly larger than outer one; porodonts moderately slender, setiform, posterolateral to the outermost tooth (Figs. 5–6); some scattered setae on the ventral side of coxosternite.

Tergites smooth, without wrinkles, backside slightly hunched; T1 generally trapeziform, posterior margin narrower than anterior margin, narrower than T3 and cephalic plate; T3 slightly narrower than cephalic plate; TT7, 8 and 10 broader than other tergites; T7 slightly rectangular, about 0.5 times as long as wide, posterior margin of T7 straight (Fig. 7); posterior margin of TT1, 3, 5 weakly concave, TT8, 10, 12 concave, T14 lateral deeply concave, middle straight (Figs. 8–9); TT1, 3 and 5 with continuous lateral and posterior

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marginal ridges, other tergites with discontinuous posterior marginal ridges; posterior angles of all tergites lacking triangular projections (Fig. 8); tiny setae scattered very sparsely over the surface.

Sternites narrower posteriorly, generally trapeziform, comparatively smooth, setae emerging from pores scattered very sparsely over the surface (Figs. 10–12).
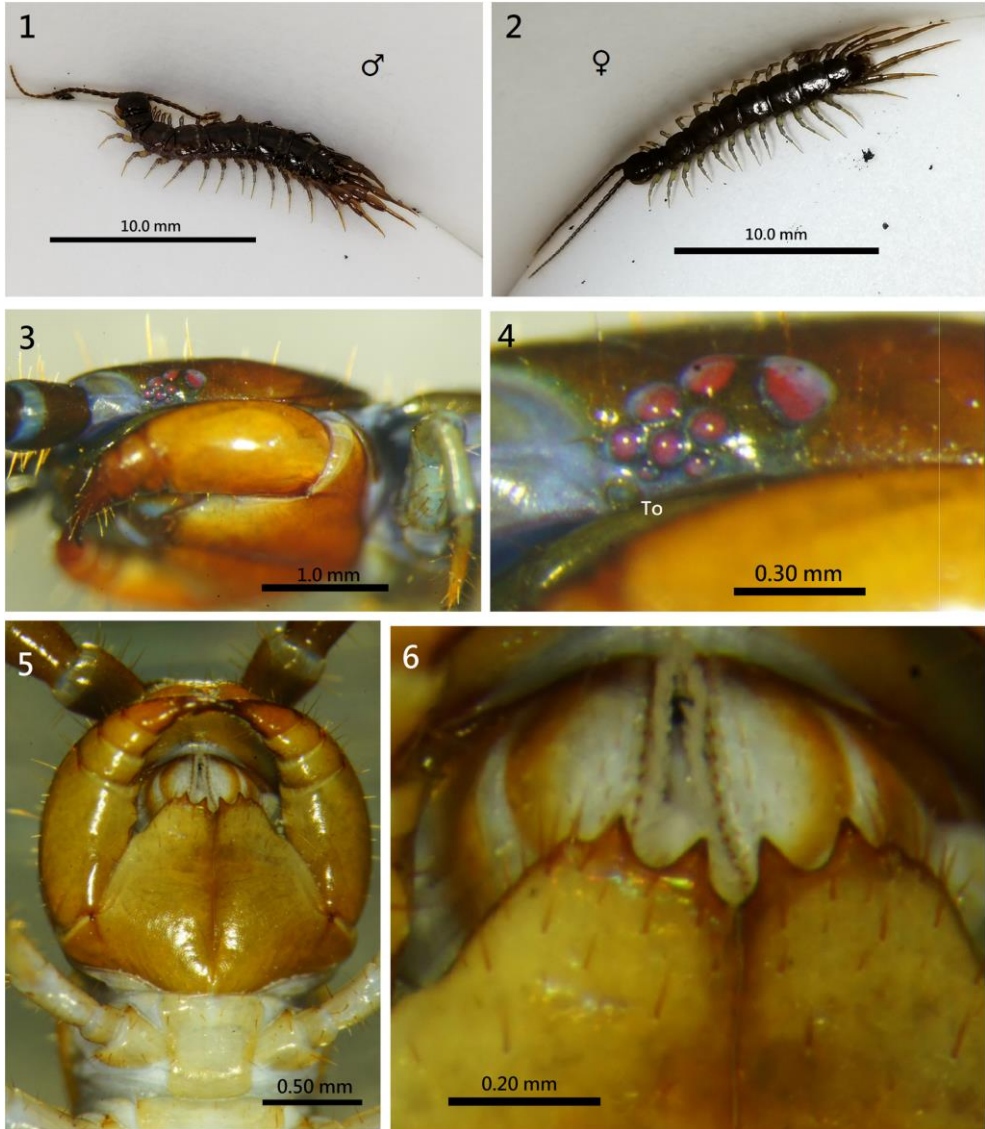
Figures 1–6. *Lithobius* (*Ezembius*) *keelungensis* sp. nov. 1 = habitus, male, legs 14–15 thick; 2 = habitus, female; 3 = lateral view of the head; 4 = eight ocelli and Tömösváry's organ (To) on the left side; 5 = ventral view of the head; 6 = 2+2 coxosternal teeth and porodonts (1 & 3–6: NMNS8103-001; 2: NMNS8103-004).

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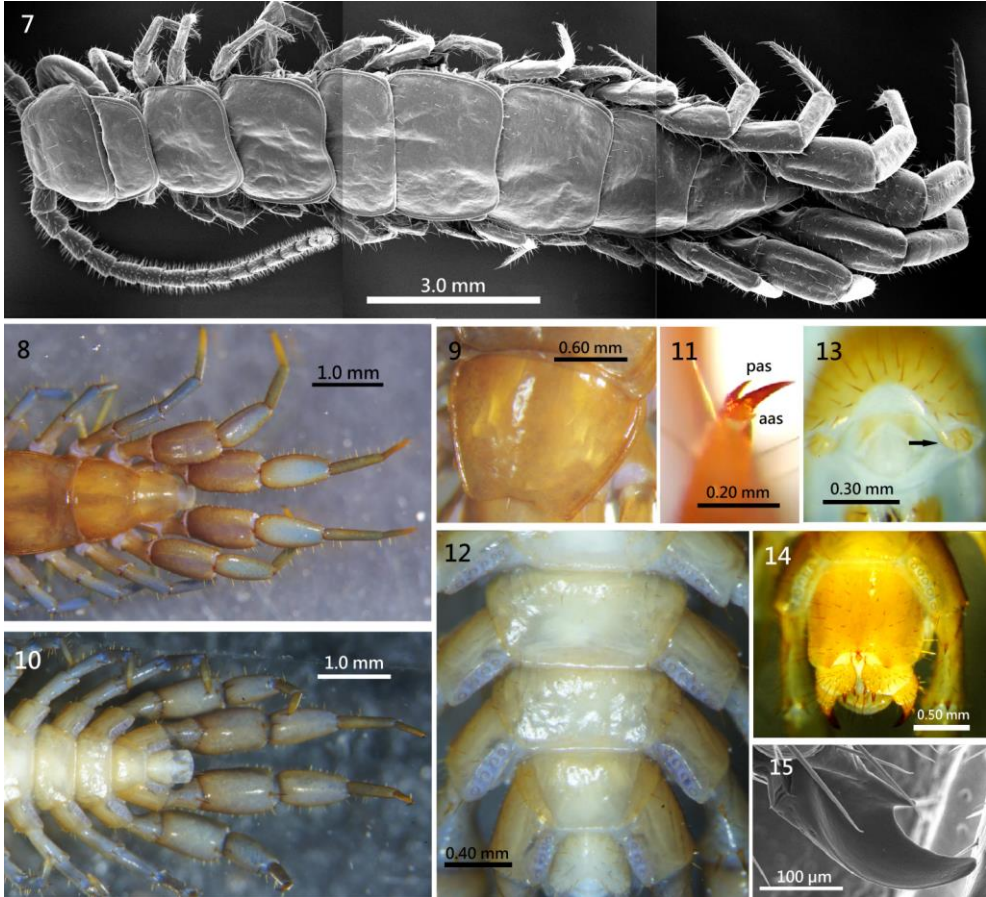
Figures 7–15. *Lithobius* (*Ezembius*) *keelungensis* sp. nov. 7 = male, habitus, dorsal view by SEM; 8 = posterior body on male, dorsal view; 9 = 14th tergite; 10 = posterior body on male, ventral view; 11 = 14th claw with short anterior (aas) and long posterior accessory spines(pas); 12 = coxal pores of 12–15th leg; 13 = male first genital sternite and gonopods (arrow); 14 = female first genital sternite and gonopods; 15 = claw of female gonopod (7: NMNS8103-005; 8–13: NMNS8103-001; 14: NMNS8103-004; 15: NMNS8103-004).

Legs: tarsi well-defined on all legs; all legs with fairly long claws, curved ventrally; thick posterior accessory spines present on base of all claws; long and slender anterior accessory spines present on claws 1–13; very short anterior accessory spines on 14th claws (Fig. 11); legs 15 lack anterior spine. Male secondary sexual characters (see below) present on thick 14th and 15th legs (Figs. 8–10); female without secondary sexual characters. Leg plectrotaxy as in Table 1. Coxal pores 4–6, round, inner pores small, coxal pore field set in a relatively shallow

groove, margin of coxal pore-field with slightly eminence (Fig. 12).

Male secondary sexual characters: 14–15th femora and tibiae markedly thick (Figs. 8–10), and 14–15th femora with a deep furrow on each dorsal surface; male 14–15th tibiae oval, with a wide shallow excavation on each dorsal surfaces (Figs. 7–8). Male first genital sternite: wider than long, usually well chitinized; posterior margin quite deeply concave between the gonopods, without a medial bulge; comparatively

long setae scattered evenly on the ventral surface; male gonopods short and small, as a semispherical bulge with 3 long setae, apically well chitinized (Fig. 13).

Female first genital sternite: wider than long; posterior margin of the genital sternite deeply concave, with a medial bulge (Fig. 14); short to long setae sparsely scattered over the ventral surface of the genital segment. Female gonopod: first article fairly broad, bearing up to 23 long setae, arranged in four irregular rows; 2+2 sharp coniform spurs, inner spur smaller (Fig. 14); second article with 7–9 rather long setae arranged in two irregular rows on its ventral side; third article usually with 2–3 long setae on its ventral surface; point of terminal claw undivided, a small sharp lateral denticle on the base of the terminal claw (Fig. 15).

Remarks. Wang (1956, 1959) recorded *Chinobius sachalinus* Verhoeff, 1937, with six specimens, *Chinobius pachypedatus* Takakuwa, 1941 with three specimens and *Chinobius sulcipes* (Attems, 1934) with two specimens from Taiwan, without any morphological descriptions. None of Wang's specimens could be located in Taiwan, and we consider Wang's records uncer-

tain. According to the descriptions of Takakuwa (1941*b*), Matic (1973), Zalesskaja (1978) and Eason (1996), the male secondary sexual characters – markedly thick male 14–15th femora and tibiae – are present in *L.* (*Chinobius*) *sachalinus* Verhoeff, 1937, *L. pachypedatus* Takakuwa, 1938 and *L. sulcipes* (Attems, 1927) from Japan and Eastern Russia. Takakuwa (1941*b*) redescribed *L. pachypedatus* with 1+5 ocelli on each side, and male 15th femora without any furrows, *L. sulcipes* with seven ocelli in two rows on each side, and male 14–15th femora and 15th tibiae with a deep furrow, and *L.* (*C.*) *sachalinus* with nine ocelli on each side, male 15th femora and tibiae with a furrow, and 14th femora with a longitudinal arched swelling with dense setae. The same character-set of *L.* (*C.*) *sachalinus* is also found in Matic's key (1973) and Zalesskaja's description (1978). Furthermore, Zalesskaja (1978) and Eason (1996) added the female characters for *L.* (*C.*) *sachalinus*: 2+2 spurs on the female gonopod, and gonopodal claw without denticles but with two or three large teeth on its medial ridge. However, *L. keelungensis* sp. nov. differs from *L. pachypedatus*, *L. sulcipes* and *L.* (*C.*) *sachalinus* by its different ocelli arrangement, female gonopodal claw and male 14–15th legs as shown in Table 2.

Table 1. Leg plectrotaxy of *Lithobius* (*Ezembius*) *keelungensis* sp. nov.

leg pair	Ventral					Dorsal				
	C	t	P	F	Ti	C	t	P	F	Ti
1	–	–	p	amp	m	–	–	p	a	a
2	–	–	p	amp	m	–	–	p	ap	a
3	–	–	p	amp	am	–	–	p	ap	a
4	–	–	mp	amp	am	–	–	p	ap	ap
5–10	–	–	mp	amp	am	–	–	ap	ap	ap
11–12	–	–	mp	amp	am	–	–	amp	ap	ap
13	–	–	amp	amp	am	–	–	amp	ap	ap
14	–	m	amp	amp	am	–	–	amp	p	p
15	–	m	amp	am	a	–	–	amp	p	–

Table 2. Main morphological characters of four species of *Lithobius* from East Asia.

Species	L. (E.) keelungensis sp. nov.	L. (C.) pachypedatus	L. (C.) sulcipes	L. (C.) sachalinus
Description from	This paper	Takakuwa (1938, 1941*b*)	Takakuwa (1941*b*)	Takakuwa (1941*b*) Matic (1973) Zalesskaja (1978) Eason (1996)
Antennae	20 articles	20–21 articles	19–22 articles	19–20 articles
Ocelli	1+2,3,2; arranged in 3 rows	1+5; arranged in 2 rows	1+6; arranged in 2 rows	1+5~8; arranged in 2 rows
Male 15th femur	A deep dorsal furrow	No furrow	A deep dorsal furrow	A dorsal furrow
Male 15th tibia	A wide dorsal furrow	No furrow	A deep dorsal furrow	A dorsal furrow
Male 14th femur	A dorsal furrow; absence of dense setae on dorsoposterior surface	No furrow; absence of dense setae on dorsoposterior surface	A deep dorsal furrow; absence of dense setae on dorsoposterior surface	A dorsal furrow; several setae clustered on dorsoposterior surface
Coxal pore	4–6, round	3–6, round	4–5, round	4–6, round
Male gonopod	3 long setae	Several setae	No data	3 long setae
Female gonopod	2+2 spurs; claw with a large denticle on tip, a small sharp lateral denticle on base	3+3 spurs; claw with a denticle on tip, and a small tooth on its medial ridge	2+2 spurs; claw divided, biapiculate	2+2 spurs; claw without denticles, but with two or three large teeth on its medial ridge

Genus *Lithobius* Leach, 1814

Subgenus *L.* (*Monotarsobius*) Verhoeff, 1905

Lithobius (*Monotarsobius*) *qingquanensis* sp. nov.

(Figures 16–25)

Material examined. Holotype, ♂ (NMNS81 03-006), garden, Qingquan, Hsinchu County, Taiwan, 24°34.36'N, 121°06.34'E, 570 m in elevation, 13 Mar. 2019, leg. Jui-Lung Chao.

Etymology. Refers to the type locality.

Diagnosis. A *Lithobius* (*Monotarsobius*) species with 17–18 elongate antennal articles; body colour brown; 3 ocelli arranged in one row, middle ocellus largest; Tömösváry's organ in front of ocelli, slightly smaller than anterior ocellus; 2+2 coxosternal teeth; porodonts posterolateral to the outermost tooth; all tergites lack posterior triangular projections; TT1, 3 and 5 with continuous lateral and posterior ridges; posterior margin of TT1, 3, 5, 8, 10 and 12 weakly concave, posterior margin of T14 concave; tarsi fused on legs 1–13, well-defined on legs 14–15; male secondary sexual characters on dorsal surface of 15th femur, a longitudinal excavation on central surface, and a small wart-like outgrowth with about 15 slightly curved setae on posterointernal surface; both 15th tibia and 15th tarsus I oval in male, with a wide shallow excavation on the dorsal surface; coxal pores 3433, round; male gonopods with two long setae.

Description. Body length: 8 mm. Body colour: brown (Fig. 16). Antennae with 17–18 articles; most articles markedly longer than wide;

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distal article about 2.8 times as long as wide (Fig. 17); abundant setae on antennal surface, less so on basal articles, gradual increase in density to around fifth article, then more or less

Figures 16–25. *Lithobius* (*Monotarsobius*) *qingquanensis* sp. nov. 16 = habitus, male; 17 = antennae; 18 = three ocelli and Tömösváry's organ (To) on the left side; 19 = anterior body, dorsal view; 20 = ventral view of the head; 21 = 2+2 coxosternal teeth and porodonts; 22 = posterior body and 15th leg, dorsal view; 23–24 = 15th femur, lateral view; 25 = male first genital sternite and gonopods (16–25: NMNS8103-006).

constant in number. 3 ocelli on each side, arranged in one row, middle ocellus largest (Fig. 18); ocelli domed, translucent, usually darkly pigmented. Tömösváry's organ comparatively small, nearly rounded, in front of ocelli, slightly smaller than the anteriormost ocellus (Fig. 18). Cephalic plate smooth, convex, width subequal to length, posterior marginal ridge moderately broader and weakly concave (Fig. 19); setae scattered sparsely over the whole surface. Forcipular coxosternite with 2+2 large triangular teeth, outer tooth slightly larger than inner one, the line of their apices recurved (Figs. 20–21); porodonts moderately slender, setiform, posterolateral to the outer tooth (Figs. 20–21); some scattered setae on ventral side of coxosternite.

Tergites smooth, without wrinkles, backside slightly hunched; T1 generally trapeziform, poste-

rior margin narrower than anterior margin, narrower than T3 and cephalic plate (Fig. 19); TT1, 3 and 5 with continuous lateral and posterior ridges; posterior margin of TT1, 3, 5, 8, 10 and 12 weakly concave, posterior margin of T14 concave; all tergites lack posterior triangular projections; tiny setae scattered very sparsely over the surface.

Sternites narrower posteriorly, generally trapeziform, comparatively smooth, setae emerging from pores scattered very sparsely over the surface.

Legs: tarsi fused on legs 1–13, well-defined on legs 14–15; all legs with fairly long claws, curved ventrally; anterior accessory spine long and slender on legs 1–13, lacking on legs 14–15; thick posterior accessory spine on all legs; leg plectrotaxy as in Table 3.

Table 3. Leg plectrotaxy of *Lithobius* (*Monotarsobius*) *qingquanensis* sp. nov.

leg pairs	Ventral					Dorsal				
	C	t	P	F	Ti	C	t	P	F	Ti
1	–	–	–	–	–	–	–	p	a	a
2	–	–	–	m	m	–	–	p	am	a
3–4	–	–	–	m	m	–	–	p	a	a
5	–	–	–	m	m	–	–	p	ap	a
6	–	–	–	m	m	–	–	p	amp	ap
7–9	–	–	–	m	m	–	–	p	ap	ap
10	–	–	a	m	m	–	–	p	ap	ap
11	–	–	a	m	m	–	–	mp	ap	ap
12	–	–	mp	m	m	–	–	mp	ap	ap
13	–	–	mp	m	m	–	–	mp	p	ap
14	–	m	mp	m	–	–	–	amp	–	–
15	–	m	mp	m	–	–	–	amp	–	–

Male secondary sexual character on dorsal surface of 15th femur: a longitudinal excavation on central surface (Fig. 22), several long setae scattered sparsely over the surface, and a small wart-like outgrowth bearing about 15 slightly curved setae present on dorsoposterior surface (Figs. 23–24); both 15th tibia and tarsus I oval, with a wide shallow excavation on the dorsal surface (Fig. 22).

Coxal pores: 3433, round, inner pores small, coxal pore field set in a relatively shallow groove, margin of coxal pore-field with slightly eminence (Fig. 25).

Male sternite 15: trapeziform, posterolaterally narrower than anterolaterally, posterior margin straight, long setae scattered sparsely over the surface (Fig. 25). Male first genital

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sternite: wider than long, usually well chitinized; posterior margin quite deeply concave between gonopods, without a medial bulge; comparatively long setae evenly scattered on ventral surface; male gonopods short and small, as a semi-spherical bulge with two long setae, apically slightly chitinized (Fig. 25).

Remarks. Murakami (1965) described a *Lithobius* (*Monotarsobius*) species from Japan, *L.* (*M.*) *tuberculatus* Murakami, 1965, with a male secondary sexual character, a wart-like outgrowth with several long curved setae on the dorsoposterior surface of male 15th tibiae. Matic (1970) described two *Lithobius* (*Monotarsobius*) species from Korea, *L.* (*M.*) *dziadoszi* Matic, 1970 and *L.* (*M.*) *riedeli*, Matic, 1970. A wart-like outgrowth with several short setae on the dorsoposterior surface of 15th femora is present in male *L.* (*M.*) *dziadoszi*, and a similar outgrowth with several short setae on the dorsoposterior surface of 15th tibiae in male *L.* (*M.*) *riedeli*. However, *L.* (*M.*) *qingquanensis* sp. nov. differs from *L.* (*M.*) *dziadoszi* by its 3 ocelli arranged in one row, and Tömösváry's organ slightly smaller than the adjoining ocellus, contrasting with *L.* (*M.*) *dziadoszi* with 7 ocelli arranged in two irregular rows, and Tömösváry's organ larger than the adjoining ocellus. *L.* (*M.*) *qingquanensis* sp. nov. differs from *L.* (*M.*) *tuberculatus* and *L.* (*M.*) *riedeli* by its wart-like outgrowth on 15th femora, contrasting with *L.* (*M.*) *tuberculatus* and *L.* (*M.*) *riedeli* with their wart-like outgrowth on 15th tibiae.

Key to the known Taiwanese species of the genus *Lithobius* Leach, 1814

1. Posterior angles of TT9, 11 and 13with triangular projecttions …………………………………………..……**2**
– Posterior angles of TT9, 11 and 13 without triangular projecttions ………...……….…......……………………….…..…**4**

2. Male secondary sexual characters present on leg 14 or 15 ... …………………………………………………………..**3**
– Male secondary sexual characters absent …………….....…… ………………..……………...…..*L. bidivisa* Takakuwa, 1939

3. Posterior angles of T7 with a triangular projection; a small tunnel at top of a longitudinal excavation on dorsal surface of male 14th tibia …….…..……….…..*L. ongi* Takakuwa, 1939
– Posterior angles of T7 without projections; about 40 long setae longitudinally arranged on ventral face of male 15th tibia, most setae concentrated in posterior part ……………. …………….……………….…..*L.trichopus* Takuwa, 1939

4. Tarsi fused on legs 1-13, well-defined on legs 14-15 ……. …………………………….**5**, subgenus *L.* (*Monotarsobius*)
– Tarsi well-defined on all legs …...**9**, subgenus *L.* (*Ezembius*)

5. Male secondary sexual characters present on leg 15 ….…...**6**
– Male secondary sexual characters absent ………...…….…..**7**

6. A large swelling on ventral surface of male 15th femur, apical region of swelling bearing numerous small pores ….. …...…….…...*L.*(*M.*) *meifengensis* Chao, Lee & Chang, 2018
– A small wart-like outgrowth bearing ca. 15 slightly curved setae present on dorsoposterior surface of male 15th femur .. ………………………….…...*L.* (*M.*) *qingquanensis* sp. nov.

7. 2222 coxal pores; terminal claw of female gonopod divided, biapiculate ……...*L.* (*M.*) *obtusus* Takakuwa, 1941
– 3-5 coxal pores; terminal claw of female gonopod undivided ………………………………………………………..**8**

8. 5555 coxal pores; a small sharp tooth on the base of terminal claw of female gonopod ……………………………….. ……………………..…*L.* (*M.*) *ramulosus* Takakuwa, 1941
– 3–4 coxal pores; terminal claw of female gonopod with irregular internal and external ridges ……………………….. ….. *L.* (*M.*) *holstii* (Pocock, 1895)

9. Male secondary sexual characters present both on leg 14-15:14-15th femora and tibiae thick, 14-15th femora with a furrow on each dorsal surfaces; female gonopods with 2+2 spurs …………………...……… *L.* (*E.*) *keelungensis* sp. nov.
– Male secondary sexual characters absent; female gonopods with 3+3 spurs ………………………………………...**10**

10. Female gonopodal claw bipartite, a large denticle on tip, a small sharp lateral denticle on base of terminal claw ….………………………….*L* (*E.*) *bidens* Takakuwa, 1939
– Female gonopodal claw undivided, without a lateral denticle …………………………...*L.* (*E.*) *lineatus* Takakuwa, 1939

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Two new species of centipedes, *Tygarrup daliensis* sp. nov. (Mecistocephalidae) and *Australobius cangshanensis* sp. nov. (Lithobiidae), from Southwestern China

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Abstract. Two new species of Chilopoda from Yunnan Province, China, are described as new: *Tygarrup daliensis* sp. nov. (Geophilomorpha, Mecistocephalidae) and *Australobius cangshanensis* sp. nov. (Lithobiomorpha, Lithobiidae). *Tygarrup daliensis* sp. nov. differs from other *Tygarrup* species by its each side of clypeal plagula with up to 15 setae, arranged in three irregular rows; labral posterior ala rough, with about 10 longitudinal slanting stripes near to mid-piece tooth; mandible with 9 pectinate dentate lamellae, 1st mandibular pectinate lamella bearing 6 teeth; each coxopleuron of last leg-bearing segments with about 50 pores of various size. *Australobius cangshanensis* sp. nov. is distinguished from congeners by a row of about 60 short setae transversely on each posterior part of 6th and 7th sternites; forcipular coxosternite with 7–10 coxosternal teeth, and porodonts between 5th and 6th or between 4th and 5th innermost teeth.

Keywords. Cangshan, Chilopoda, Dali, taxonomy, Yunnan.

INTRODUCTION

The centipedes of Southwest China were rarely investigated. The Institute of Entomoceutics Research, Dali University, collected and deposited many insect, spider and myriapod specimens from the Yunnan region over the last ten years. We studied specimens of centipedes from Dali University and some new material collected by ourselves. Our study recorded six known species of centipedes in the region (Tab. 1): *Mecistocephalus rubriceps* Wood, 1862, *Bothropolys yoshidai* Takakuwa, 1939, *Cermatobius longicornis* (Takakuwa, 1939), *Scolopendra dehaani* Brandt, 1840, *Scolopendra subspinipes mutilans* L. Koch, 1878 and *Cryptops doriae* Pocock, 1891. Moreover, we revealed two new species, *Tygarrup daliensis* sp. nov. (Geophilomorpha, Mecistocephalidae) and *Australobius cangshanensis* sp. nov. (Lithobiomorpha, Lithobiidae).

MATERIAL AND METHODS

The material was studied using stereo-microscope and SEM. Type specimens are preserved in 75% alcohol and deposited in the department of Biology, National Museum of Natural Science (NMNS), Taichung, Taiwan. Terminology for external anatomy follows Bonato *et al.* (2010). The following abbreviations are used in the text and tables: a—anterior, C—coxa, F—femur, m—median, p—posterior, P—prefemur, t—trochanter, T/TT—tergite/tergites, Ti—tibia.

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Table 1. The records of six species of Chilopoda from the Yunnan Province, China.

Species	Material examined
Mecistocephalus rubriceps Wood, 1862	1♂ (NMNS8103-66), bush, Lufeng County, 12 Nov 2018, leg. H.W. Chang & D.Q. Rao
	1♂2♀♀ (NMNS8103-65), bush, Maotianshan, Chengjiang County, 13 Nov 2018, leg. H.W. Chang & D.-Q. Rao
	2♂♂2♀♀ (NMNS8103-067), bush, Dian Lake, Kunming City, 14 Nov 2018, leg. H.W. Chang & D.Q. Rao
Bothropolys yoshidai Takakuwa, 1939	1♂3♀♀ (NMNS8103-063), forest floor, Weibaoshan, Weishan County, 18 Nov 2018, leg. J.L. Chao
Cermatobius longicornis (Takakuwa, 1939)	1♀ (NMNS8103-064), bush, Maotianshan, Chengjiang County, 13 Nov 2018, leg. H.W. Chang & D.Q. Rao
Scolopendra dehaani Brandt, 1840	Dali University Coll., forest floor, Cangshan, Dali City, 15 May 2011, leg. Z. Z. Yang
Scolopendra subspinipes mutilans L. Koch, 1878	Dali University Coll., forest floor, Cangshan, Dali City, 15 May 2011, leg. Z. Z. Yang
Cryptops doriae Pocock, 1891	1♂1♀ (NMNS8103-68), bark, Cangshan, Dali City, 29 Oct 2011, leg. L. Yang
	1♂ (NMNS8103-69), bush, Cangshan, Dali City, 17 May 2011, leg. H.W. Chang
	1♂ (NMNS8103-70), bush, Lijiang City, 08 May 2011, leg. H.W. Chang
	1♂1♀ (NMNS8103-71), forest floor, Weibaoshan, Weishan County, 18 Nov 2018, leg. J.L. Chao

TAXONOMY

Order Geophilomorpha Pocock, 1895

Family Mecistocephalidae Bollmann, 1893

Genus *Tygarrup* Chamberlin, 1914

Tygarrup daliensis Chao, Lee, Yang & Chang, sp. nov.

(Figures 1–11)

Material examined. Holotype: ♀ (NMNS8103-013), forest floor, Cangshan, Dali City, Yunnan Province, 25°42'N, 100°07'E, 2500 m, 08 May 2011, leg. Yuan He. *Paratypes:* 3♀♀ (NMNS8103-014), same data as holotype. *Other material:* 1♂, 1♀ (NMNS8103-015), same locality as holotype, 29 Oct 2011, leg. Z.Xu. Bao; 1♀ (NMNS8103-016), same locality as holotype, 14 Jul 2010, leg. R.Y. Nan; 2♀♀ (NMNS8103-017), rotten wood, Weishan County, Yunnan Province, 25°10'N, 100°21'E, 2506 m, 16 Nov 2018, leg. Z.-Z. Yang & J.L. Chao; 1♀ (NMNS8103-018), forest floor, Tengchong County, Yunnan Province, 25°01'N, 98°29'E, 1718 m, 17 Jul 2011, leg. L. Yang.

Etymology. Refers to the type locality.

Diagnosis. A *Tygarrup* species invariably with 45 leg-bearing segments. Body length about 40 mm. Head 1.4 times as long as wide. Each clypeal plagula with about 15 setae, arranged in three irregular rows, each seta inside an insula. Ventral surface of labral posterior ala rough, each side with about 10 longitudinal slanting stripes near mid-piece tooth; posterior margin of labral ala without a fringe. Mandible with 9 pectinate dentate lamellae, 1st lamella bearing 6 teeth, average intermediate lamella bearing ca. 16 teeth. Forcipular articles I with a large denticle, II and III each with a small denticle, tarsungulum with a basal denticle. Sternal

sulcus apparently not furcated. Each coxopleuron of last leg-bearing segments with about 50 pores of various size, without a macropore distinct from other pores.
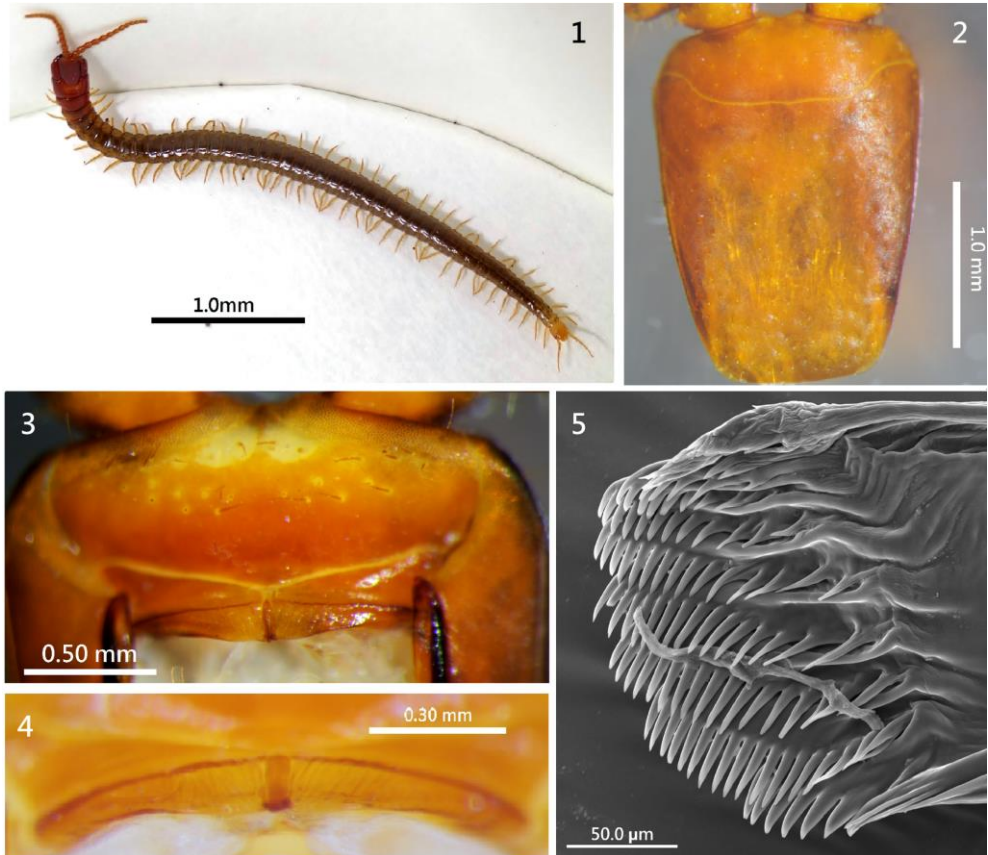
Figures 1–5. *Tygarrup daliensis* sp. nov. 1 = habitus, dorsal view; 2 = cephalic plate; 3 = clypeus and labrum; 4 = labrum; 5 = mandibular dentate lamellae (1–4: NMNS8103-017; 5: NMNS8103-016).

Description. A total of 45 leg-bearing segments. Body length of adults up to about 40 mm. Body colour: head, forcipular segment and 1st leg-bearing segment dark red, last leg-bearing segment and legs yellow, other leg-bearing segments yellow with dark patches (Fig. 1). Antennae: with 14 articles. Cephalic plate: about 1.4-times as long as wide, transverse suture uniformly rounded (Fig. 2). Clypeus: areolate part only present along anterior margin of head, areolate part without smooth insulae, a long seta on each side of the areolate part; an entire plagula covering most of clypeus, without a mid-longitudinal areolate stripe; each clypeal plagula with 11–15 setae, arranged in three irregular rows as follows: 4–7 setae along each anterior margin of plagula (1–2 intermediate, 3–5 lateral), and 7–8 setae arranged in two irregular rows on each side of the plagula (Fig. 3); each seta inside a smooth insula. Labrum: anterior ala triangular, medial margin reduced to a vertex; posterior margin of each side-piece sinuous; ventral surface of labral posterior ala rough, each side with about 10 longitudinal slanting stripes near mid-piece tooth (Fig. 4); posterior margin of labral ala without a fringe.

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Spiculum absent (Fig. 3). Buccae without setae. Mandible: 9 pectinate dentate lamellae (Fig. 5) with variable teeth (Tab. 2).

Table 2. Number of teeth on every mandibular dentate lamella in *Tygarrup daliensis* sp. nov.

Pectinate lamella	1st	2nd	3rd	4th	5th	6th	7th	8th	9th
Number of teeth	6	18	17	16	15	12	10	8	8

First maxillae: lateral lappet lacking, each coxal projection about 1.4 times as long as wide, internal margin with some setae; each telopodite about 4 times as long as wide, distal articles curved inward (Fig. 6). Second maxillae: article I of telopodite about 4 times as long as wide; article III about 2.4 times as long as wide, densely covered with setae (Fig. 6); apical claw very small (Fig. 7). Forcipules: trochantero-prefemur about 1.3 times as long as wide, with a large distal tooth; both femur and tibia with a small tooth (Fig. 8); tarsungulum with a large basal denticle.
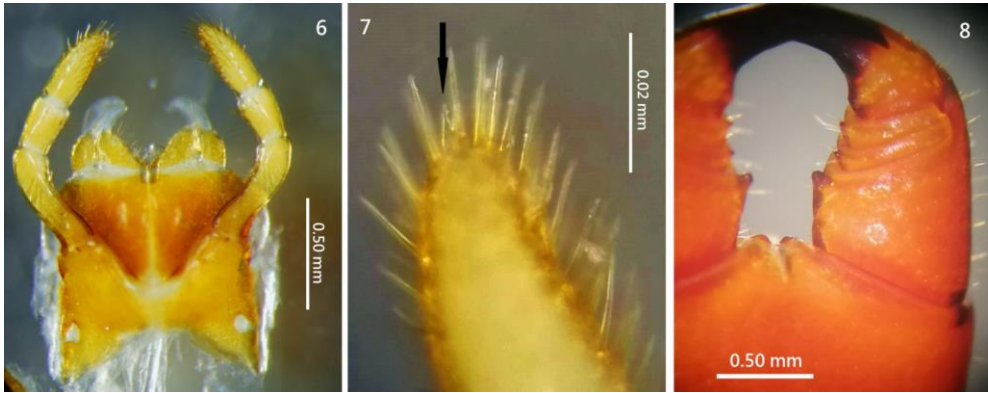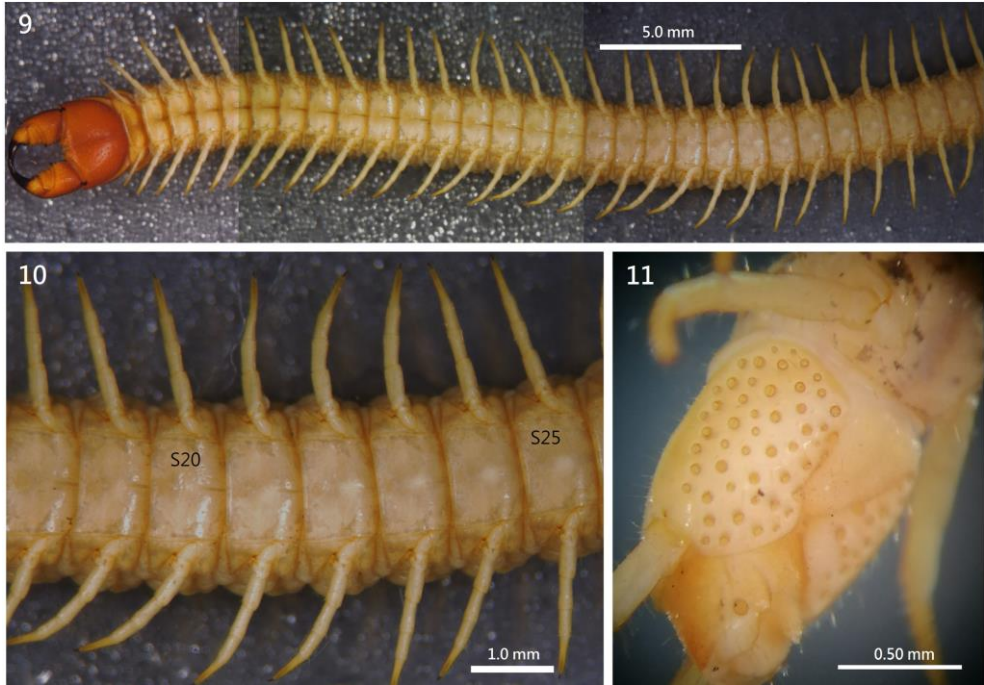

Figures 6–8. *Tygarrup daliensis* sp. nov. 6 = first and second maxillae; 7 = apical claw (arrow) of second maxillae; 8 = forcipules (6–7: NMNS8103-016; 8: NMNS8103-015).

Sternites: sternal sulcus not furcated, apparently present from 1st to 23rd sternites (Figs. 9–10); sternal pores lacking in both sexes. Last leg-bearing segment: last sternite about 1.2 times as long as wide; about 50 pores of various sizes on each coxopleuron, without a macropore distinct from other pores (Fig. 11). A large anal pore on each ventro-lateral sides of telson (Fig. 11).

Remark. Fourteen species have hitherto been described within the genus *Tygarrup* Chamberlin, 1914, with only one species, *Tygarrup poriger* (Verhoeff, 1942), from Shigatse, China. Verhoeff (1942) originally described a new genus *Brahmaputrus* and type species *B. poriger*, with 45 leg-bearing segments; each side of clypeal plagula with 6 setae; mandible with 9 pectinate lamellae, 1st lamella with 3 teeth; each coxopleuron of last leg-bearing segments with 21–22 pores of various sizes. Crabill (1968) considered the genus *Brahmaputrus* Verhoeff, 1942, as a synonym of *Tygarrup* Verhoeff, 1942. Shinohara (1965) described *Tygarrup nepalensis* from Himalaya, with 45 leg-bearing segments; each side of clypeal plagula with 8 setae; mandible with 8–9 pectinate lamellae, 1st lamella with 3 teeth; each coxopleuron of the last leg-bearing segment with 20 pores of various sizes. *Tygarrup daliensis* sp. nov. differs from other *Tygarrup* species by its clypeal plagula with more setae, arranged in three irregular rows; ventral surface of labral posterior ala rough; mandible with more pectinate dentate lamellae and teeth; each coxopleuron of the last leg-bearing segment with more pores (Tab. 3).

Figures 9–11. *Tygarrup daliensis* sp. nov. 9 = anterior leg-bearing segments, ventral view; 10 = 18th–25th sternites; 11 = last leg-bearing segment, lateral view (9–11: NMNS8103-015).

Table 3. Main morphological characters of the eight known Asian species of *Tygarrup* Chamberlin, 1914.

Tygarrup species		*T. daliensis* sp. nov.	*T. poriger*	*T. nepalensis*	*T. javanicus*
Description from		This paper	Verhoeff (1942) Crabill (1968)	Shinohara (1965)	Verhoeff (1937) Titova (1983) Bonato *et al.* (2004) Bonato & Minelli (2010)
Clypeal setae (pair)	areolate part	1	0	1	1
	plagula	11–15	6	8	5–7
Mandible	lamellae	9	9	8–9	6
	teeth of 1st lamella	6	3	3	5
Coxopleural pores		50	21–22	20	23–24

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Table 3 (continued). Main morphological characters of the eight known Asian species of *Tygarrup* Chamberlin, 1914.

Tygarrup species		*T. crassignathus*	*T. singaporiensis*	*T. takarazimensis*	*T. triporus*
Description from		Titova (1983)	Verhoeff (1937) Titova (1983)	Miyoshi (1957) Uliana *et al.* (2007)	Titova (1983)
Clypeal setae (pair)	areolate part	0	0	1	1
	plagula	2–3	12	10	6–7
Mandible	lamellae	6	4–5	8	6
	teeth of 1st lamella	5	?	5	5
Coxopleural pore		? (numerous)	40	20	? (numerous)

Order Lithobiomorpha Pocock, 1895

Family Lithobiidae Newport, 1844

Genus *Australobius* Chamberlin, 1920

Australobius cangshanensis Chao, Lee, Yang & Chang, sp. nov.
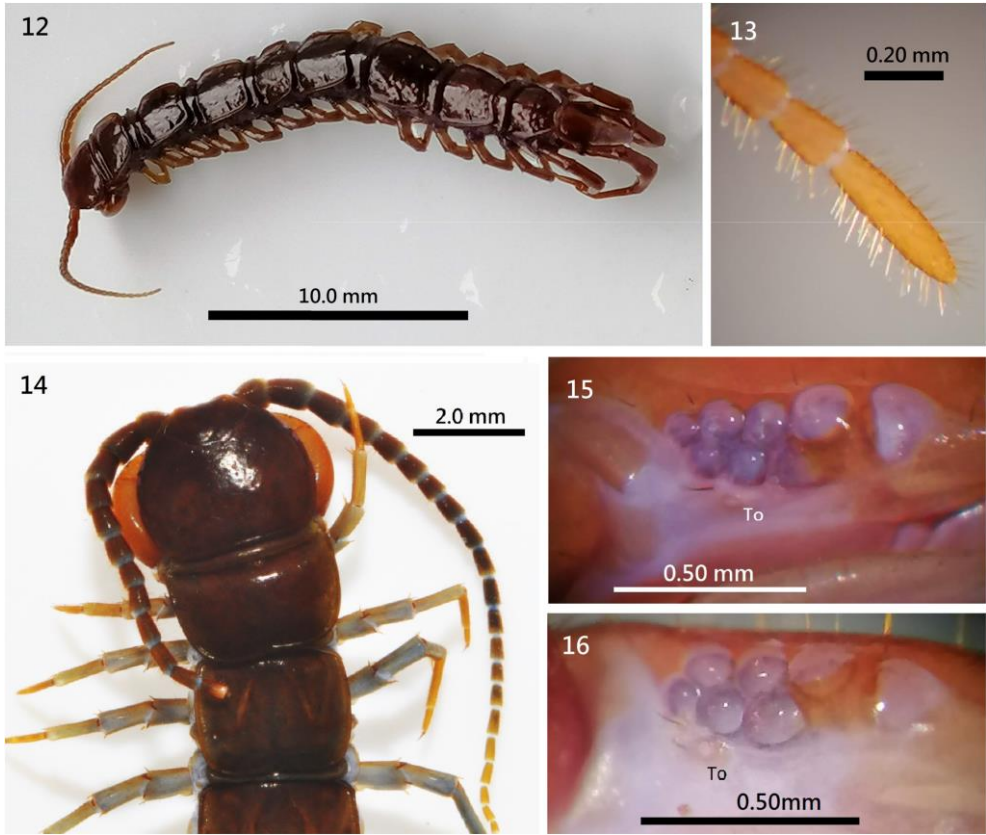
(Figures 12–25)

Material examined. Holotype: ♂ (NMNS81 03-007), forest floor, Cangshan, Dali City, Yunnan Province, 25°42'N, 100°07'E, 2500 m, 29 Aug 2010, leg. H.B. Pu, K.C. Zhang & Z.Z. Yang. *Paratypes:* 8♂♂, 1♀ (NMNS8103-008 & 009): same data as holotype. *Other material:* 4♀♀ (NMNS8103-010), same locality as holotype, 12 Jul 2010, leg. H.B. Pu; 1♀ (NMNS8103-011), forest floor, Weibaoshan, Weishan County, Yunnan Province, 25°10'N, 100°21'E, 2501m, 11 Nov 2018, leg. J.L. Chao; juvenile 2♂♂, 2♀♀ (NMNS8103-012), Lijiang City, Yunnan Province, 08 May 2011, leg. H.W. Chang.

Etymology. Refers to the type locality.

Diagnosis. A species of the genus *Australobius* Chamberlin, 1920, normally with 23+23 elongate antennal articles; body length approximately 26 mm; cephalic plate markedly wider than all tergites; 7–8 ocelli, [1+4(3), 3], posterior ocellus comparatively large. Tömösváry's organ smaller than adjacent ocelli; forcipular coxosternite with 7–10 coxosternal teeth, porodont between 5th and 6th or between 4th and 5th

innermost teeth; posterior angles of all tergites lacking triangular projections; a transverse row of about 60 short setae transversely on the posterior part of both 6thand 7th sternites; coxal pores 5–7, ovate; female gonopods with 3–5 slender spurs, terminal claw undivided; male gonopods with two long setae.

Description. Body length: 26 mm. Body colour: dark brown (Fig. 12). Antennae with 23 articles; all articles markedly longer than wide; distal article much longer than wide, up to 3.9 times as long as wide (Fig. 13); abundant setae on antennal surface, less so on basal articles, gradual increase in density to around fourth article, then more or less constant in number. Cephalic plate smooth, width subequal to length, posterior marginal ridge moderately broader and weakly concave; cephalic plate markedly wider than all tergites (Fig. 14), setae scattered sparsely over whole surface. Seven or eight ocelli on each side, [1+4(3), 3], one posterior, three or four dorsal, three ventral, arranged in two irregular rows; posterior ocellus comparatively large; ocelli domed, translucent, usually darkly pigmented (Figs. 15–16). Tömösváry's organ comparatively small, nearly rounded; situated under the second ventral seriate ocellus, smaller than adjacent ocelli (Figs. 15–16). Forcipular coxosternite subtrapezoidal, anterior margin narrow, external side slightly longer than internal side; median longitudinal cleft moderately deep; anterior border with 10+9 large triangular coxosternal teeth in the adult, or with 7+8 teeth in juveniles; porodont slender, between 5th and 6thinnermost teeth in

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Figures 12–16. *Australobius cangshanensis* sp. nov. 12 = habitus, dorsal view; 13 = distal articles of antennae; 14 = head and anterior trunk; 15 = eight ocelli and Tömösváry's organ (To) on left side; 16 = seven ocelli and Tömösváry's organ on left side (12–13: NMNS8103-007; 14: NMNS 8103-011; 15: NMNS8103-007; 16: NMNS8103-012).

specimens with a total of 9 or 10 teeth (Figs. 17–18), between 4th and 5th innermost teeth in those with a total of 7 or 8 teeth (Fig. 19); some scattered setae on the ventral side of coxosternite.

Tergites smooth, without wrinkles, back side slightly hunched; T1 generally trapeziform, posterior margin narrower than anterior margin; T1 slightly narrower than cephalic plate, wider than other tergites; posterior margin of TT1, 3 and 5 weakly concave; posterior margin of TT8, 10, 12, 14 and 15 deeply concave. TT1, 3, 5, 8, 10 and 12 with continuous lateral and posterior marginal ridges, other tergites with lateral mar-

ginal ridges. Posterior angles of all tergites lacking triangular projections; tiny setae scattered very sparsely over the surface. Sternites narrower posteriorly, generally trapeziform, comparatively smooth, setae emerging from pores scattered very sparsely over the surface. A transverse row of about 60 short setae on the posterior part of both 6th and 7th sternites (Figs. 20–21). Legs: tarsi well-defined on all legs; all legs with fairly long claws, curved ventrally; anterior and posterior accessory spines on legs 1–13, anterior accessory spines slender and short, posterior one thick and long, posterior accessory spine longer than anterior one; legs14 and 15 lack accessory spines. Leg plectrotaxy as in Table 4.
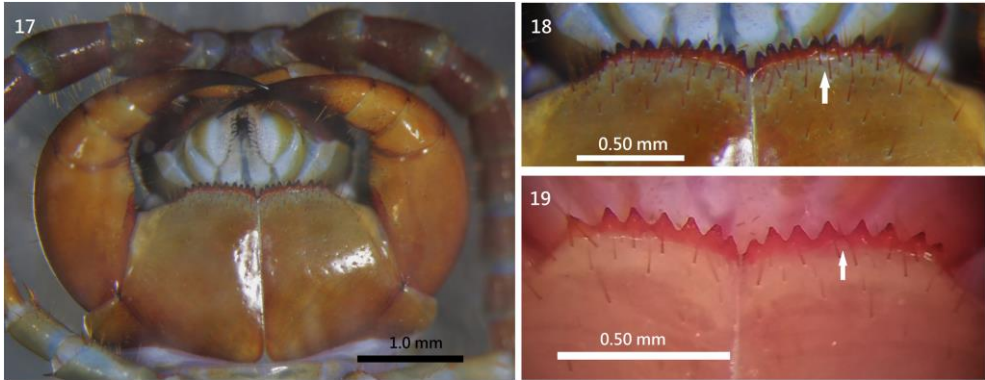
Figures 17–19. *Australobius cangshanensis* sp. nov. 17 = head and forcipules, ventral view; 18 = porodont nodes (arrow) between 5th and 6th innermost coxosternal teeth; 19 = porodont nodes (arrow) between 4th and 5th innermost coxosternal teeth (17–18: NMNS 8103-011; 19: NMNS8103-012).

Table 4. Leg plectrotaxy of *Australobius cangshanensis* sp. nov.

| leg pairs	Ventral					Dorsal				
	C	t	P	F	Ti	C	t	P	F	Ti
1	–	–	ap	m	m	–	–	ap	a	a
2–5	–	–	ap	amp	am	–	–	ap	ap	a
6–13	–	–	ap	amp	amp	–	–	amp	ap	ap
14	–	m	amp	amp	ap	m	–	amp	p	–
15	–	m	amp	amp	a	m	–	amp	–	–

Coxal pores: 6665 in males, 7777 in females, ovate; coxal pore field set in a relatively shallow groove, margin of coxal pore-field with slightly eminence (Figs. 22–24). Male sternite 15: generally trapeziform, posterolaterally narrower than anterolaterally, posterior margin concave, long setae scattered sparsely over the surface (Fig. 22). Male first genital sternite: wider than long, usually well chitinized; posterior margin quite deeply concave between the gonopods, without a medial bulge; comparatively long setae scattered evenly on ventral surface; male gonopods short and small, as a semi-spherical bulge with 2 long setae, apically slightly chitinized (Fig. 23). Female sternite 15: generally trapeziform, anterolaterally broader than posterolaterally, posterior margin straight, long setae scattered sparsely over the surface; sternite of the genital segment well chitinized, wider than long; posterior margin of the genital sternite straight; short to long setae sparsely scattered over the ventral surface of genital segment (Fig. 24). Female gonopod: first article fairly broad, bearing 15–18 long setae, arranged in three irregular rows; 3–5 slender spurs, inner spur smaller; second article with 8–10 rather long setae arranged in two irregular rows on its ventral side; third article usually with 3–5 long setae on its ventral surface; terminal claw undivided (Fig. 25).

Remarks. Seven species of *Australobius* have hitherto been described from China (Ma *et al.* 2008*a*, 2008*b*, Qin *et al.* 2014, Li *et al.* 2018, Dyachkov 2017). Ma *et al.* (2008*b*) first described *A. nodulus* from Tibet, as with a transverse band of setae on the posterior part of both 6th and 7th sternites in male; 11 ocelli, [2+4, 5], posterior ocellus largest, penultimate ocellus large, other ocelli small, and arranged in two

rows; 6+6 coxosternal teeth. Li *et al.* (2018) described *A. tracheoperspicuus* from Guizhou, with 6th and 7th sternites with about 30 setae each, arranged in two irregular rows; no ocelli; and 5+5 coxosternal teeth. However, *Australobius cangshanensis* sp. nov. has a row of ca. 60 setae on each 6th and 7th sternites; with a different ocelli arrangement, and with more coxosternal teeth.
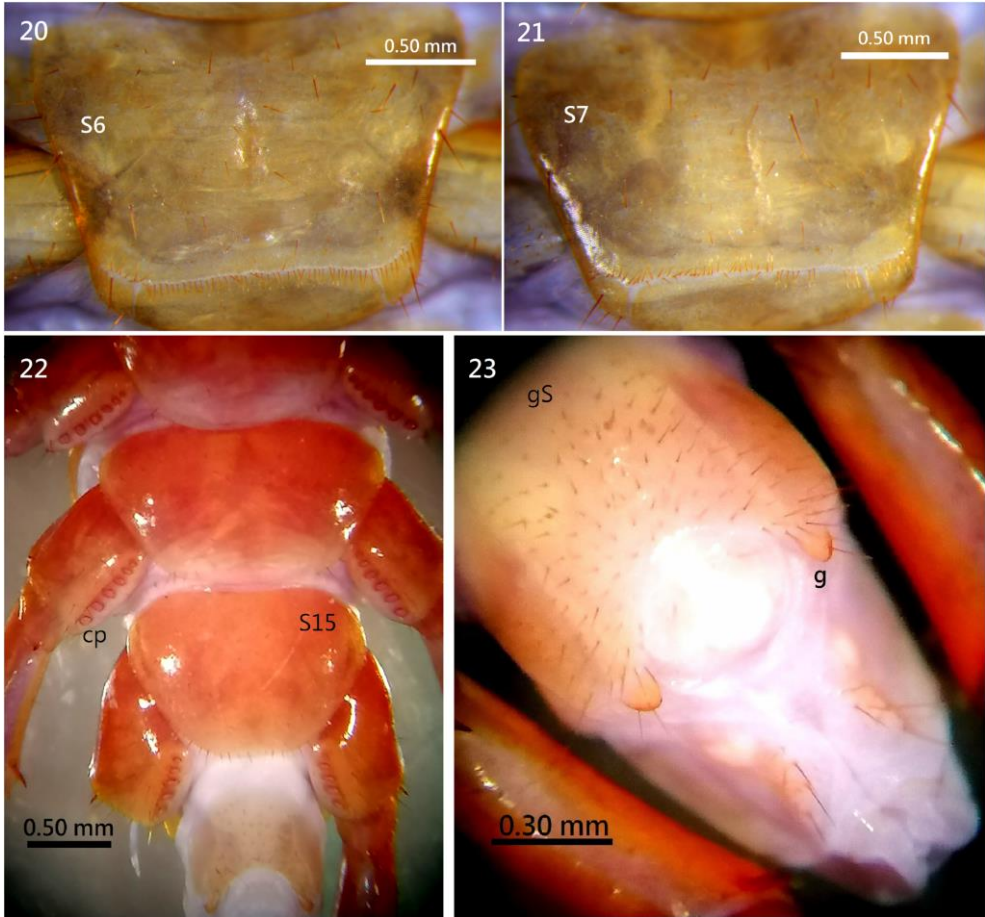
Figures 20–-23. *Australobius cangshanensis* sp. nov. 20 = 6th sternite (S6); 21 = 7th sternite (S7); 22 = coxal pores (cp) of 13-15th legs, 15th sternite (S15); 23 = male first genital sternite (gS) and male gonopods (g) (20–21: NMNS 8103-011; 22–23: NMNS8103-008).

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Figure 24–25. *Australobius cangshanensis* sp. nov. 24 = coxal pores of 15th legs, female first genital sternite and female gonopods; 25 = claw of female gonopod (24–25: NMNS 8103-011).

Key to the known Chinese species of the genus *Australobius* Chamberlin, 1920

1. At least four ocelli on each side of cephalic plate **2**
– No ocelli on cephalic plate ....
…….....*A. tracheoperspicuus* Li, Pei, Guo, Ma & Chen, 2018

2. Four ocelli on each side of cephalic plate, Tömösváry's organ larger than adjacent ocelli …………………………
....*A. tetrophthalmus* (Loksa, 1960)
– More than seven ocelli on each side of cephalic plate, Tömösváry's organ smaller than adjacent ocelli ………....**3**

3. Porodonts present ……………………………….........**4**
– No prodonts ....*A. apicicornis* Qin, Lin, Zhao, Li, Xie, Ma, Su & Zhang, 2014

4. Large posterior tergites wrinkled; a bulge present on terminal part of male 15th tibiae ……………………………
………………………………….*A. magnus* (Trozina, 1894)
– Large posterior tergites smooth; no bulge on the terminal part of male 15th tibiae ………………………....…....**5**

5. Antenna with 31 articles; 5–6 forcipular coxosternal teeth ...
....*A. nodulus* Ma, Song & Zhu, 2008
– Antenna with less than 31 articles ……..…………………..**6**

6. Antenna with 29 articles; 7–8 small blunt forcipular coxosternal teeth ……………..
……………..*A. polyspinipes* Ma, Liu, Lu, Hou & Pei, 2018
– Antenna with less than 29 articles …………………..........**7**

7. Antenna with 26 articles; 2–4 forcipular coxosternal teeth ...
...................................*A. anamagnus* Ma, Song & Zhu, 2008
– Antenna with 23 articles; 7–10 triangular forcipular coxosternal teeth …..………………..–*A. cangshanensis* sp. nov.

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Changes in surface active myriapod communities during the restoration of woodland to wood pasture: a long-term study

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Abstract. The myriapod communities of an area of woodland restored to wood pasture through tree felling was compared with a control site in dense woodland, using pitfall trapping over a 28-year period. 14 species of millipede and 13 of centipede were recorded. Numbers of individual species varied over time even within the control plot. There were significantly more centipede individuals and species and more millipede species in the control plot than the restoration area. NMDS ordination indicated three groupings for the millipedes in the restored area with the community changing following the initial restoration to a tight cluster but then further movement in later years. In contrast the control community showed little variation. 2015 showed the greatest change from other years, probably due to high abundance of two species of polydesmid millipede that year, in both plots. The results are discussed in comparison with other studies looking at the impact of the edge effect of forests. The community of the restored area has perhaps not changed as much as expected, which may indicate a high degree of resilience, although it may be acting more like a forest clearing than an edge.

Keywords. Millipedes, centipedes, habitat restoration, beech trees, forest edge.

INTRODUCTION

Burnham Beeches is a 383 ha nature reserve comprising beech dominated woodland (*Fagus sylvatica* L.) 40 km west of London. It is part of a Natura 2000 site (i.e. a site of European nature conservation importance), for Atlantic acidophilous beech forests (Natura 2000 code 9120). The main reason for the designation is its population of 400–500 year-old beech trees that were for centuries cut as pollards, producing a crop of wood every 15–20 years (Le Sueur 1931). The trees were set in wood pasture grazed by domestic livestock, probably a mixture of cattle, equines and pigs. The southern 220 ha of the nature reserve was common land which, although owned by the Lord of the Manor, gave local people rights to graze their livestock and cut the trees for fuel wood. Old descriptions and photographs indicate that the majority of the area was 'savannah-like' with scattered trees and some patches of scrub in a largely open environment. The soils are acidic with ground vegetation being similar to heathland, with *Calluna vulgaris* (L.) (ling/common heather) and grasses typical of acid soils.

In recent years, the idea that most of Europe, prior to human influence, was climax woodland with more or less continuous tree cover has been challenged. Recent research has indicated that it was more likely to have been dominated by a type of savannah with large herbivores driving the development of scrub and woodland and maintaining a greater proportion of open areas with scattered trees (Vera 2000). In medieval times, southern England had abundant areas of wood pasture but most were abandoned or destroyed in the early 20th century through loss to agriculture or building development, or through lack of grazing. These medieval wood pastures, although heavily managed, were perhaps arguably a more accurate reflection of the natural vegetation of the region than was previously thought.

At one time almost all the beech and oak (*Quercus* sp.) trees within Burnham Beeches were managed as pollards, cut at regular intervals to produce a crop of wood which was probably largely used by local people for domestic fuel. Repeated cutting causes the trees to develop a knobbly area, around the point of cutting, developing decay pockets and water pools which provide micro habitats for many saproxylic invertebrates. Cutting also enables the trees to live longer than uncut trees so the older generation of pollards are around 500 years old. Over 60 red listed species have been recorded (Read 2010) on the reserve, almost all associated with these old trees. Tree management through pollarding ceased at Burnham Beeches around 200 years ago; grazing also declined so that by the 1920s this merely involved a few donkeys. In 1951 the nature conservation value of the area was recognised and the area was designated as being important for nature conservation in a UK context. However, by the 1980s the old trees had become swamped by younger secondary woodland, dominated by *Betula* spp. (birch) and *Ilex aquifolium* (L.) (holly), resulting from cessation of grazing, and were dying through lack of light. In addition, they had become very top heavy because of the lapse in their cutting cycle, resulting in trees splitting apart as the larger branches became too heavy for the ageing trunk beneath. Since then, substantial restoration work has been carried out to attempt to rescue the trees and to restore the wood pasture in which they stand. This has included tree clearance and the re-instatement of grazing using cattle, ponies and, in some years, pigs in the autumn. Wood pasture is increasingly being recognised as a distinct habitat in the UK and restoration is being carried out in a range of locations. However, this restoration has only recently started and documenting changes taking place is valuable to both assess the importance of the habitat and the implications of restoration. Substantial work has been carried out on the trees at Burnham Beeches (Read *et al.* 2010) and the preliminary impacts on ground vegetation and some ground active spiders has been reported (Read 2000). The impact of felling younger trees to give more light to ancient ones in terms of tree response and saproxylic species (those associated with decaying

wood) of invertebrate was examined by Alexander *et al.* (2010) however little work has been published on the effects of similar management on surface-active invertebrates. Myriapods can provide an interesting insight to the changes taking place as a shaded woodland floor with abundant leaf litter, is replaced by a grassy sward with a much greater exposure to light. Millipedes being detritivores might be considered more likely to be impacted than the more predatory groups of centipedes, for example.

There are other studies that have documented myriapod communities in similar environments, including disturbance effects on forests due to tree clearance (Smith *et al.* 2017 and Stašiov & Svitok 2014) the latter in beech forests, studies of gradients between forested and open areas (Bogyó *et al.* 2015, De Smedt *et al.* 2016) and studies on the impact of forest fragmentation (Riutta *et al.* 2012). None of these situations are quite equivalent to wood pasture but are similar.

The current study reports on the results of part of a larger project looking at changes in the ground active invertebrates during restoration of wood pasture over a period of nearly 30 years. In general, most studies cover relatively short periods of time and typically use different sites at different stages of succession as a substitute for following long term changes (e.g. Bogyó *et al.* 2015)- The work of Tajovsky (2000), and Tajovsky *et al.* (2017) is notable for the long time scales of recording myriapod communities, even though not always continuous, one such study covered a time scale of 25 years (Tajovsky *et al.* 2017).

MATERIALS AND METHODS

Two areas were sampled. The restoration area was actively managed for nearly 30 years to restore wood pasture (through tree felling, re-instatement of grazing and periodic control of bracken and bramble). The tree clearance was carried out in two phases, winter 1991/92 and March 1994 during which the number of mature trees in the vegetation plot was reduced from 19 to 6 and shrub layer holly from 20% to a single

bush. A control site nearby was also surveyed where no restoration had taken place and which remained densely vegetated with beech/holly woodland throughout the study (although at several times work in the vicinity may have made minor changes to the light levels).

Pitfall traps (plastic vending machine cups) 8 cm in diameter and 10 cm deep were installed, containing 50 ml of 4% formalin and a few drops of detergent, with wooden rain covers held about 3 cm above them on large nails. The quantity of fluid was sufficient to ensure captures remained in fluid except on a few occasions when the number of wood ants was very high. Ten traps were installed in each site in a 5 x 2 formation with traps 2 m apart, a format regularly used in the UK (Read 1987). Traps were emptied and re-set every two weeks during the season taking care to ensure that the lip of the cups were flush with the ground surface. Traps were first installed in the restored area in 1990 and in the control (unrestored area) in 1992 and run each year. Catches were sorted and the Myriapoda were identified to species level where possible and adults distinguished from immatures. Data presented here are for millipedes and centipedes for each year up to and including 2017. Although pitfall trapping has been used in previous studies (for example Stašiov & Svitok 2014), its validity as a method of comparing myriapod communities has been questioned and there are clear short comings (see for example Gerlach *et al.* 2009, Tuf 2015) but they are still regularly used in quantitative studies for example De Smedt *et al.* (2019) and in the UK Environmental Change Network (2020). Indeed, despite the considerable debate over the years regarding pitfall trapping as a suitable technique for sampling surface active invertebrates, the technique remains reasonably popular because it is relatively easy (and cheap) to operate and usually provides statistically viable results (Wheater *et al.* 2020). Myriapoda have long been sampled using pitfall traps (e.g. Van der Drift 1963) and the method was used here because of the need to trap in a way that drew least attention to members of the public and was feasible to run by volunteers, without taking up too much time and/or needing specific expertise to deploy.

Trapping usually took place between April and October/November but for operational reasons the trapping periods varied slightly between years, with two years when it started later (in early June in 1992 and in early May in 1996) and a further two years when it finished earlier (late September in 1993 and 1994). To include as much of the data as possible for analysis, the longest period of time for each year was used where the two trapping grids (i.e. restoration and control areas) were in agreement. As the number of days varied between years the analysis was carried out on numbers of myriapods per 100 trapping days.

Vegetation was also monitored annually around the pitfall traps. For the experimental area the plot was 30 x 30 m in size and was located just to one side of the traps. For the control, due to the shape of the woodland block, it was 20 x 45 m with the pitfall traps central to the plot. Each year 25 random quadrats, 0.25 m^2, were thrown (positions determined using random number tables) and percentage cover estimated for all species. A mean percentage cover figure was calculated for the whole plot per year and multiplied by the frequency to give a value that was arcsine transformed before ordination since the data were not normally distributed.

A notable feature of this part of Burnham Beeches is the high density of wood ant (*Formica rufa* L.) nests. This species forages on the ground and also in the tree canopies, which it reaches by walking along the ground using trails that are variable in location and extent. Thus, this species was found in high numbers in the pitfall traps at certain times and is generally very abundant on the surface across both areas where the traps were located. As wood ants are predatory and opportune generalists, their presence can have profound effects on the populations of other invertebrates (e.g. Fowler & MacGarvin 1985 and Punttila *et al.* 2004), including surface active species (e.g. Reznikova & Dorosheva 2004). The impact is usually negative, but some species are positively associated with wood ant abundance (for example the staphylinid beetle *Pella humeralis* (Gravenhorst)) and on others there may be no apparent impact.

Table 1. Species of millipede found in the two sites.

Millipedes	Restored site mean ± SE per year (percentage of years occurring: *n* = 28)	Control site mean ± SE per year (percentage of years occurring: *n* = 26)
Glomeris marginata (Villers, 1789)	6.8 ± 1.13 (82.1%)	19.9 ± 5.80 (96.2%)
Nanogona polydesmoides (Leach, 1814)	0.3 ± 0.17 (21.4%)	0.1 ± 0.04 (7.7%)
Chordeuma proximum Ribaut, 1913	1.2 ± 0.38 (57.1%)	6.8 ± 1.67 (96.2%)
Nemasoma varicorne C.L. Koch, 1847	0.02 ± 0.02(3.6%)	0 (0%)
Proteroiulus fuscus (Am Stein, 1857)	0.7 ± 0.19 (57.1%)	1.0 ± 0.22 (57.7%)
Tachypodoiulus niger (Leach, 1814)	8.2 ± 0.09 (100%)	11.7 ± 1.58 (100%)
Cylindroiulus britannicus (Verhoeff, 1891)	4.0 ± 1.63 (35.7%)	0.9 ± 0.36 (26.9%)
Cylindroiulus caeruleocinctus (Wood, 1864)	0.02 ± 0.02(3.6%)	0.02 ± 0.021 (3.8%)
Cylindroiulus parisiorum (Brolemann & Verhoeff, 1896)	0.07 ± 0.00 (7.1%)	0.02 ± 0.02 (3.8%)
Cylindroiulus punctatus (Leach, 1815)	5.1 ± 0.69 (100%)	4.1 ± 0.57 (100%)
Ophyiulus pilosus (Newport, 1842)	0.07 ± 0.03 (14.3%)	0.1 ± 0.05 (15.4%)
Polydesmus angustus Latzel, 1884	124.7 ± 20.00 (100%)	90.4 ± 20.08 (100%)
Polydesmus denticulatus C.L. Koch, 1847	33.4 ± 8.20 (89.3%)	94.5 ± 22.72 (100%)
Brachydesmus superus Latzel, 1884	0.07 ± 0.05 (7.1%)	0.3 ± 0.15 (19.2%)

Analysis comprised repeated measures ANOVA (by year) using Tukey-Kramer multiple comparison tests (Wheater & Cook 2000), using StatView v5.0, to explore potential differences between the sites on the basis of the numbers of individuals per 100 days trapping, the number of species, the proportion of immature animals compared to the number of adults (millipedes), and various measures of species diversity (Shannon *H'*, Simpson 1-*D*, Berger-Parker 1/*d*, and Evenness *J'* based on the Shannon index – Wheater & Cook 2015). The communities of millipedes and centipedes were ordinated separately using NMDS, with the Gower distance measure (Wheater *et al.* 2020), using PAST v3 (Hammer *et al.* 2001). Species turnover was measured as change in ordinational space between years, calculated as differences in ordinational space across the first three major ordination axes using an extension of the Pythagorean theorem. Correlations between the axes of major variation for myriapods and vegetation variables was completed using FCStats v2.1a (Wheater & Cook 2015, Wheater *et al.* 2020).

RESULTS

A total of 14 species of millipedes and 11 species of centipedes were found in the wood pasture restoration area compared to 13 species of millipedes and 12 species of centipedes in the control site (Tabs. 1–2). Figures 1–9 show the abundance of selected species which were caught in sufficient numbers to illustrate patterns of variation over time. Most of the species found were common British species with the most unusual in a UK context being the millipedes *Chordeuma proximum* and *Cylindroiulus parisorum* and the centipedes *Lithobius muticus* and *L. macilentus*. *Chordeuma proximum* has a strong southwest distribution in the UK and is an Atlantic species strongly associated with woodlands and may be associated with acid sandy soils (Lee 2006). The relatively high numbers caught, including juveniles, especially in late springs, indicate it is well established at Burnham Beeches. *Cylindroiulus parisorum* in

contrast is a predominately south eastern species and rather less well recorded in the UK. Although there is some suggestion of an association with synanthropic habitats in continental Europe, where it is very sparsely distributed (Kime & Enghoff 2017), in the UK this species has been associated with decaying wood and loose bark (Lee 2006) so the finding in a nature reserve known for its decaying wood habitat is not unexpected. *Lithobius macilentus* has been found across the UK but the records are very patchy and it has not been found in the south

west (Barber pers. comm.). The majority of the records are for woodland where it also appears to be most abundant (Barber & Keay 1988), it is only known from females in the British Isles and is the only British *Lithobius* apparently showing parthenogenesis (Barber pers. comm.). There were just 2 individuals caught during this project, both in the control plot. *Lithobius muticus* has a strong south eastern distribution in the UK and is a characteristic scrub and woodland species. It was regularly caught in the traps, especially in the restoration area.

**Table 2.** Species of centipede found in the two sites.

Centipedes	Restored site mean ± SE per year (percentage of years occurring: $n = 28$)	Control site mean ± SE per year (percentage of years occurring: $n = 26$)
Strigamia acuminata (Leach, 1814)	0.2 ± 0.07 (17.9%)	1.6 ± 0.33 (84.6%)
Strigamia crassipes (C.L. Koch, 1835)	0.7 ± 0.27 (46.4%)	1.9 ± 0.46 (61.5%)
Geophilus easoni Arthur *et al.*, 2001	1.0 ± 0.25 (67.9%)	1.9 ±0.42 (84.6%)
Geophilus flavus (De Geer, 1778)	0.1 ± 0.04 (21.4%)	0 (0%)
Geophilus insculptus Attems, 1895	0 (0%)	0.03 ± 0.03 (3.8%)
Geophiulus truncorum (Bergsoe & Meinert, 1886)	0.1 ± 0.05 (14.3%)	0.3 ±0.09 (34.6%)
Cryptops hortensis Donovan, 1810	0.2 ± 0.06 (25.0%)	0.4 ± 0.11 (38.5%)
Lithobius forficatus (Linnaeus, 1758)	8.0 ± 1.06 (100%)	15.0 ± 1.02 (100%)
Lithobius macilentus L. Koch, 1862	0 (0%)	0.1 ± 0.05 (11.5%)
Lithobius muticus C.L. Koch, 1847	8.0 ± 0.89 (100%)	1.2 ± 0.31 (61.5%)
Lithobius variegatus Leach, 1813	2.9 ± 0.90 (71.4%)	4.8 ± 0.88 (96.2%)
Lithobius crassipes L. Koch, 1862	0.3 ± 0.11 (28.6%)	0.6 ± 0.28 (26.9%)
Lithobius microps Meinert, 1868	0.04 ± 0.03 (7.1%)	0.03 ± 0.03 (3.8%)

The numbers of individuals in each species varied considerably with some only being found twice but other species being found in their hundreds. Numbers of *Cylindroiulus punctatus* declined over time in both plots whereas *Cylindroiulus britannicus* and *Glomeris marginata* increased over time (for *C. britannicus* from complete absence in the early years and *Glomeris marginata* from very low numbers to quite

high). *Chordeuma proximum* shows a very spikey pattern and in some years it is much more abundant than others. The two larger polydesmid species were caught in very high numbers in 2015. Generally, *Polydesmus denticulatus* was relatively more abundant in the control plot and *P. angustus* in the restoration plot but both showed a spike in 2015 which was especially pronounced in the control plot.

Centipede species were also variable with some predominantly found in the control plot (like *Strigamia acuminata*), others (like *Lithobius muticus*) more abundant in the restoration plot. *Lithobius variegatus* was more abundant in the restoration plot in the early years but numbers declined over time while they increased in the control plot. Generally, there were more species in the control plots than the restoration areas.
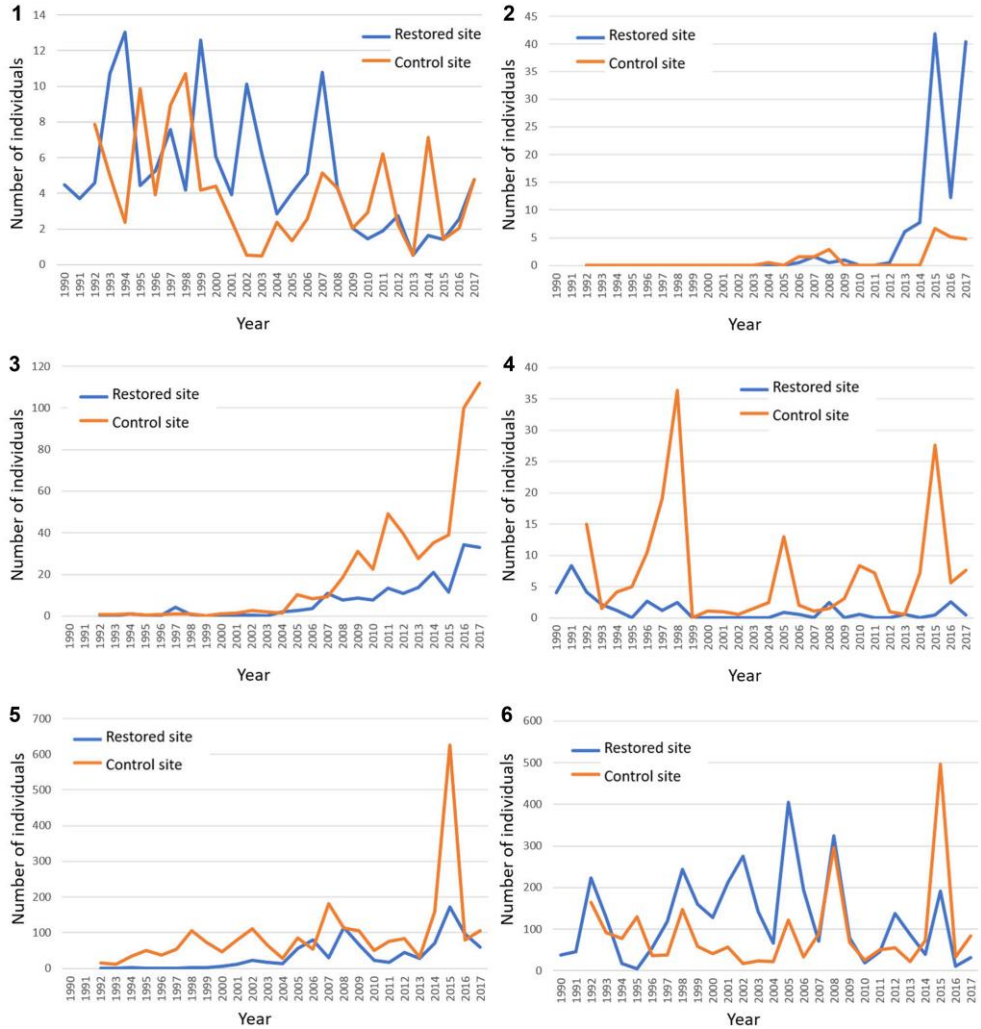
Figures 1–6. Numbers of individuals in various myriapod species in restoration and control plots over time.
1 = *Cylindroiulus punctatus*; 2 = *Cylindroiulus britannicus*; 3 = *Glomeris marginata*;
4 = *Chordeuma proximum*; 5 = *Polydesmus denticulatus*; 6 = *Polydesmus angustus*.
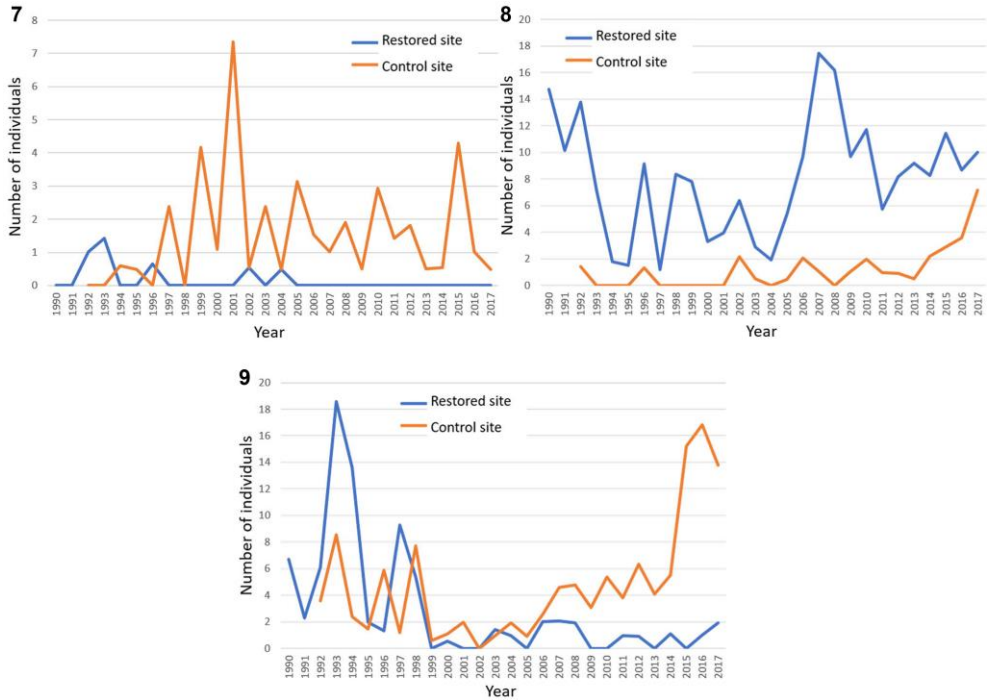
Figures 7–9. Numbers of individuals in various myriapod species in restoration and control plots over time.
7 = *Strigamia acuminata*; 8 = *Lithobius muticus*; 9 = : *Lithobius variegatus*.

Table 3. Analysis of variance for millipede numbers and diversity (with year as a repeated measure).

Millipedes	$F_{1,25}$	P	Comments
Numbers of individuals per 100 trapping days	1.006	0.3254	No significant difference between sites
Number of species	4.475	0.0445	Control significantly higher than restored site
Proportion of immatures to matures	7.933	0.0093	Control significantly higher than restored site
Shannon index (H')	0.393	0.5362	No significant difference between sites
Simpson index (1-D)	13.935	0.0010	Restored site significantly higher than control site
Berger-Parker index ($1/d$)	8.014	0.0090	Control significantly higher than restored site
Evenness (J')	0.035	0.8535	No significant difference between sites

Comparison between the two sites (restored vs. control) showed that the numbers of individuals per 100 days trapped were not significant between the two areas for millipedes (Tab. 3) but showed significantly more centipedes in the control area than in the restored site (Tab. 4). Figure 10 illustrates the patterns found in terms of the number of millipedes per 100 trapping days in the two sites. Similar patterns can be seen at the two sites over time except for a more dramatic increase in 2015 for the control site. Figure 11 clearly shows that the number of centipedes per 100 trapping days is consistently lower in the restored site, the restored site has

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two major peaks (one at the beginning of the survey and one part way through), whilst the control is reasonably stable with an increase at the end. For both classes, the control area had significantly more species than the restored site (Tabs. 3–4). The proportion of immatures to adults was significantly higher in the control site for millipedes, but not for centipedes.

Table 4. Analysis of variance for centipede numbers and diversity (with year as a repeated measure).

Centipedes	$F_{1,25}$	P	Comments
Numbers of individuals per 100 trapping days	6.779	0.0153	Control significantly higher than restored site
Number of species	9.441	0.0051	Control significantly higher than restored site
Proportion of immatures to matures	2.093	0.1604	No significant difference between sites
Shannon index (*H'*)	0.384	0.5411	No significant difference between sites
Simpson index (1-*D*)	0.120	0.7324	No significant difference between sites
Berger-Parker index (1/*d*)	2.391	0.1346	No significant difference between sites
Evenness (*J'*)	0.074	0.7882	No significant difference between sites
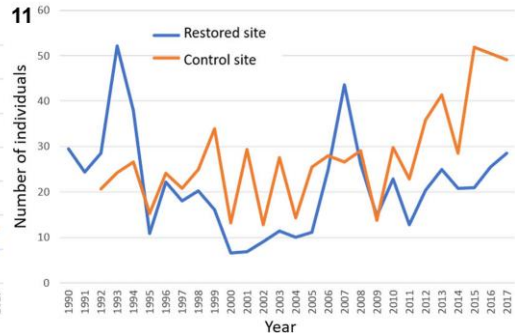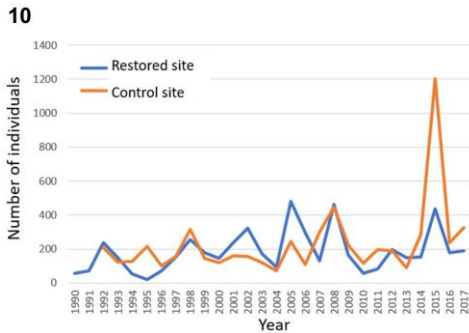
Figures 10–11. Numbers of myriapods per 100 trapping days over time. 10 = millipedes; 11 = centipedes.
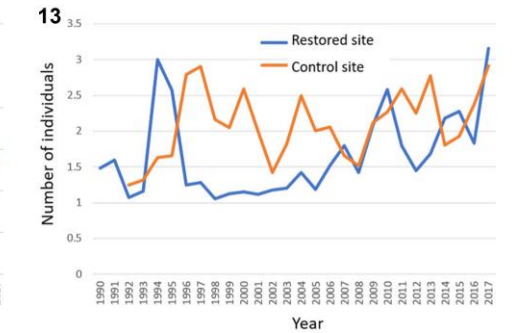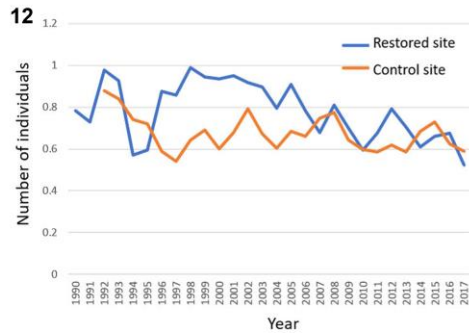
Figures 12–13. Indices over time for millipedes. 12 = Simpsons diversity index; 13 = Berger Parker Index.

No significant differences were found between the sites in terms of any of the diversity measures for centipedes. However, for millipedes, Simpson's index was significantly lower in the restored site, whilst Berger-Parker's index was higher in the control site. Figure 12 shows that the Simpson index for millipedes has remained more or less consistent over time for the control site, whereas for the restored site it has declined over time, becoming less diverse. Since this index is more influenced by the presence of common species, this implies that there are fewer common species in the restored site over time. The Berger-Parker index was also significantly different between sites and showed a clear increase over time for the restored site (Fig. 13). This suggests that species dominance has decreased over time, possibly related to the overall decline of several species including *C. punctatus* (Fig. 1) and *P. angustus* in the later few years (Fig. 6).

The NMDS biplots (Fig. 14) for millipedes show some separation along coordinate 1 (the axis of major variation) with the communities in the restored site for some early years lying to the left of the biplot, close to a large (fairly tight) cluster comprising the bulk of the data and the later years (2015–2017) being somewhat spread out to the right. This indicates that perhaps some changes did take place early on after restoration began, there was then a period of consolidation and then some larger changes occurred much later in the process. Although a similar spread of data can be seen on the biplot for the control site (with change occurring from bottom left to top right – Fig. 15), the data for the first 23 years are generally much more tightly clustered, implying a more consistent community structure over time. For the centipedes no obvious patterns emerged for either the restoration area or the control and similar groupings were found in the plots for the restoration and the control.
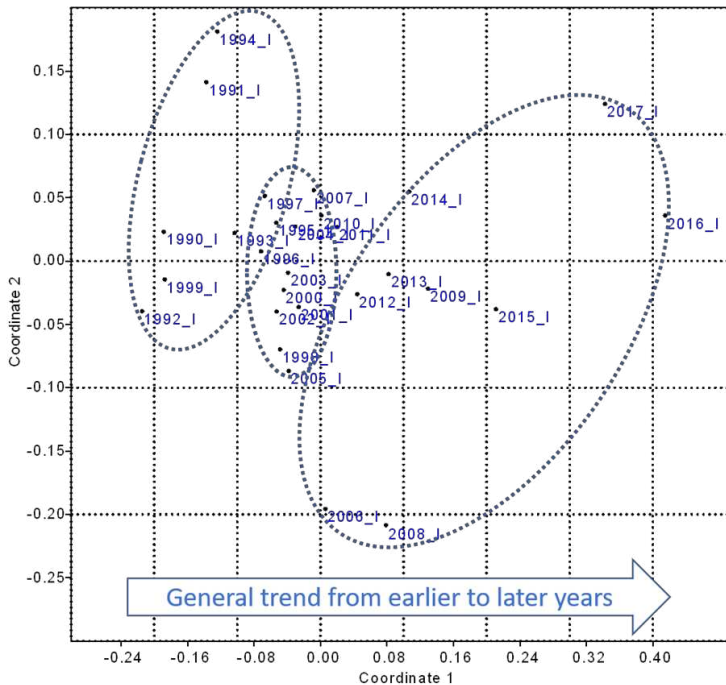

Figure 14. NMDS biplot of millipede communities over time for the restored site. Showing a general trend from early to later years along coordinate 1 (ellipses indicate groupings of early to later years).
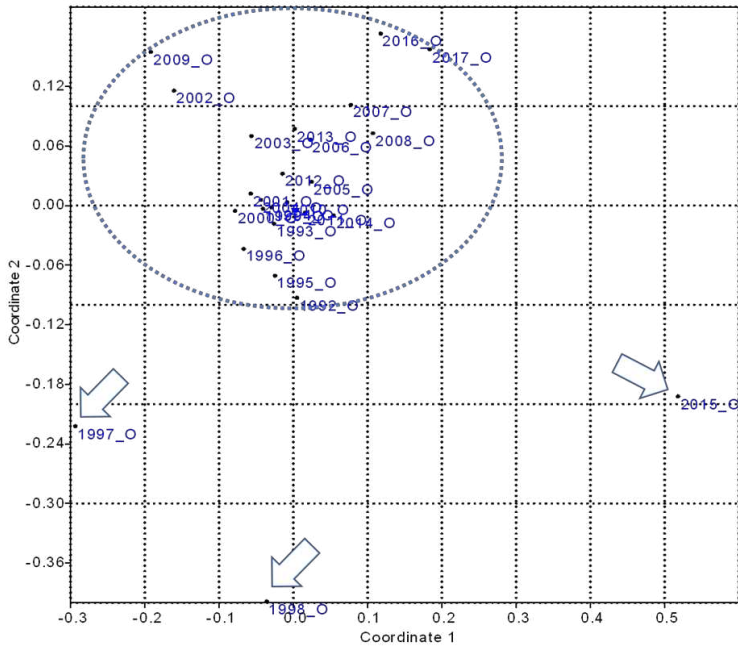
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Figure 15. NMDS biplot of millipede communities over time for the control site. Showing a fairly tight grouping of years and three possible outliers (arrowed).
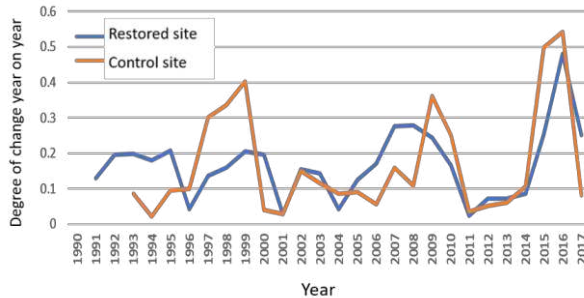
Figure 16. Degree of change in multidimensional space over time for millipedes. Indicating amount of community change.

Using change in multidimensional space as a measure of change in community structure between years, there were no differences between sites for either millipedes or centipedes. However, it can be seen for millipedes that the major change at both sites was in 2015 and 2016 (Fig. 16). If these dates are omitted from the analysis, the restored site can be seen to have a higher degree of change over time than the control site (repeated measures ANOVA $F_{1,24}$ = 11.392, $P = 0.0029$). For centipedes the amount of change between years is similar, although the patterns differ across the years with no discernible pattern.

The myriapod communities were then compared with the vegetation. Spearman Rank Correlations between the coordinate 1 scores from

the ordination of the millipede and centipede communities and various measurements of the vegetation (number of plant species, individuals and diversity indices) were carried out. For the control plot there were no significant correlations, suggesting that the vegetation diversity is not a major influence on the myriapod communities. For the restoration plot the only significant correlations were found between the number of plant species and Shannon diversity, for both millipedes and centipedes (Tab. 5). Thus, the separation between the myriapod communities appear to be influenced by the number of species of plant including variation in the development of leaf litter (quantity and quality) providing resources such as food and shelter as well as influencing the microclimatic conditions.

Comparing the numbers of wood ants with the numbers of individuals and species of both centipedes and millipedes through Spearman Rank Correlation Coefficients revealed no significant relationships. Neither were there any significant results when compared with ordination coordinate 1.

Ordination (NMDS) of the vegetation data for the restored area shows no particular clusters of years and a change in community structure from left to right over time. The change in multidimensional space shows that between each year the rate of change is relatively low. In contrast, the plot for the control site shows a tight cluster of years with one major outlier (1999) and aside from this one year, the rate of change is also relatively low.

Table 5. Significant correlations between coordinate 1 scores for myriapod communities and vegetation in the restoration plot.

Factor	Tied r_s	n	Tied P	Direction of relationship
Millipedes:				
Number of plant species	0.46397	26	0.01696	Positive
H' (Shannon) for plants	0.50632	26	0.00831	Positive
Centipedes:				
Number of plant species	0.46397	26	0.01696	Positive
H' (Shannon) for plants	0.50632	26	0.00931	Positive

DISCUSSION

Species found included a small number that can be considered interesting for the area. Despite the length of sampling time some species were only discovered in very low numbers (e.g. 2 individuals of *L. macilentus*). The number of centipede species found (13) compares with 10–21 found in previous studies from beech woodland in continental Europe (Stašiov & Svitok 2014), despite the limitations of pitfall trapping as a method and the relatively impoverished UK fauna. Although the UK has fewer species of millipede than other European countries at the same latitude, 14 species of millipedes were recorded which compares favourably with that

of a forest edge in Belgium (De Smedt *et al.* 2016) where 10 species were found. Relative abundance of species were different however, in Belgium *Proteroiulus fuscus* was the most dominant and made up 33% of catch. This species was also found in the current study, but in low numbers.

Two species of centipede were only found in the control plot (*Geophilus insculptus* and *Lithobius macilentus*), but they both were encountered as very low numbers of individuals. *Geophilus flavus* was only found in the restoration plot and although at low numbers this was recorded in several years. This appears to be an eastern and northern species in the UK, is regularly encountered in disturbed places like urban

and suburban locations and is found in grassland and pasture more frequently than woodland (Barber pers. comm.). Analysis of distribution records for preferred habitat in the UK found that *Geophilus insculptus* was equally likely to be found in the surface, leaf litter and subsurface layers and that *G. flavus* had a marked tendency to occur above ground (Barber & Keay 1988). The millipede *Nemasoma varicorne* was only found in the restoration area but again as just one individual. *N. varicorne* is not a species that would be expected to be found in pitfall traps regularly as it is very much an under-bark species on standing trees (see Lee 2006 for review of favoured tree species in the UK) but has also been recorded from pitfall traps (Kime 1997). The numbers of each species found in the two sampling areas over time were not evenly distributed and varied over time. Some showed clear differences between the control and restoration areas for example *Lithobius muticus* was consistently more abundant in the restoration area. Others showed changes over time within specific plots, for example *Cylindroiulus punctatus* became less abundant in the restoration plot over time, perhaps not surprising as this is a species living in decaying wood during the summer in France (Geoffroy 1981) and the quantity in this plot will have declined. Some species showed changes in abundance over time that appeared to be unrelated to restoration work being carried out. *Cylindroiulus britannicus* and *Glomeris marginata* were absent or almost absent at the beginning of the sampling period but now represent a substantial part of the millipede catch. *Chordeuma proximum* shows great variation between years within the control plot, which has not changed in other ways, and where the vegetation has remained very similar over time. The two main species of polydesmid millipede found also showed variation in numbers between the years, especially *P. angustus*. Captures in 2015 were notable with particularly large numbers of both species being trapped throughout the year.

The extreme variation in numbers found over time, not apparently always related to the restoration activity carried out, are interesting in highlighting apparently natural variation in myriapod activity over different years. The fact that the data for the last three years shows a similar spread to that found in the restored site, suggests that something other than the management implementation is impacting on the communities. The impact of trapping at the edges of the activity period for some species is also noteworthy. The traps may not be reflecting true abundance but are of course known to be dependent on the amount of activity and have strong bias for and against some species (Gerlach *et al.* 2009). The fact that some species became much more abundant over time would indicate that overtrapping is not having an obvious negative impact.

There were significant differences between total number of species found at the sites for both millipedes and centipedes, in both cases with the control being higher than the restoration area (i.e. the woodland had more species than an area perhaps equivalent to a forest edge, and the undisturbed habitat had more species than a disturbed one). Over time it might have been expected that a disturbed forest edge type habitat might have supported more species and this is what other work has found. For example, Stašiov & Svitok (2014) recorded a higher species richness of centipedes with increasing intensity of forestry thinning, although millipede species richness remained more or less the same. De Smedt *et al.* (2016) found that the species richness in oak woodland was lower in the centre of the forest than at edges and the activity density (measured by pitfall trapping) of millipedes was higher in the forest edges than the centre of deciduous forests across a range of latitudes and forest ages (De Smedt *et al.* 2019) although no relationship was found with centipedes. Tajovský (2000) found that both the number of species and the density of millipedes increased in abandoned fields. Both peaked at between 3–6 years after abandonment, and then declined; it was suggested that the development of scrub caused temporary population increases. Bogyó *et al.* (2015) recorded significantly fewer millipede species in grassland compared to forests, although forest edges had even more than either.

High myriapod species richness has been recorded by Spitzer *et al.* (2008) in sparse stands

(30% canopy cover) of singled coppice woodland with low deer numbers, compared to areas of high deer numbers (which they equated to wood pasture) or dense woodland. Although the managed site in this study has the appearance of a forest edge it is still located within a larger block of woodland. Perhaps it has not yet gained species that would be typical of more open habitats, as they are less able to colonise, than a true forest edge.

In terms of numbers of individuals there was no significant difference between the sites for the millipedes but there were higher numbers of centipedes in the control plot. It might have been expected that the numbers of millipede, being decomposers, would be higher in the control site where there is more leaf litter but the results do not show this and indicate that there is sufficient food source for them. Perhaps the scrub and grassland plant species are compensating for the lower levels of tree leaf litter. Generalist predators may be more adaptable in the face of change; for example, spider numbers have been reported to increase as beech woodland canopy is opened up (Černecká *et al.* 2019). However, in this study centipedes seem to have declined in numbers. Perhaps those that are more active, like the lithobiomoph centipedes have been able to respond more rapidly to changing conditions than the generally slower moving millipedes. Alternatively, perhaps they are treating this area as a woodland clearing and are simply crossing it. *L. muticus* seems to be doing reasonably well in the restored area, perhaps it's more its preferred habitat than dense woodland.

In contrast other studies have shown significant differences. Bokor (1993) found double the abundance of centipedes in ecotones as in forest. De Smedt *et al.* (2016) found that the abundance of millipedes declined about 7 m inside the forest edge and Bogyó *et al.* (2015) recorded the highest abundance of millipedes at the forest edge. Again, these studies indicate that forest edges are better than dense forest in terms of number of individuals whereas in our study the open area could be acting more as a forest clearing than a true edge.

For millipedes the control plot has a significantly higher proportion of immatures to matures. This could be because there were more immatures or because there were fewer adults in this area. This former would make more sense, within the woodland the ground is covered in leaf litter which is likely to be a more suitable substrate for breeding than the more open grassland and scrub of the restored area.

Of the diversity indices calculated there was no relationship between the sites for the centipedes but for millipedes the restored site was significantly higher for Simpson (indicating an increase in the number of common species) and the control was higher for Berger-Parker (where a high value in the most frequently found species impacts negatively on the index), although no difference was found with the Shannon index or Evenness. This suggests that the restored area is dominated by a number of relatively common species. This perhaps is not surprising, with a relatively small number of species responding positively to perturbations during the restoration and habitat management work.

Stašiov & Svitok (2014) calculated evenness and found that the highest scores for centipedes were found in unthinned forest and for millipede in forests with moderate levels of thinning. Shannon for both groups was found to increase with increasing intensity of past thinning.

All previous studies have shown the importance of forest edges, ecotones and forestry thinning which appears to have positive impacts for both centipedes and millipedes. De Smedt *et al.* (2016) described ecotones and forest edges as being warmer and with deeper leaf litter, as well as being possibly higher in pH and nitrogen deposition which would favour decomposers. Bogyó *et al.* (2015) also states that they have a higher percentage of leaf cover and more deadwood. All of these factors suggest that they could be very good places for myriapods. In contrast, Ruitta *et al.* (2012) tested a hypothesis that decomposition would be slower at the forest edge and found that the soil was moister and decomposition of ash and oak was faster in the forest interior compared with the edge where decomposition and moisture was more limited.

The macrofauna accelerated decomposition regardless of moisture levels, but the authors felt that forest fragmentation was an important ecosystem process. De Smedt *et al.* (2018) showed that moisture content was a more important factor in the speed of good quality leaf litter breakdown than temperature indicating that moisture could be a constraint in more open habitats. Spitzer *et al.* (2008) concluded that areas where the tree cover had been cleared to 30% and left to regenerate, with low grazing pressure, were most important for species of conservation concern, which were referred to as 'relic species'. They recommended preserving highly heterogeneous and sparse canopy conditions and restoring such conditions in selected areas to benefit open woodland specialists. David (2009) concluded that habitat heterogeneity at a landscape scale seemed to be good for millipedes, even at the cost of fragmentation. While this may be true at a large scale, this study has questioned the validity of this statement at a small scale.

The present study appears to have supported the view that forest fragmentation has a negative impact on decomposer communities as the unmanaged control plot was better in terms of both species and numbers of centipedes and numbers of millipede species. Notwithstanding, aside from the physical characteristics, Tracz (2000) described ecotones as having two roles, as barriers and a transit zone and they clearly have a very important role to play as warm and sheltered places for certain species. The level of leaf litter accumulation will depend on the species of tree/shrub and the physical characteristics of the ground and this could be very variable, contributing to a patchy nature of the grass/scrub/tree mosaic.

Characterisation of communities through ordination indicated some changes in ordinal space over time for the millipedes in the restoration plot. There appears to be some change relatively soon after large scale changes to the vegetation and then a period of consolidation with little change, followed by more substantial changes in the later years. Examination of the change in more detail indicates that the main year of difference was 2015 (the change will be

reflected twice for this unusual year, between 2014–15 and again 'back' from 2015–16). The ordination for the control plot also shows some changes in later years with 2015 a particularly different year to any others. 2015 is particularly notable for the 10-fold increase in captures of *Polydesmus angustus* and *Polydesmus denticulatus*, which were consistently high during the year, especially in the summer months. There are several possible reasons for this, of which climatic aspects are one. Peak adult activity of *P. denticulatus* is reported to be in June and July (Lee 2006) but while adults of *P. angustus* have been found at this time they are usually scarce over the summer (Lee 2006). Blower (1985) noted that *P. angustus* can be found in large numbers around cultivated land, with the subadults highly aggregated, and that it is a relatively fleet footed species. Other Polydesmids, notably species of the family Paradoxosomatidae have been reported to swarm in Nigeria (Lewis 1971) and Tasmania (Mesibov 2014). David (2012) measured the intrinsic rate of increase in laboratory populations of *P. angustus* subjected to seasonal conditions and calculated that a small group of 10 females at the start of a breeding season can potentially grow to over 3,000 females for the next year. It was considered that outbreaks of this species in favourable field conditions could be generated by a small number of fertilised females.

Relating the myriapod communities with the ground vegetation showed no significant relationships with the control plot, which is to be expected as this has not greatly changed over the years of study. However, the number of species of plant in the plots around the traps and their diversity, measured using the Shannon index, shows a positive correlation with coordinate 1 of the ordination of the millipede communities. This indicates that the number of plant species does have an impact on the millipede communities, with plant species being positively correlated along coordinate 1 of the ordination separating the millipede communities over time. A key feature of the restoration has been the increase in diversity of the ground vegetation which is a function of the grazing as well as tree clearance. Therefore, it is not surprising that the 'new' millipede communities in these restored

areas are related to the change in vegetation. However, the movement in the millipede communities in recent years, both in the control as well as the restoration site, suggests that there is more than vegetation causing these changes. Perhaps, in addition to the alteration in management, we are seeing some impact of wider environmental changes including changing climate and broader management changes (such as clearing within dense woodland) on both communities.

Previous work has also indicated the importance of vegetation on myriapod communities. Bogyó *et al.* (2015) used DCCA to separate out three communities of grass, forest and forest edge and found that changes in millipede abundance was highly correlated with vegetation structure. Scheu (1996) found that while there was a continuous change in floral composition from arable fields to beech woodland it was moisture levels and leaf litter that were the key determinants explaining a substantial part of the variation in communities of millipedes using CCA. Neither moisture levels nor aspects of leaf litter were measured in the present study however they are potentially a major influence on invertebrates inhabiting the leaf litter zone. Poser (1990) found that, while there were more lithobiid centipedes and higher numbers of *Strigamia accuminata* in plots with augmented litter, there were more edaphic centipedes in areas without litter. Increased leaf litter depth as a result of heavy metal pollution was a driver for a study by Read & Martin (1990). A significant positive correlation was found between numbers of millipedes and litter depth. However, this seemed to be largely explained by *G. marginata*, numbers of which were positively correlated with litter depth and when this species was removed the results were not significant. De Smedt *et al.* (2016) found a strong decrease in numbers of *G. marginata* on a transect into woodland, the abundance of this species was different to other species being more abundant at the forest edge where it was suggested that the leaf litter might be of better quality due to the lower carbon to nitrogen ratio (although in this study it was not more abundant). It was also postulated that *G. marginata* was very desicca-

tion tolerant so less restricted to the forest interior than other species.

CONCLUSIONS

Long-term studies of ground active invertebrates are relatively rare and this study has given some insight into communities, both where there has been active restoration work for habitat conservation and in a comparable woodland area that has not been actively managed. In the latter, plant and invertebrate communities generally changed very little over time, although some species did become more, or less, abundant and for a few species there were surprisingly big changes over time. This perhaps indicates a degree of turn-over which may be related to longer term climatic changes, but with just a single plot this is difficult to evaluate further.

The area restored to wood pasture, as might be expected, showed a higher degree of change, which in part does appear to be related to the changes in vegetation that has taken place in this area. Changes in the millipede communities, in particular, appear to have shifted in recent years, a relatively long time after the major part of the restoration work was carried out. While some of this may be due to external, possibly climatic changes, some species may have been advantaged or disadvantaged by the tree clearance, the impact of which has over-ridded more 'global' changes. It seems that 2015 was an exceptional year, when the abundance of a couple of common millipede species increased dramatically, including in the control site. The restored plot appears to have changed quite dramatically as a result of the restoration, from abundant leaf litter and decaying wood under tree canopy, to a grass and herb dominated sward with lower levels of patchily distributed leaf litter and decaying wood. It is therefore remarkable that the myriapod communities have proved so resilient.

The value of woodland vs. wood pasture as a habitat for myriapods requires further study and this was not an intended aim of the work. While the woodland control was consistently

better than the restoration area for numbers of millipede and centipede species as well as overall numbers of centipedes, the community did not change as much as might have been expected. This either demonstrates a high degree of resilience as a remnant of the previous woodland, or that wood pasture retains sufficient pockets of woodland like habitat to support good populations of these groups, or that the current degree of restoration is producing clearings within woodland rather than effecting a more major change. The wood pasture restoration is intended to favour the saproxylic communities rather than the myriapod communities, but it is perhaps re-assuring that they have not been significantly negatively impacted as a result of the management work.

Long-term studies such as this one are also useful in revealing variation in species abundances over time in areas with no apparent change in management. The control site, over a nearly 30 year period, has shown large changes in abundances for a small number of species. These may show long-term trends or big variations between individual years. This indicates how much variation there can be between individual years and shows the importance of long-term studies such as this.

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Present status of the millipede fauna of Hungary, with a review of three species of *Brachyiulus* Berlése, 1884 (Diplopoda)

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Abstract. Since 2005, the last comprehensive species list of the millipedes of Hungary, several new species to the fauna have been approved. Here we provide an updated summary of all Hungarian Diplopoda, comprising altogether 107 species. *Brachyiulus pusillus* (Leach, 1815) and *Chondrodesmus riparius* Carl, 1914, based on recent collections, are considered as new to the fauna of Hungary. We give special remarks to the following taxa: *Julus curvicornis* Verhoeff, 1899, *Typhloiulus polypodus* (Loksa, 1960), *Hungarosoma bokori* Verhoeff, 1928, *Heteracrochordum evae* (Loksa, 1960), *Ochogona* spp., *Haasea hungarica* (Verhoeff, 1928), *Mastigona* spp., and some Polydesmidae. In addition, the taxonomical relationship between *B. bagnalli* (Brolemann, 1924), *B. lusitanus* (Verhoeff, 1898), and *B. pusillus* is discussed in detail. With 21 figures.

Keywords. *Brachyiulus pusillus*, *Chondrodesmus riparius*, faunal list, new occurrences.

INTRODUCTION

The millipede fauna (Diplopoda) of the territory of Hungary was summarized several times in the past 25 years by Korsós (Korsós 1994, 1998, 2001, 2005). In 2005, on a poster for the 13th International Congress of Myriapodology, Bergen, Norway, the number given was 101 species (Korsós 2005), which testified a gradual increase depending on the research efforts. Since then, four new species were subsequently added to the fauna of the country: *C. caeruleocinctus* (Wood, 1864) in Bogyó & Korsós (2010), *Megaphyllum silvaticum* (Verhoeff, 1898) in Lazányi & Korsós (2010), *Cylindroiulus burzenlandicus* Verhoeff, 1907 and *Leptoiulus liptauensis* (Verhoeff, 1899) in Bogyó et al. (2012). In our presentation during the 18th International Congress of Myriapodology, Budapest (Korsós & Lazányi 2019) we discussed the occurrences of 106 species, including the recently collected *Brachyiulus pusillus* (Leach, 1815) and *Chondrodesmus riparius*

Carl, 1914. These are formally added here to the species list of Hungarian millipedes. In the present paper, we also change the list according to formerly omitted literature records. Thus, we remove *Mastigona vihorlatica* (Attems, 1899) [= *M. bosniensis* (Verhoeff, 1897) by Hauser 2004], and add *Ochogona phyllophaga* (Attems, 1899) and *Polydesmus subscabratus* Latzel, 1884.

LIST OF MILLIPEDES (DIPLOPODA) OF HUNGARY

In the followings, we give an updated list of the millipede fauna of Hungary, with 107 species in total. In contrast to the earlier species lists (Korsós 1994, 1998) we do not include the subspecific category as subspecies are sometimes based on uncertain characters. We follow the systematic arrangement of Diplopoda by Shear (2011) down to the family level; lower taxa are presented in alphabetic order. In a few cases, status changes in species taxonomy are

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mentioned in parentheses, as compared to the species list in Korsós (1998). New locality records are also given for three species. An asterisk (*) marks the species which have already published data from Hungary, but not included in the earlier faunal lists, two asterisks (**) mark the species presented here as new to the Hungarian fauna. Superscript numbers ([n]) refer to the remarks section of the present paper.

POLYXENIDA

Polyxenidae

1. *Polyxenus lagurus* (Linnaeus, 1758)

GLOMERIDA

Glomeridellidae

2. *Glomeridella minima* (Latzel, 1884)

Glomeridae

3. *Glomeris hexasticha* Brandt, 1833

4. *Glomeris klugii* Brandt, 1833 (= *G. conspersa* C. L. Koch, 1847 in Korsós 1998)

5. *Glomeris ornata* C. L. Koch, 1847

6. *Glomeris pustulata* (Fabricius, 1781)

7. *Glomeris tetrasticha* Brandt, 1833 (= *G. connexa* C. L. Koch, 1847 in Korsós 1998)

8. *Haploglomeris multistriata* (C. L. Koch, 1844)

9. *Trachysphaera costata* (Waga, 1857)

10. *Trachysphaera gibbula* (Latzel, 1884)

11. *Trachysphaera schmidtii* Heller, 1858

POLYZONIIDA

Polyzoniidae

12. *Polyzonium germanicum* Brandt, 1837

JULIDA

Blaniulidae

13. *Archiboreoiulus pallidus* (Brade-Birks, 1920)

14. *Blaniulus guttulatus* (Fabricius, 1798)

15. *Boreoiulus tenuis* (Bigler, 1913)

16. *Choneiulus palmatus* (Němec, 1895)

17. *Cibiniulus phlepsii* (Verhoeff, 1897)

18. *Nopoiulus kochii* (Gervais, 1847)

19. *Proteroiulus fuscus* (Am Stein, 1857)

Julidae

20. *Allajulus dicentrus* (Latzel, 1884)

21. *Allajulus groedensis* (Attems, 1899)

22. *Brachyiulus bagnalli* (Brolemann, 1924) [10]

23. *Brachyiulus lusitanus* Verhoeff, 1898 [10]

24. **Brachyiulus pusillus* (Leach, 1815) [10]

25. *Cylindroiulus abaligetanus* Verhoeff, 1901

26. *Cylindroiulus arborum* Verhoeff, 1928

27. *Cylindroiulus boleti* (C. L. Koch, 1847)

28. *Cylindroiulus burzenlandicus* Verhoeff, 1907

29. *Cylindroiulus caeruleocinctus* (Wood, 1864)

30. *Cylindroiulus horvathi* (Verhoeff, 1897)

31. *Cylindroiulus latestriatus* (Curtis, 1845)

32. *Cylindroiulus luridus* (C. L. Koch, 1847)

33. *Cylindroiulus meinerti* (Verhoeff, 1891)

34. *Cylindroiulus parisiorum* (Broelemann & Verhoeff, 1896)

35. *Cylindroiulus truncorum* (Silvestri, 1896)

36. *Enantiulus nanus* (Latzel, 1884)

37. *Enantiulus tatranus* (Verhoeff, 1907)

38. **Julus curvicornis* Verhoeff, 1899[1]

39. *Julus scandinavius* Latzel, 1884

40. *Julus scanicus* Lohmander, 1925

41. *Julus terrestris* Linnaeus, 1758

42. *Kryphioiulus occultus* (C. L. Koch, 1847)

43. ***Leptoiulus baconyensis*** (Verhoeff, 1899)

44. ***Leptoiulus cibdellus*** (Chamberlin, 1921)

45. ***Leptoiulus liptauensis*** (Verhoeff, 1899)

46. ***Leptoiulus proximus*** (Němec, 1896)

47. ***Leptoiulus saltuvagus*** (Verhoeff, 1898)

48. ***Leptoiulus simplex*** (Verhoeff, 1894)

49. ***Leptoiulus trilineatus*** (C.L.Koch, 1847)

50. ***Leptoiulus trilobatus*** (Verhoeff, 1894)

51. ***Leptoiulus tussilaginis*** (Verhoeff, 1907)

52. ***Megaphyllum bosniense*** (Verhoeff, 1897)

53. ***Megaphyllum projectum***Verhoeff, 1894

54. ***Megaphyllum silvaticum*** (Verhoeff, 1898)

55. ***Megaphyllum transsylvanicum*** (Verhoeff, 1897)

56. ***Megaphyllum unilineatum*** (C. L. Koch, 1838)

57. ***Mesoiulus paradoxus*** Berlése, 1886

58. ***Ommatoiulus sabulosus*** (Linnaeus, 1758)

59. ***Ophyiulus pilosus*** (Newport, 1842)

60. ***Pachypodoiulus eurypus*** (Attems, 1894)

61. ***Styrioiulus pelidnus*** (Latzel, 1884)

62. ***Styrioiulus styricus*** (Verhoeff, 1896)

63. ***Typhloiulus polypodus*** (Loksa, 1960)[2]

64. ***Unciger foetidus*** (C. L. Koch, 1838)

65. ***Unciger transsilvanicus*** (Verhoeff, 1899)

66. ***Xestoiulus imbecillus*** (Latzel, 1884)

67. ***Xestoiulus laeticollis*** (Porat, 1889)

Nemasomatidae

68. ***Nemasoma varicorne*** C. L. Koch, 1847

CALLIPODIDA

Dorypetalidae

69. ***Dorypetalum degenerans*** (Latzel, 1884)

CHORDEUMATIDA

Chordeumatidae

70. ***Chordeuma sylvestre*** C. L. Koch, 1847

71. ***Melogona broelemanni*** (Verhoeff, 1897)

72. ***Melogona transsilvanica*** (Verhoeff, 1897)

Hungarosomatidae

73. ***Hungarosoma bokori*** Verhoeff, 1928[3]

Trachygonidae

74. ***Heteracrochordum evae*** (Loksa, 1960)[4]
(= *Acrochordum evae* Loksa, 1960 in Korsós 1998)

Craspedosomatidae

75. ***Craspedosoma raulinsii*** Leach, 1814

76. ***Ochogona caroli*** (Rothenbühler, 1900)[5]

77. ***Ochogona elaphron*** (Attems, 1895)[5]

78. [*]***Ochogona phyllophaga*** (Attems, 1899)[5]

79. ***Ochogona triaina*** (Attems, 1895)[5]

Haaseidae

80. ***Haasea flavescens*** (Latzel, 1884)

81. ***Haasea hungarica*** (Verhoeff, 1928)[6]

82. ***Hylebainosoma tatranum*** Verhoeff, 1899

Mastigophorophyllidae

83. ***Haploporatia eremita*** Verhoeff, 1909

84. ***Mastigona bosniensis*** (Verhoeff, 1897)[7]

85. ***Mastigona mutabilis*** (Latzel, 1884)[7]

86. ***Mastigona transsylvanica*** (Verhoeff, 1897)[7]

POLYDESMIDA

Chelodesmidae

87. [**]***Chondrodesmus riparius*** Carl, 1914[8]

Paradoxosomatidae

88. ***Oxidus gracilis*** (C. L. Koch, 1847)

89. ***Stosatea italica*** (Latzel, 1886)

90. ***Strongylosoma stigmatosum*** (Eichwald, 1830)

Oniscodesmidae

91. ***Amphitomeus attemsi*** (Schubart, 1934)

Pyrgodesmidae

92. ***Cynedesmus formicola*** Cook, 1896

93. ***Poratia digitata*** (Porat, 1889)

Polydesmidae

94. ***Brachydesmus attemsii*** Verhoeff, 1895

95. ***Brachydesmus dadayi*** Verhoeff, 1895[9]

96. ***Brachydesmus superus*** Latzel, 1884

97. ***Brachydesmus troglobius*** Daday, 1889[9]

98. ***Polydesmus collaris*** C. L. Koch, 1847

99. ***Polydesmus complanatus*** (Linnaeus, 1761)

100. ***Polydesmus denticulatus*** C. L. Koch, 1847

101. ***Polydesmus edentulus*** C. L. Koch, 1847

102. ***Polydesmus germanicus*** Verhoeff, 1896

103. ***Polydesmus monticola*** Latzel, 1884

104. ***Polydesmus polonicus*** Latzel, 1884

105. ***Polydesmus schaessburgensis*** Verhoeff, 1898[9]

106. *****Polydesmus subscabratus*** Latzel, 1884[9]

107. ***Polydesmus transylvanicus*** Daday, 1889[9]

REMARKS TO THE SPECIES LIST

[1]*Julus curvicornis* Verhoeff, 1899

The species was described by Verhoeff from present-day Hungary ("Bükk-Gebirge, Oberungarn", Verhoeff 1899b), and mentioned several times by Karel Tajovský that it should occur near the East Slovakian border (Tajovský

pers. comm.). We have recently found a sample in the HNHM collection, originated from the Institute of Systematic Zoology, University of Budapest, with one adult and one juvenile male and an adult female (Szalajka valley, Bükk Mts, 29 June 1951). The tube contained a simple handwritten label ("*Julus curv.*") by Imre Loksa (1923−1992), former professor at the university. The male gonopods are in complete agreement with the drawings by Verhoeff (1899b, 1928).

[2]*Typhloiulus polypodus* (Loksa, 1960)

The species has been described by Loksa (1960) as *Allotyphloiulus polypodus*, from the Forrás Cave near Lillafüred, Bükk Mts., northeastern Hungary. Its generic allocation is still undecided. Vagalinski et al. (2015) in their revision listed it in *Typhloiulus* Latzel, 1884, whereas in the Millibase it is under the genus *Allotyphloiulus* Verhoeff, 1905 (Sierwald & Spelda 2018). (It is completely missing from the Fauna Europaea database.) For a long time, the species was only known from the type locality, when Mock et al. (2002) found a female identified as *Typhloiulus* cf. *polypodus* in the Gombasecká Cave in the Slovak Karst.

[3]*Hungarosoma bokori* Verhoeff, 1928

This species was described by Verhoeff (1928) based on a single female from the Abaliget Cave, South Hungary, collected by Elemér Bokor (1887−1928) Hungarian cave zoologist. He gave a detailed description of the specimen's eyes and body segments with paraterga and setae, with figures. Verhoeff (1928) also speculated about the systematic position of this chordeumatidan: according to his opinion the genus *Hungarosoma*, although related to *Brachychaeteuma*, finds its nearest relative in Japan, in the genus *Macrochaeteuma*, showing a peculiar connection between the millipede fauna of Southeast Europe and Asia (Verhoeff 1928). Several years after the description of another species, *Hungarosoma inexpectatum* Ceuca, 1967, Ceuca (1974) erected the family Hungarosomatidae for the two species alone. This was generally not accepted, and *Hungarosoma* was

later erroneously assigned to Anthroleucoso-
matidae (Hoffman 1980, Enghoff 2013). Fol-
lowing all these, for a long time *Hungarosoma
bokori* was considered a unique and endemic
member of the Hungarian fauna, a troglobiont
(Korsós 1994, 1998), and it still stands as such in
the databases of Fauna Europaea (Enghoff 2013)
and Millibase (Sierwald & Spelda 2018). Mock et
al. (2014, 2016) finally presented a detailed de-
scription of a freshly collected male, as well as a
careful study of all available museum material.
They even carried out a molecular research, in
which *H. bokori* came out as an independent line-
age supporting the validity of the family Hun-
garosomatidae (Mock et al. 2016).

However, in a more recent paper Antić et al.
(2018) called for attention to a curious similarity
between the illustrations of *Ceratosoma cervinum*
Verhoeff, 1899 (Verhoeff 1899a: figs 19–23; and
Mršić 1987: p. 67, fig. 10 I, J), and the illustra-
tions of *Hungarosoma bokori* (Mock et al. 2016:
pp. 245, 247, figs 15, 16). They concluded that
they all show the male gonopods of the same spe-
cies, however schematic are the figures of
Ceratosoma cervinum Verhoeff, 1899 (now ac-
cepted as *Ochogona cervinum* (Verhoeff, 1899)
(Antić et al. 2018)). They did not formally estab-
lish a synonymy, and because their observation is
based only on the drawings, here we still follow
the consensus taxonomy and consider *H. bokori* a
good species in its own status. In agreement with
Haľková & Mock (2018) we believe that a proper
synonymy can only be proven if the original
specimens of *Ceratosoma cervinum* sensu
Verhoeff are compared under the microscope to
the *H. bokori* material.

Our concept on the geographic distribution of
H. bokori has nevertheless changed substantially,
since the extensive collections by our Czech and
Slovakian colleagues showed that its occurrence
surpasses the Carpathian Basin by far (see the
map in Mock et al. 2016: fig. 19). Hence its en-
demic status to Hungary (Korsós 1998) is now
revised.

[4]*Heteracrochordum evae* (Loksa, 1960)

The species was originally described by
Loksa (1960) from a beech forest near Bánkút,
Bükk Mts, north-eastern Hungary, as a new
subgenus *Heteracrochordum* Loksa, 1960 in the
genus *Acrochordum* Attems, 1899. There is one
female specimen found in the HNHM, with only
a species label handwritten by Loksa but with-
out further details, which we believe could be
part of the syntype series. In Loksa's paper, four
specimens are listed as part of the type series,
one female from 15 September 1949, and one
male and two juveniles from 20 July 1954, from
the same locality (Loksa 1960), all of them sup-
posedly deposited in the Department of Zoosys-
tematics, Eötvös Loránd University. Since those
specimens could not be located, we consider the
HNHM specimen as the female syntype.

Heteracrochordum is accepted now as a val-
id genus (Sierwald & Spelda 2018, Mock et al.
2019), known only by its type species, which is
considered as endemic to the Carpathian Basin
(Korsós 1998). The family Trachygonidae is
supposedly under revision by Mock et al.
(2019), as they said in the presentation during
the 18th International Congress of Myriapod-
ology in Budapest. They have found new records
of *Heteracrochordum evae* in two distinct
regions in Slovakia (Driencany, Burda Mts in
Mock et al. 2019), representing the northern-
most limits of the family distribution.

[5]*Ochogona* species

We accept four species as occurring in Hun-
gary, which are discussed below:

Ochogona caroli (Rothenbühler, 1900): Ma-
terial studied: Bakony Mts, Zirc, Pintér Hill,
1941.X.19, leg. L. Szalay & I. Kovács, det. L.
Szalay (3215/1943, five vials, gonopods sepa-
rated: My. 1331, 1333, 1334, 1336, 1337); Zirc,
Pintér Hill, 1941.X.21, leg. L. Szalay & I. Ko-

vács, det. L. Szalay (3215/1943, gonopods separated in vial: My. 1338); Bakony Mts, Miklós Pál Hill, 1965.X., leg. I. Loksa & Zs. Szombathelyi, det. I. Loksa.

Ochogona elaphron (Attems, 1895): Material studied: Kőszegi Mts., 1937.XI.1, leg. A. Visnya Aladár, det 3160/1942, det. L. Szalay L. (3160/1942, My. 1330), revid. I. Loksa (200/1955); Kőszegi Mts., 1938.XI.2., leg. A. Visnya, det. L. Szalay (3162/1942, My 1332& 1335).

Ochogona triaina (Attems, 1895): Material studied: Kőszegi Mts., 1937.XI.1, leg. Bpesti Egyet. Állatrendsz. Int., det. L. Szalay (3160/1942, My 1329), 1 male and 1 female,gonopods in genitalia vial.

With these three species we follow Szalay (1942, 1944) who considered them separate species as it can be seen on the labeling of the HNHM specimens. Loksa (1968) for Szalay's *Ochogona caroli* specimens from Pintér Hill, 1941, and for his own 1968 Miklós Pál Hill sample described *O. c.* ssp. *hungaricum*, as well as another ssp. *somloense* from Somló Hill (Loksa 1968). The tubes in the HNHM contain only hand-written labels by Loksa (in the case of Somló Hill with the name "*Ceratosoma caroli evae*", Somló 67.X.); however we consider them as part of the original syntype series of *O. c. somloense*. Together with Verhoeff's *Ceratosoma caroli* ssp. *nubium* Verhoeff, 1921, we do not differentiate them from the nominal species *Ochogona caroli*.

In the collection material there are *O. elaphron* and *O. triaina* vials with labels suggesting their co-occurrence (especially because they seem to be collected at once). Dr. László Szalay had worked with the genus in details; in his material gonopods are dissected, so here we rely on his results (Szalay 1942) and accept the occurrence of both species in Hungary.

Ochogona phyllophaga (Attems, 1899): This fourth species we add here to the species list of millipedes of Hungary. Antić & Akkari (2020) called our attention to this species, of which the original literature record by Attems (1899: p. 315) was unfortunately overlooked by us. Attems in his description of *Atractosoma phyllophagum* Attems, 1899, listed "St. Gotthard in Ungarn, ganz nahe der steirischeu Grenze" as type locality of the species, which clearly corresponds to Szentgotthárd, a small town in the westernmost part of present-day Hungary. We hope to find new specimens of this species, but even until then we have to consider it as a member of the Hungarian fauna.

[6]*Haasea hungarica* (Verhoeff, 1928)

The genus *Haasea* has recently been comprehensively revised by Antić & Akkari (2020). For *Haasea hungarica*, they listed several new localities (Lower Austria, Slovenia, Serbia, and southern Romania), hence widening its distribution over the Carpathian Basin (see map by Antić & Akkari 2020: fig. 40). Its former endemic status to Hungary according to earlier authors (Verhoeff 1928, Szalay 1942, Korsós 1998) can now be revised. Tabacaru's subspecies (*Orobainosoma hungaricum orientale* Tabacaru, 1965) from the Romanian Banat is a junior subjective synonym of *Haasea hungarica* (Antić & Akkari 2020).

[7]*Mastigona* species

In the former species lists, five species of the genus *Mastigona* (previously *Heteroporatia*) were recorded from present-day Hungary (Korsós 1998, 2005). Here we consider only three species as valid: *M. bosniensis* (Verhoeff, 1897), *M. mutabilis* (Attems, 1899), and *M. transsylvanica* (Verhoeff, 1897). The fourth, *M. vihorlatica* (Attems, 1899) was already considered as a junior synonym of *M. bosniensis* by Hauser (2004), although he did not express it explicitly, and the fifth, *M. mehelyi* (Verhoeff, 1897), was synonymized with *M. bosniensis* by Lazányi & Korsós (2009). *M. transsylvanica* was recorded from Jósvafő, Northeast Hungary by Matic & Ceuca (1969).

Fig. 1. *Chondrodesmus riparius* from Törökbálint.

[8]*Chondrodesmus riparius* **Carl, 1914**
(Fig. 1)

This exotic species was first found in Hungary by Benedek Török, an employee at the Plantart Horticulture in Törökbálint near Budapest in May 2015. A few specimens were seen in the pots of imported *Phoenix* palm. One year later a dozen specimen were recorded in an office building in Budapest by Liza Takács, spreading out also from imported indoor plant pots. These findings represent new records for the Hungarian millipede fauna.

The species was originally described from Colombia, tropical South America, and in Europe it was first found in Umeå, Sweden (2000), later in Söderköping, Sweden (2006), then in Copenhagen, Denmark and as well as in Bonn, Germany (Anderson & Enghoff 2007, Enghoff 2008). Most probably it is distributed throughout the continent by horticultures and household megastore networks (like IKEA). It is unlikely to survive in natural environments.

[9]**Polydesmidae**

Brachydesmus dadayi Verhoeff, 1895, *B. troglobius* Daday, 1889, and *Polydesmus*

schaessburgensis Verhoeff, 1898 were all dealt with as endemic species to Hungary by Korsós (1998). *B. dadayi* was recorded from Bulgaria already by Strasser (1973), and recently from Slovakia (Haľková & Mock 2018). Distribution of *B. troglobius* was discussed in detail by Angyal et al. (2017) (Slovenia, Serbia and Montenegro). *P. schaessburgensis* was found as a new species to the fauna of Bulgaria (Bachvarova et al. 2017). With this keeping in mind, no polydesmids can now be considered as an endemic species to the Carpathian Basin.

In addition, based on a formerly omitted literature record, we here add *Polydesmus subscabratus* Latzel, 1884 to the Hungarian fauna. The species was mentioned already by Daday (1889) from Sátoraljaújhely, extreme northeast of Hungary, and from Velejte (= Veľaty), southeastern Slovakia. Haľková & Mock (2018), however, still handle these as unconfirmed records, until fresh specimens are collected.

Polydesmus transylvanicus Daday, 1889 was first recorded from Hungary by Kutas (2000): Szeged, Tisza-Maros rivers confluence, 5 Nov. 1996, leg. E. Hornung (3 males, 10 females, 2 juveniles). Haľková & Mock (2018) also recorded it from as far as eastern Slovakia.

[10]REVIEW OF THE HUNGARIAN SPECIES OF *BRACHYIULUS*

The genus *Brachyiulus* Berlese, 1884 was revised by Vagalinski & Lazányi (2018). They gave a complete morphological redescription of the genus, and listed seven species: *B. apfelbeckii* Verhoeff, 1898, *B. bagnalli* (Brolemann, 1924), *B. jawlowskii* Lohmander, 1928, *B. lusitanus* Verhoeff, 1898, *B. pusillus* (Leach, 1815), *B. stuxbergii* (Fanzago, 1875) and *B. varibolinus* Attems, 1904. The distribution of the genus covers Central and Eastern Europe, the Balkans, Italy, and even the Caucasus and Kazakhstan.

Brachyiulus bagnalli was the only species hitherto reported in Hungary (Korsós 1994, 1998). However, this species was previously mentioned in the literature as *B. pusillus* (pl. Loksa 1956), and just later clarified to be *B. bagnalli* (Dziadosz 1964, Korsós 1994). *B. lusitanus* was only mentioned once from the country, in an unpublished thesis (Sziráki 1966), and remained dubious till now (Korsós 1994, 1998). According to literature distribution data (Kime & Enghoff 2017, Vagalinski & Lazányi 2018) three species occur in Central Europe: *B. bagnalli*, *B. lusitanus*, and *B. pusillus*. Here we give descriptive data and definite occurrences of the three species in Hungary.

All material investigated belong to the HNHM. Methods are the same as in Lazányi & Korsós (2011).

TAXONOMIC PART

Brachyiulus bagnalli (Brolemann, 1924)
(Figs 2–3, 8–9, 14–15, 21)

Microbrachyiulus Bagnalli Brolemann, 1924: pp. 108–109.

Brachyiulus bagnalli: Schubart 1934: p. 276.

Brachyiulus pusillus ssp. *Kaszabi* Loksa, 1956: p. 389, fig. 5.

Brachyiulus pusillus: Sziráki 1966: p. 43, figs 78–79.

Brachyiulus bagnalli: Vagalinski & Lazányi 2018: pp. 16–17.

Material investigated. Vizsoly, backwater of Hernád, 21 June 2002, leg. Hegyessy G., det. Bogyó D.; Vizsoly, backwater of Hernád, 29 July 2002, leg. Hegyessy G., det. Bogyó D.; Tarcal, Ördög mine, 15 May 1999, leg. Hegyessy G., det. Bogyó D.; Szécsény, Pöstény steppe, 7 June 2005, leg. Hegyessy G., det. Bogyó D.; Szécsény, Pöstény steppe, 30 June 2005, leg. Hegyessy G., det. Bogyó D.; Mezőzombor, Szarka farm, 5 July 2005, leg. Hegyessy G., det. Bogyó D.; Mezőzombor, Szarka farm, 1 Aug. 2006, leg. Hegyessy G., det. Bogyó D.; Szentistvánbaksa, Baksa stack, 22 May 2002, leg. Hegyessy G., det. Bogyó D.; Zalkod, Palocsa, 9 May 2002, leg. Hegyessy G., det. Bogyó D.; Közép-tiszai Landscape Protection Area, Kisköre, Patkós, willowy, 1 Apr. 1995, leg. Korsós Z., det. Korsós Z. 1995; Apaj, beneath logs, 7 Apr. 1991, leg. Farkas B., det. Korsós Z. 1994; Pusztaszeri Landscape Protection Area, Baks, Palásti forest, oak forest, 4 June 1994, leg. Z. Korsós, det. Korsós Z. 1994; County Pest, Szentendre, Northern boundary, floodplain of the Danube, 25 June 1995, leg. Korsós Z., det. Korsós Z.; County Pest, Makád, 27 Mar. 1989, leg. Merkl O., det. Korsós Z. 1989; County Pest, Szob, Danube shore, 27 Dec. 1988, leg. Korsós Z., det. Korsós Z. 1989; Budapest, Békásmegyer, Róka hill, 30 Mar. 1989, leg. Szederkényi N., det. Korsós Z. 1989; Budapest, Népsziget, 100m, willowy, under bark, 15 Mar. 1990, leg. Merkl O., det. Korsós Z. 1990; Budapest, Hajógyári island, willowy, leaf litter, 4 Mar. 1990, leg. Merkl O., det. Korsós Z. 1990; Budapest, Hajógyári island, 1 Apr. 1991, leg. Merkl O., det. Korsós Z. 1991; Budapest, Gellért hill, Somlói street 12, leaf litter, 10 Feb. 1998, leg. Fürjes I., det. Korsós Z.; Budapest, Gellért hill, Somlói street, 10 May 1989, leg. Fürjes I., det. Korsós Z. 1989; Fertőújlak, det. Korsós Z. 1995; Lébény, Nyíres, 30 Mar. 2000, leg. Podlussány A., det. Korsós Z.; County Somogy, Balatonszentgyörgy, Gulya Restaurant, 30 May 1994, leg. British Myriapod Group; County Somogy, Balatonfenyves, Hotel Fenyves, 29 May 1994, leg. R. E. Jones; Szeged, alluvium on the shore of Tisza, 8 Mar. 1937, leg. K. Czógler, det. Korsós Z. 1986;

County Baranya, Drávapalkonya, floodplain, willowy, 8 Nov. 1995, leg. Korsós Z. 1995; Fertő-Hanság National Park, Mosonszolnok, Öreg forest, 11 Oct. 1995, leg. Horváth Edit, det. Korsós Z.; Tihany, 16 June 1972, Loksa material, det. Lazányi E. 2019; County Fejér, Baracska, beneath bark of fallen tree, 3 Apr. 1988, leg. Korsós Z., det. Korsós Z. 1988; Fertő-Hanság National Park, along the road leading to Nyíres, 18 Apr. 1996, leg. Horváth Edit; Budapest, Csillag hill, 30 Mar. 1990, leg.

Szederkényi N, det. Korsós 1990; Budapest, Csillag hill, 1 Feb. 1989, leg. Szederkényi N, det. Korsós Z. 1989; Budapest, Városmajor, park, 5 Apr. 1990, leg. Korsós Z., det. Korsós Z.; Budapest, Városliget, 8 Apr. 1989, leg. Korsós Z., det. Korsós Z. 1989.

Descriptive notes

Males. Length: 10.1–11.8 mm, height: 0.6–0.8 mm; number of body rings: 33+(1–2)+T; stadium: VIII.

Figures 2–7. SEM figures of *Brachyiulus* male gonopods, from mesal (upper row) and lateral views (lower row). 2–3 = *B. bagnalli* (County Pest, Szob, Danube shore, 27 Dec. 1988, leg. Z. Korsós), left and right gonopods, respectively, but both flipped horizontally to facilitate comparison; 4–5 = *B. lusitanus* (County Somogy, Balatonfenyves, 29 May 1994, leg. British Myriapod Group), right and left gonopods, respectively; 6–7 = *B. pusillus* (Törökbálint, Plantart Horticulture, 14 May 2015, leg. Z. Korsós), left and right gonopods, respectively, but both flipped horizontally to facilitate comparison. Abbreviations: *ap*: anterior process, *fc*: flagellum channel, *lp*: lateral process, *P*: promere, *s*: solenomere. Scale bars: 0.2 mm.

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Anal valves with 9–10 setae on the valve, and another 9–10 on the mesal margin of the valve. Subanal scale less pointed than in *B. lusitanus*.

Gonopods (Figs 2–3, 8–9): Opisthomere without mesoanterior process; lateral process (*lp*) wide, divided into two parts: the anterolateral one forming a flattened, thin lamella with furrows, the mesocaudal part slightly pointed, without furrows.

Females. Length: 11.7–12.4 mm, height: 0.8–0.9 mm, number of body rings: (33–35)+(2)+T, stadium: VIII.

Prefemur and femur (*pf* and *f* on Fig. 15, respectively) of mature female's 2nd leg-pair more elongated than the respective parts of *B. lusitanus* females (length/width ratio is around 1.5–1.7 for both parts).Anal valve with around 8 setae on the valve, and 8 on its mesal margin.

Vulva (Fig.14): Not as elongated as by *B. lusitanus* (length/width ratio never reaching 2). Apical opening (*o*) is rounded, with a conspicuous central area. Bursa apically with 10–14 (max. 18) setae, *i.e.* considerably less setose than *B. lusitanus*. Side sclerites (*sc*) with 4 setae.
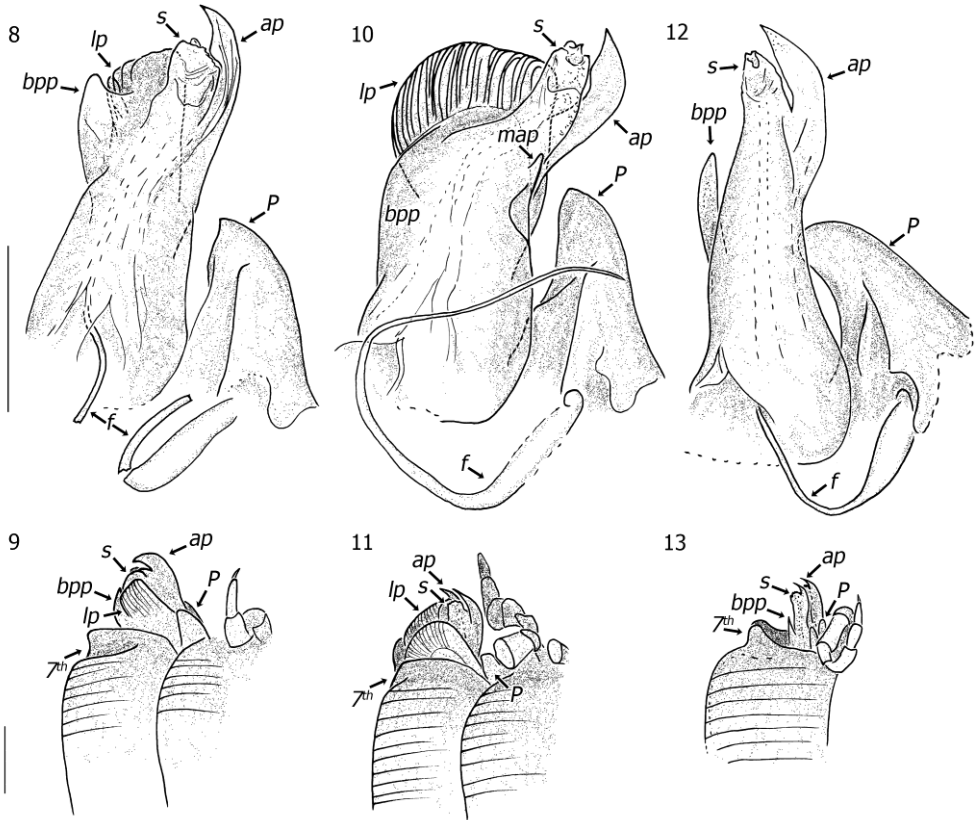
Figures 8–13. *Brachyiulus* male gonopods: from mesal view and *in situ* from left. 8–9 = *B. bagnalli* (Budapest, Népsziget, 15 Mar. 1990, leg. O. Merkl), right gonopods, and *in situ*; 10–11 = *B. lusitanus* (Törökbálint, Plantart Horticulture, 14 May 2015, leg. Z. Korsós); right gonopods, and *in situ*; 12–13 = *B. pusillus* (Törökbálint, Plantart Horticulture, 14 May 2015, leg. Z. Korsós), left gonopods flipped horizontally to facilitate comparison, and *in situ*. Abbreviations: *ap*: anterior process, *f*: flagellum, *lp*: lateral process, *map*: mesoanterior process, *P*: promere, *s*: solenomere, *7th*: pleurotergite of the 7th body ring. Scale bars: 0.2 mm.

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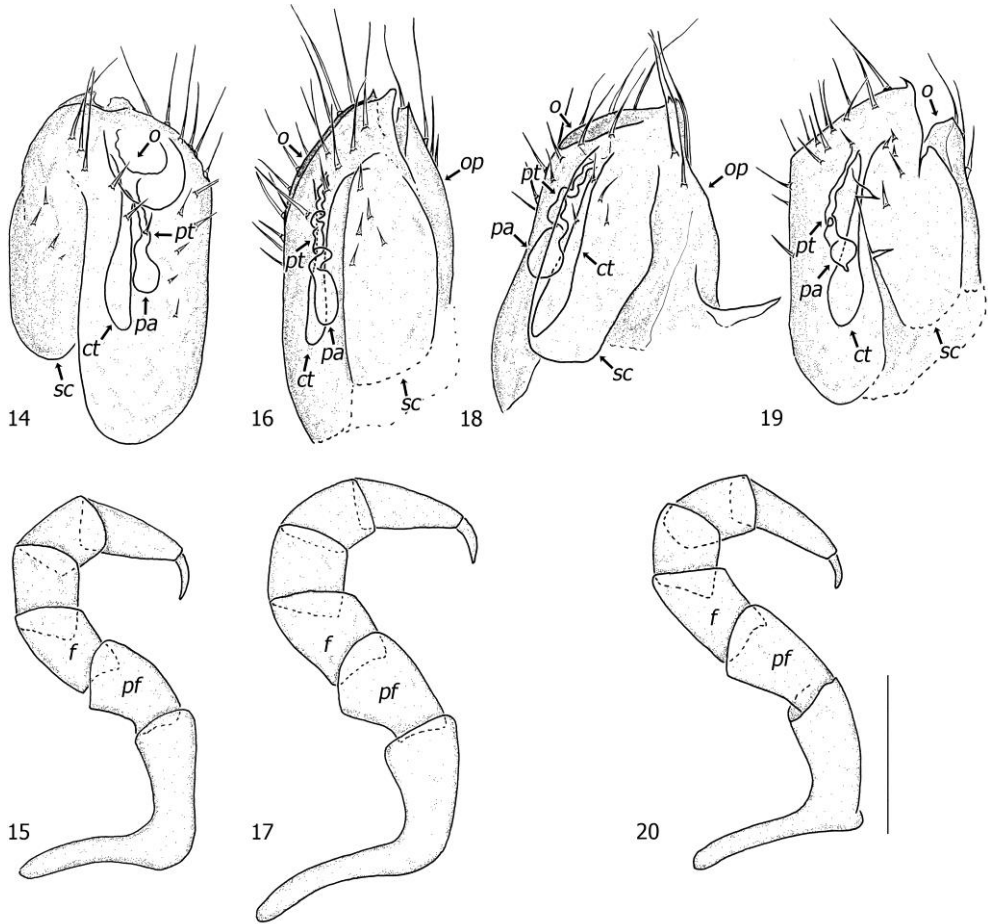
Figures 14–20. *Brachyiulus* vulvae and female 2nd legs. 14–15 = *B. bagnalli* (Pusztaszeri Landscape Protection Area, Baks, Palásti forest, 4 June 1994, leg. Z. Korsós), right vulva and right 2nd leg from caudal view; 16–17 = *B. lusitanus*, (Szombathely, private home, Oct. 1998, leg. Cs. Szinetár), left vulva from caudo-lateral and right 2nd leg from caudal view; 18 = *B.* aff. *pusillus* (Törökbálint, Plantart Horticulture, 14 May 2015, leg. Z. Korsós), left vulva from lateral view; 19–20 = *B. pusillus* ("*Microbrachyiulus litoralis* Verh." Bayern, III.3.127), left vulva from caudo-lateral view, and left 2nd leg from caudal view but flipped horizontally to facilitate comparison. Abbreviations: *ct*: central tube, *f*: femur, *o*: opening, *op*: operculum, *pa*: posterior ampulla, *pf*: prefemur, *pt*: posterior tube, *sc*: side sclerite. Scale bars: 0.2 mm.

Central tube (*ct*) elongated, distally slightly widening, at least 1.5 times longer than posterior tube (*pt*). Posterior tube (*pt*) wavy or just slightly folded (i.e. less folded than in *B. lusitanus*), ending in an elongated posterior ampulla (*pa*).

Distribution. Central European and Balkan species (Kime & Enghoff 2017, Vagalinski & Lazányi 2018). In Hungary it is found mostly in natural habitats (Fig. 21). However, it also occurs in rural habitats as cities, parks. In these latter places it can co-occur with *B. lusitanus*.

Remarks. In Hungary, this species is most similar to *B. lusitanus* at first sight. The opisthomere of *B. bagnalli* does not have a mesoanterior process as in *B. lusitanus* (**map** on Fig. 10), the well-developed basoposterior process is

partly fused with the lateral process (***bpp*** and ***lp*** on Figs 2–3, 8–9). The lateral process is thinner than in *B. lusitanus*.

Both males and females have around 8–10 seate on the anal valves (and 8–10 more on the mesal margin of the anal valves), not only 2–5 (5–

6, respectively) as in *B. lusitanus* and *B. pusillus*.

Since the poor original description of *B. pusillus* there has been a lot of confusion about many *Brachyiulus* species (for discussion see Vagalinski & Lazányi 2018). Although Brolemann (1924) corrected the misunderstanding
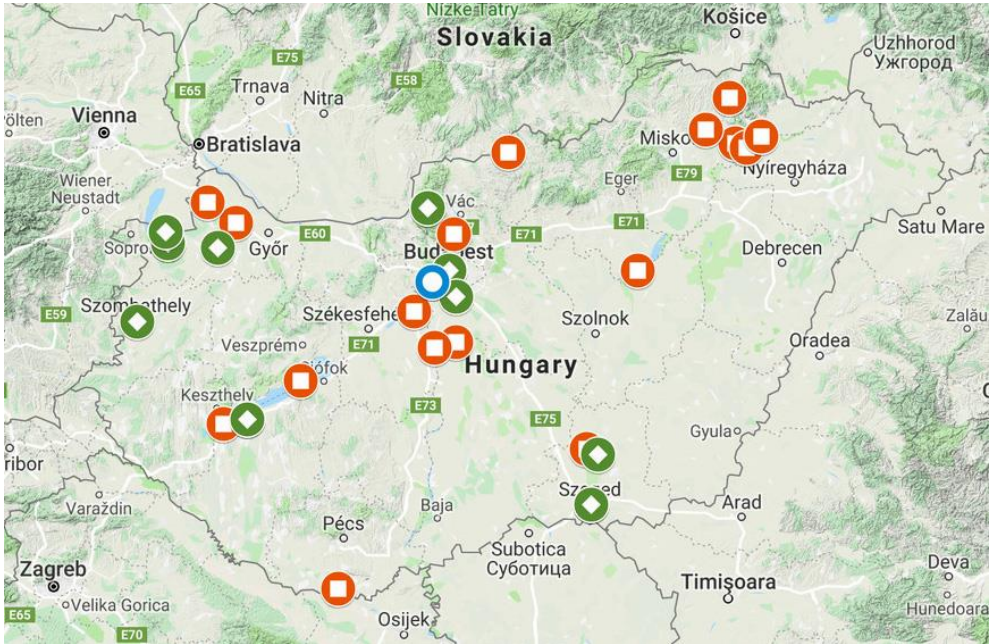

Figure 21. Distribution of three *Brachyiulus* species in Hungary.
Brachyiulus bagnalli ⬜, *Brachyiulus lusitanus* ◆, *Brachyiulus pusillus* ○

around the "Hungarian" *B. pusillus* by establishing a new name, *B. bagnalli*, and Dziadosz (1964) drew attention to this problem, the information did not become widely known. Loksa was still aware only of *B. pusillus* when he found the real *B. bagnalli* in Hungary (Loksa 1956), and therefore he described it as a new subspecies: *B. pusillus* ssp. *Kaszabi* Loksa, 1956 (later synonymised with *B. bagnalli* by Korsós 1994). As a student of Loksa, Sziráki has also referred to the species as *B. pusillus* (Sziráki 1966).

Brachyiulus lusitanus (Verhoeff, 1898)
(Figs 4–5, 10–11, 16–17, 21)

Brachyiulus pusillus, lusitanus (sic!) Verhoeff, 1898: pp. 153–154, fig. 28.

Brachyiulus lusitanus: Sziráki 1966: p. 42.

Brachyiulus lusitanus: Vagalinski & Lazányi 2018: pp. 17–18, figs 6–9.

Brachyiulus bagnalli partim.: Korsós 1998: p. 90.

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Material investigated (all det. Lazányi E.). Budapest, Margitsziget, 30 Apr. 1990, leg. Merkl O.; Budapest, Népliget, 6 Apr. 1990, leg. Róka Sz. & Korsós Z.; Budapest, Zugló, 27 Mar. 1990, leg. Korsós Z.; Budapest, Zugló, 15 Mar. 1989, leg. Korsós Z.; Budapest, Zugló, Vezér street, garden, 19 Mar. 1989, leg. Korsós Z.; Budapest, Zugló, garden, 29 Oct. 1988, leg. Korsós Z.; Budapest, 1096, Ernő street 21., inner garden, leaf litter, 19. Apr. 2019, leg. E. Lazányi; Dunaharaszti, garden, 11 Nov. 1989, leg. Sziráki Gy.; County Pest, Szob, Danube shore, 27 Dec. 1988, leg. Korsós Z.; Mindszent, Nagyhalom, 4 Oct. 1985, leg. Hornung E; Szeged, Lake Fehér, from willow, 28 Apr. 1996, leg. Korsós Z.; Csorna, Lócsi channel, 17 June 1997, leg. Horváth E.; County Somogy, Balatonfenyves, 29 May 1994, leg. British Myriapod Group; Szombathely, private home, Oct. 1998, leg. Szinetár Cs.; Fertő-Hanság, Fertőújlak, Ürgedomb, 10 Oct. 1995, leg. Podlussány A.; Törökbálint, Plantart Kft., 14 May 2015, leg. Z. Korsós; Fertő-Hanság National Park, along the road leading to Nyíres, 18 Apr. 1996, leg. Horváth E.; Budapest, Csillaghegy, 30 Mar. 1990, leg. Szederkényi N.; Budapest, Csillaghegy, 1 Feb. 1989, leg. Szederkényi N.; Budapest, Városmajor, park, 5 Apr. 1990, leg. Korsós Z.; Budapest, Városliget, 8 Apr. 1989, leg. Korsós Z.

Descriptive notes

Males. Length: 10.4–10.5 mm, height: 0.8 mm; number of body rings: 33+2+T; stadium: VIII.Subanal scale somewhat more pointed than in *B. bagnalli*.

Gonopods (Figs 4–5, 10–11): Opisthomere with hardly detectable mesoanterior process (*map* on Fig. 10); lateral process wide, shovel-like, with numerous furrows (*lp*).

Females. Length: 11.6–15.6 mm, height:1–1.1 mm, number of body rings: (32–36)+(1–2)+T, stadium: VIII–IX. Prefemur and femur (*pf* and *f* on Fig. 17, respectively) of mature female's 2nd leg-pair more stout than the respective parts of *B. bagnalli* females (length/width ratio around 1.2–1.5 for prefemur, and around 1.3 for femur).

Anal valve with around 2–4 setae on the valve, and 5–6 on its mesal margin. Prefemur and femur (*pf* and *f* on Fig. 17, respectively) of mature female's 2nd leg-pair more stout than the respective parts of *B. bagnalli* females (length/width ratio around 1.2–1.5 for prefemur, and around 1.3 for femur).

Vulva (Fig. 16): More elongated as by *B. bagnalli* (length/width ratio around 2). Apical opening (*o*) a bit U-shaped, not rounded. Bursa apically with 20–26 setae, *i.e.* considerably more setose than *B. bagnalli*. Side sclerites (*sc*) with 3–5 setae. Central tube (*ct*) elongated, distally slightly widening, just 1.1–1.3times longer than posterior tube (*pt*). Posterior tube (*pt*) considerably folded, ending in an elongated or drop-shaped posterior ampulla (*pa*).

Distribution. Subcosmopolitan species (Kime & Enghoff 2017, Vagalinski & Lazányi 2018). In Hungary it is also found in mostly urban, rural habitats, gardens, parks, horticultures (Fig. 21). However, occasionally it may occur in natural habitats, too.

Remarks. In Hungary this species is most similar to *B. bagnalli* at first sight. The opisthomere of *B. lusitanus* does have a mesoanterior process (*map* on Fig. 10) contrary to *B. bagnalli*, but this process is hard to detect. The other difference is that the opisthomere's lateral process forms a wide, shovel-like lamella (*lp* on Figs 4–5, 10–11) which can be seen even *in situ* (Fig. 11). Basoposterior process (*bpp*) not so prominent. Anal valves are covered with only a few setae (2–5 on the valves and 5–6 on the anal valve's mesal margin of the valves) compared to *B. bagnalli* (8–10 and 8–10, respectively), but this feature does not distinguish the species from *B. pusillus*. Tadler gave beautiful detailed drawings about the species' gonopods and vulva and their fitting during copulation (Tadler 1996: figs. 2, 6, 9, 12 and 15). During copulation the vulva remains in the vulval sac. The short promerite touches the female's second leg-pair, while the considerably longer opisthomerite is deeply introduced to the vulval sac. The solenomerite fits into the opening (central funnel), and the apical process protrudes into the slit between the valvae (Tadler 1996).

The species was mentioned from Hungary in the doctoral thesis of Sziráki (1966), but only as information received from Loksa by personal communication (Sziráki, *pers comm.*). The data presented here are the first reliable Hungarian records of the species.

Brachyiulus pusillus (Leach, 1815)
(Figs 6–7, 12–13, 18–20, 21)

Julus pusillus Leach, 1815: pp. 379–380.

Brachyiulus (Microbrachyiulus) littoralis Verhoeff, 1898: Brolemann 1924: pp. 108–109.

Brachyiulus pusillus: Vagalinski & Lazányi 2018: pp. 18–19.

Material investigated. Pest County, Törökbálint, Plantart Horticulture., 14 May 2015, leg. B. Török, det. Lazányi E. 2019; *Microbrachyiulus litoralis* Verh. Bayern, III.3.127.

Descriptive notes

Males. Length: 8.5–11.9 mm, height: 0.7–1 mm; number of body rings: (29–35)+(1–2)+T; stadium: VIII.Anal valves with 2–3 setae on the valve and 5–6 setae on its mesal margin. Subanal scale somewhat pointed.

Gonopods (Figs 6–7, 12–13): Opisthomere: without mesoanterior process, lateral process vestigial (*lp*), basoposterior process (*bpp*) short, thin, pointed.

Females. There were two adult *B. pusillus* females in the German sample (from Bayern), and three females in the Hungarian sample, but here males of both *B. lusitanus* and *B. pusillus* were found. Based on comparison with both the German (*B. pusillus*) and with other Hungarian material (*B. lusitanus*) we presume that there were *B. pusillus* females in the sample from Törökbálint. However, we give descriptive data separately for females of the two samples because the adult female individuals from Bayern were smaller, just in stadium VII.

Females from Bayern: Length: 10.2–11mm, height: 1–1.1 mm, number of body rings: (29–31)+(2–3)+T, stadium: VII. Anal valves with 2–3 setae on the valve and 5–6 setae on its mesal margin. Prefemur and femur (*pf* and *f* on Fig. 20, respectively) of mature female's 2nd leg-pair elongated (length/width ratio around 1.6–1.62 for prefemur, and around 1.64–1.78 for femur). Vulva (Fig.19): less elongated compared to *B. lusitanus* (length/width ratio 1.63–1.7). Bursa apically with 14–16 setae, side sclerites (*sc*) with 2–5 setae. Central tube (*ct*) elongated, distally more or less widening, around 1.5 times longer than posterior tube (*pt*). Posterior tube (*pt*) moderately folded, ending in a mostly drop shaped posterior ampulla (*pa*), distally pointed.

Females from Törökbálint: Length: 11.5–14 mm, height: 1–1.1 mm, number of body rings: (32–36)+(1–2)+T, stadium: VIII–IX. Vulvae: Anal valves with 2–3 setae on the valve and 5–6 setae on its mesal margin. Vulva (Fig. 18): elongated (length/width ratio varies between 1.85–2.34). Bursa apically with 14–20 setae, side sclerites (*sc*) with 3–5 setae. Central tube (*ct*) elongated, distally slightly widening, around 1.4–1.5 times longer than posterior tube (*pt*). Posterior tube (*pt*) moderately folded, ending in a mostly drop shaped posterior ampulla (*pa*).

Distribution. Central and Western Europe, introduced to other regions (Kime & Enghoff 2017, Vagalinski & Lazányi 2018). In Hungary, the species is known only from horticulture, so its presence seems to be resulting from anthropochory (Fig. 21).

Remarks. The gonopods of this species differ significantly from those of the other two *Brachyiulus* species occurring in Hungary. The opisthomere is thin, elongated, its lateral process (*lp* on Figs 6–7, 12–13) is not lamellar, but vestigial compared to other congeneric species. The basoposterior process (*bpp*) is well-developed, but short, thin.Although the gonopods of *B. pusillus* are obviously different from the Hungarian congeners, female vulvae show intermediate characters between *B. bagnalli* and *B. lusitanus*.

As already mentioned in the discussion above the *B. bagnalli* section, the name "*B. pusillus*" has been erroneously cited many times from Hungary. The true *B. pusillus* is here reported as new to the Hungarian fauna.

CONCLUSIONS

The millipede fauna of Hungary presently consists of 107 species, showing a mixture of European, Mediterranean, Alpine-Atlantic, Carpathian and synanthropic elements. The Carpathian Basin itself, due to its relatively well-defined situation with the surrounding mountain chains, contains a relatively high ratio of endemism in different animal groups (Varga 2018). Earlier, Korsós (1998) counted 10 species and 15 subspecies of millipedes as endemic to Hungary, i.e. 10.2%, 15.3%, respectively (compared to the earlier 96 species number). They were believed to occur mostly in caves and relict (such as glacial) habitats. With the accumulated distribution records from the surrounding countries, however, there remained only 2 species (1.8%), *Heteracrochordum evae* and *Typhloiulus polypodus*, both described by Loksa(1960) from the Bükk Mts, which could be considered as endemic millipedes to the Carpathian Basin. They have probably new occurrences in neighbouring Slovakia as well. Due to the taxonomical uncertainties we do not comment on the subspecific category.

At the same time, however, influences of the surrounding Carpathian Mountains, especially from the north, represented by the Slovakian Tatras, and the east by Transylvania, as well as that of the foothills of the Alps in the west of Hungary are considered as important factors when describing the composition of the millipede fauna. Altogether, 15 species (14%) represent rare mountainous elements which are more common in the forests of the embracing mountain chains of the Carpathians. A considerable number of species are supposed to be brought into the country by the two big rivers, the Danube and the Tisza, from the west and east, respectively. And at last, synanthropic, introduced elements (13 species) also add up to 12% of the total fauna.

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