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The troglophilic population of *Lithobius peregrinus* Latzel, 1880 (Chilopoda, Lithobiomorpha) from Gaura cu Muscă Cave – first record of the species in Romania: morphological variations, asymmetry, teratology and behaviour

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Abstract

The current study presents the first confirmed record of *Lithobius peregrinus* Latzel, 1880, in Romania, based on specimens collected from Gaura cu Muscă Cave (Banat Mountains). Over a three–year period (2022–2024), 39 specimens were sampled, revealing significant morphological variations, asymmetries, and teratological features. Morphological assessments, including variations in ocelli count, coxosternal teeth, plectrotaxy, and gonopod structures, were conducted. Directional asymmetry was analyzed, showing significant right–side bias in antennal segment counts but no clear asymmetry in other measured traits. Behavioural observations highlighted the close water affinity of this centipede, with individuals frequently found near water bodies, possibly contributing to its dispersal ability. The study also discussed the broader cave affinities of *L. peregrinus*, comparing its current geographic distribution to related species and highlighting changes in the cave microclimate that may have impacted its subterranean adaptations. These findings contribute to the understanding of the ecological preferences and morphological diversity of the species, enhancing the knowledge of centipede biodiversity in Romania.

Keywords
Biodiversity, centipedes, developmental/regenerative abnormalities, Lithobiidae, subterranean

Introduction

The centipede *Lithobius peregrinus* (Latzel, 1880) was first reported in the Romanian fauna by Brolemann (1930), based on two male specimens collected by Montandon in Bucharest (2♂♂, Brölemann collection, registration "no 3765, *Lithobius peregrinus* Latz., Roumanie, Bucarest, Montandon") (Zapparoli 1992). However, the uncertainty surrounding this first report on the presence of this species in Romania was clarified when Zapparoli (1992) re-examined the material and reclassified it as *Lithobius nigripalpis* L. Koch, 1867, a fairly common species in the southern part of the country. Moreover, subsequent studies of Matic (1966), Negrea (1965, 1994, 2006) and Negrea and Negrea (1969) did not confirm the presence of *L. peregrinus* in Romania.

According to Zapparoli (1992) the uncertainty associated with the improper identification of this centipede species is mainly due to the fac that only the males are collected, combined with the inherent difficulty of distinguishing the males of both species, especially when they are in their early epimorphic stage. As the description of Brolemann (1930) is not consistent with *L. peregrinus*, consequently, the current paper presents the first record of the centipede *L. peregrinus* in the Romanian fauna.

Based on morphological characteristics, *L. peregrinus* was traditionally classified within the *L. piceus* (L. Koch, 1862) group, alongside *L. viriatus* Sseliwanoff, 1880, and *L. nigripalpis*. However, recent molecular analyses combined with maximum–likelihood trees derived from 18S rRNA and 28S rRNA data (Ganske et al. 2021), have identified a distinct group that includes the species *L. agilis* C.L. Koch, 1847, *L. atkinsoni* Bollman, 1887, *L. erythrocephalus* C. L. Koch, 1847, *L. schuleri* Verhoeff, 1925 and *L. stygius* Latzel, 1880. Within this group, *L. stygius* is a troglobitic species, while *L. erythrocephalus* exhibits cave affinities and is considered troglophilic.

The most comprehensive inventory of Chilopoda from Romanian caves is the catalogue of cavernicolous centipedes (Negrea 1994) which comprises 46 taxa (one scutigeromorph, 27 lithobiomorphs, 13 geophilomorphs and 5 scolopendromorphs, respectively) collected from 240 caves and artificial cavities. The order Lithobiomorpha is the only one with endemic troglobitic species in this list (viz. *Harpolithobius oltenicus* Negrea, 1962, *Lithobius dacicus* Matic, 1958 and *L. decapolitus* Matic, Negrea & Prunescu, 1962, respectively) and an endemic trogloxene subspecies (*H. banaticus banaticus* Matic, 1961) (Negrea 1994). Recently, two more troglobitic species have been described, namely *Cryptops speleorex* Vahtera, Stoev & Akkari, 2020 (ord. Scolopendromorpha) (Vahtera et al. 2020) and *Geophilus zagreus* Baba & Giurginca in Baba et al. 2024 (ord. Geophilomorpha), both from the famous Movile Cave, located in the Dobrogea region (southeast of Romania). Besides the abovementioned centipedes, there are no clear examples of trogloxenic or troglophilic species consistently monitored in caves and present in all sections over an extended period. Typically, the centipedes were just occasionally observed in the vestibular area of caves, with only a few individuals venturing into the intermediate or deeper sections. Such behaviour was observed by Negrea (1994) in the following species, which led to their classification as troglophiles: *Scutigera coleoptrata* (Linnaeus, 1758), *Eupolybothrus transsylvanicus* Latzel, 1882; *Lithobius agilis*; *L. crassipes* L. Koch, 1862; *L. erythrocephalus*; *L. forficatus* (Linnaeus, 1758); *L. piceus* as well as *Cryptops hortensis* (Donovan, 1810) and *C. parisi* Brolemann, 1920. We highlight the case of *L. crassipes*, previously identified as the dominant species in 20–meter drilling in the limestone of SE Dobrogea, suggesting its ability to successfully colonize the limestone fracture networks in the area (Negrea 2004). Ilie (2007) also reported numerous epimorphic stages of *S. coleoptrata* found in traps placed in drillings at a depth of 0.8 meters in the Doman Valley (Banat Mountains), indicating a preference for limestone crevices until reaching later epimorphic stages. The noteworthy cases of *L. erythrocephalus* and *H. anodus dentatus* Matic, 1957, are discussed later in the present study.

The study of the fauna from the Southern Banat Mountains started approximately six decades ago, with the investigation of the Gaura cu Muscă Cave, the Cave from Pepa, the Cave from Dumbrăvița Mică, the Gura Ponicovei Cave, the Cave no. 1 and no. 2 from Gura Ponicovei and the Veterani Cave (Negrea and Negrea 1969). In addition to these caves, 34 other caves from the Banat Mountains were examined and identified as hosting centipedes, but none of them belong to *L. peregrinus* or the morphologically similar species such as *L. piceus* or *L. nigripalpis* (Negrea 1994). Subsequently, Matic (1971) published data on the centipedes in the area that would be flooded after the construction of the Iron Gates I dam, selecting 17 sampling sites and named 27 species (one scutigeromorph, 14 lithobiomorphs, five scolopendromorphs and seven geophilomorphs). He later added another eight species to the list in the monographic book dedicated to the Iron Gates area (Matic 1975). Supplementary information on the Chilopoda from this region was provided by Victoria Ilie, whose work primarily focused on the Reșița – Moldova Nouă synclinorium, especially the Anina Mountains. The study used complementary sampling techniques and included data from the mesovoid shallow substratum (MSS), resulting in a remarkable diversity of Chilopoda, with 44 species recorded from a pool of 1483 collected specimens (Ilie 2003, 2007; Ilie et al. 2003).

Historic data of centipedes collected from caves located in the Danube Gorges (Negrea and Negrea 1969; Negrea 1971) included:

Scutigera coleoptrata and *Lithobius crassipes* (numerous specimens); Gaura cu Muscă Cave; the aphotic sections of the cave on clay and guano.

Lithobius sp., Dumbrăvița Cave; without further comment.

Harpolithobius banaticus Matic, 1961; *H. polonezenus* (Chamberlin,1952) (identified as *H. anodus dentatus*); *Eupolybothrus transsylvanicus*; *Lithobius agilis*; *Geophilus impressus* C.L. Koch, 1847 (first cited as *Geophilus* sp.); *Pachymerium ferrugineum* (C.L. Koch, 1835); *Strigamia acuminata* (Leach, 1816); Gura Ponicovei Cave; most species were found in the aphotic segment of the cave on the floor, on clay, detritus and guano.

Lithobius agilis; Cave no. 1 from Gura Ponicovei; on the floor in the disphotic and aphotic segments of the cave, on humid clay in a mixture of detritus and the excrements of herbivorous animals.

Lithobius burzenlandicus Verhoeff, 1931; Cave no. 2 from Gura Ponicovei; on the floor in the disphotic and aphotic segment on clay, stones and in detritus and the excrements of herbivorous animals.

Scutigera coleoptrata; *Harpolithobius banaticus*; *Lithobius burzenlandicus*; Veterani Cave; in the disphotic zone, on the clay substratum covered by woody debris.

Materials and methods

Sampling site

Gaura cu Muscă Cave (Fig. 1) (44°39'53"N, 21°41'57"E) is an active cave located in the southern end of the Locvei Mountains, a subrange of the Banat Mountains (southwest Romania). It is located on the left bank of the Danube Gorges, with its entrance facing the River Danube, 3 km downstream from Coronini (Onac et al. 2006).

The cave is relatively short (254 m), with the main entrance of the cave leading into a vestibule and followed by a fossil gallery on the right, a 42–meter–long passage with a partially walled entrance. On the left, is a system of galleries fed by a permanent underground emergent stream, flow rate varying throughout the year. As can be seen on the cave map (Fig. 1), the main sampling areas were situated in the left gallery, including the aphotic zone of the Water Gallery, which lies between the entrance and the next chamber, followed afterwards by the Bat Chamber, which in turn is the widest section with the richest dry guano deposits. The Water Gallery can be bypassed via the more accessible Bat Gallery. This section is rich in clay and occasionally contains small patches of guano and mustelid feces. The deepest part of the Water Gallery, along with the base of the chimney, which is often covered in guano, also provided valuable sampling locations. For even further simplification in text, the main sections of the cave were also abbreviated as follows: the entrance of Water Gallery located after the curve in the aphotic area near the Bat Chamber is marked as W.G. ent.; the deep parts of Water Gallery, situated after the Bat Gallery, is marked as W.G. deep; Bat Chamber and Bat Gallery are referred to as B.Ch. and B.G. respectively.

The Gaura cu Muscă Cave is located in the Iron Gates National Park and is one of the prominent subterranean touristic points in the Sf. Elena Karstic Plateau, alongside the U Lomu Cave and the Potoc Cave. However, previous field campaigns failed to locate the latter two caves, which is most likely due to blocked entrances, as Botoșăneanu et al. (1967) already pointed out the precarious condition of the caves.

The material was collected from the Potoc Valley near the Sf. Elena locality (44°40'24.12"N, 21°43'24.08"E) and from the same valley alongside the Danube River (44°39'40.42"N, 21°44'16.38"E). Additional sampling sites were set in the Danube Gorges or near Gaura cu Muscă Cave, such as Gaura Haiducească

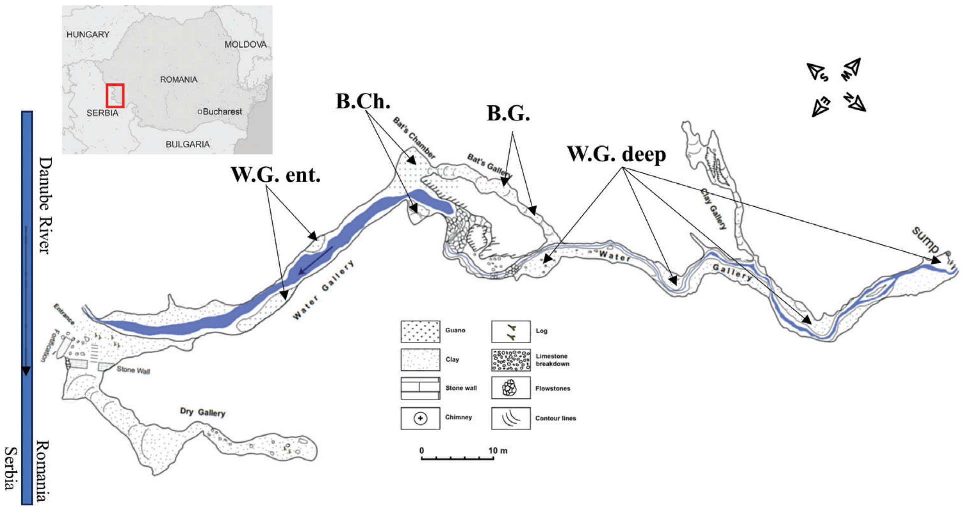

Figure 1. Map of the Gaura cu Muscă Cave with the main sampling locations within the cave (after Onac et al. 2015 modified). W.G. ent. (entrance of the Water Gallery); B.Ch. (Bat Chamber); Bat Gallery (B.G.); Water Gallery, deeper section of the cave (W.G. deep).

Cave (44°43'52.92"N, 21°44'21.62"E), Velebny Zlabek Cave (44°39'55.54"N, 21°43'57"E), Ponicovei Valley, Gura Ponicovei Cave and the artificial Ponicova Tunnel. Recent data from other natural and artificial caves in the Banat Mountains are also presented in the current study.

The Banat Mountains are situated in the southwest of Romania and represent a subunit of the Carpathian Mountains. The area is characterized by a pronounced sub–Mediterranean climate with oceanic influences, rendering the region more prone to aridity and drought compared to other parts of the country (Halbac–Cotoara–Zamfir 2012). This climate pattern is particularly evident in the Moldova Veche area, where Gaura cu Muscă cave is located. This region also records the highest average temperatures in Banat Mountains (i.e. 12 °C during 1986–2012, see Dunca 2018) and an average annual precipitation rate of 750 mm, with the highest rainfall occurring in the summer months (Onac et al. 2015). The limestone formations near the Danube are covered by deciduous woodlands, dominated by Turkey oak (*Quercus cerris* L.). These forested ecosystems are further enriched with Hungarian oak (*Quercus frainetto* Ten.), Downy oak (*Quercus pubescens* Willd.), and Silver lime (*Tilia tomentosa* Moench) (Schneider–Binder 2014).

Sampled material

Over a three–year period (2022–2024), 39 specimens of *L. peregrinus* were sampled from Gaura cu Muscă Cave, with the species being found during each of the five visits. The assessment of the precise postembryonic stage of *L. peregrinus* was challenging due to the lack of specific previous studies on the biology of this species. However, this assessment was successfully done based on the works of

Barber and Eason (1986), Andersson (1976), as well as the updated developmental terminology of Stojanović et al. (2023). Out of the 39 collected specimens, 37 were *matures* like. Additionally, one specimen was an *immaturus* and another was in stage *anamorph 3*, with just 10 pairs of developed legs.

The samples collected (leg.) by Șt. Baba are further referred in text as ȘtB, RO for Robert Opran, RP for Rodica Plăiașu and AM for Andreea Mîrleneanu. We also collected and identified 74 specimens through singling from other caves in the Banat Mountains and from the edaphic fauna in the gorges area.

The specimens were stored in the Centipede Collection of the "Emil Racoviță" Institute of Speleology (ERIS) from Bucharest, Romania.

The specimens of *L. peregrinus* (Fig. 2A) are listed below, with their corresponding inventory collection numbers (i.e. CH1946 to CH1984) used throughout the text for referencing specific specimens:

Romania • 2 ♀♀ (ERIS CH1952, CH1955); 28 Sep. 2022; ȘtB leg. and det.; W.G. ent., on the walls of the aphotic area, just before the B.Ch. • 1 ♂ (ERIS CH1967); 28 Sep. 2022; ȘtB leg. and det.; B.Ch., on the wall section partially covered with guano • 1 ♂ (ERIS CH1971); 28 Sep. 2022; RO leg.; ȘtB det.; B.G., on the floor covered with clay • 1 ♂ (ERIS CH1946); 28 Sep. 2022; RO leg.; ȘtB det.; W.G. deep, on sand • 3 ♀♀ (ERIS CH1968, CH1961, CH1948); 5 Feb. 2023; ȘtB leg and det.; B.Ch., on an accumulation of guano situated on the cave floor • 1 ♂ (ERIS CH1977); 5 Feb. 2023; ȘtB leg. and det.; W.G. deep, on the wall of the last section • 1 ♂, 1 ♀ (ERIS CH1966, CH1981); 6 May 2023; ȘtB leg.; W.G. ent., on a stone surrounded by water and on the humid wall • 2 ♂♂ (ERIS CH1950, CH1958); 6 May 2023; ȘtB leg. and det.; B.Ch., on the wall • 1 ♀ (ERIS CH1959); 6 May 2023; ȘtB leg. and det.; B.G., on the floor near fresh guano • 3 ♀♀ (ERIS CH1960, CH1974, CH1982); 6 May 2023; ȘtB leg. and det.; W.G. deep, on the walls and on the sand very close to the water • 1 ♂ (ERIS CH1965); 27 Feb. 2024; ȘtB leg. and det.; W.G. ent., on the wall • 1 ♂, 1 ♀ (ERIS CH1975, CH1969); 27 Feb. 2024; ȘtB leg. and det.; B.Ch., on a pile of guano accumulated on the floor • 2 ♂♂, 1 ♀ (ERIS CH1953, CH1954, CH1963); 27 Feb. 2024; ȘtB leg. and det.; B.G., on the ceiling and on the floor close to guano • 1 ♂, 3 ♀♀ (ERIS CH1957, CH1947, CH1964, CH1972); 27 Feb. 2024; ȘtB and RO leg.; ȘtB det.; W.G. deep, on the walls, close to the chimney • 1 ♂, 1 anamorph (ERIS CH1951, CH1983); 17 Jul. 2024; ȘtB leg. and det.; B.Ch., on the humid walls • 1 ♂, 3 ♀♀; (ERIS CH1979, CH1956, CH1970, CH1980); 17 Jul. 2024; ȘtB leg. and det.; B.G., on the floor; • 3 ♂♂, 3 ♀♀ (ERIS CH1962, CH1973, CH1984, CH1949, CH1976, CH1978); 17 Jul. 2024; ȘtB, RP, RO, and AM leg.; ȘtB det; partially submerged stones, sand, and walls.

The material was collected by hand, with tweezers, and fixed in 70% ethanol. A Zeiss Stemi 508 stereomicroscope with an Axiocam 208 camera was used to capture images of the main morphological characteristics and to make the taxonomic drawings. Additional images were captured with the Optika SZM2 stereomicroscope paired with the Canon EOS 2000D, which was also used for photographing inside the cave. Most image were performed with ZEN 2011 (Blue Edition) software, while additional image processing was performed using Adobe Photoshop CS6.

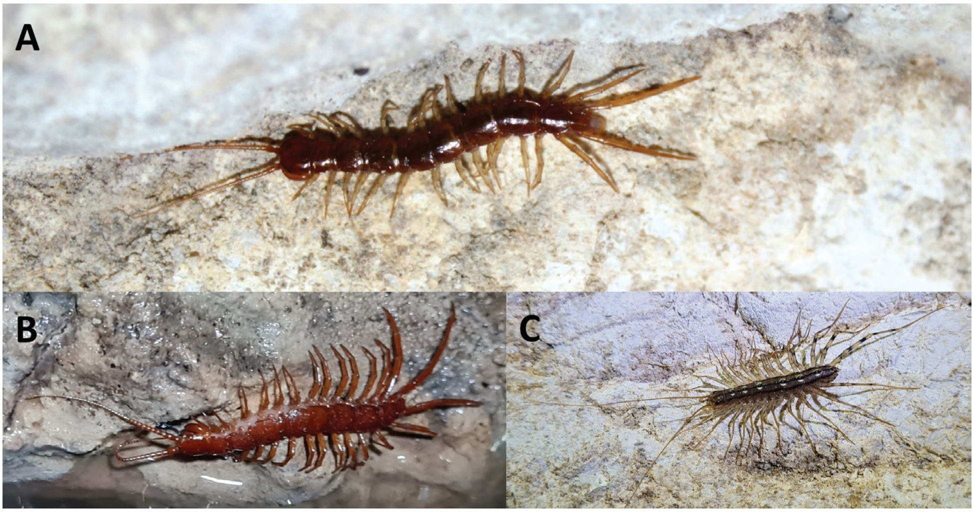

Figure 2. A *Lithobius peregrinus* Latzel, 1880 habitus, dorsal view, photographed in situ in Gaura cu Muscă Cave – Bat Chamber, left wall (February 27, 2024) **B** *Eupolybothrus transsylvanicus* Latzel, 1882 habitus dorsal view (May 6, 2023) **C** *Scutigera coleoptrata* Linnaeus 1758, habitus dorsal view (February 27, 2024). Photocredit: Șt. Baba.

Morphological measurements were performed using ImageJ, a Java–based software specifically designed for image processing and quantitative analysis. Each measurement was performed three times, as with the counting of the various morphologic structures. The measurements of the leg articles were obtained from specimens presumed to belong to the latest epimorphic stage. The terminology for the external centipede morphology follows Bonato et al. (2010). All photographs and subsequent drawings were made by Șt. Baba and the ink drawings by A. Giurginca.

Abbreviations for centipede morphology, particularly plectrotaxy: **LP** – leg pair (numbered between LP 1 and LP 15); **D** – dorsal; **V** – ventral; **a** – anterior; **m** – median; **p** – posterior; **c** – coxa; **t** – trochanter; **P** – prefemur; **F** – femur; **T** – tibia.

The assessment of directional asymmetry was performed using MiniTab Statistic Software, LLC. Directional asymmetry (hereafter DA) refers to consistent differences in measurements between the right and left sides of an individual, typically indicating potential biases that occur in normal rates of development or function. To evaluate the overall trend of asymmetries, the mean differences between left and right side (hereafter L–R) values of various characters were calculated. For each trait dataset, the mean DA was assessed, based on the standard deviations of these differences and paired one–sample t–tests. This analysis method was largely derived from Palmer and Strobeck (1986).

The air temperature and relative humidity in the cave were recorded using the Tinytag Plus (TGP–4500) temperature and relative humidity data logger, which was enclosed in a waterproof housing. The logger was programmed with a recording interval of one hour and operated continuously from March 22, 2020, to January 22, 2021.

Samples from the Emil Racoviță Institute of Speleology collection

Following Negrea (2006) on the potential misidentification of *L. piceus* in southern Romania, and the fact that *L. peregrinus* was traditionally classified within this morphologic group, we conducted a comprehensive examination of all specimens previously identified as *L. piceus* and *L. nigripalpis* within the centipede collection of the ERIS from Bucharest. The ERIS centipede collection contains material identified by Șt. Negrea and V. Ilie. Although our findings support Șt. Negrea's suspicion that some specimens were mislabeled or misidentified, none of the examined material belonged to *L. peregrinus*.

The following material was verified from Ștefan Negrea collection (samples from Romania only):

Samples reviewed and confirmed as *L. piceus* (on the original label: *L. piceus gracilitarsis*) • 2 ♂♂ (ERIS SN212); Cernei Mountains, Prisaca de la Șchiopu 1 Cave; 25 Jul. 1958; I. Tabacaru leg.; Șt. Negrea det. • 1 ♂ (ERIS SN213); Vârghișului Gorges, Cave No. 60; 13 Mar. 1959; T. Orghidan leg.; Șt. Negrea det.

Samples reviewed and confirmed as *L. nigripalpis* (on the original label: *L. piceus bulgaricus*) • 2 ♂♂, 1 ♀ (ERIS SN320); Gura Dobrogei Cave; 24 Nov. 1958; L. Botoșeneanu leg.; Șt. Negrea det.

Samples reassigned to *L.* cf. *nigripalpis*; ȘtB det. (on the original label: *L. piceus piceus*): • 1 anamorph (ERIS SN148); Limanu Cave; 28 Mar. 1961; M. Dumitrescu and T. Orghidan leg.; Șt. Negrea det. • 2 anamorphs (ERIS SN149); Limanu Cave; 20 Oct. 1961; M. Dumitrescu leg.; Șt. Negrea det.; • 1 ♂ (ERIS SN150); Limanu Cave; 21 Oct. 1961; M. Georgescu leg.; Șt. Negrea det.

The following material was verified from Victoria Ilie collection (samples from Romania only):

Samples reviewed and most of them confirmed as *L. piceus* • 1 ♂ (ERIS VI898); Vârghiș Valley, Cave 1200/12 (cave index no.); 15 May 2002; V. Ilie leg. and det.; entrance of the cave • 1 ♀ (ERIS VI897); Peștera Mare de la Merești Cave; 17 May 2002; A. Giurginca leg.; V. Ilie det.; entrance of the cave • 1 ♀ (ERIS VI889); Sighiștel Valley; 7 Jul. 2003; V. Ilie leg. and det.; edaphic • 2 ♀♀ (ERIS VI890, VI891); Sighiștel Valley; 9 Jul. 2003; V. Ilie leg. and det.; edaphic • 1 ♂ (ERIS VI894); Vârghiș Valley; 17 Sep. 2003; V. Ilie leg. and det.; edaphic • 1 ♂ (ERIS VI900); Carașului Valley; 9 Oct. 2003; V. Ilie leg. and det.; leaf litter; damaged material, unable to confirm.

Most samples reviewed and confirmed as *L. piceus* (on the original label: *L. piceus gracilitarsis*) • 1 ♀ (ERIS VI899); Sighiștel Valley; 7 Sep. 2000; V. Boitan leg. and det.; edaphic • 1 ♂ (ERIS VI940); Vârghiș Valley; 15 Sep. 2004; V. Ilie leg. and det.; limestone pavement, Winkler 1; label rectified on the verso to *Lithobius* sp.; 7 specimens; reassigned as *L. burzenlandicus* (5 ♀♀, 2 ♂♂); ȘtB det. • 2 ♂♂, 1 ♀ (ERIS VI895, VI896); Vârghiș Valley; 15 Sep. 2004; V. Ilie leg. and det.; edaphic; corrected as *L. piceus* (1 ♂, 1 *agenitalis*); ȘtB det. • 1 ♂, 1 ♀ (ERIS VI893); Vârghiș Valley; 17 Sep. 2004; V. Ilie leg. and det.; edaphic.

Most of the specimens reviewed and confirmed as *L. nigripalpis* • 1 ♂ (ERIS VI873); Grădinari Forest [now part of the Comana Forest, Giurgiu]; 19–21 Oct. 1976; I. Tabacaru leg.; V. Ilie det. • 1 ♀ (ERIS VI870); Dolj County, Bratovoești; 15 Mar.–6 May 2001; A. Babalean leg.; V. Ilie det. • 2 ♀♀ (ERIS VI387); Piscul Sadovei; 9 Aug. 2001; A. Babalean leg.; V. Ilie det.; • 1 ♂ (ERIS VI871) Dolj County, Piscul Sadovei; 17 Jun.–9 Aug. 2001; A. Babalean leg.; V. Ilie det. • 1 *imm.* (ERIS VI875); Dolj County, Bucovăț; 29 Mar.–5 May 2001; A. Babalean leg.; V. Ilie det.; • 1 *imm.* (ERIS VI875); Dolj County, Bucovăț; 20–26 May 2002; A. Babalean leg.; V. Ilie det. • 1 ♂ (ERIS VI869); Vârghiș Valley; 15 Sep. 2004; V. Ilie leg. and det.; limestone pavement; reassigned as *L. burzenlandicus*; ȘtB det. • 1 ♂ (ERIS VI375); Bucharest, National Stadium Park; 25 Jun. 2005; A. Giurginca leg.; V. Ilie det.

Sample originally labeled as *L. piceus* group, reassigned to *L. erythrocephalus* • 1 ♂; Banat Mountains, 6 Aug. 2005; V. Ilie leg. and det.; decomposing wooden logs.

Results and discussions

Below, we present new data on Chilopoda from Banat Mountains caves, along with edaphic samples collected from the Danube Gorges, as part of the collective effort to pursuit the geographic distribution of the centipede *L. peregrinus* has additional locations to be included in its distribution in Romania (those situated in the Danube Gorges are marked with "*"):

Harpolithobius dolffusi Verhoeff, 1901; • 1 ♂; left slope of Carașului Gorges, Peștera cu Prăbușiri Cave; 8 Jul. 2023; A. Nae leg.; ȘtB det.; *H. banaticus* • 1 ♀; same data • 1 ♀; *Lithobius forficatus*; same data.

Eupolybothrus tridentinus Fanzago, 1874 • 1 ♂; Carașului Gorges, Ilma Tunnel; 45°02'12"N, 21°51'24"E; 22 Sep. 2023; ȘtB and RP leg.; ȘtB det.; intermediate part of the cave, vegetal detritus • 1 anamorph; *Eupolybothrus* sp.; same data.

Lithobius burzenlandicus • 2 ♂♂, 1 ♀; Aninei Mountains, Sfânta Elena Cave; 45°01'33"N, 21°46'30"E; 4 Jul. 2023; ȘtB, RP, and AM leg.; ȘtB det.; entrance of the cave, loosened soil and vegetal detritus *L. forficatus* • 1 ♀; same data; *L. mutabilis* • 2 ♀♀; same data *L. microps* • 1 ♂; same data; *Lithobius* sp. • 1 anamorph; same data.

Harpolithobius banaticus • 1 ♀; Dognecei Mountains, Melia Tunnel; 45°21'10"N, 21°46'56"E; 30 Jun. 2023; ȘtB leg. and det.; intermediate part of the cave, decomposing wood.

Harpolithobius polonezenus (Chamberlin, 1952) • 1 ♀; Almăjului Mountains, *Gura Ponicovei Cave; 44°35'44"N, 22°15'21"E; 2 Jun. 2022; ȘtB and RP leg.; ȘtB det.; Concrețiunilor Gallery, on clay and guano; *Lithobius erythrocephalus* • 1 ♂; same data as for preceding; *L. forficatus* • 1 anamorph; 2 Jun. 2022; ȘtB and RP leg.; ȘtB det.; entrance of the cave; *L. erythrocephalus* • 1 ♀, 2 anamorphs; 13 Apr. 2022; ȘtB and RP leg.; ȘtB det.; Concrețiunilor Gallery, on clay and guano; *Eupolybothrus transsylvanicus* • 2 anamorphs; same data; *L. erythrocephalus* • 4 ♀♀, 5 ♂♂, 2 anamorphs; same data; *L. erythrocephalus* • 2 ♀♀, 3 ♂♂, 7 anamorphs; 13 Apr. 2022; ȘtB, RP, RO, and AM leg.; ȘtB det.; wood debris at the entrance of the Main Gallery facing the Danube River; *Geophilus* cf. *impressus* • 1 ♀; 13 Aug. 2024; ȘtB leg.; ȘtB det.; 50 m from the entrance in the disphotic zone, under a log.

Lithobius microps • 1 ♂; Almăjului Mountains, *Ponicova Tunnel; 44°35'28"N, 22°15'20"E; 4 Jul. 2023; ȘtB, RO, and RP leg.; ȘtB det.; entrance of the tunnel, mix of loosened soil and vegetal detritus; *L. muticus* C.L. Koch, 1847 • 1 ♂, 1 anamorph; same data as for preceding; *Cryptops croaticus* Verhoeff, 1931 • 1 specimen; same data; *Henia illyrica* Meinert, 1870 • 2 ♀♀; same data.

Lithobius muticus • 1 ♀; Dognecei Mountains, Aurora Tunnel; 45°16'13"N, 21°43'40"E; 4 Jul. 2023; ȘtB leg. and det.; the entrance of the tunnel, under a stone.

Lithobius erythrocephalus • 1 ♂; Locvei Mountains, Gaura Haiducească Cave; 44°43'53"N, 21°44'23"E; 4 Jul. 2023; ȘtB, RO, and RP leg.; ȘtB det.; aphotic segment, 100 m from the insurgency entrance, under stones and in vegetal detritus; *Harpolithobius dolffusi* • 1 ♀; same data; *Lithobius forficatus* • 1 anamorph; same data.

Eupolybothrus transsylvanicus • 2 ♀♀; Almăjului Mountains, Ponicova Valley; 19 Jul. 2024; ȘtB leg.; ȘtB det.; leaf litter; *Lithobius aeruginosus* L. Koch, 1862; • 1 ♂; ibidem; 19 Jul. 2024; ȘtB leg.; ȘtB det.; superficial soil under the leaf litter; *L. burzenlandicus* • 1 ♂; ibidem; 13 Aug. 2024; ȘtB leg.; ȘtB det.; leaf litter; *L. parietum* • 1 ♂, 1 ♀; ibidem; 19 Jul. 2024; ȘtB leg.; ȘtB det.; under a stone; *Cryptops croaticus* • 1 specimen; ibidem; 19 Jul. 2024; AM leg.; ȘtB det.; under a stone; *Clinopodes flavidus* C.L. Koch, 1847 • 2 ♀♀; ibidem; 19 Jul. 2024; RO and RP leg.; ȘtB det.

Eupolybothrus transsylvanicus • 2 ♀♀; Locvei Mountains, Potoc Valley near Sf. Elena village, 19 Jul. 2024; RP, RO, and AM leg.; ȘtB det.; humid leaf litter; *Lithobius forficatus* • 1 ♂; ibidem, 19 Jul. 2024; RP, RO, and AM leg.; ȘtB det.; under a stone near the spring; *L. muticus* • 1 ♀; ibidem; 19 Jul. 2024; RP, RO, and AM leg.; ȘtB det.; leaf litter; *Cryptops croaticus* • 1 specimen; ibidem; 19 Jul. 2024; ȘtB leg.; ȘtB det.; under a stone; *C. parisi* • 1 specimen; ibidem; 19 Jul. 2024; ȘtB leg.; ȘtB det.; leaf litter.

Eupolybothrus transsylvanicus; • 1 ♂; Locvei Mountains, Potoc Valley near the Danube Gorges; 19 Jul. 2024; ȘtB, RP, and AM leg.; ȘtB det.; humid leaf litter close to the river; *Lithobius agilis* • 1 ♀; ibidem; 19 Jul. 2024; ȘtB, RP, and AM leg.; ȘtB det.; leaf litter; *Clinopodes flavidus* • 2 ♀♀; ibidem; 19 Jul. 2024; ȘtB, RP, and AM leg.; ȘtB det.; under a stone;

We did not find *L. peregrinus* during these field trips, but several noteworthy observations were made. We recorded 56 specimens of 14 centipede species in both natural and artificial caves of the Banat Mountains, and another 18 specimens belonging to 11 Chilopoda species from soil samples in the Danube Gorges. All species have already been recorded from the area, as mentioned in previous studies. The rarest species, *E. tridentinus*, was critically assessed by Șt. Negrea (2010), who reported its occurrence at only seven Romanian locations. We have documented the eighth location, for the first time in an artificial cavity. The only other known subterranean location in these mountains where the species was previously recorded was Peștera Albă from the Comarnic Valley. *Harpolithobius* specimens from Gura Ponicovei Cave fit exactly into the *H. anodus dentatus* description by Matic (1957), which according to Zapparoli (1999) is a junior synonym of *H. polonezenus*, whose taxonomic status is subject to considerable uncertainty and requires further investigation for a precise assessment of synonymy (Negrea 2004). In the case of *L. erythrocephalus*, our perennial observations show that the species has a great potential to colonize caves, including in Gura Ponicovei Cave.

This species has also been recorded in the deeper sections of caves in various European countries, such as Dobšiná Cave in Slovakia (Papáč et al. 2020). In Croatia, this species is considered troglophilic (Ozimec 2002). Furthermore, morphological intraspecific variation among cave–dwellers were observed in certain regions of Slovenia, suggesting that some subterranean subpopulations may have gradually become isolated from external populations (Kos et al. 2023).

Coexisting species in Gaura cu Muscă Cave

Among other invertebrates Negrea and Negrea (1969) cited two other centipedes collected in the Gaura cu Muscă Cave, namely *L. crassipes* and *S. coleoptrata*. In our opinion the cave served as a refuge for the *S. coleoptrata* (Fig. 2C) during the winter months, with the Bat Gallery being particularly favored by the warm air currents. In February 2024, 43 specimens were counted along the cave, from the vestibule to the deeper areas. In contrast, only up to seven specimens were observed during autumn and spring, with no sightings recorded during the summer. We can also add records of two males of *E. transsylvanicus* (Fig. 2B).

We consider it noteworthy to mention also the bat species that inhabit the cave throughout the year, namely *Rhinolophus ferrumequinum* (Schreber, 1774), *Rhinolophus euryale* Blasius, 1853, *Myotis capaccinii* Bonaparte, 1837 and *Miniopterus schreibersii* (Kuhl, 1817) (Nagy and Postawa 2010). These bats produce important guano deposits, that serve as the primary source of organic matter for several groups of invertebrates at the base of the cave's food web, especially in the Bat Chamber, the Bat Gallery, and on the wall below beneath the chimney, that marks the end of the accessible section of the cave.

Recently sampled biological material from the cave

The aquatic Arthropoda fauna (collected using quantitative methods) consisted mainly of amphipods, dominated by the epigean *Gammarus balcanicus* Schäferna, 1923 and *Niphargus illidzensis pannonicus* S. Karaman, 1950; O. Pacioglu, ȘtB leg.; O. Pacioglu det.; together with several larvae of the dragonfly *Cordulegaster bidentata* Selys, 1843; O. Pacioglu, RO, ȘtB leg.; O. Pacioglu det.

The terrestrial Arthropoda fauna included the following: Order Araneae, *Pholcus phalangioides* (Füssli, 1775) • 1 ♀; *Lepthyphantes leprosus* (Ohlert, 1865) • 1 ♀; *Metellina merianae* (Scopoli, 1763) • 1 ♀; *Porrhomma convexum* (Westring, 1851) • 1 ♀; 17 Jul. 2024; ȘtB leg.; A. Nae det.; the walls of the cave; Order Opiliones, *Paranemastoma ancae* Avram, 1973 • 2 specimens; 17 Jul. 2024; RP leg. and det.; the entrance of the cave, on the walls; Order Isopoda, Suborder Oniscidea, *Ligidium germanicum* Verhoeff, 1901 • 1 ♂, 1 ♀; *Cylisticus convexus* (De Geer, 1778) • 1 ♀; *Porcellionides pruinosus* (Brandt, 1833) • 1 ♀; 27 Feb. 2024; RO and ȘtB leg.; A. Giurginca det.; Bat Chamber, on the floor covered by clay and guano; *Mesoniscus graniger* (Frivaldsky, 1865) • 2 ♀♀; 18 Jul. 2024; ȘtB leg.; A. Giurginca det.; W.G. deep, guano; Class Diplopoda, Order Julida, *Nopoiulus kochii* (Gervais, 1847) • 1 ♂, 1 ♀; 27 Feb. 2024; ȘtB leg.; A. Giurginca det.; humid stones partially covered with clay and guano and surrounded by water.

The photic section of the entrance gallery was scattered with numerous Odonata exuviae on the walls during our visit to the cave on July 17, 2024. Also, staphylinids were always observed on the guano deposits in the B.Ch.

Morphologic variability and left–right asymmetry

As previously mentioned by Barber and Eason (1986), there is an insufficient knowledge regarding the intraspecific variability of *L. peregrinus*. The same authors have made a thorough description of the immature stages of this species, emphasizing the frequent occurrence of L–R variations in certain meristic characters, such as the denticles on the forcipular coxosternite and the coxal pores. Our aim was to expand the knowledge gap on this variability, by referring to traits that have received less attention so far and by investigating certain aspects of the L–R asymmetry and teratology.

Measurements of specimens' length, the length/width ratio of the head capsule, the degree of development of genital structures along with other meristic characteristics, suggest that many of the previously analyzed specimens may not have reached the later epimorphic stages and the maximum new higher limit for some characters is given.

Size. Adults: 19–25.9 mm, tergite 3 (*ca* 2.8 mm) and tergite 10 (*ca* 3.2 mm), widest.

Head. Cephalic plate as wide as tergite 3, 2.4–3.1 mm wide and 2.2–2.7 mm long. Cephalic capsule is mostly smooth, with rare puncta and visible transverse suture on the anterior part of the dorsal side. In most specimens, broader than long, only with a few exceptions, where it was as long as wide. It is noteworthy that this ratio tends to decrease in smaller individuals, while in larger ones, it generally varied from 1.03 to 1.14.

Antennae. They typically reached the midpoint of the fifth tergite, although at full extension they may extend beyond and adjoin the sixth tergite, and comprised 39 to 53 articles, as noted by Zalesskaja (1978), which provided an upper limit of 54. The last article is at least twice as long as the previous one; all articles were covered with relatively dense setae.

Asymmetry. Only three specimens had the same number of antennomeres on both sides of the head, with differences in the rest ranging 1–7 articles. Seven specimens had damaged antennae and were excluded from further DA assessment. Mean Asymmetry was –1.93 (i.e. rightward bias on average), the standard deviation of asymmetry was 3.64 and significant ($p < 0.01$, t test), suggesting consistent rightward bias. A mean absolute difference of ~3.2, indicates considerable side-to-side variation in addition to the net directional difference. Even when analyzing specimens with scarred antennae, the right side exhibited higher average number of antennal articles compared to the left side.

Ocelli. In most specimens, the number of ocelli ranged from 17 to 23, maximum 26 (Fig. 3A), arranged in four–five rows, clearly delimited dorsally by the ocellar branch. Tömösváry's organ was consistently about three times smaller in diameter then the largest ocelli and 0.15–0.2 times the length of the cephalic plate across individuals. We believe that it is inaccurate to describe its size as comparable to a small ocellus, as suggested in other descriptions, as the smallest ocelli can be significantly reduced. One specimen (CH1957) had an ectopic ocellus located above the superior row of ocelli and beyond the antennocellar suture (Fig. 3B).

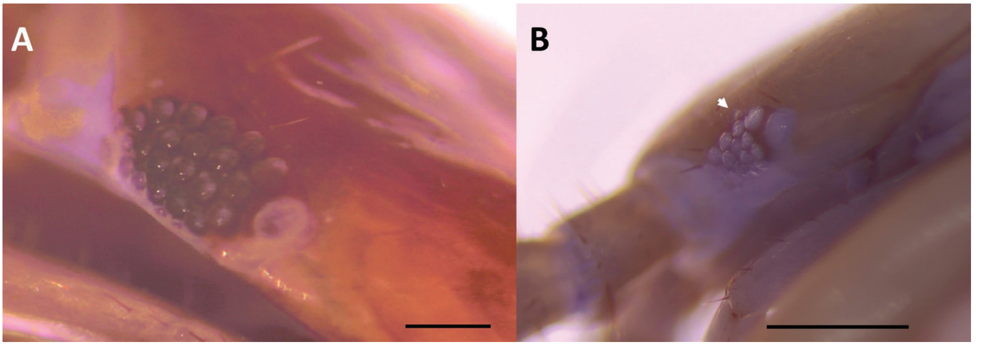

Figure 3. *Lithobius peregrinus* Latzel, 1880. Left ocelli (lateral view) of **A** CH1982 **B** CH1957; arrow indicates the ectopic ocelli. Scale bars: 0.2 mm (**A**); 0.5 mm (**B**).

Asymmetry. A large female with a maximum of 26 ocelli on one side and 25 on the other. Twenty–one specimens showed a different number of ocelli on each side, with a maximum difference of two ocelli between the sides. With a mean asymmetry of 0.11 and standard deviation of 1.15, the difference was not significant ($p > 0.05$, t student). There is no significant L–R bias despite a slight asymmetry with, on average, 0.8 ocelli difference between the sides for any given specimen.

Forcipular coxosternite and its anterior margin. The anterior margin of forcipular coxosternite was slightly rounded/ellipsoid, the teeth were subconical, only the superior half or even starting from the base is dark brownish and strongly sclerotised (Fig. 4A, B). The number, placement, size and spacing of the teeth were irregular features, with the number of teeth typically ranging from 5 to 8 in epimorphic stages, although reaching up to 10 on one side (Fig. 5A, B), which was only observed in the presence of ectopic, possibly abnormal teeth. The porodont was positioned marginally before the development of the 4th tooth. After the development of additional teeth, it usually occupied an intermediary position between the last two lateral teeth (or penultimate two in rare occasions), regardless of the number or size of the teeth. There was no distinct diastema present between the teeth on either side of the porodont, a feature also noted by Barber and Eason (1986), previously considered a reliable taxonomic feature. The spacing between the teeth varied randomly, and in some cases, the teeth were so close together that they appeared almost fused (observed in five specimens).

Besides the presence of subconical normal teeth, there were reduced teeth (sometimes extremely reduced) and blunt teeth with usually marginal position (observed in six specimens). Although it is common for the marginal or medial denticle to be smaller, 12 specimens had one or two reduced teeth in the middle part, while only 10 specimens had relatively uniform denticles. Two specimens had smaller ectopic teeth, the tips of which usually did not reach the base of the first row of teeth. One specimen had six teeth on the right side and eight on the left side (Fig. 5C, D), with the ectopic tooth positioned below the third and fourth median teeth. Another specimen had

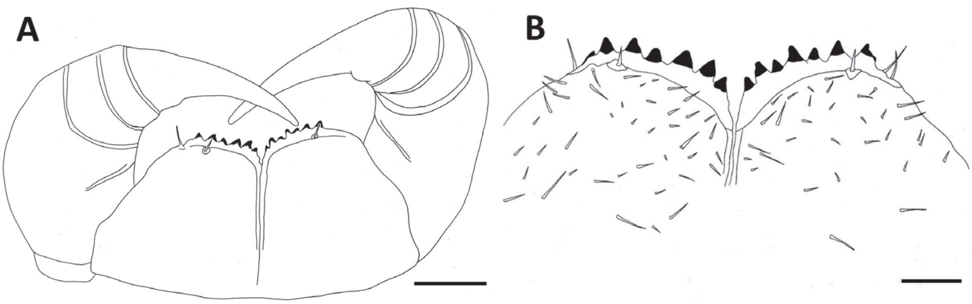

Figure 4. *Lithobius peregrinus* Latzel, 1880 **A** forcipular segment of CH1977, ventral view **B** detail of the anterior margin of the forcipular coxosternum of the same specimen. Scale bars: 0.5 mm (**A**); 0.2 mm (**B**).

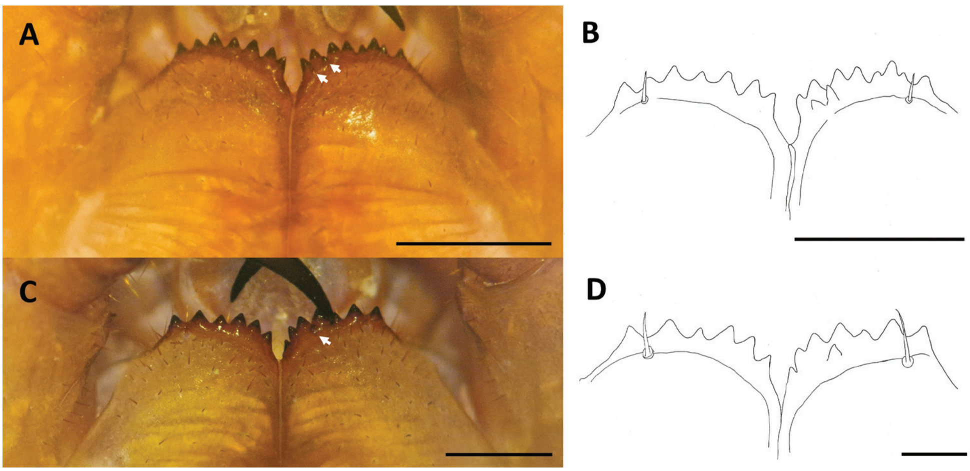

Figure 5. *Lithobius peregrinus* Latzel, 1880 **A, C** forcipular segment of CH1982 and CH1967, ventral view **B, D** drawings of the anterior margin of the forcipular coxosternum of CH1982 and CH1967, respectively; arrows indicate the additional teeth. Scale bars: 0.5 mm (**A, B, C**); 0.2 mm (**D**).

seven denticles on the right side and 10 on the left (two of them ectopic, between the first and second median tooth and between the second and third tooth) (Fig. 5A, B).

Asymmetry. More than half of the examined specimens (i.e. 20) showed an asymmetrical number of teeth on each side. Typically, only one extra tooth was present on one side, but four specimens showed a more pronounced asymmetry with at least two additional teeth. Mean asymmetry: –0.03; standard deviation: 1.04; t–statistic: –0.16; ($p > 0.05$, t–test) no statistically significant directional bias. Slight asymmetry of about 0.7 teeth difference on average between the sides.

Tergites. Tergite 1 had rounded posterior corners, while the remaining tergites had a slightly concave posterior edge, although the concavity was less pronounced in the imbricated tergites. Tergite 10 was the widest. Tergite 9, tergite 11, and tergite 13 had characteristic posterior projections.

Asymmetry. CH1964 showed normal projection on the right side of tergite 9, while there is no projection on the left side (Fig. 6A).

Coxal pores. In larger specimens, legs 13 and 14 generally had the greatest number of pores, with eight or nine and at least five–six pores observed on the coxae of legs 12 and 15. The pores were oval in earlier epimorphic stages and tended to elongate as the individual matured; the proximal pore was usually still round even in older specimens.

Asymmetry. Although they were regularly arranged (with few exceptions, e.g. CH1964, Fig. 6B), symmetrical pore numbers were observed on all corresponding coxae in 15 specimens. Mean Asymmetry: 0.16; standard deviation: 1.32; t–statistic: 0.75; $p > 0.05$, t–test, without significant differences. Nevertheless, specimens exhibited a slight asymmetry of 0.9 pores on average (centered around zero) suggesting that some specimens have the same number of pores on each side, while others differ by up to two or three pores.

Male genitalia. In larger males, the number of setae on each side of the first sternite has been counted as about 40 to 50, exceeding earlier data from the literature (Barber and Eason 1986; Zapparoli 1992), which described the second genital sternite with a much smaller number of setae (approximately 20 or 30). The second genital sternite is nude, with variable shape and sometimes completely divided into two halves. Male gonopods are inconspicuous in some specimens, flattened, closely adjacent, and each consists of a single article bearing up to 10 setae on the distal half.

Female genitalia. First genital sternite on average slightly longer than wide (0.9 mm long and 0.8 mm wide) with about 30 setae on each half, most of them clustered on the distal lateral margin. Most females possessed normally structured gonopods with two spurs on the first gonopodal segments that had a characteristic serrated apical margin (Fig. 7A). Approximately 20–25 setae were scattered over the ventral surface of this segment. They were as long as the spurs, some even longer. The distal segment had a large,

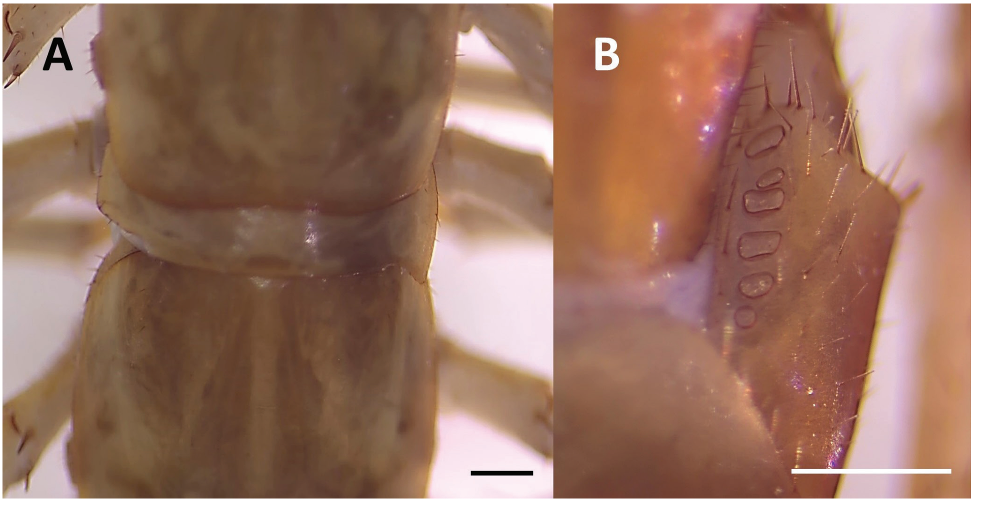

Figure 6. *Lithobius peregrinus* Latzel, 1880 **A** the 9th tergite (CH1964), dorsal view **B** right coxa of the 15th leg pair (CH1964), ventral view. Scale bars: 0.5 mm (**A, B**).

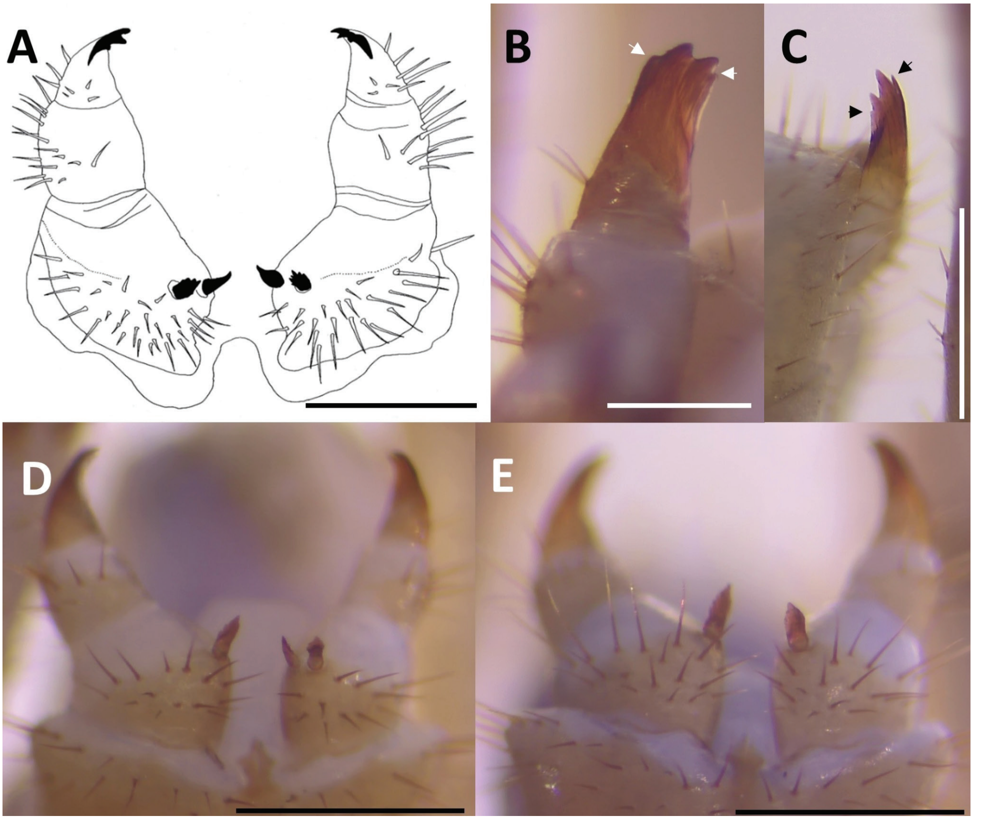

Figure 7. A *Lithobius peregrinus* Latzel, 1880. Typical female gonopods (CH1959), ventral view **B, C** lateral denticles of the gonopodal claw (CH1982), ventral and dorsal, respectively **D, E** gonopodal spurs of CH1954 and CH1956, respectively. Scale bars: 0.2 mm (**B**); 0.5 mm (**A, C, D, E**).

slightly concave claw with three denticles, the smallest located on the lateral side (with an anterior orientation), consistent with previous redescriptions (Barber and Eason 1986; Zapparoli 1992) (Fig. 7A). About 10 setae were visible on the third segment, with two or three additional setae at the base of the claw. However, in larger females (two of the females examined: CH1982 and CH1970), the gonopods appear to develop an additional tip on the claw, resulting in a fourth internal lateral denticle (Fig. 7B, C). It is not uncommon for certain species to show variation in the number of denticles on the gonopodal claw. For example, *L. muticus* from the Romanian fauna typically possesses two well–developed denticles and occasionally an additional one (Matic, 1966). However, an additional fourth tip has been documented.

Two specimens exhibited two spurs on one side and one spur on the opposite (CH1954 and CH1949) (Fig. 7D), whereas a significant portion of our sample (five females) had one pair of spurs (CH1974, CH1955, CH1952, CH1947, CH1956) (Fig. 7E). There was no evidence of damage or loss, as none of these females had scars on the gonopods, indicating that this condition was not due to injury.

Last pair of legs. The last pair of legs had a tarsus equipped with two claws, similar to all the previous legs. However, the inner claw was significantly smaller. The length of the leg segments (in mm) for specimens in the later epimorphic stages (CH1982, CH1981, CH1979, CH1978) were on average: leg 14: trochanter + prefemur = 1.8, femur = 1.6, tibia = 2, tarsus 1 = 2, tarsus 2 = 1; leg 15: trochanter + prefemur = 2.2, femur = 2.3, tibia = 2.6, tarsus 1 = 2.4, tarsus 2 = 1.4.

Plectrotaxy. The most comprehensive plectrotaxy described is that of Barber and Eason (1986), who based their results on a small introduced population. While there was little variation in plectrotaxy in our sample, we discuss further some relevant aspects related to variation and asymmetry. Individuals in the late epimorphic stages had 96–103 spines dorsally on each side (L–R) and about 115–119 ventrally (Table 1). Certain L–R asymmetries are observed when an additional spine is present in specific positions. However, when this occurred in a segment that exhibited the complete formula of anterior, median, and posterior spines, it appeared as though one of these spines was duplicated. The additional spine is usually positioned in close proximity to, or even in direct contact with, the adjacent spine, as opposed to certain species where a four–spine formula is typical and the distances between the spines is relatively uniform as in *L. borealis* Meinert, 1868, which possesses an additional spine on the dorsal part of the prefemur of the 15th leg. Zapparoli (2009) provided an intriguing account of *L. lapidicola* Meinert, 1872, which was discovered in a cave in Sardinia (Grotta di San Giovanni, Cagliari). The specimen showed an additional prefemur spine on the 15th left leg, while the corresponding right leg was mutilated, a pattern not consistently observed in other taxa.

Variations on ventral side. Transition from VmpP to VampP on the posterior part of the body started mainly in LP 11 (eight specimens) and LP 12 (22 specimens), with the presence of numerous asymmetries (VmpP/VampP) on the paired legs (13 specimens).

Table 1. *Lithobius peregrinus* leg plectrotaxy from the Gaura cu Muscă Cave (in brackets: variable and asymmetrical spines).

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

Asymmetry: Mean directional asymmetry: –0.19; standard deviation: 0.95; t–statistic: –1.23; p–value: 0.24. No directional asymmetry was detected (p > 0.05, t–test). The mean difference of about 0.19 indicates that, the right side had slightly more ventral spines overall than the left side.

In one specimen (CH1977) the asymmetrical presence of an additional spine on 15 VamTi(right)/VaTi(left) was observed; in another (CH1946) a spine was missing on 13 VaC(left)/V–C(right). The most extreme case is CH1980, which has an additional spine on the prefemur and femur of the left leg 14. Additionally, on the same left side, an extra spine is present on the prefemur of the leg 15: 14 VaampP (left); 14 VaampF (left); 15 VaampP (left).

Variations on dorsal side. The transition from DmpP to DampP in the anterior region of the body shows the highest degree of variability. This transition was observed in the following pairs of legs: leg 2 (five specimens), leg 3 (12 specimens), leg 4 (seven specimens), leg 5 (six specimens), leg 6 (five specimens), and leg 10 (two specimens), with a total of 16 asymmetries (DmpP/DampP) observed in these legs. Additionally, the transition from DaT to DapT on LP 2 and LP 3 was characterized by 11 cases of asymmetry (DaT/DapT) on the paired legs.

In the posterior region of the body, spinulation was progressively reduced, with five asymmetries observed at LP 12 and LP 13 (DapF/DpF). LP 12 DaC was present only asymmetrically (DaC/D–C) on three cases (CH1972, CH1973 and CH1956) as it was already observed previously by Zalesskaja (1978), but in comparison to her observations we also noted ventrally, as mentioned above.

Asymmetry: mean asymmetry: –0.06; standard deviation: 1.07; t–statistic: –0.31; p–value: 0.76. Observed asymmetry is moderate, with an average absolute difference of ~0.83 dorsal counts.

Development and regenerative abnormalities

Teratological studies on centipedes are primarily focused on geophilomorphs. Simaiakis et al. (2007) examined *Himantarium gabrielis* (Linnaeus, 1767) and reported segmental anomalies in two specimens from museum collections. Mitić et al. (2011) documented similar trunk segment anomalies in *Clinopodes flavidus* and *C. trebevicensis* Verhoeff, 1898 (a synonym of *C. carinthiacus* (Latzel, 1880) according to Bonato et al. 2011), based on extensive material from Serbia, and suggested that such anomalies occur naturally, albeit at low rate. More recently, Fusco et al. (2015) investigated the potential for severe developmental anomalies due to geographic isolation in *Haplophilus subterraneus* (Shaw, 1794), but found no definitive evidence in the Poznań population.

Recent teratological observations in scolopendromorphs include a bifurcated ultimate leg in *Cryptops parisi* (Stojanović et al. 2019). The authors also listed additional cases of schistomely, especially present in geophilomorphs. Vega-Román et al. (2025) also report various teratological features on the appendages of the species of *Akymnopellis* Shelley, 2008 from Chile.

For lithobiomorphs some developmental anomalies were described by García Ruiz (1994) in relation to variations in leg size for *Lithobius borealis* Mainert, 1864 and *L. castaneus* Newport 1844. Mitić and Makarov (2007) observed rare morphological anomalies on the antennae and tergite projections of *Eupolybothrus transsylvanicus* (eight out of 1,128 specimens), with regenerative anomalies in the same population later discussed by Mitić et al. (2010). The occurrence of a single spur on each female gonopod, or in some cases, the presence of an additional spur on one of the gonopods, is considered a developmental anomaly (Lewis 1987). In Romania, this condition was first reported by Negrea (2004) in an abnormal female of *L. crassipes* with an additional spur on both gonopods found in limestone drillings near Movile Cave. Later, Giurginca and Baba (2016) observed this in *L. melanops* Newport, 1845 from the Călugărească Forest, a fragmented plain forest along the Ialomița River. In a study on epimorphic development, Mitić and Tomić (2008) recorded *E. transsylvanicus* females with 1+1 and 3+3 spurs on the gonopods. Additionally, a female of *Harpolithobius dolffusi* from the Gaura Haiducească Cave with 1+1 spurs was found in our analyzed material. Certain subspecies of *L. lucifugus* L. Koch, 1862 were previously classified based on anomalies in the pattern of coxal pores. Specifically, some specimens showed an additional row containing low number of additional pores, while others showed smaller pores interspersed among the typical ones. These observations were summarized by Borek (1958). Regenerative anomalies are more common: some recent observations by Tuf and Dányi (2017) provide another example of regenerative teratology affecting the coxal pores of *L. sibiricus* Gerstfeldt, 1858.

Observed abnormalities

In the *L. peregrinus* population from the Gaura cu Musca Cave, the presence of bifid spines was observed, which are clearly divided (e.g., CH1981: 3 DampP right leg; CH1967: 13 VampP left leg) (Fig. 8A, B). Additionally, double spines were found in specific positions (e.g., CH1966: 14 DaaC left leg; CH1949: 14 DaaC left leg; CH1976: 13 DammpP left leg; CH1967: 2 DamppP right leg) (Fig. 9A, B, C). Female gonopods with only one pair of spurs (1+1) (CH1974, CH1955, CH1952, CH1947, CH1956) or with 2+1 spurs (CH1954 and CH1949) (Fig. 7B, C). A spine–covered outgrowth, possibly a schistomely was present on the prefemur of the left side of the 15th leg of CH1980, likely formed during the regeneration process or because a possible injury (Fig. 10A, B). Located on the ventral side, the outgrowth had an approximate diameter of 0.22 mm and features eight spines arranged in a concentric pattern. Directly below the regenerative outgrowth, a dark, scab–like scar was visible on the ventral surface only: this usually is formed after at least five days after the injury (Fründ 1992). Additionally, four anterior spines are positioned above the structure, deviating from the typical VampP pattern, the anterior leg also has two instances of additional spines: 14 VammpP and 14 VaampF left leg (Fig. 9D). This is possible the second case of schistomely recorded at the genus *Lithobius* and the first one affected the ultimate legs (see Demange 1959; Stojanović et al. 2019).

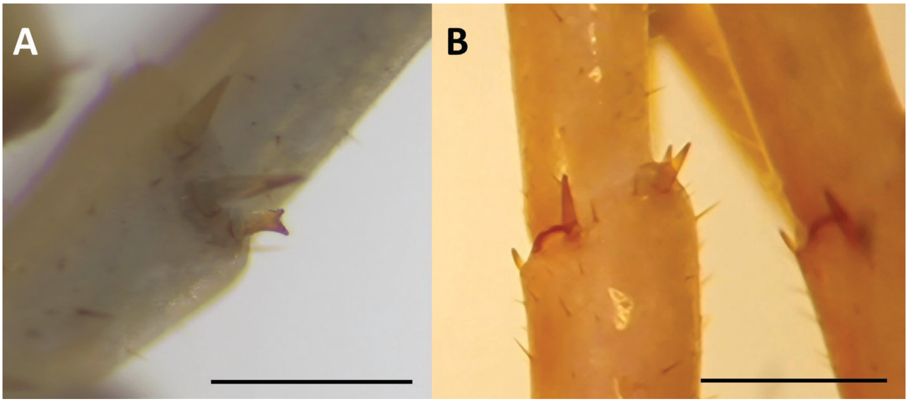

Figure 8. *Lithobius peregrinus* Latzel, 1880 **A** bifid anterior spine of CH1967, 13 VampP left leg **B** bifid posterior spine of CH1981, 3 DampP right leg. Scale bars: 0.5 mm.

Bilateral L–R asymmetry of morphological characters

Left–right asymmetry in invertebrates focused on certain model laboratory organisms such as *Drosophila melanogaster* Meigen, 1830 and on the chirality of snails (reviewed by Okumura et al. 2008). It is also noteworthy that in insects, fluctuating asymmetry in bilaterally symmetrical traits has been proposed as an indicator of environmental stress, as such asymmetry tends to increase under stressful conditions that disrupt normal developmental processes (Hoffmann et al. 2005). For example, asymmetric variation has been documented as a typical morphological response associated with insecticide exposure (Vilaseca et al. 2022).

Frasnelli et al. (2012) investigated various aspects of L–R asymmetry in the behaviour and nervous system of invertebrates. Interesting results were reported from social bees and fruit flies showing further evidence for the preference of using olfaction predominantly through one of their antennae (Letzkus et al. 2006). Spiders also show asymmetric behaviour in the use of legs during predation (Heuts and Lambrechts 1999).

Compared to other invertebrates, L–R asymmetry in centipedes has received limited scientific attention, with most assessments based primarily on observations. However, few data are available in the literature. Attems (1930) was among the first to document asymmetry, noting uneven distribution of teeth–bearing blocks (subdivisions of the mandibular lamella) in the scolopendromorph *Cormocephalus westwoodi* Newport, 1844. Similarly, Trauberg (1932) reported a left–side bias in the number of ocelli, antennal articles and coxal pores analyzing a sample of 417 *L. forficatus* specimens collected from Latvia. In contrast, Andersson (1976) analyzed a similarly sized sample of the same species reared in a controlled environment and found no significant bias, with both sides showing comparable values. Tracheal spiracles are known to exhibit L–R asymmetry, with those missing on one side of the body being compensated for by tracheae on the opposite side (Hilken et al. 2011). A personal communication by Nunes and collaborators (presented at the 17th

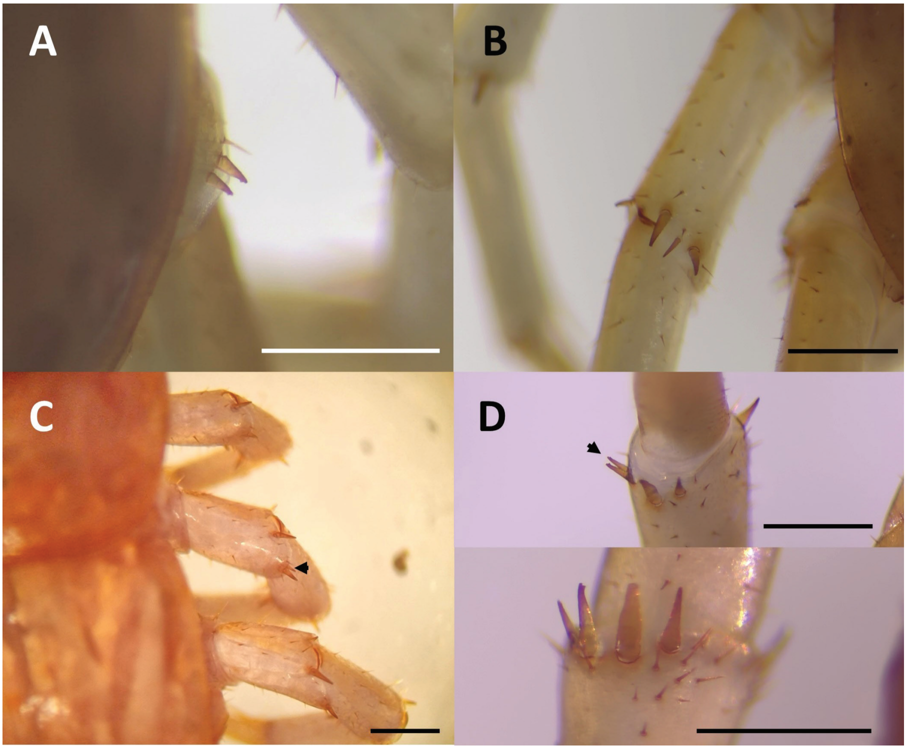

Figure 9. *Lithobius peregrinus* Latzel, 1880. Additional spines in the following positions **A** CH1966: 14 DaaC left leg **B** CH1976: 13 DammpP left leg **C** CH1967: 2 DamppP right leg **D** CH1980: 14 VammpP and 14 VaampF left leg. Scale bars: 0.5 mm.

International Congress of Myriapodology, Thailand, 2017) revealed that the number of antennomeres varies in certain Brazilian geophilomorphs, especially schendylids, an unusual feature in a group typically characterized by 14 fixed antennal segments. They also noted a variation in the number of articles in the ultimate legs. Translational fluctuating asymmetry was analyzed using geometric morphometrics, a method relevant for assessing developmental stability. Eight species of geophilomorphs (from the genera: *Stenotaenia* C.L. Koch, 1847 and *Stigmatogaster* Latzel, 1880) were considered for this study (Savriama et al. 2016). Additionally, allometric studies on the forcipular apparatus were conducted using a geometric morphometric approach on five geophilomorph species. No clear evidence of directional asymmetry was found, with only the species of *Strigamia* Gray, 1843 being found to have marginal significance with regard to the size of tarsungulum (Baioco et al. 2017).

In the *L. peregrinus* population from the Gaura cu Muscă Cave, the L–R asymmetry was mainly reflected in the sensory organs, especially in the antennae (Fig. 11). A slight rightward bias was observed in the number of forcipular coxosternite teeth and in the dorsal and ventral plectrotaxy, while a slight leftward bias was observed in the number of ocelli and coxal pores. Each case also had notable outliers (Fig. 11).

Figure 10. *Lithobius peregrinus* Latzel, 1880. Spine-covered regenerative outgrowth on the prefemur of the left 15th leg of specimen CH1980, ventral view **A** overview **B** close-up detail. Scale bars: 0.5 mm (**A**); 0.2 mm (**B**).

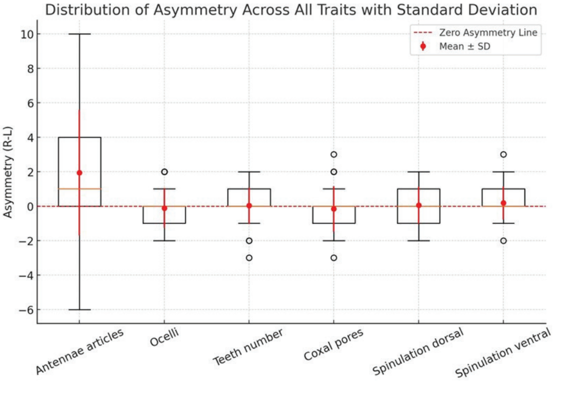

Figure 11. Distribution of DA (L–R) over the traits (no. of antennomeres, no. of ocelli, no. of forcipular denticles, no. of coxal pores, dorsal and ventral plectrotaxy). Red dots with error bars indicate the mean ± SD, the dashed red line marks zero asymmetry, and specimen dots represent outliers.

Antennae are important sensorial organs for centipedes and are equipped with sensilla that serve various functions, including mechanoreception, chemoreception, hygroreception and thermoreception (Müller et al. 2011). In *L. peregrinus* from the Gaura cu Muscă Cave the right antenna was often longer and had more antennomeres on average. Additionally, among specimens with visibly damaged antennae (which were excluded from the primary assessment), three specimens had both broken antennae and undergoing regeneration, four had damage to the right antenna and two to the left antenna. Although more data are needed, these results suggest a possible tendency toward left–sided "handedness". Although no clear evidence of antennal breakage was observed, it is reasonable to assume that such an event occurred during their lifespan, probably due to predation, as discrepancies of up to seven antennal articles between sides exceed the expected natural variation.

In the case of coxosternal dentition, asymmetry is considered a common intraspecific variation in Lithobiidae with more than two or three denticles (Matic 1966). For example, in the Romanian fauna, *L. parietum* (five–six teeth), *L. forficatus* (five–seven teeth) and *L. nigripalpis* (five to six teeth) typically exhibit a symmetrical tooth arrangement, while *L. piceus* (three to five teeth) displayed asymmetrical arrangement and all have a sometimes–asymmetrical L–R number of denticles. *Lithobius peregrinus* like *L. piceus* has an asymmetrical arrangement of the teeth and variable tooth size. However, no comprehensive studies have yet evaluated the degree of directional asymmetry across multiple morphological traits to determine whether it is random or correlated on the same side.

In terms of plectrotaxy, most asymmetries are due to a developmental delay on one side, especially in the transitional areas where spines form. A new, very small spine may appear on one side, and as the animal continues to grow, a corresponding spine typically develops on the other side, as observed in studies of centipede development such as Andersson (1976) and Mitić and Tomić (2002).

The presence and prevalence of scars

Considering the occurrence of scars, including the clearly regenerated legs, multiple visual inspections of the specimens revealed the following aspects: CH1982 exhibited regeneration process on the left leg 8, indicated by the presence of a regenerative bud. CH1958 had a scar on the 13th article of the right antenna. CH1974 had a scar on the left half of the forcipular coxosternite, just below the rostrum. CH1966 exhibits asymmetry in the antennae, with the right antenna containing 32 articles, some of which are deformed, while the left antenna contains 43 articles. Additionally, blunt, broken teeth with scars are present on the left side of the coxosternite.

CH1967 shows scars on both antennae, the left one being affected on the 7th article and the right one on the 8th article. CH1946 presents broken antennae, with the right antenna undergoing regeneration (8 articles) and the left antenna comprising 23 antennomeres, with the last one showing no scars. In CH1968, both antennae were broken, with the left one regenerated and containing 16 articles, while the right antenna bearing a scar on the 9th article. This specimen also shows small, cicatrized wounds on the dorsal part of the cephalic capsule.

CH1964 showed a regenerated right antenna, with the 23rd and 24th articles in the middle region slightly deformed and more than twice as long as the neighboring articles, while the last antennal articles were smaller than usual. This specimen had a total of 39 right antennal articles, while the left antenna comprised 48 articles. CH1954 had the left leg 15 without visible scars, but significantly reduced in length and without a complete set of dorsal spines, while the right leg 13 had a broken and cicatrized tarsus.

CH1978 had a damaged left antenna with 20 articles, but without visible scarring, while the right antenna contains 44 articles. CH1980 has a scar on the left leg 15, which is also reduced in length. CH1970 has three consecutive regenerated legs on the left side.

Overall, 29.7% of specimens showed evidence of body wounds, a percentage comparable to that reported by Fründ (1992) for most centipede populations studied.

Distribution and cave affinities

Zapparoli (1992) has listed the following locations as certain for the presence of this species: Albania, Bosnia and Herzegovina, Bulgaria, Croatia, Georgia (region of the Caucasus), Greece, Italy, Montenegro, North Macedonia, Serbia, the Russian region of the Caucasus, and noted other locations as uncertain. We consider this study as a point of reference and discuss new occurrence data from 1992 onwards.

Recently, a stable population has been confirmed in Russia and Crimea, with material collected from the Abrau Peninsula near the city of Krasnodar (Korobushkin et al. 2016) and near Sevastopol (Zuev 2016) with a new location also added in Georgia (Kiria at al. 2023). According to Iorio and Geoffroy (2019), the species is native to the Ardèche region of France and prefers karst areas where it is typically found near cave entrances and in shallow subterranean habitats, although it can also be found on the surface in forested and rocky areas. A new record from Slovenia, mentioning an unspecified location, was provided by Ravnjak and Kos (2015). Stoev (2001a) mentioned new localities from the Šar Planina Mountains (North Macedonia), the same author evaluated centipede material from Albania without reconfirming the presence of the species, although some material comes from speleological expeditions (Stoev 1997, 2001b). Zapparoli (2002) provided new localities from mainland Greece, while other studies have revised the material from the Greek islands, reidentifying *L. peregrinus* specimens from the southern Aegean Archipelago, including the frequently cited Kephalonian locality (Ionian Island) and Crete, as *L. nigripalpis* (Simaiakis et al. 2004, 2005).

Some introduced populations in Europe, are recorded from the island of Malta (Zapparoli et al. 2004) and from the Island of Minorca (Spain), among others, as Sammler et al. (2006) mention in a personal comment by Zapparoli.

Outside Europe, this species has been recorded in Panama, the Bermuda Islands, and South Africa, as well as in Tasmania (Mesibov 1994), New Zealand (Auckland Museum), and Australia (www.ala.org.au). However, records from southern Australia and New Zealand remain uncertain until the specimen data are further verified.

The nearest historic localities to our study are in Bulgaria, including Borovets Hill, Yambol, the Toundzha Plain, and Primorsko near the Ropotamo River on the Black Sea Coast (Stoev 2002), and in Serbia, where it was previously documented in the Potpećka Pećina Cave, Požega, near Užice (Mitić and Tomić 2002). Additionally, D. Stojanović has recently recorded the species in several other locations, including caves (personal communication):

Serbia • 2 ♀♀; Ribnička pećina Cave, Ribnica Gorge, village Paštrić, near Mionica; 44°12'19.44"N, 20°04'41.23"E; ~260 m a.s.l.; 4 Aug. 2023; M. Šević, D. Stojanović leg.; D. Stojanović det.; IZB ChL092, ChL093 • 1 ♂, 1 ♀; Šalitrena pećina Cave, Ribnica Gorge, village Brežđe, near Mionica, 44°11'26.99"N, 20°05'32.64"E,

~290 m a.s.l.; 2 Sep. 2023; M. Šević, D. Stojanović leg.; D. Stojanović det.; IZB ChL094, ChL121 • 3 ♂♂, 6 ♀♀, 3 immatures; same locality; 10 Nov. 2022; D. Stojanović, D. Antić leg.; D. Stojanović det.; IZB ChL122.

Furthermore, P. Stoev (personal communication) report its occurrence in Kosovo*: Kosovo* • 5 ♂♂, 1 ♀; Shpella e Banuar Cave (Gërgavica), near Zatriqit village, Rahovec Municipality, 42°27'09.4"N, 20°38'30.5"E; 12 Apr. 2017; H. Dundarova leg.; P. Stoev det.

It is worth mentioning the observed affinities for subterranean habitat of this species: beside the above–mentioned observations from France, Serbia and the region of Kosovo*, it was also found in a cave from in the Ambrolauri Region (Georgia) (Zapparoli 1992); Cave Grotta del Bus Mescapel (Lombardia, Bergamo) and Cave Grotta del Covolo della Guerra (Veneto, Venice) both from Italy (Zapparoli 1992); as well as in the MSS in Greece (Zapparoli 2002). The species has also been found in artificial subterranean cavities, such as the Catacombs of Paris (Iorio and Jacquemin 2024). Although Zapparoli (1992) considered the report from the subterranean environment of Pont–Saint–Esprit (Cévennes, Gard) as doubtful, Iorio and Jacquemin (2024) claim that this locality has been confirmed and that it is probably an introduced population.

Historical microclimatological assessments within the Gaura cu Muscă Cave during 1962, 1965, and 1966 (Negrea and Negrea 1969), specifically within the Bat Chamber, documented air temperatures ranging from approximately 15.5 °C to 15.8 °C, as recorded during summer and early autumn (end of July and end of September). The temperature measurements, which were taken exclusively during the summer in the deeper section of the active gallery, were between 13.5 °C and 15 °C. Additionally, a relative humidity (RH) of 94% was measured in the Bat Chamber and 96% in the deeper section of the active gallery (Negrea and Negrea 1969). More recent data collected using a data logger (Tinytag Plus: TGP–4500) between March 2020 and January 2021 in the Bat Chamber showed and average air temperature of 14.79 °C and an average relative humidity of 92.82% (Fig. 12). It is more relevant to compare the data recorded by the logger during the same months in

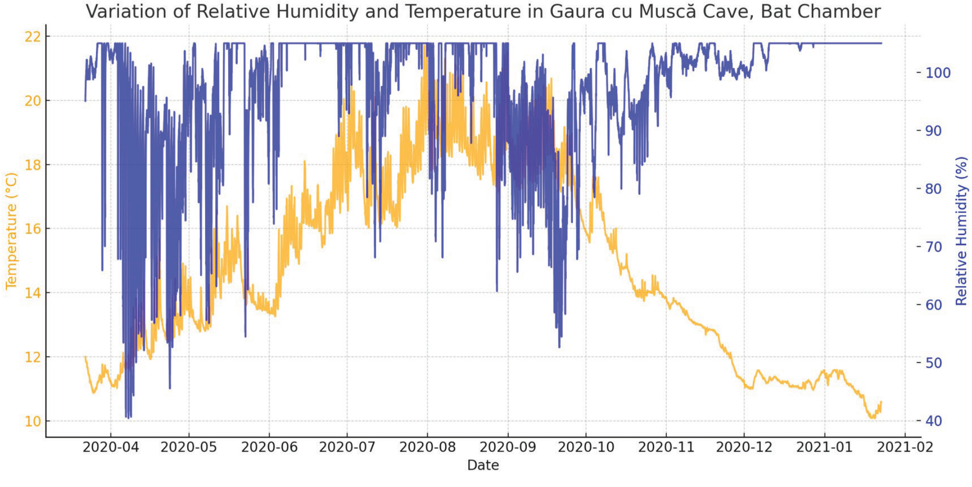

Figure 12. Air temperature (°C) and relative humidity (%RH) recorded hourly inside the Bat Chamber of Gaura cu Muscă Cave, from March 2020 to January 2021.

which the historical data was collected. The analysis reveals that the average temperature in July 2020 was 17.97 °C (between a minimum of 16 °C and a maximum of 21.7 °C) with a relative humidity (RH) of 96.8% (minimum 63.1%, maximum 100%). In September, the average temperature was 18.1 °C (ranging from 15.9 °C to 18.2 °C) with an RH of 81% (minimum 47.6%, maximum 100%). These results indicate a significant alteration in the microclimatic conditions in the cave. It is important to note that the Bat Chamber is located approximately 45 meters from the entrance, which could influence these fluctuations.

Origin of the Romanian population of *Lithobius peregrinus*

The ecological specificity and the biogeographical context of the Banat Mountains, suggest a natural, relict population at the northern-most distribution limit of the species *L. peregrinus*. The presence of a small and very localized (for now, at least) population in the Locvei Mountains and the species apparent affinity for stable and humid environments align well with established patterns observed in other arthropods exhibiting cave colonization behavior and could explain the current restriction to caves of *L. peregrinus* in Romania, with no evidence of an epigean population to the best of our knowledge. In this scenario, the species preferred the well–known environmental stability of the hypogean habitat (Prous et al. 2004). Other groups of epigean arthropods are known to exhibit similar behaviour, demonstrating a remarkable capacity for colonizing caves during hot summer months. Following cave colonization, some individuals remained in these subterranean environments for the duration of their lives, as observed in *Paranemastoma silli* subsp. *silli* (Herman, 1871) from Cloșani Cave and Lazului Cave (Plăiașu et al. 2017).

Behavior

Two females were observed laying eggs (Fig. 13A) (July 17, 2024), and two specimens in anamorphic stages were spotted near fissures, suggesting that these areas may serve as developmental sites until the juveniles grow large enough to venture into the larger galleries to hunt.

The species was often found on stones surrounded by water (Fig. 13B). It frequently sits close to the water's edge, with its antennae almost touching the surface. On several occasions, while attempting to collect specimens from cave walls, we observed centipedes falling into the water and quickly dived down to hide in limestone cracks or under submerged stones. This behavior has also been documented in other centipede species (Dányi et al. 2019).

Jeekel (1963) in his note on *Lithobius provocator* Pocock, 1891 a junior synonym of *Lithobius peregrinus* Latzel, 1880, was also amazed about the presence of this species in Bermudes and stated:

> "*That a species from Southeastern Europe has established itself in localities as far from its homeland as in the present case seems quite unique. One can only wonder on what occasion and under what circumstances L. peregrinus has been transported to these remote places*."

We could assume that this unusual ability to spread could be favored by this behavior.

Figure 13. *Lithobius peregrinus* Latzel, 1880 **A** egg laying female photographed on the wall of Bat Chamber (July 17, 2024) **B** specimen on a humid stone surrounded by water in the deeper part of the cave (May 6, 2023).

Conclusions

We studied a troglophilic population of *Lithobius peregrinus*, a species recorded in Romania for the first time, in the present study. The population was monitored over a period of three year. The studied specimens showed a number of remarkable asymmetries and teratological anomalies in important external morphological characters relevant for taxonomic identification. In addition to numerous asymmetrical spines on the paired legs, anomalies were observed in the teeth on the forcipular coxosternite and in the number of ocelli and antennal articles. All previous descriptions, as documented by Barber and Eason (1986), and Zapparoli (1992), provided primarily unilateral assessments of meristic characters, with some evidence of L–R differences. While the degree of asymmetry in most characters was notable, there was no evidence of directional asymmetry or consistent correlation of asymmetry between sides, except for antennae. This bias observed in antennae may result from multiple factors, particularly those related to predation, as found in similar studies of spider legs (Heuts and Lambrechts 1999). The plausibility of left–"handedness" cannot be dismissed. However, in view of the limited sample size and the specific conditions in the cave, we do not want to generalize our results. Nevertheless, further data collection could provide sufficient evidence to support or refute this pattern.

Furthermore, developmental and regenerative anomalies were documented, such as double spines in certain positions, strongly bifurcated spines, single spurs on each basal article of both gonopods and a spine–covered regenerative outgrowth, possible a schistomely (Fig. 10A, B). The significant morphological variability observed within this relatively small sample can be partly attributed to the well–documented phenomenon that cave–dwelling organisms generally have a prolonged lifespan compared to their surface–dwelling counterparts (Lunghi and Bilandžija 2022). It is well known that centipedes, even in epimorphic development, may acquire additional ocelli, coxal pores, or spines following each moulting event and that they undergo through several moulting stages during their lifetime (Voigtländer 2007; Rosenberg et al. 2011). Moreover, given the lack of seasonality of the subterranean climate, the troglophilic life stage is a factor identified by Descamps et al. (1988) as influencing moult rate, as it affects the physiological activity and may contribute to structural modifications, leading to increased variability. Although it is well established that certain centipede species can enter and even thrive in cave environments (Negrea 1994; Vahtera et al. 2020; Kos et al. 2023), the factors that enable some species to successfully adapt compared to others remains unclear.

The several possibilities for the origin of the Romanian population of *L. peregrinus* (natural *versus* introduced) will be evaluated in further research using molecular data in a larger European context.

Acknowledgments

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