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Original paper

Redescription and new records of *Lithobius demavendicus* Matic, 1969 from Iran (Chilopoda: Lithobiomorpha: Lithobiidae)

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Summary. The Iranian endemic species *Lithobius demavendicus* Matic, 1969 is rediscovered and redescribed based on newly collected specimens. Previously, the species was known only from an incomplete, most probably subadult male lacking the ultimate pair of legs, collected at high altitudes on Mount Damavand, a well-known inactive volcanic mountain in northern Iran. The new records confirm its occurrence on this mountain and at lower altitudes, and also indicate a troglophilic tendency for the species, as reflected by its repeated occurrence in caves in the northeastern part of the country. The first complete description of females and adult males is provided, together with an account of changes in morphological characters during late postembryonic development. A brief comparison with morphologically similar species was conducted, and the taxonomic status of *L. demavendicus* is discussed.

Keywords: centipedes, caves, development, Middle East, Mount Damavand, redescription.

INTRODUCTION

As one of the most species-rich genera within the class Chilopoda, the genus *Lithobius* Leach, 1814 is known from a wide range of habitats and has an almost global distribution (Zapparoli and Edgecombe 2011; Ganske et al. 2021). They represent one of the most important components of the soil food web and mainly inhabit forest habitats, but also occur in open habitats, dry areas, caves and anthropogenic environments (Zapparoli 2003). The vast majority of its representatives have a Palearctic distribution, although some species are native to, or have been introduced into, other regions of the world (e.g. Johns 2010; Mercurio 2010; Vega-Román and Ruiz 2018; Thofern et al. 2021). According to ChiloBase, a catalogue of all known centipede species of the world (Bonato et al. 2016), the genus currently comprises more than 550 species. Numerous synonyms are also listed for many species, and may therefore represent only an approximation of the final number of valid species. Recent integrative taxonomic studies have revised the status of several taxa, confirming the validity of some species, synonymizing others, and reinstating certain former synonyms to species rank (eg. Akkari et al. 2024; Kos et al. 2025). In addition, new species of *Lithobius* continue to be described worldwide at a relatively high rate (eg. Zuev 2017; Dyachkov and Farzalieva 2018; Farzalieva 2018; Iorio and Voigtländer 2019; Stojanović et al. 2021; Iorio and Racine 2022; Pei et al. 2021, 2022; Dyachkov 2024; Serra Sorribes 2024; Iorio et al. 2025). Altogether, these ongoing taxonomic advances contribute to a refined assessment of species diversity within the genus and to a better understanding of its taxonomic complexity.

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As pointed out by Zapparoli (2003), many *Lithobius* species were described in the past in a very concise manner and on the basis of unstable characters. A considerable number of species remains poorly known, largely due to incomplete original descriptions that do not present the full range of morphological characters and are often based on only a few selected traits. Moreover, species descriptions are frequently based on a limited sample size, or sometimes even a single specimen, without an assessment of intraspecific variability and lacking subsequent records (e.g. Folkmanová 1940; Verhoeff 1943; Matic and Stenzer 1977). An additional problem is that the developmental stage of the type specimen(s) has often not been taken into account. External morphological characters important for the description and identification of *Lithobius* species change, to a greater or lesser extent, through different developmental stages during ontogeny (e.g., Voigtländer 2007; Stojanović et al. 2023). Consequently, a number of species have been described on the basis of juvenile or subadult specimens exhibiting incomplete morphological characters, which further complicates the taxonomy and species delimitation within the genus. Thus, although assessment of the taxonomic status of many species via incorporation of additional data on morphological variability remains challenging, this represents a crucial step toward understanding the global success of this largest group of centipedes.

In this study, we present the first new records of the Iranian endemic species *Lithobius demavendicus* Matic, 1969, more than a half a century after its original description. Until now, the species was known only from a single holotype, a male with incomplete morphology (i.e., lacking the ultimate pair of legs, which bear some of the most taxonomically important characters for delimiting *Lithobius* species). This specimen was collected by the late Italian entomologist and biospeleologist Prof. Valerio Sbordoni (1942–2024) in August 1966 at high altitude (ca. 3000–3200 m a.s.l.) on Mount Damavand, a well-known inactive volcanic mountain in northern Iran (Tehran Province), without any additional habitat data provided in the original description (Matic 1969: 98). The species epithet refers to the type locality. The holotype is deposited in the Collezione Scientifica dell'Istituto Nazionale di Entomologia (Rome), as stated by Matic at the beginning of the original description. Following its description, the species was largely overlooked and has since been mentioned only once in a checklist of Iranian Chilopoda (Zarei et al. 2020: 138). Based on newly collected material from Mount Damavand and from northeastern Iran, we confirm the presence of the species at lower altitudes and document its relatively frequent occurrence in different parts of the caves in the area. Here we provide a complete description of the adult male morphology and the first description of females, together with notes on morphological variability across different postembryonic developmental stages, supported by illustrations of taxonomically important characters. Finally, a brief comparison with morphologically similar species and comments on the taxonomic status of *L. demavendicus* are presented.

MATERIAL AND METHODS

In total, 31 specimens of *Lithobius demavendicus* were newly collected, of which eight are from Mount Damavand, a mountain that includes the type locality of the species, and the rest were found in caves, soil, and leaf litter in northeastern Iran. The material was collected by hand with an aspirator, as well as by using pitfall traps and a Berlese funnel. All specimens were identified, photographed, measured, and assigned to a developmental stage. Analyses were conducted using a Nikon SMZ 1270 binocular stereomicroscope equipped with a Nikon DS-Fi2 camera and a Nikon DS-L3 camera controller at the University of Belgrade – Faculty of Biology, Institute of Zoology (IZB), Belgrade, Serbia. Taxonomically relevant external morphological characters necessary for species identification were photographed and are illustrated in Figs 1 and 2. Additionally, instances of abnormal phenotypes observed among the examined specimens are presented in Fig. 3.

Specimen identification was based on diagnostic features from the original species description (Matic 1969). For each specimen, a unique collection registration number was assigned and specimens were preserved in separate, labeled plastic vials filled with 70% ethanol. The material is deposited in the collections of the Institute of Zoology, University of Belgrade – Faculty of Biology, Belgrade, Serbia (IZB collection) and Zoology Museum of Ferdowsi University of Mashhad, Mashhad, Iran (ZMFUM collection).

Terminology and abbreviations used throughout the text and tables follow Bonato et al. (2010): a = anterior, C = coxa, D = dorsal, F = femur, L = leg, m = median, p = posterior, Pf = prefemur, T = tergite, TO = Tömösváry's organ, TT = tergites, Ti = tibia, Tr = trochanter, V = ventral. Developmental stages terminology and abbreviations follow Stojanović et al. (2023): AG = agenitalis, IM = immaturus, PM = praematurus, PS = pseudomaturus, M = maturus.

Focus-stacked images were processed using Zerene Stacker software. Final images and plates were processed using Adobe Photoshop CS6. The occurrence map (Fig. 4) was created using Google Earth Pro (version 7.3.6.9345) and Adobe Photoshop CS6.

RESULTS

The analysed material comprised 31 specimens collected from nine localities. It included 12 maturus (four males, eight females), three AG, seven IM (four males, three females), five PM (three males, two females), and four PS specimens (all females). The material was examined to document ontogenetic changes in morphological characters. All examined stages were epimorphic; anamorphic stages were not present in the sample.

The analysis of the examined material shows that *Lithobius demavendicus* has a considerably wider distribution than previously known, extending beyond Mount Damavand, where the species had hitherto been the only recorded locality. In addition to its rediscovery on Mount Damavand, the species was found at eight other sites, six of which are caves (AL Cave, Bazangan Cave, Bidak Cave, Kardeh Cave, Poostin-Dooz Cave, and Mazdavand (Mozdouran) Cave), located along the border between Iran and Turkmenistan (Fig. 4).

Based on this material, the first complete description of the species, including both sexes and different postembryonic stages, is provided. The newly documented distribution considerably expands the known range of the species and contributes to a better understanding of its variability and development.

Taxonomy

Class Chilopoda Latreille, 1817
Order Lithobiomorpha Pocock, 1895
Family Lithobiidae Newport, 1844
Genus *Lithobius* Leach, 1814
***Lithobius demavendicus* Matic, 1969**
Literature records: Matic 1969: 98.; Zarei et al. 2020: 138 (in list).

Material examined

IRAN: ● 2♂♂, 2♀♀ (both sexes with one M and IM stage); Mazandaran Province, Larijan District, foot of Mount Damavand, Upper Abgarm Larijan (collector mark: DM 2024); 35°54′30″N, 52°11′08″E; 2309 m a.s.l.; hand-collected under a rock; 26 October 2024; leg. M. Mehrafrooz Mayvan; ZMFUM. ● 2♂♂ (M, PM), 1♀ (M), 1AG; ibidem; IZB (IZB ChL139). ● 2♂♂ (M, IM), 1♀ (M); Razavi Khorasan Province, Mashhad City, Kardeh Village, AL Cave (collector mark: ALCA 211); 36°40′00.2″N, 59°39′19.9″E; 1693 m a.s.l.; hand-collected with an aspirator in the dark zone of the cave; 13 October 2023; leg. M. Mehrafrooz Mayvan; ZMFUM. ● 2♀♀ (M, PM); Razavi Khorasan Province, Mashhad City, Kardeh Village, AL Cave (collector mark: ALCA 2001); 36°40′00.2″N, 59°39′19.9″E; 1693 m a.s.l.; dark zone of the cave; hand-collected with an aspirator; 26 May 2024; leg. M. Mehrafrooz Mayvan; ZMFUM. ● 1♂ (PM), 2♀♀ (PS, PM); ibidem; IZB (IZB ChL140). ● 2♀♀ (PS, IM); Razavi Khorasan Province, Sarakhs County, near Bazangan Village, Bazangan Cave (collector mark: BACA 258); 36°18′29″N, 60°22′19″E; 1401 m a.s.l.; dark zone of the cave; pitfall trap containing propylene glycol; 18 June 2022; leg. M. Mehrafrooz Mayvan; ZMFUM. ● 1AG; North Khorasan Province, Bojnourd City, near Bidak Village, Bidak Cave (collector mark: BICA 207); 37°26′30″N, 57°13′14″E; 1327 m a.s.l.; dark zone of the cave; hand-collected with an aspirator; 23 June 2022; leg. M. Mehrafrooz Mayvan; ZMFUM. ● 1♂ (IM); Razavi Khorasan Province, Mashhad City, Dehbar Village (collector mark: DE 06 Ar); 36°14′48″N, 59°17′07″E; 1702 m a.s.l.; extracted with a Berlese funnel from soil and litter; 1 July 2023; leg. M. Mehrafrooz Mayvan; ZMFUM. ● 1♀ (IM); North Khorasan Province, Shirvan City, Gelyan Village (collector mark: GE 17 Ar); 37°13′46″N, 57°53′24″E; 1344 m a.s.l.; extracted with a Berlese funnel from soil and litter; 1 July 2023; leg. M. Mehrafrooz Mayvan; IZB (IZB ChL141). ● 1♂ (PM), 2♀♀ (M); Razavi Khorasan Province, Mashhad City, Kardeh Village, Kardeh Cave (collector mark: KRCA 293); 36°40′15.9″N, 59°40′37.6″E; 1458 m a.s.l.; dark zone of the cave; hand-collected with an aspirator; 10 August 2023; leg. M. Mehrafrooz Mayvan. ● 1♂ (M), 1♀ (PS), 1AG; ibidem; IZB (IZB ChL142). ● 1♂ (IM), 1♀ (PS); North Khorasan Province, Shirvan City, Lujali Village, Poostin-Dooz Cave (collector mark: PUCA 930); 37°38′16″N, 57°52′43″E; 1785 m a.s.l.; pitfall traps with plastic cups containing propylene glycol; 22 June 2022; leg. M. Mehrafrooz Mayvan; ZMFUM. ● 1♀ (M); Razavi Khorasan Province, Sarakhs County, Mazdavand City, Mazdavand (Mozdouran) Cave (collector mark: UN 94 Ar), 36°09′05″N, 60°32′59″E; 1056 m a.s.l.; dark zone of the cave; hand-collected with an aspirator; 18 June 2022; leg. M. Mehrafrooz Mayvan. ● 1♀ (M); ibidem; IZB (IZB ChL143).

Re-description

Measurements. Body length of maturus specimens: males 12.6–17.6 mm (mean 14.6 mm), females 11.6–19.6 mm (mean 14.0 mm); maximum trunk width: males 1.7–1.9 mm (mean 1.7 mm), females 1.3–1.9 mm (mean 1.6 mm). Measurements by developmental stages: AG—body length 5.8–6.7 mm (mean 6.2 mm), trunk width ca. 0.7 mm; IM—body length 8.0–8.7 mm in males (mean 8.3 mm) and 7.1–9.6 mm in females (mean 8.0 mm), trunk width 0.8–1.0 mm (mean 0.9 mm) in both sexes; PM—body length 10.6–11.0 mm in males (mean 10.8 mm) and 10.3–10.5 mm in females (mean 10.4 mm), trunk width 1.2–1.4 mm (mean 1.3 mm) in both sexes; PS—females with body length 11.1–12.7 mm (mean 11.9 mm) and trunk width 1.5–1.7 mm (mean 1.5

mm); males at this stage were not collected.

Colouration (Figs 1, 2). Yellowish brown, fairly uniform along entire body; head region (cephalic capsule and forcipular segment) slightly darker. Specimens in early developmental stages, as well as in early phases of each stage, markedly paler.

Antennae (Figs 1A, 2A). Between $^1/_2$–$^1/_3$ of body length; proportion lower in younger subadult stages, with mean ratios of 0.35 (AG), 0.36 (IM), 0.39 (PM), and 0.42 (PS), gradually increasing with stage progression and reaching the highest values in adults (0.34–0.49; mean 0.42). Antennae approximately 3.6–4.7 times longer than cephalic capsule, distally narrowing (Fig. 1A), showing a pattern of proportional increase through postembryonic stages that correlates with body length. Composed of 19–23 antennal articles, usually 20; terminal article about 2.5 times longer than wide and 1.5 times longer than penultimate article (Fig. 2A). All articles bearing numerous setae.

Cephalic capsule (Fig. 1A–B). Approximately as long as wide; measurements consistent across developmental stages:

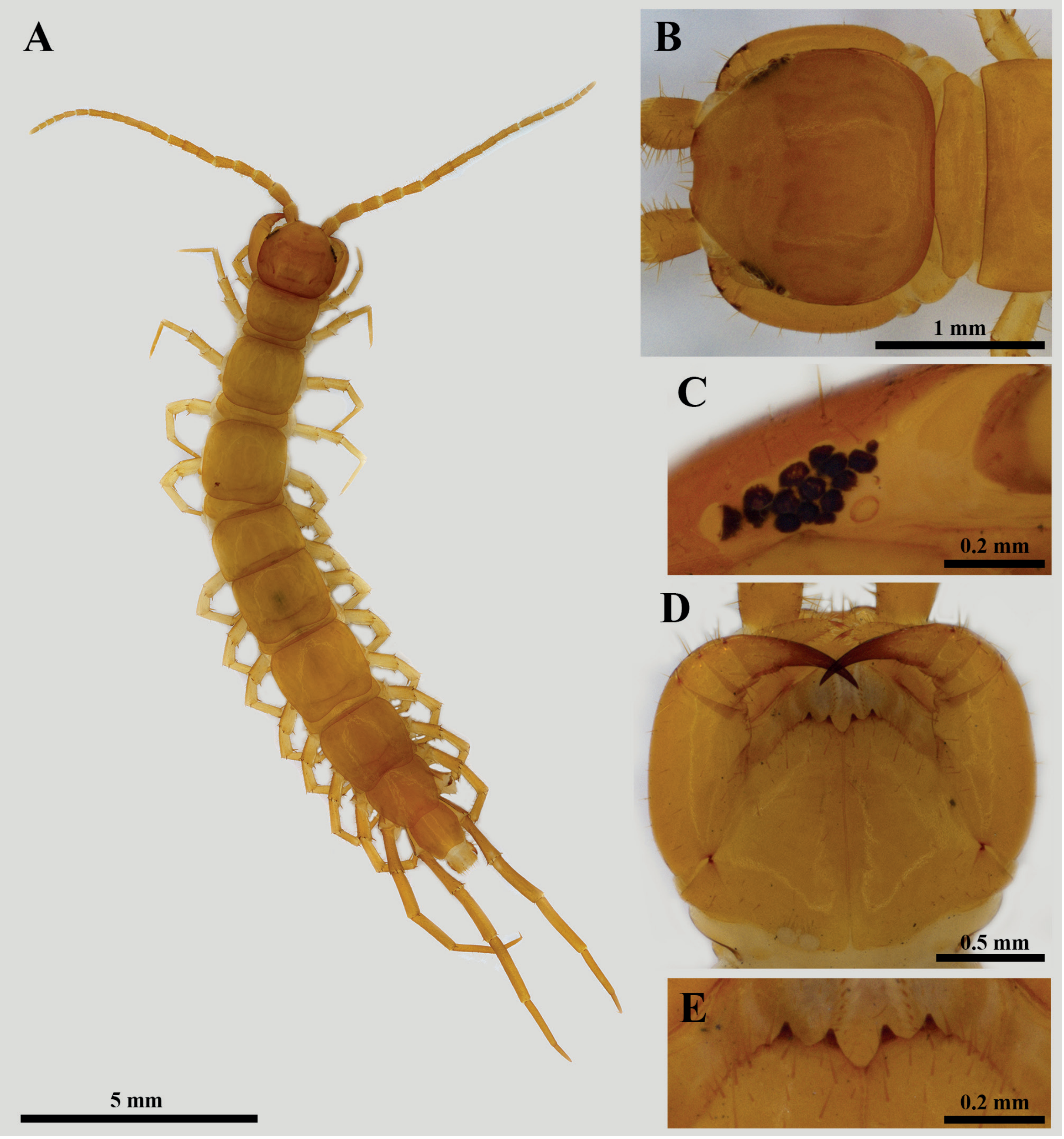

Fig. 1. *Lithobius demavendicus* Matic, 1969. **A**, habitus, female, dorsal view (DM4, ZMFUM); **B**, cephalic capsule, male, dorsal view (DM5, ZMFUM); **C**, right aggregate of ocelli and Tömösváry organ, male, lateral view (DM5, ZMFUM); **D**, forcipular segment, male, ventral view (DM5, ZMFUM); **E**, anterior margin of the forcipular coxosternite, male, ventral view (DM5, ZMFUM).

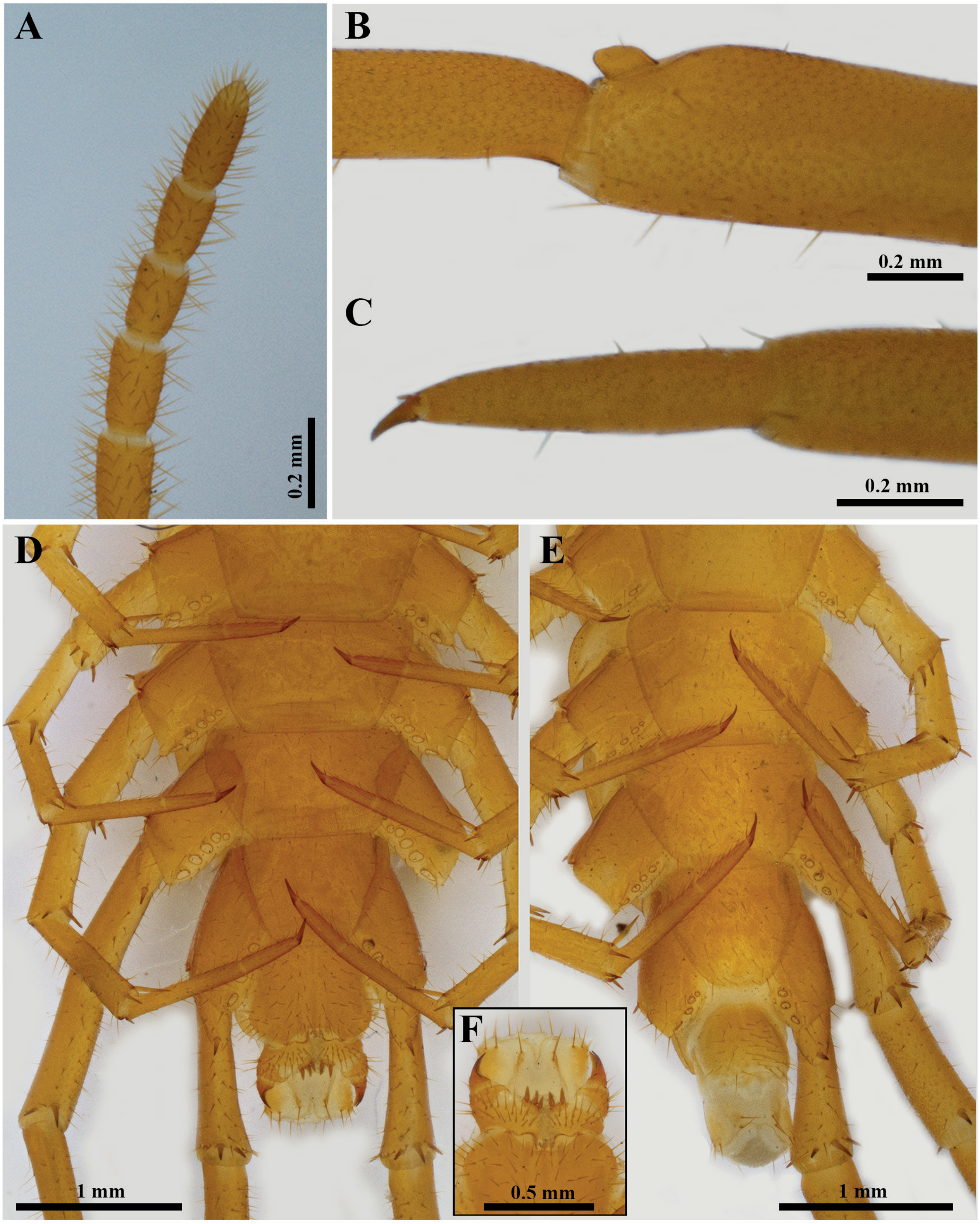

Fig. 2. *Lithobius demavendicus* Matic, 1969. **A**, apical articles of the left antennae, male, dorsal view (DM5, ZMFUM); **B**, dorsal subdistal wart-like process on tibia of left ultimate leg, male, posteroventral view (DM5, ZMFUM); **C**, pretarsus of left ultimate leg, male, posteroventral view (DM5, ZMFUM); **D**, posterior part of body, female, ventral view (DM4, ZMFUM); **E**, posterior part of body, male, ventral view (DM5, ZMFUM); **F**, postpedal segments, female, ventral view (DM4, ZMFUM).

AG 0.98–1.05 (mean 1.02), IM 0.96–1.07 (mean 1.01), PM 0.93–1.03 (mean 0.99), PS 0.96–1.10 (mean 1.01), M 0.90–1.05 (mean 0.98). Cephalic plate with almost straight posterior margin and narrowing anteriad (Fig. 1B).

Ocelli (Fig. 1C). Grouped in a triangular cluster, 9–14 (typically 11) on each side in adults, mostly arranged in three irregular rows. The two most posterior ocelli are the largest, almost twice the size of the median ones located on the anterior and dorsal sides of the cluster's central part, while the antero-ventral row contains the smallest ocelli. During post-embryonic development, the number of ocelli increases with stage: 5 in AG (all specimens), 6–7 in IM, 8–9 in PM, and 9–11 in PS.

Tömösváry's organ (Fig. 1C). Oval to ellipsoid, medium-sized (smaller than the largest posterior ocelli and larger than the adjacent ones in adults); positioned anteroventral to ocelli. During postembryonic development, size of TO relative to ocelli (located adjacent to two largest posterior ocelli) changes, being smaller in AG and IM stages, equal in PM, and larger in PS and M stages.

Forcipular segment (Fig. 1D). Coxosternite subtrapezoidal; anterior margin narrowed, with external side slightly higher than internal side. Dental margin typically with 2+2 small, pointed teeth of equal size. Developmental anomalies in number and/or shape of coxosternal teeth were observed in three specimens: reduction to 1+2 teeth in a female from Mount Damavand (DM6, ZMFUM; Fig. 3A); increase to 4+3 teeth by insertion of smaller teeth between regular ones, with apical bifurcation of the inner right tooth in another female from the same locality (DM4, IZB ChL139; Fig. 3B); and apical bifurcation of both left-side teeth in a female from Kardeh Cave (KR3, ZMFUM; Fig. 3C). Medial diastema moderately deep, V-shaped, with approximately equal width and depth (Figs 1D–E, 3A–D). Porodont generally slender, setiform, positioned posterolateral to the lateral tooth on weakly defined shoulders of the forcipular coxosternite (Fig. 1E). An unusual case of porodont, setiform on the left side and stout on the right side, was recorded in a PS female from Bazangan Cave (BA2, ZMFUM; see Fig. 3D). Forcipular tarsungulum curved, approximately 2.5 times longer than the basal width. Chaetotaxy of forcipular coxosternite and telopodites as shown in Fig. 1D.

Tergites (Fig. 1A). Posterior angles of all tergites rounded, without triangular projections. T1 rectangular, anterior margin slightly wider than posterior margin, posterior edges distinctly rounded. TT 2, 4, 6, 7, 9, and 11 with straight posterior margins. TT 3 and 13 with slightly concave posterior margins. TT 5, 8, 10, 12, and 14 with the posterior margin distinctly concave. With the exception of TT 3, 5, 8, 10, and 12, which are as long as wide, all other tergites are distinctly wider than long.

Legs. Tarsi of all legs divided; tarsal articulation weakly expressed but visible in L1–10, somewhat more pronounced in L11–12, and well defined in L13–15. Leg-pairs 1–13 with relatively long, curved claws bearing slender anterior accessory spines. Penultimate legs with both an anterior accessory spine and a small posterior accessory claw; ultimate legs with a small posterior accessory claw only, located on the inner side (Fig. 2C). L14 and L15 significantly longer than the walking legs. In males, ultimate legs bear a subdistal dorsal tibial wart-like process (tibial protuberance) (Fig. 2B); this structure is absent in females. The tibial wart-like process is clearly differentiated from the PM stage onward and absent in earlier stages. Pores of telopodal glands on the inner side of penultimate and ultimate legs present in both sexes. Plectrotaxy of adults and its variation through developmental stages are summarized in Tables 1–7. Unusual spinulation involving duplication of the dorsal anterior spine on the L13 coxa and the dorsal medial spine on the L15 prefemur, both on the left side, was observed in a male collected from Mount Damavand (DM5, ZMFUM) (Fig. 3E; see also Table 2).

Coxal pores (Fig. 2D–E). Rounded to elliptic, clearly visible in adults. Their number increases progressively through developmental stages: in AG, usually 1,2,2,2, otherwise 2,1(2),1(2),1; in IM, from 2,2(3),2(3),2(3) to 2(3),3,3,3;

Table 1. Plectrotaxy of maturus female of *Lithobius demavendicus* Matic, 1969 (DM4, IZB ChL139). Brackets indicate asymmetry (spine present on one side only).

Legs	Ventral					Dorsal				
N	Cx	Tr	Pf	F	Ti	Cx	Tr	Pf	F	Ti
1			p	amp	m			p	a	a
2			p	amp	m			p	a(p)	a
3-5			p	amp	m			p	ap	ap
6-10			mp	amp	am			ap	ap	ap
11			(a)mp	amp	am			amp	ap	ap
12			amp	amp	am	a		amp	p	ap
13		(m)	amp	amp	am	a		amp	p	p
14		m	amp	mp	am	a		amp	p	p
15		m	amp	am		a		amp	p	

Table 2. Plectrotaxy of maturus male of *Lithobius demavendicus* Matic, 1969 (DM5, ZMFUM). Brackets indicate asymmetry (spine present on one side only).

Legs	Ventral					Dorsal				
N	Cx	Tr	Pf	F	Ti	Cx	Tr	Pf	F	Ti
1			p	am	m			p	a	a
2			p	amp	m			p	a(p)	a(p)
3-4			p	amp	m			p	ap	ap
5			p	amp	(a)m			p	ap	ap
6			p	amp	(a)m			ap	ap	ap
7-8			p	amp	am			ap	ap	ap
9-10			mp	amp	am			ap	ap	ap
11			(a)mp	amp	am			ap	ap	ap
12			amp	amp	am	(a)		ap	ap	(a)p
13			amp	amp	am	2a		amp	p	(a)p
14		m	amp	mp	am	a		amp	p	p
15		m	amp	am		a		a2m	p	

Table 3. Plectrotaxy of pseudomaturus female of *Lithobius demavendicus* Matic, 1969 (DM7, IZB ChL139). Brackets indicate asymmetry (spine present on one side only).

Legs	Ventral					Dorsal				
N	Cx	Tr	Pf	F	Ti	Cx	Tr	Pf	F	Ti
1			p	am	m			p	a	a
2			p	am(p)	m			p	ap	ap
3-5			p	amp	m			p	ap	ap
6			p	amp	(a)m			p	ap	ap
7-11			mp	amp	am			ap	ap	ap
12			mp	amp	am			amp	(a)p	ap
13			amp	amp	am	a		amp	p	ap
14		m	amp	ap	m	a		amp	p	p
15		m	amp	mp		a		amp	p	

Table 4. Plectrotaxy of praematurus male of *Lithobius demavendicus* Matic, 1969 (DM1, IZB ChL139). Brackets indicate asymmetry (spine present on one side only).

Legs	Ventral					Dorsal				
N	Cx	Tr	Pf	F	Ti	Cx	Tr	Pf	F	Ti
1			p	m	m			p	a	a
2-8			p	am	m			p	ap	ap
9			mp	amp	m			ap	ap	ap
10-11			mp	amp	am			ap	ap	ap
12			amp	amp	am	a		amp	ap	ap
13			amp	amp	am	a		amp	p	ap
14		m	amp	am	m	a		(a)mp	p	p
15		m	amp	mp		a		amp	p	

in PM, from 2,3(4),4,4 to 3,4(5),5,4; in PS, from 2(3),3,4,4 to 4,5,5,4. In the maturus stage, minimum counts of 3,4,4,3 and maximum counts of 4,5,5,5 and 3(4),5,6,4 were recorded.

Ultimate leg-bearing segment (Fig. 2D–E). Intermediate tergites in both sexes with slightly concave to straight posterior margins; sternite of the ultimate leg-bearing segment identical in both sexes; trapeziform, posteriorly narrowed, as long as wide; anterior margin about twice as long as posterior; with scattered short setae.

Postpedal segments. Male (Fig. 2E): first genital sternite longer than wide, with scattered setae; posterior margin convex between gonopods, without medial bulge. Gonopods

Table 5. Plectrotaxy of immaturus female of *Lithobius demavendicus* Matic, 1969 (DM2, ZMFUM). Brackets indicate asymmetry (spine present on one side only).

Legs	Ventral					Dorsal				
N	Cx	Tr	Pf	F	Ti	Cx	Tr	Pf	F	Ti
1				m	m			p		
2-5				am	m			p	ap	ap
6-8			p	am	m			p	ap	ap
9			p	amp	am			ap	ap	ap
10-11			mp	amp	am			ap	ap	ap
12			mp	amp	am	(a)		amp	ap	ap
13			amp	amp	am	(a)		amp	(a)p	(a)p
14		m	amp	am	m	a		amp	p	p
15		m	amp	mp		a		amp	p	

Table 6. Plectrotaxy of agenitalis of *Lithobius demavendicus* Matic, 1969 (BICA 207, ZMFUM). Brackets indicate asymmetry (spine present on one side only).

Legs	Ventral					Dorsal				
N	Cx	Tr	Pf	F	Ti	Cx	Tr	Pf	F	Ti
1				m	m					
2				m	m				p	
3-4				m	m				p	a
5				m	m				ap	a
6				am	m				ap	a(p)
7-9				am	m			p	ap	ap
10			m	am	m			p	ap	ap
11			m	am	m			p	(a)p	(a)p
12			m(p)	am	m			mp	p	p
13			mp	am	m			mp	p	p
14			m(p)	am	m			amp	p	p
15			amp	am				amp		

Table 7. Plectrotaxy of agenitalis of *Lithobius demavendicus* Matic, 1969 (DM8, IZB ChL139). Brackets indicate asymmetry (spine present on one side only).

Legs	Ventral					Dorsal				
N	Cx	Tr	Pf	F	Ti	Cx	Tr	Pf	F	Ti
1				m	m					
2				m	m					a
3				m	m				a	a
4-5				m	m				ap	a
6-9				m	m				ap	p
10			m	m	m				(a)p	(p)
11			m	m	m			(p)	p	p
12			m	am	m			mp	(p)	(p)
13			m	m	m			mp		
14			m(p)	m	m			mp		
15			amp	m				mp		

short, bulge-like, single-segmented, with one anterior seta. Penis moderately long, bilobed, asetose. Female (Fig. 2D, F): first genital sternite as long as wide, with scattered setae; posterior margin deeply concave, with well-sclerotized medial bulge. Gonopods with broad first articles bearing 16–25 relatively long setae in three rows and usually 2+2 coniform spurs (rarely 3+2); second articles with 4–5 long ventral and 3–4 dorsolateral setae; third articles with 1–2 dorsolateral setae; claws moderately curved, bidentate, denticles subequal.

Re-evaluated diagnosis. Distinguished from all other morphologically similar species (i.e., taxa characterized by the presence of a subdistal, wart-like tibial process (tibial protuberance) on the dorsal side of the ultimate legs (L15) in males; see Discussion) by the following combination of characters: forcipules with 2+2 coxosternal teeth with setiform porodonts; antennae composed of 19–23 articles; up to 14 ocelli arranged in 2–3 irregular rows; Tömösváry's organ oval, medium-sized, larger than the surrounding ocelli; all tergites without a posterior triangular projections; L14 and L15 with two and one accessory claw, respectively; ultimate legs of males with a subdistal tibial wart-like process; female gonopod with 2+2 to 2+3 gonopodal spurs and a bidentate claw.

DISCUSSION

The findings presented here contribute to a better understanding of the biology of *Lithobius demavendicus*, particularly with regard to its distribution, morphology, ecology, taxonomy, and possible phylogeny. Certainly, the discovery of male specimens with ultimate legs present, females allowing for the observation of genital traits, and juveniles showing developmental morphological changes together provide a clearer and more complete understanding of species' morphology. The presented results of the species redescription suggest that Matic (1969) described *L. demavendicus* based most likely on a subadult specimen lacking the ultimate pair of legs. This conclusion can be reached by a straightforward comparison of selected morphological characters, such as body size, number of ocelli, and number of coxal pores, with the corresponding values in the examined specimens. The condition of the characters in the holotype presented by Matic (1969) corresponds to that of subadult specimens at the late praematurus/early pseudomaturus stage from the examined material (for details on stage determination, see Stojanović et al. 2023). As expected, most measurements and several numerical characters in the largest newly collected, unquestionably adult specimens show higher values compared to the holotype. Specifically, body length increases from 10 mm to almost 20 mm, number of antennal articles from 22 to 23, number of ocelli from 8–9 up to 14, and number of coxal pores from 1–2 to 3–5. However, the remaining diagnostic characters reported by Matic unequivocally confirm that these specimens belong to the same species.

The developmental anomalies recorded in forcipular teeth and spinulation in *Lithobius demavendicus* (Fig. 3) are generally not so uncommon; similar cases have been reported in other lithobiomorphs (e.g., Lewis 1987, 1988; García Ruiz 2002, 2006; Iorio 2008). Variation in the number of coxosternal teeth can be considered a common occurrence in some species due to developmental stage or intraspecific variability; however, in most species typically possessing 2+2 teeth, such variation is much rarer. A similar case of coxosternal teeth bifurcation was reported in some *Lithobius* species from Germany by Lindner (2008), presented at the 14th International Congress of Myriapodology in Görlitz, Germany. No consistent pattern in the occurrence of abnormalities was observed, as they did not appear to occur more frequently in specimens from any particular population or locality within the examined material. To the best of our knowledge, the only previously reported teratological case of a porodont in lithobiomorphs is that of Zapparoli (1994), a bifurcation of the right porodont in *Lithobius erdschiasius* Verhoeff, 1943 from Turkey. The occurrence of both types of porodonts (stout and setiform) within a single specimen (usually a character used to separate different species or even species groups) as observed in the female from Bazangan Cave (Fig. 3D), is exceptional and has not previously been documented.

Additionally, spine duplication (as shown in Fig. 3E) has not been reported in the literature as a distinct anomaly, likely because it occurs relatively frequently (pers. obs.) and is most likely associated with developmental changes. The presence of a double spine on the ventromesal side of the praefemur of leg 15 (double VpP spine) is recognized as an important taxonomic character for the identification of *Lithobius borealis* Meinert, 1868 (see Eason 1964; Koren 1992). This character is so well known that Zapparoli (2009) used the term "*L. borealis*-like spine" to describe a similar feature observed in a female of *Lithobius lapidicola* Meinert, 1872 collected from a cave in Sardinia. Eason (1964) previously reported this condition as common in *L. lapidicola*. More recently, Baba et al. (2025) reported cases of double spines in several specimens of *Lithobius peregrinus* Latzel, 1880 collected from a cave in Romania.

The relationship of *Lithobius demavendicus* to other similar taxa remains unclear, and its position is still insufficiently resolved. To address these uncertainties, further research is required, including the systematic collection of morphologically similar species across a wider geographic area encompassing Iran and neighboring countries, as well as the application of an integrative taxonomic approach combining morphological and molecular data. In this context, the term "morphologically similar species" should include taxa characterized by the presence of a subdistal tibial wart-like process (tibial protuberance) dorsally on the ultimate legs (L15) of males. This distinctive morphological feature occurs in a relatively limited number of species, most of which are distributed in Central Asia. In some species, the wart-like process is also present on the tibiae of the penultimate legs (L14) in males (e.g. *L. worogowensis* Eason, 1976, or *L. princeps* Stuxberg, 1876; see Eason 1976; Zalesskaja 1978) and should therefore be regarded as an important taxonomic character.

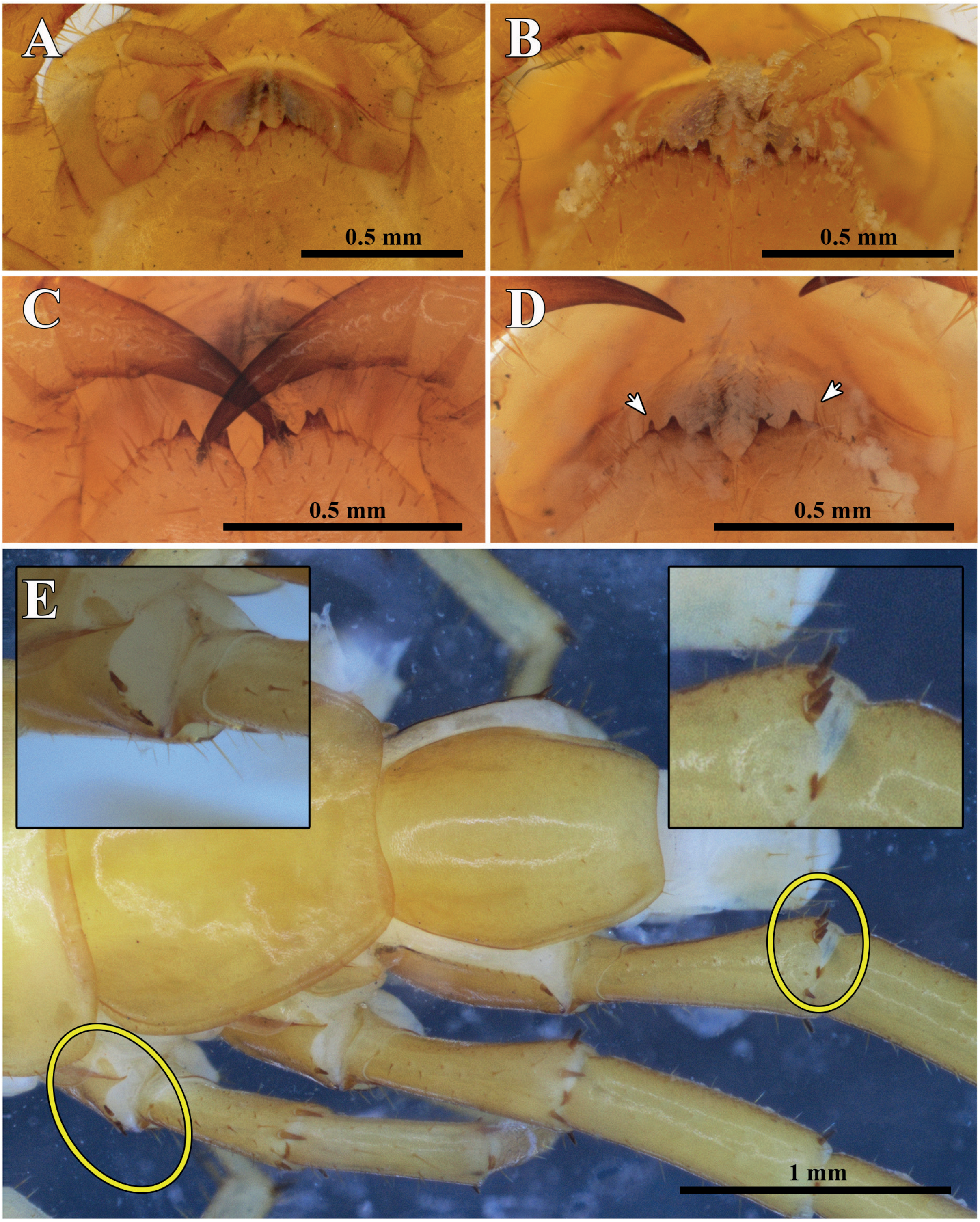

Fig. 3. Recorded anomalies in *Lithobius demavendicus* Matic, 1969. **A**, coxosternal teeth, female, ventral view (DM6, ZMFUM); **B**, coxosternal teeth, female, ventral view (DM4, IZB ChL139); **C**, coxosternal teeth, female, ventral view (KR3, ZMFUM); **D**, coxosternal teeth, female, ventral view (BA2, ZMFUM); **E**, terminal part of the body (unusual spinulation), male, dorsal view (DM5, ZMFUM). White arrows indicate different porodonts on the same specimen; yellow circles frame unusual spinulation.

Although its functional role is not yet fully understood, the tibial wart-like process is clearly associated with reproductive behavior (Kenning et al. 2017). Studies on the widespread European species *Lithobius nodulipes* Latzel, 1880 have demonstrated that this structure contains various sensory and glandular elements and, together with its sexual dimorphism, likely plays a role in reproduction, particularly during courtship and mating (Roithmair et al. 2023). It's worth mentioning that Eason (1997) noted that the wart-like growth on the tibia of *Australobius magnus* (Trotzina, 1894), known from Kazakhstan, Kyrgyzstan, and Nepal, is observed only in the largest males (i.e., the most sexually mature specimens). As in *L. demavendicus*, in which this structure is present from the PM stage onwards, this feature in *A. magnus* appears to be age-dependent, providing indirect evidence of its role in the reproductive process.

Bearing in mind the absence of the ultimate legs in the holotype, Matic (1969) considered *L. alaicus* Trotzina, 1894 (currently regarded as a junior synonym of *L. giganteus* Sseliwanoff, 1881; see Eason 1986) to be one of the morphologically most similar species to *L. demavendicus*. To distinguish between these two species, he referred to several minor differences in the number of antennal articles, the number of coxal pores, and leg spinulation. The same characters, albeit with greater confidence and including the number of ocelli, were used to separate *L. demavendicus* from a group of Central Asian species, such as *L. czekanowskii* Sseliwanoff, 1881 (currently a junior synonym of *L. princeps* Stuxberg, 1876), *L. giganteus*, *L. loricatus* Sseliwanoff, 1881 (currently *Disphaerobius loricatus* (Sseliwanoff, 1881), after Farzalieva et al. 2017), *L. brandtii* Sseliwanoff, 1881, *L. potanini* Sseliwanoff, 1881, and *L. porathi* Sseliwanoff, 1881.

Matic (1969) also confidently stated that *L. ferganensis* (Trotzina, 1894) can be readily distinguished from *L. demavendicus*. The discovery of a subdistal tibial wart-like process in the present redescription allows *L. demavendicus* to be easily separated from species lacking this structure, such as *L. giganteus* (including its junior synonym *L. alaicus*), *L. potanini*, and *L. porathi*. In contrast, *L. princeps* is characterized by the presence of a similar structure on the tibia of the penultimate legs (L14), as well as by a significantly higher number of ocelli and differences in female gonopods (see Eason 1976).

The remaining two species, *Lithobius brandtii* and *L. ferganensis*, are the only taxa mentioned by Matic (1969) that possess a subdistal tibial wart-like process on the ultimate legs and were compared with *L. demavendicus*. In addition to these two species, Zalesskaja (1978) listed seven further Asian species from the territory of the former USSR that share the same structure dorsally on the tibiae of the ultimate legs in males. These species are *L. javanicus* (Zalesskaja, 1978), *L. lenkoranicus* (Zalesskaja, 1976), *L. magnus* Trotzina, 1894 (a junior synonym of *Australobius magnus* (Trotzina, 1894); see Eason 1997), *L. praeditus* Zalesskaja, 1975, *L. sseliwanoffi* Garbowski, 1897, *L. tuberculipes* (Folkmanová, 1958), and *L. turkestanicus* (Attems, 1904) (= *L. curtipes turkestanicus* Attems, 1904).

Eason (1997) proposed the synonymization of the last three species listed above, along with *L. nodonotatus* (Verhoeff, 1943), as junior synonyms of *L. ferganensis* following a revision based on external morphology. An exception is *L. tuberculipes*, known from the Caucasus (Krasnodar region, Russia) and Turkey, which differs markedly in its smaller body size and proportionally reduced values of several characters, such as the number of ocelli, number of coxal pores, and leg spinulation. For the remaining taxa, however, their morphological similarity appears to justify the synonymizations proposed by Eason (1997).

Based on a specific combination of morphological characters, *Lithobius ferganensis*, which is distributed relatively close to Iran (Armenia, Kazakhstan, Kyrgyzstan, southern Russia (Stavropol), Tajikistan and Turkey; see Zalesskaja 1978; Dyachkov 2023), shows remarkable similarity to *L. demavendicus*. Both species also share similar ecological preferences: *L. ferganensis* is known from higher altitudes and has been frequently recorded from caves. The present study indicates that *L. demavendicus* has a significantly wider distribution than previously reported, as well as a broader range of habitat types and altitudinal distribution (approximately 1000–3200 m a.s.l.), similar to the literature data available for *L. ferganensis*. The two species can be distinguished morphologically by differences in leg spinulation (somewhat reduced in *L. ferganensis*) and in the shape of the female gonopodal claws; however, the most reliable diagnostic character is the absence of an accessory claw on the praetarsus of the ultimate legs in *L. ferganensis* (vs. a double claw in *L. demavendicus*).

Lithobius demavendicus can be readily distinguished also from species *Australobius magnus* and *L. praeditus* based on clear differences across the entire set of easily recognizable morphological characters. In contrast, the situation is more complex in the case of *L. brandtii*, *L. javanicus*, and *L. lenkoranicus*. Several additional species described after Matic (1969) and Zalesskaja (1978) should also be noted. These species possess a wart-like process on the tibia of the ultimate legs and show some similarities to *L. demavendicus*: *L. evsyukovi* Zuev, 2017 from the Caucasus, *L. monocoxaporus* Dyachkov & Farzalieva, 2018, and *L. trisspurus* Dyachkov & Farzalieva, 2018, both from South Kazakhstan.

The species *Lithobius brandtii*, known from Nikolayevsk-on-Amur (Khabarovsk Krai, southeastern Russia; see Zalesskaja 1978), also possesses an accessory claw on the praetarsus of the ultimate legs; however, in contrast to *L. demavendicus*, it is characterized by a smaller Tömösváry's organ, tridentate gonopodal claws in females, and somewhat reduced leg spinulation.

Further, *Lithobius javanicus*, a species known from Tajikistan and Uzbekistan (Zalesskaja 1978; Farzalieva 2006; Dyachkov 2022, 2023), is likewise morphologically similar, but differs in having fewer, depigmented ocelli, the absence of an accessory claw on the praetarsus of ultimate legs, and unidentate gonopodal claws in females.

The most similar species to *L. demavendicus*, and probably the most closely related, is *L. lenkoranicus*, known from Azerbaijan and Georgia (Zalesskaja 1978; Kiria et al. 2023). This species differs from *L. demavendicus* in its more reduced spinulation and in the specific morphology of the female gonopodal claws, which are also bidentate, but with a significantly enlarged inner tooth and a smaller, laterally positioned outer tooth. It is possible that *L. lenkoranicus* represents a junior synonym of *L. demavendicus*, which was described later; however, this remains uncertain, and further analyses, particularly those incorporating molecular data, are required to test this hypothesis.

Among the more recently described species, the most notable resemblance is shown by *L. evsyukovi*, known from the Caucasus (North Ossetia–Alania, Russia; see Zuev 2017). This species differs from *L. demavendicus* in having somewhat more pronounced spinulation, female gonopods with a tridentate claw, a somewhat larger wart-like process on the tibia of male ultimate legs (based on the original description; see Zuev 2017: 21, figs 24–25), and the absence of accessory claws on the L15 pretarsus. The species *L. monocoxaporus* and *L. trisspurus*, both from South Kazakhstan, also differ from *L. demavendicus* in lacking accessory claws on the L15 pretarsus. Additionally, *L. monocoxaporus* possesses a noticeably smaller number of ocelli, reduced spinulation, and fewer coxal pores than *L. demavendicus*, as well as a tridentate gonopodal claw in females, whereas in *L. trisspurus* the female gonopods are less setose and bear 3+3 gonopodal spurs.

Comparison with all related species discussed above reveals morphological differences that justify recognizing

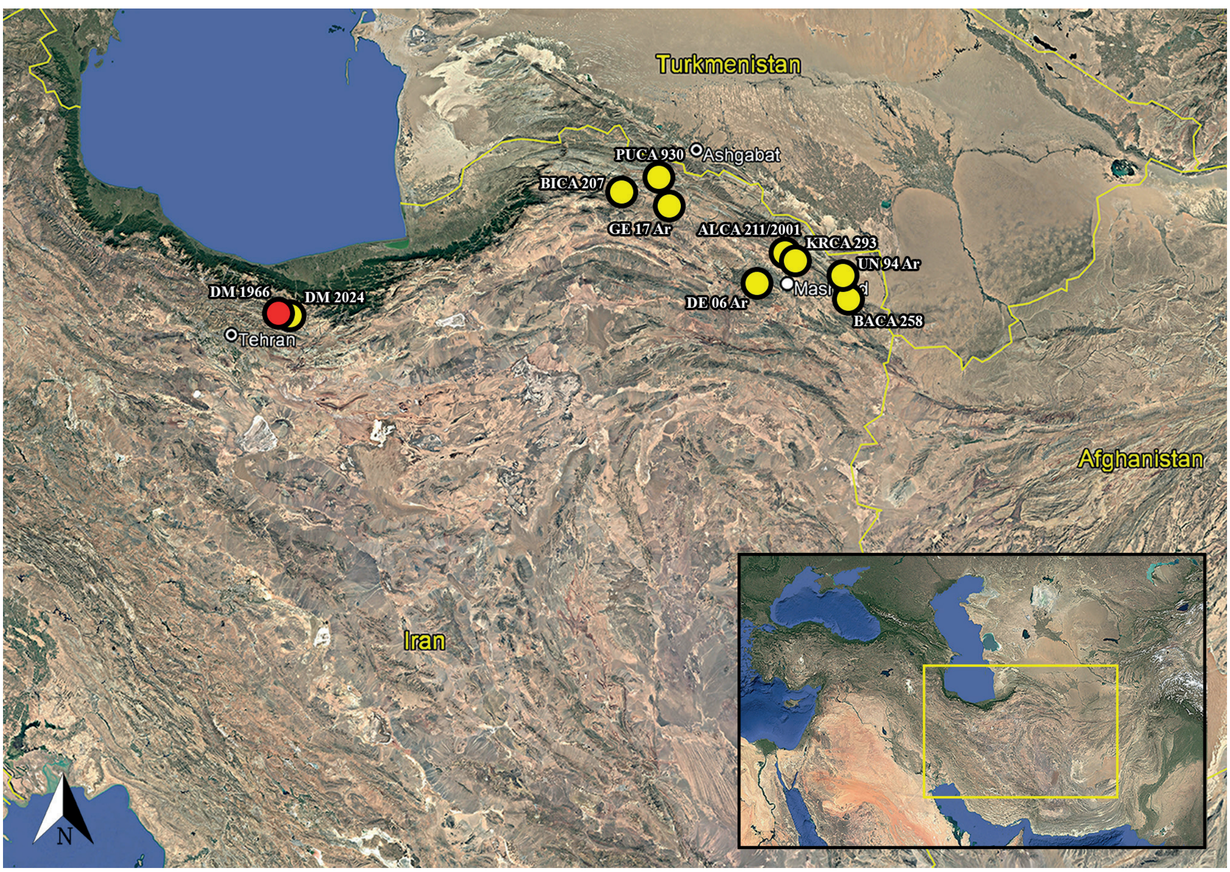

Fig. 4. Finding localities of *Lithobius demavendicus* Matic, 1969 (red circles = literature record; yellow circles = new records). Localities: ALCA 211 – AL Cave; BACA 258 – Bazangan Cave; BICA 207 – Bidak Cave; DE 06 Ar – Dehbar Village; DM 1966 – Damavand Mountain, literature record, collected in 1966; DM 2024 – Damavand Mountain, new records, collected in 2024; GE 17 Ar – Gelyan Village; KRCA 293 – Kardeh Cave; PUCA 930 – Poostin-Dooz Cave; UN 94 Ar – Mazdavand (Mozdouran) cave.

Lithobius demavendicus as a valid species and support Matic's original taxonomic decision. Nevertheless, we acknowledge that future integrative studies incorporating molecular data may yield results that challenge or refine this conclusion, as has been the case in some recent studies suggesting that hidden diversity is not unusual in centipedes, especially cave-dwelling ones (see Kos et al. 2023, 2025).

Finally, the present study indicates the occurrence of *L. demavendicus* in subterranean habitats, as this species is here recorded for the first time in such ecosystems. The cave specimens presented here were collected from different locations within caves (six in total), without any particularly noticeable pattern in the preference for specific microhabitats, except that all specimens were consistently found in dark zones with slightly increased substrate humidity, often in deeper parts of the caves. The frequent presence of this species in caves, although it was originally regarded as epigean, suggests its troglophilic character, i.e. a facultative association with subterranean ecosystems. In addition to specimens collected under rocks on Mount Damavand, one specimen from each of two localities was extracted from soil and leaf litter using a Berlese funnel. All these findings suggest that *L. demavendicus* has a broad ecological range.

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REFERENCES

Akkari N, Macek O, Edgecombe GD. 2024. Revision of some historical types of the genus *Lithobius* Leach, 1814 (Chilopoda, Lithobiomorpha) from the 1949/50 Austrian Iran Expedition, with new molecular data for *L. iranicus* Attems, 1951. Zootaxa. 5424(4):401–422. https://doi.org/10.11646/zootaxa.5424.4.1.

Baba ŞC, Giurginca A, Plăiașu R, Opran R, Mîrleneanu A, Pacioglu O. 2025. 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. Subterranean Biology. 52:69–102. https://doi.org/10.3897/subtbiol.52.154132.

Bonato L, Chagas Junior A, Edgecombe GD, Lewis JGE, Minelli A, Pereira LA, Shelley RM, Stoev P, Zapparoli M. 2016. ChiloBase 2.0 – A World Catalogue of Centipedes (Chilopoda). https://chilobase.biologia.unipd.it.

Bonato L, Edgecombe GD, Lewis JGE, Minelli A, Pereira LA, Shelley RM, Zapparoli M. 2010. A common terminology for the external anatomy of centipedes (Chilopoda). ZooKeys. 69:17–51. https://doi.org/10.3897/zookeys.69.737.

Dyachkov YuV. 2022. New records of lithobiid centipedes (Chilopoda: Lithobiomorpha) from Middle Asia. Acta Biologica Sibirica. 8:399–407. https://dx.doi.org/10.14258/abs.v8.e24.

Dyachkov YuV. 2023. On the Chilopoda fauna of the Pamir Mts, Tajikistan, with notes on the highest records of chilopod species in Middle Asia. Ecologica Montenegrina. 65:67–75. https://dx.doi.org/10.37828/em.2023.65.9.

Dyachkov YuV. 2024. *Lithobius* (*Monotarsobius*) *fomichevi* sp.n., a new species of lithobiid centipedes (Chilopoda: Lithobiomorpha) from Tajikistan, with a key to the Middle Asian species of the subgenus. Acta Biologica Sibirica. 10:303–316. https://doi.org/10.5281/zenodo.11098117.

Dyachkov YuV, Farzalieva GSh. 2018. Two new species of lithobiid centipedes (Chilopoda: Lithobiomorpha: Lithobiidae) from southern Kazakhstan. Arthropoda Selecta. 27(3):210–218. http://doi.org/10.15298/arthsel.27.3.03.

Eason EH. 1964. Centipedes of the British Isles. London, New York: Frederick Warne & Co Ltd.

Eason EH. 1976. The type specimens and identity of the Siberian species described in the genus *Lithobius* by Anton Stuxberg in 1876 (Chilopoda: Lithobiomorpha). Zoological Journal of the Linnean Society. 58(2):91–127. https://doi.org/10.1111/j.1096-3642.1976.tb00822.x.

Eason EH. 1986. On the synonymy of *Lithobius giganteus* Sseliwanoff 1881 and the taxonomic status of *Porobius* Attems 1926 (Chilopoda). Annalen des Naturhistorischen Museums, Wien. 87B:181–192.

Eason EH. 1997. On some Lithobiomorpha from the mountains of Kizghizia and Kazakhstan (Chilopoda). Arthropoda Selecta. 6(1-2):117–121.

Farzalieva GSh. 2006. New species of the lithobiid genus *Lithobius* (*Monotarsobius*) (Chilopoda: Lithobiomorpha: Lithobiidae) from eastern Kazakhstan. Arthropoda Selecta. 15(2):99–117.

Farzalieva GSh. 2018. *Lithobius* (*Monotarsobius*) *tanagolus* sp.n., a new lithobiid species (Chilopoda, Lithobiomorpha) from southern Siberia, with remarks on the closely related *L.* (*M.*) *holstii* (Pocock, 1895). Arthropoda Selecta. 27(1):22–30. https://doi.org/10.15298/arthsel.27.1.02.

Farzalieva GSh, Nefediev PD, Tuf IH. 2017. Revision of *Disphaerobius* Attems, 1926 (Chilopoda: Lithobiomorpha: Lithobiidae: Pterygoterginae), a centipede genus with remarkable sexual dimorphism. Zootaxa. 4258(2):121–137. https://doi.org/10.11646/zootaxa.4258.2.2.

Folkmanová B. 1940. O novýc balkánských jeskynních Chilopodech ve sberech DR. K. Absolona. Species novae Chilopodorum cavernicolorum Balcanicorum in coll. Dr. K. Absolon. Vestnik Ceskoslovenské Zoologické Spolecnosti v Praze. 8:47–58.

Ganske AS, Vahtera V, Dányi L, Edgecombe GD, Akkari N. 2021. Phylogeny of Lithobiidae Newport, 1844, with emphasis on the megadiverse genus *Lithobius* Leach, 1814 (Myriapoda, Chilopoda). Cladistics. 37(2):162–184. https://doi.org/10.1111/cla.12431.

García Ruiz A. 2002. Diversos casos de estructuras anormales observadas en quilópodos (Myriapoda, Chilopoda) de Andalucia (España) [Various cases of abnormal structures observed in chilopods (Myriapoda, Chilopoda) from Andalusia (Spain)]. Boletin de la Sociedad Entomológica Aragonesa. 31:199–200.

García Ruiz A. 2006. Effects on a community of centipedes (Chilopoda) of cadmium accidentally released. Norwegian Journal of Entomology. 53:191–194.

Iorio É. 2008. Contribution à l'étude des chilopodes (Chilopoda) des Alpes–Maritimes, incluant une clé d'identification des lithobiomorphes Lithobiidae de Provence–Alpes–Côte d'Azur [Contribution to the study of chilopods (Chilopoda) of the Alpes-Maritimes, including an identification key to the lithobiomorphs Lithobiidae of Provence–Alpes–Côte d'Azur]. Bulletin de la Société Linnéenne de Provence. 59:127–190.

Iorio É, Racine A. 2022. Description of an unexpected troglobitic species of the genus *Lithobius* Leach, 1814 from a Pyrenean cave in France, with a synthesis on the troglobitic centipedes from Pyrenees (Myriapoda: Chilopoda). Annales de la Société Entomologique de France (N.S.). 58(3):265–280. https://doi.org/10.1080/00379271.2022.2089233.

Iorio É, Racine A, Jacquemin G, Zapparoli M. 2025. Description of a new *Lithobius* species from southern France, with a character observed for the first time in the European lithobiids (Chilopoda: Lithobiomorpha). Annales de la Société entomologique de France (N.S.). 61(1):47–61. https://doi.org/10.1080/00379271.2025.2461090.

Iorio É, Voigtländer K. 2019. The Lithobiomorpha of the continental Iberian Peninsula (Chilopoda): new data, description of a new species of the genus *Lithobius* (s. str.), checklist and identification key. Mémoires de la Société Linnéenne de Bordeaux. 18:1–98.

Johns PM. 2010. Phylum Arthropoda. Myriapoda: centipedes, millipedes, pauropods, and symphylans. In: Gordon DP, editor. New Zealand inventory of biodiversity. Volume 2. Kingdom Animalia. Chaetognatha, Ecdysozoa, Ichnofossils. Christchurch: Canterbury University Press. p. 90–97.

Kenning M, Müller CHG, Sombke A. 2017. The ultimate legs of Chilopoda (Myriapoda): a review on their morphological disparity and functional variability. PeerJ. 5:e4023. https://doi.org/10.7717/peerj.4023.

Kiria E, Barjadze S, Tuf IH. 2023. Checklist of Georgian centipedes (Myriapoda: Chilopoda). Caucasiana. 2:177–188. https://doi.org/10.3897/caucasiana.2.e108535

Koren A. 1992. Die Chilopoden-Fauna von Kärnten und Osttirol. Teil 2. Lithobiomorpha. Carinthia II. 51:3–139.

Kos A, Delić T, Kos I, Kozel P, Polak S, Zagmajster M. 2023. The overview of lithobiomorph centipedes (Chilopoda, Lithobiomorpha) from caves of Slovenia. Subterranean Biology. 45:165–185. https://doi.org/10.3897/subtbiol.45.101430.

Kos A, Akkari N, Delić T, Komerički A, Stojanović D, Zagmajster M. 2025. Disentangling the cave centipede *Lithobius stygius* species complex through molecular phylogenetics and redescription of *L. stygius* s. str. Scientific Reports. 15:42687. https://doi.org/10.1038/s41598-025-26880-7.

Lewis JGE. 1987. On some structural abnormalities in *Lithobius* and *Cryptops* (Chilopoda) and their possible significance. Bulletin of the British Myriapod Group. 4:3–6.

Lewis JGE. 1988. Abnormal coxopleural teeth in *Lithobius forficatus* L. Bulletin of the British Myriapod Group. 5:36–37.

Lindner N. 2008. Some structural abnormalities in centipedes and millipedes. In: Xylander W, Voigtländer K, editors. 14th International Congress of Myriapodology. Abstract Book. 117.

Matic Z. 1969. Contributo alla conoscenza dei Lithobiidae dell'Iran (Chilopoda Lithobiomorpha) [Contribution to the knowledge of the Lithobiidae of Iran (Chilopoda Lithobiomorpha)]. Fragmenta Entomologica. 6(2):87–114.

Matic Z, Stentzer I. 1977. Beitrag zur Kenntnis der Hundertfüssler (Chilopoda) aus Slowenien. Biološki Vestnik. 25:55–62.

Mercurio RJ. 2010. An annotated catalog of centipedes (Chilopoda) from the United States of America, Canada and Greenland (1758–2008). Bloomington: Xlibris Corporation.

Pei S, Ma H, Liu H, Lu Y, Liang K. 2021. *Lithobius* (*Monotarsobius*) *femoratus* sp.n., a new centipede species from China (Chilopoda: Lithobiomorpha: Lithobiidae). Arthropoda Selecta. 30(4):497–501. https://doi.org/10.15298/arthsel.30.4.05.

Pei S, Ma H, Liu H, Liang K, Lu Y. 2022. *Lithobius* (*Monotarsobius*) *aterrimus* sp.n., a new centipede species from China (Chilopoda: Lithobiomorpha: Lithobiidae). Arthropoda Selecta. 31(2):166–172. https://doi.org/10.15298/arthsel.31.2.04.

Roithmair Z, Edgecombe GD, Wanninger A, Akkari N. 2023. Sexually dimorphic characters of the ultimate legs in lithobiid centipedes (Myriapoda, Chilopoda, and Lithobiomorpha): Morphology and implications for reproductive behavior. Journal of Morphology. 284(2):e21549. https://doi.org/10.1002/jmor.21549.

Serra Sorribes A. 2024. *Lithobius hemihydrobius* (Chilopoda, Lithobiomorpha) una nova espècie cavernícola amb comportament semiaquàtic [*Lithobius hemihydrobius* (Chilopoda, Lithobiomorpha), a new cave-dwelling species with semiaquatic behavior]. Publicacions del Centre de Recursos de Biodiversitat Animal. 20:1–2.

Stojanović DZ, Antić DŽ, Makarov SE. 2021. A new cave-dwelling centipede species from Croatia (Chilopoda: Lithobiomorpha: Lithobiidae). Revue Suisse de Zoologie. 128(2):425–438. https://doi.org/10.35929/RSZ.0054.

Stojanović DZ, Vujić VD, Jovanović ZS, Milovanović JZ, Dudić BD, Ilić BS, Makarov SE. 2023. Morphological variation during post-embryonic development in the centipede *Lithobius melanops*: traditional and geometric morphometrics approaches. Contributions to Zoology. 92(3):316–348. https://doi.org/10.1163/18759866-bja10044.

Thofern D, Dupérré N, Harms D. 2021. An annotated type catalogue of the centipedes (Myriapoda: Chilopoda) held in the Zoological Museum Hamburg. Zootaxa. 4977(1):1–103. https://doi.org/10.11646/zootaxa.4977.1.1.

Vega-Román E, Ruiz VH. 2018. Catalogue of Chilean centipedes (Myriapoda, Chilopoda). Soil Organisms. 90(1):27–37.

Verhoeff KW 1943. Über Chilopoden aus westbalkanischen Höhlen. Zeitschrift für Karst- und Höhlenkunde. 1942-43(3):133–152.

Voigtländer K. 2007. The life cycle of *Lithobius mutabilis* L. Koch, 1862 (Myriapoda: Chilopoda). Bonner zoologische Beiträge. 55(1):9–25.

Zalesskaja NT. 1978. Определитель многоножек-костянок СССР (Chilopoda, Lithobiomorpha). Москва: Издательство „Наука". [Identification key to the lithobiid centipedes of the USSR (Chilopoda, Lithobiomorpha). Moscow: Nauka Publishers].

Zapparoli M. 1994. Chilopodi di Turchia. IV. Specie del genere *Lithobius* Leach 1814 s. str. (Chilopoda Lithobiomorpha) [Chilopods of Turkey. IV. Species of the genus *Lithobius* Leach, 1814 s. str. (Chilopoda, Lithobiomorpha)]. Fragmenta Entomologica. 25(2):175–256.

Zapparoli M. 2003. The present knowledge on the European fauna of Lithobiomorpha. Bulletin of the British Myriapod and Isopod Group. 19:20–41.

Zapparoli M. 2009. An annotated catalogue of the epigeic and cave centipedes (Chilopoda) of Sardinia. Zootaxa. 2318:56–168. https://doi.org/10.11646/zootaxa.2318.1.6

Zapparoli M, Edgecombe GD. 2011. Chilopoda – taxonomic overview: Order Lithobiomorpha. In: Minelli A, editor. Treatise on Zoology – Anatomy, Taxonomy, Biology. The Myriapoda. Volume I. Leiden: Brill. p. 371–389.

Zarei R, Rahimian H, Mirmonsef H, Bonato L. 2020. Geophilomorpha from Alborz Mountains and a checklist of Chilopoda from Iran. Zootaxa. 4780(1):132–146. https://doi.org/10.11646/zootaxa.4780.1.6.

Zuev RV. 2017. Two new species of lithobiid centipedes (Chilopoda: Lithobiomorpha) from the northern Caucasus, Russia. Arthropoda Selecta. 26(1):15–24. https://doi.org/10.15298/arthsel.26.1.03.