

Original paper

Four new species of *Unixenus* Jones, 1944 (Diplopoda: Penicillata: Polyxenidae) from the mid-central coastal region and two islands off the coast of Vietnam

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Summary. Four new species of *Unixenus* Jones, 1944, *U. binhduinhensis* **sp. nov.**, *U. lysonensis* **sp. nov.**, *U. phanrangensis* **sp. nov.** and *U. phuquyensis* **sp. nov.**, are described from grassland habitats in the mid-central coastal region of Vietnam and two offshore islands. All four species share the diagnostic morphological characters typical of *Unixenus*. Due to their similar body size, overall morphology, and partially overlapping geographic distributions, these taxa are morphologically cryptic and difficult to distinguish using traditional taxonomic characters. Morphological comparisons suggest two closely related species groups with mainland coastal and offshore island distributions. However, molecular phylogeny reveals clear genetic differentiation among all four taxa, supporting their recognition as distinct species. This study also highlights the presence of cryptic diversity within *Unixenus* and demonstrates the importance of integrative taxonomy, incorporating molecular phylogenetics, for resolving species boundaries in morphologically conservative penicillate millipede lineages from Southeast Asia. A key to the Vietnamese species of *Unixenus* is also included in this study.

Key words: Penicillate millipedes, morphology, integrative taxonomy, cryptic diversity, phylogenetic analysis, coastal grassland habitat.

INTRODUCTION

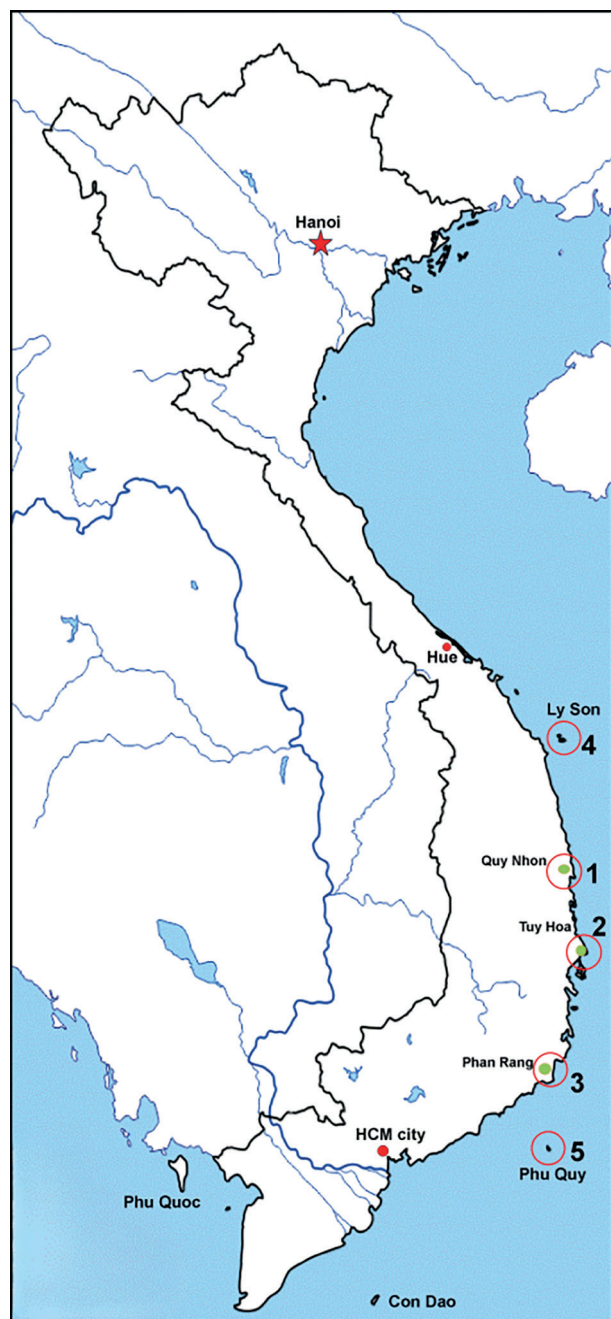
The genus *Unixenus* (Diplopoda, Polyxenidae) was established by Jones (1944) under the original name *Monoxenus* Jones, 1937 with *Monoxenus padmanabhii* Jones, 1937 from southern India designated as the type species. However, the name *Monoxenus* was already assigned to a genus in the family Cerambycidae (Coleoptera), so the genus was subsequently renamed *Unixenus* Jones, 1944. Species of *Unixenus* are widely distributed across Africa, Madagascar, India, Southeast Asia, and Australia (Huynh and Veenstra 2023). To date, 15 species have been described prior to this study.

In the mid-central coastal region of Vietnam and on two adjacent offshore islands (Fig. 1), four species of *Unixenus* Jones, 1944 were collected from grassland habitats (Fig. 2).

These species exhibit highly similar body lengths and overall morphology, which can lead to the assumption that they are a single species. Consequently, species-level identification based solely on traditional morphological characters is problematic. To overcome this morphological conservatism, molecular analyses provide a powerful tool for detecting clear genetic divergence among these lineages, supporting their recognition as distinct species within *Unixenus*. The presence of multiple morphologically similar yet genetically distinct species along the Vietnamese coast indicates that *Unixenus* is a morphologically conservative genus with substantial cryptic diversity. Accordingly, this study aims to resolve species boundaries within *Unixenus* from the mid-central region of Vietnam using an integrative taxonomic approach that combines detailed morphological examination with molecular evidence.

MATERIAL AND METHODS

Penicillate millipedes were collected from grassland habitats growing among coastal rocky outcrops across three locations in mid-central coastal region of Vietnam and from two adjacent offshore islands: (1) Quy Nhon, (2) Tuy Hoa, (3) Phan Rang, (4) Ly Son Islands (28 km off Sa Ky, Quang Ngai), and (5) Phu Quy Island (120 km off Phan Thiet). Specimens were obtained using a beating method, striking grass tussocks to dislodge individuals onto a tray. Collected specimens were preserved in 100% ethanol, although some



individuals were kept alive for photography using an Olympus TG6 camera. A map of Vietnam was obtained from d-maps.com and annotated with the locations where the specimens were collected (Fig. 1).

Morphological studies. Specimens were examined and identified as *Unixenus* species (Polyxenidae) from these five locations. Body length was measured from head to telson, excluding caudal trichomes, using an Olympus BX43 compound microscope with a DP22 camera and a Nikon SMZ800 stereoscope with an Infinity I camera, and sex was identified by reproductive organs on the second leg coxae. For taxonomic drawings, specimens were slide-mounted using a modified Short and Huynh (2010) staining technique allowing DNA extraction. Specimens preserved in 80% ethanol were transferred to 100% ethanol on glass slides, where trichomes from the body, pleural projections, and caudal region were sequentially removed and mounted on separate slides for structural examination. Slides were air-dried and mounted in DPX for analysis of trichomes and caudal hooks.

Stripped specimens of *Unixenus* were subjected to DNA extraction using the Invisorb Spin Forensic Kit, following incubation at room temperature for 12 hours and digestion at 56 °C for 1 hour. Extracted DNA was retained for genomic study. Remaining cuticles were mounted for morphometric analysis (Huynh and Veenstra 2015) and prepared for scanning electron microscopy (SEM) following the method of Huynh and Veenstra (2018a). Holotypes and paratypes of *Unixenus* were deposited in the Institute of Ecology and Biological Resources (IB), Vietnam.

Genetic studies. Genomic DNA was extracted from the number available *Unixenus* specimens collected at five locations; their DNA quantity was measured using a NanoDrop 1000 Spectrophotometer. Two genes were sequenced: *18S rRNA* (primers 1F/5R; White et al. 1990) and *CO1* (primers dgLCO1490/dgHCO2198; Meyer 2003). The *18S* marker was used for arthropod phylogeny and species differentiation within Polyxenida (Huynh and Veenstra 2018a, b, 2022; Huynh et al. 2023), while *CO1* followed the Barcode of Life (<https://www.boldsystems.org>) standard for species identification. PCR followed using the method of Huynh and Veenstra (2022). Sequences of these new *Unixenus* species were deposited in GenBank (<https://www.ncbi.nlm.nih.gov>) (*Unixenus binhdinhensis* sp. nov.: 18S – PX592948; CO1 – PX530354, *Unixenus phanrangensis* sp. nov.: 18S – PX592950; CO1 – PX530352, *Unixenus lysonensis* sp. nov.: 18S – PX592949; CO1 – PX530353, *Unixenus phuquyensis* sp.

Fig. 1. Map of Vietnam showing five collection sites in the mid central coastal region: three mainland coastal localities, Quy Nhon (Location 1), Tuy Hoa (Location 2) and Phan Rang (Location 3), and two offshore islands, the Ly Son Islands (Location 4) and Phu Quy Island (Location 5). (Map source: d-maps.com)

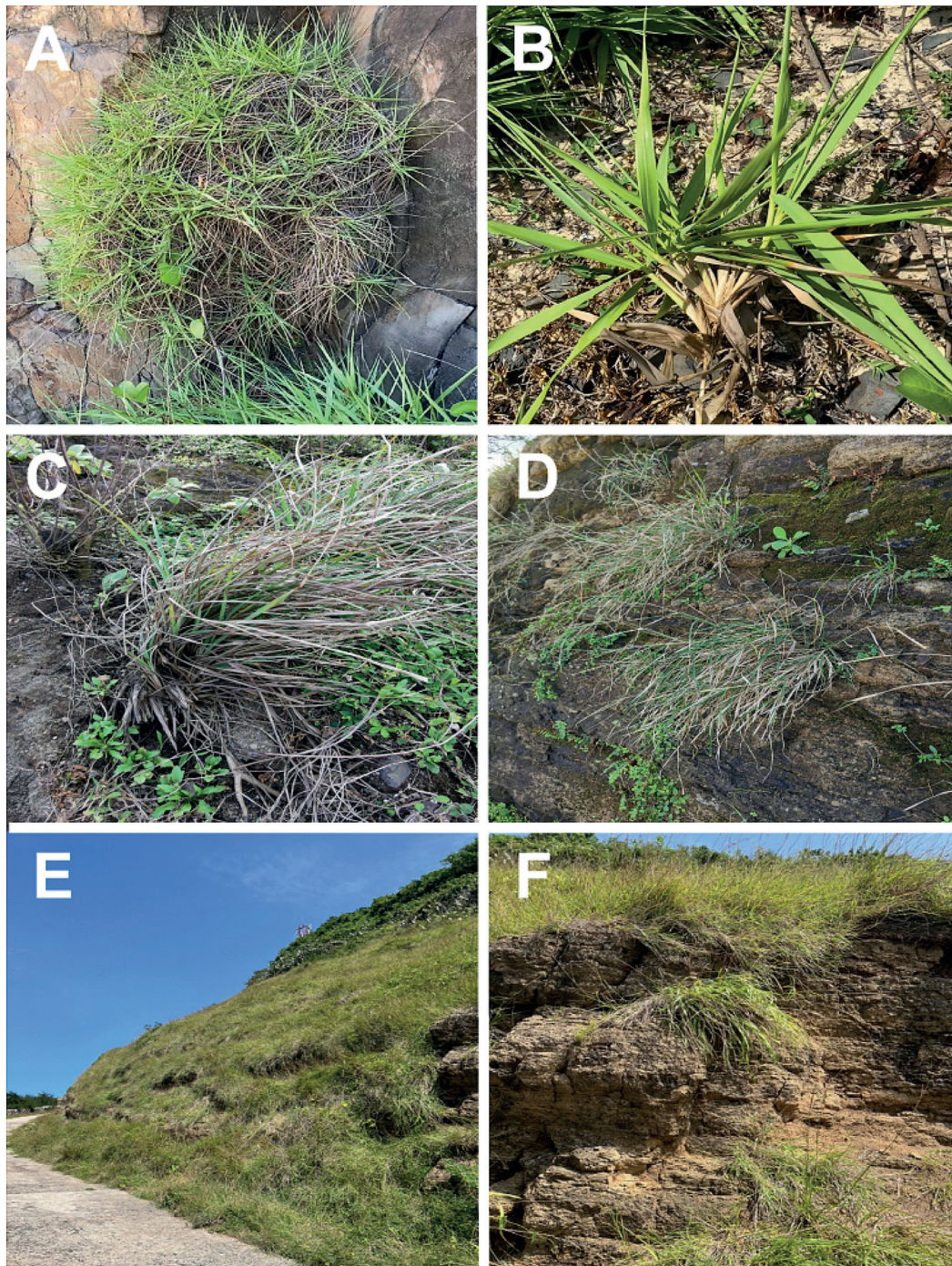


Fig. 2. Penicillate millipedes were collected from representative grass habitats at each site. **A**, grass species from coastal location 1 (Quy Nhon) and location 2 (Tuy Hoa), growing among rocky outcrops and forming dense clumps with hard, sharp leaves; **B**, detail of the tough leaf grass species at locations 1 and 2; **C**, *Poa* species from location 3 (Phan Rang); **D**, *Poa* species from location 4 (Ly Son Islands); **E–F**, grass habitat from location 5 (Phu Quy Island); **C–E**, show *Poa* species characterized by soft, elongated leaves.

nov.: 18S – PX592951; COI – PX530355). BLAST searches identified related taxa; sequences were aligned in BioEdit (Hall 1999), and phylogenetic trees were generated using MEGA 11 (Kumar et al. 2021) with maximum likelihood and bootstrap support (Fig. 17A, B). GenBank accession numbers for the sequences from penicillate millipede species and outgroups are listed in Table 1.

RESULTS

Taxonomy

Class Diplopoda de Blainville in Gervais, 1844

Subclass Penicillata Latreille, 1831

Order Polyxenida Verhoeff, 1934

Family Polyxenidae Lucas, 1840

Genus *Unixenus* Jones, 1944

Monoxenus Jones, 1937: 138; Silvestri 1948: 216.

Unixenus Jones, 1944: 94; Nguyen Duy-Jacquemin and Condé 1967: 68.

Type species. *Unixenus padmanabhahi* (Jones, 1937)

Diagnosis. The genus can be distinguished from other polyxenid genera by the following character combination: Eight ommatidia on each eye, antennomere VI with three thick bacilliform sensilla, a setiform sensillum situated anteriorly between two thick bacilliform sensilla, a conical sensillum located posteriorly. Labral surface with papillae gradually reducing in size toward posterior margin. Lateral palp of gnathochilarium with 13 conical sensilla, 1.5 times longer than medial palp. Tergal trichomes forming two latero-posterior clusters on each side of midline, with central gap, posterior rows continuous or interrupted medially. Tarsus II with setiform seta (Fig. 3A–I).

Species included: 19

Table 1. GenBank accession numbers for partial 18S rRNA and COI gene sequences of the four newly described *Unixenus* species, other penicillate millipedes, and the outgroup taxa.

Family	Genus	Species	Collecting location	18S rRNA	COI
Polyxenidae	<i>Monographis</i>	<i>Monographis condorensis</i>	Vietnam	MH729072	MH737736
		<i>Monographis dongnaiensis</i>	Vietnam	KP255446	–
		<i>Monographis phuquocensis</i>	Vietnam	MG210571	MG279505
		<i>Monographis queenslandica</i>	Australia	KF147166	MG279506
		<i>Monographis konkakinensis</i>	Vietnam	ON604951	ON627711
		<i>Monographis tamdaoensis</i>	Vietnam	ON604952	ON627712
		<i>Monographis panhai</i>	Thailand	OR075887	OR069398
		<i>Monographis thatsonensis</i>	Vietnam	ON604953	ON627713
	<i>Polyxenus</i>	<i>Polyxenus fasciculatus</i>	Europe	AF173235	MN073933
		<i>Polyxenus lagurus</i>	Europe	MF592763	MF746324
	<i>Unixenus</i>	<i>Unixenus binhdinhensis</i> sp. nov.	Vietnam	PX592948	PX530354
		<i>Unixenus corticolus</i>	Australia	MG283313	MG279507
		<i>Unixenus intragramineus</i>	Vietnam	MG210572	MG279508
		<i>Unixenus karajinensis</i>	Australia	MF592754	–
		<i>Unixenus lysonensis</i> sp. nov.	Vietnam	PX592949	PX530353
		<i>Unixenus mjobergi</i>	Australia	MF592755	–
		<i>Unixenus moniqueae</i>	Vietnam	MH729073	MH737737
		<i>Unixenus mossmanus</i>	Australia	MT656009	–
		<i>Unixenus phanrangensis</i> sp. nov.	Vietnam	PX592950	PX530352
		<i>Unixenus phuquyensis</i> sp. nov.	Vietnam	PX592951	PX530355
	Outgroups	<i>Sphaeromimus musicus</i>	Africa	FJ409961	–
		<i>Procyliosoma leae</i>	Australia	FJ409955	FJ409910
		<i>Glomeridella minima</i>	Europe	–	JN271878

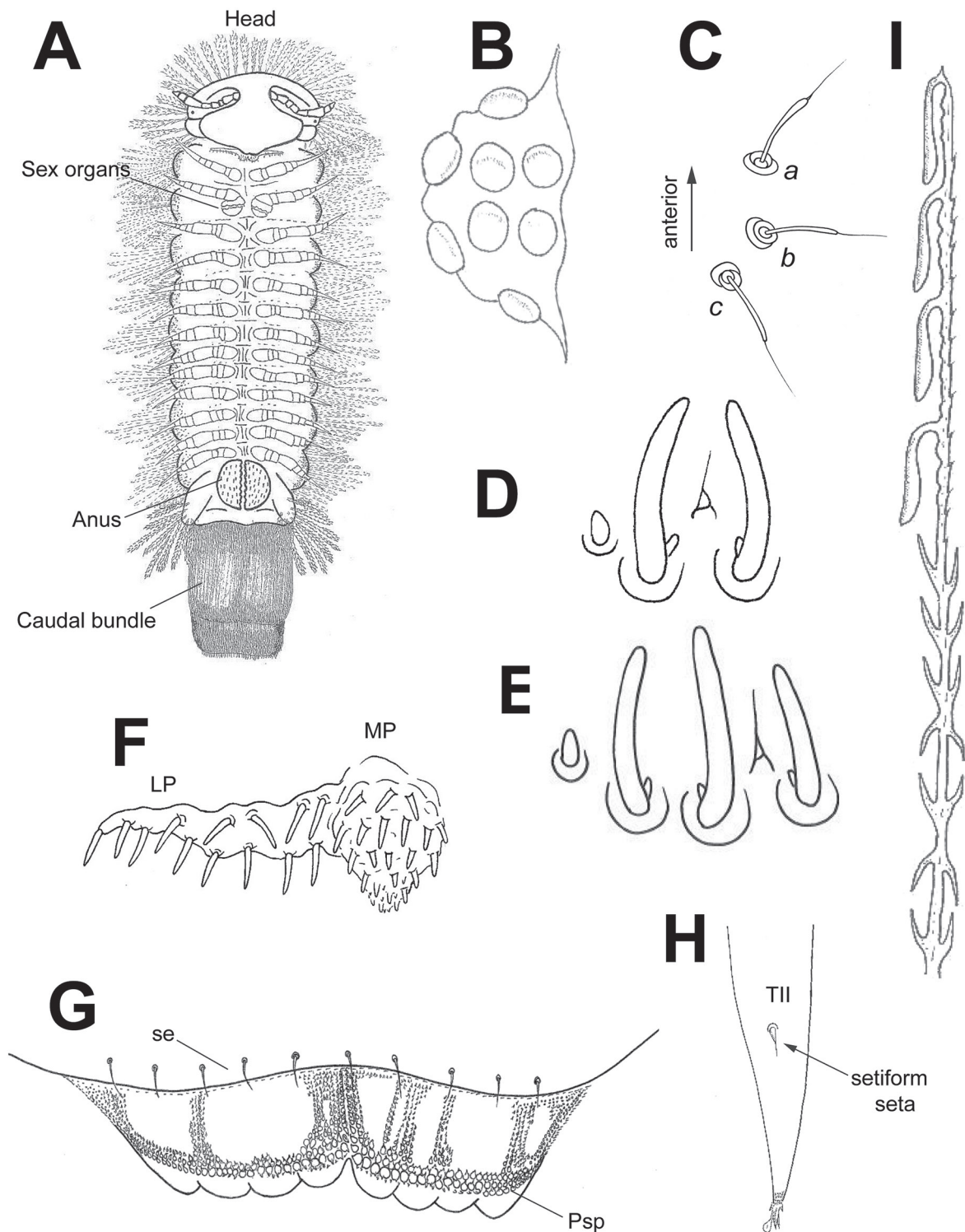


Fig. 3. General diagnosis characteristics of *Unixenus* species (Polyxenidae). **A**, ventral view of an adult with 13 pairs of legs; **B**, eye with eight ommatidia (left side); **C**, trichobothria *a*, *b*, and *c*; **D**, a typical arrangement of sensilla on antennomere VII; **E**, sensilla on antennomere VI; **F**, gnathochilarium with a lateral palp (LP), and medial palp (MP); **G**, clypeo-labrum with papillae (Psp) on the labral surface, setae (se) at the posterior margin; **H**, leg segment tarsus II with the setiform seta indicated by an arrow; **I**, caudal trichome with serial backward hooks. (Not to scale)

1. *Unixenus attemsi* Nguyen Duy-Jacquemin & Condé, 1967 (Australia)
2. *Unixenus barrabaensis* Short & Huynh, 2013 (Australia)
3. *Unixenus binhdinhensis* **sp. nov.**
4. *Unixenus broelemanni* (Condé & Jacquemin, 1962) (Madagascar)
5. *Unixenus carnarvonensis* Short & Huynh, 2013 (Australia)
6. *Unixenus corringlensis* Short & Huynh, 2013 (Australia)
7. *Unixenus corticolus* Short & Huynh, 2011 (Australia)
8. *Unixenus intragramineus* Huynh & Veenstra, 2018 (Vietnam)
9. *Unixenus karajinensis* Short & Huynh, 2011 (Australia)
10. *Unixenus lysonensis* **sp. nov.**
11. *Unixenus mjoebergi* (Verhoeff, 1924) (Australia)
12. *Unixenus moniqueae* Huynh & Veenstra, 2020 (Vietnam)
13. *Unixenus mossmanus* Huynh & Veenstra, 2021 (Australia)
14. *Unixenus myallensis* Short & Huynh, 2013 (Australia)
15. *Unixenus padmanabhahi* (Jones, 1937) (India)
16. *Unixenus phanrangensis* **sp. nov.**
17. *Unixenus phuquyensis* **sp. nov.**
18. *Unixenus thailandicus* Huynh et al., 2023 (Thailand)
19. *Unixenus vuillaumei* (Condé & Terver, 1963) (Ivory Coast)

***Unixenus binhdinhensis* sp. nov.**

Figs 4A, 5–8

Material examined. Holotype adult ♂ (IB-Myr 1044), Vietnam, Dry Rock Islet (Hon Kho), Hai Dong Village near Quy Nhon City, Binh Dinh Province (recently renamed Gia Lai Province), (lat 13.772178°, long 109.293114°; elevation 5 m), overhanging grass tussocks growing among rocks.

Paratypes, adult ♂ and adult ♀ (IB-Myr 1044), collected with the holotype, 13 July 2022, leg. C. Huynh.

Three additional specimens (adult ♀♀) (IB-Myr 1045), Vietnam, Dai Lanh Cape (lat 12.896572°, long 109.455308°; elevation 50 m), 35 km south of Tuy Hoa City, Phu Yen Province (now Dak Lak Province), similar coastal habitat to holotype, 6 February 2023, leg. C. Huynh; (Figs 1, 2A, B, 4A). All specimens mounted on slides.

Diagnosis. Body is light yellowish-brown. Antennomere VI with an anterior setiform sensillum, three thick bacilliform sensilla, intermediate sensillum distinctly placed distally, one posterior conical sensillum (Fig. 6C). Leg setae biarticulated with ridged funicle (Fig. 7B). Telotarsus with anterior setiform process equal in length to claw (Fig. 7E).

Description. Holotype male body: 1.8 mm; paratypes: 1.6–2.0 mm in both sexes; caudal bundle: 0.5 mm.

Colouration. Body is light yellowish-brown; the trichomes of pleural projections are dark black. Caudal bundle of trichomes is silvery black (Fig. 4A).

Head. Posterior vertex trichomes with 2 rows of equal-sized trichome sockets: anterior and posterior rows are oblique with a narrow gap between them. Holotype with 13 trichome sockets (L), and 12 (R) in anterior row, 7 in both posterior rows (Figs 5A, 8A). Paratypes 12–13 sockets in anterior rows, 7–9 sockets in posterior rows. Trichobothria. Three thin sensory hairs with narrow, cylindrical funicles; basal sockets equal in size and arranged in an isosceles triangular configuration, with equal distances *ab* and *bc* (Figs 3C, 8A). Clypeo-labrum. Labral surface with papillae gradually reducing in size toward posterior margin. 11 setae at posterior margin of labrum (paratypes with 10–11 setae). These setae are quite short compared to the labrum width (Figs 8E, F). Gnathochilarium. Lateral palp 1.5 times medial palp; 13 conical sensilla on the lateral palp (Figs 3F, 8F). Antennae. Antennomere VI with one anterior setiform sensillum followed by three thick bacilliform sensilla, with the intermediate bacilliform sensillum distinctly positioned distally; one conical sensillum located posteriorly in the structure (Figs 6A, C, 8B, D). Antennomere VII with a conical sensillum in posterior position, followed by 2 thick bacilliform sensilla (Ta and Tp), a setiform sensillum (s) in between these bacilliform sensilla (Figs 6B, 8C).

Body. 13 pairs of legs. Tergites typical of Polyxenidae: 10 tergal segments with 9 pleural projections, excluding the telson and caudal bundle. Collum – the first tergite with two ovate plates of trichome sockets, each pointed medially, separated by a wide gap, posterior socket rows converge posteriorly, leaving a small median gap; and a pair of lateral protuberances (Lp), bearing 6–7 sockets (Fig. 5B). Tergites II–X each with a pair of anterolateral pleural projections. Trichome sockets on these tergites form two latero-posterior, clusters on each side; posterior rows are slightly curved upward toward the midline, leaving a small weakly defined median gap (Figs 5C, 8A). The final tergite (X) bears denser, smaller trichome sockets (Fig. 5D).

Legs. Composed of eight segments: coxa, trochanter, prefemur, femur, postfemur, tibia, tarsus I, and tarsus II, following the terminology of Manton (1956). Legs 1–2 lack a trochanter (Fig. 7A), and leg 1 additionally lacks tarsus I. **Chaetotaxy.** Legs 1–13, coxae I–II each bear 1–2 biarticulated setae with a ridged funicle, whereas coxae III–XIII bear 2–3 such setae. The prefemur and femur each possess a similar seta; the femur also bears a setiform sensillum in the intermedio-posterior position. The postfemur and tibia each carry one setiform sensillum. Tarsus I without setae, tarsus II with a single setiform sensillum (Figs 7A–D).

Telotarsus. Claw slender, with an anterior lateral

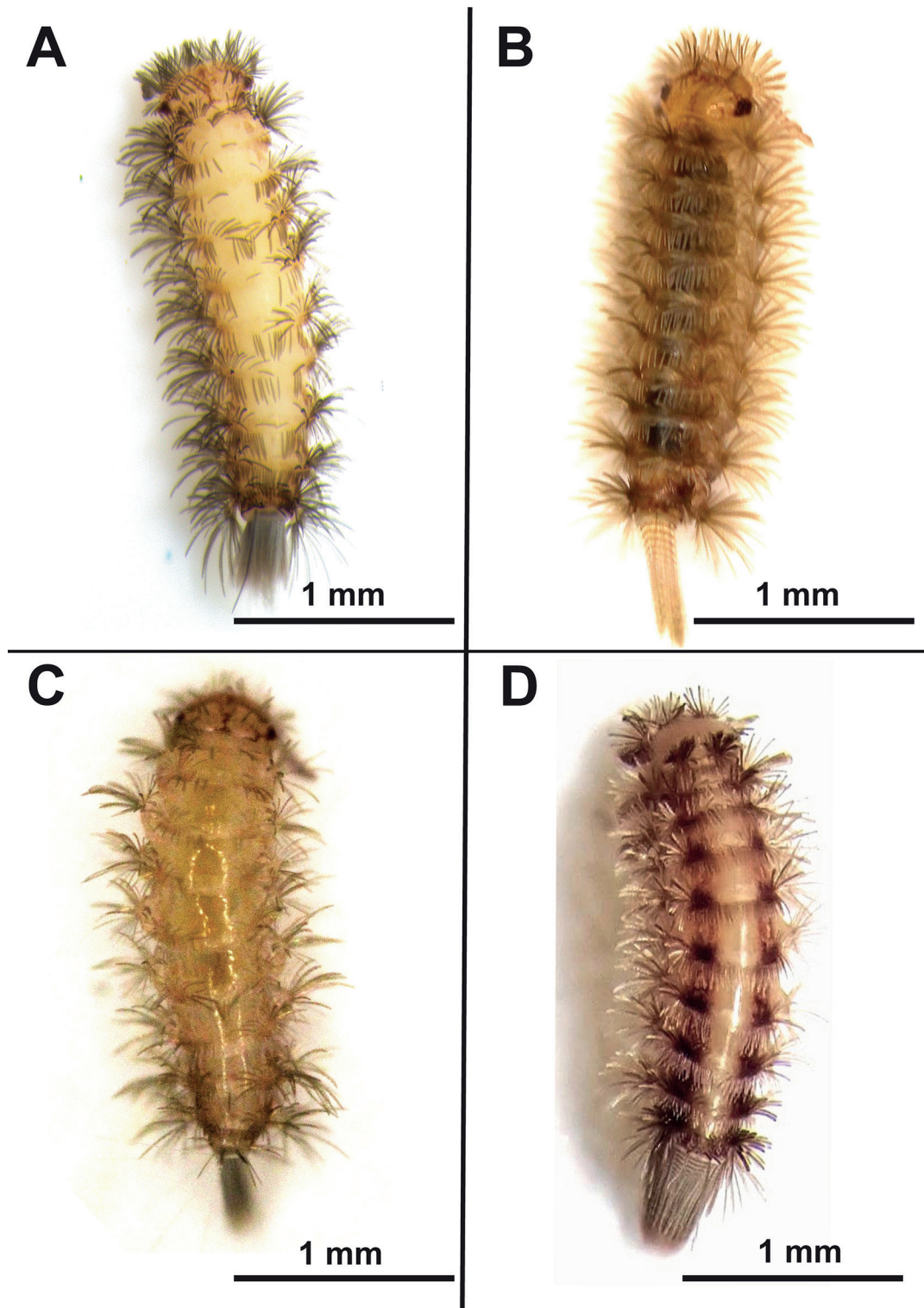


Fig. 4. *Unixenus* species (Polyxenidae) found in three locations in the mid central coastal regions and two offshore islands of Vietnam. **A**, *Unixenus binhdinhensis* **sp. nov.** from coastal location 1 (Quy Nhon) and location 2 (Tuy Hoa); **B**, *Unixenus phanrangensis* **sp. nov.** from coastal location 3 (Phan Rang); **C**, *Unixenus lysonensis* **sp. nov.** from location 4 (Ly Son Islands); **D**, *Unixenus phuquyensis* **sp. nov.** from location 5 (Phu Quy Island).

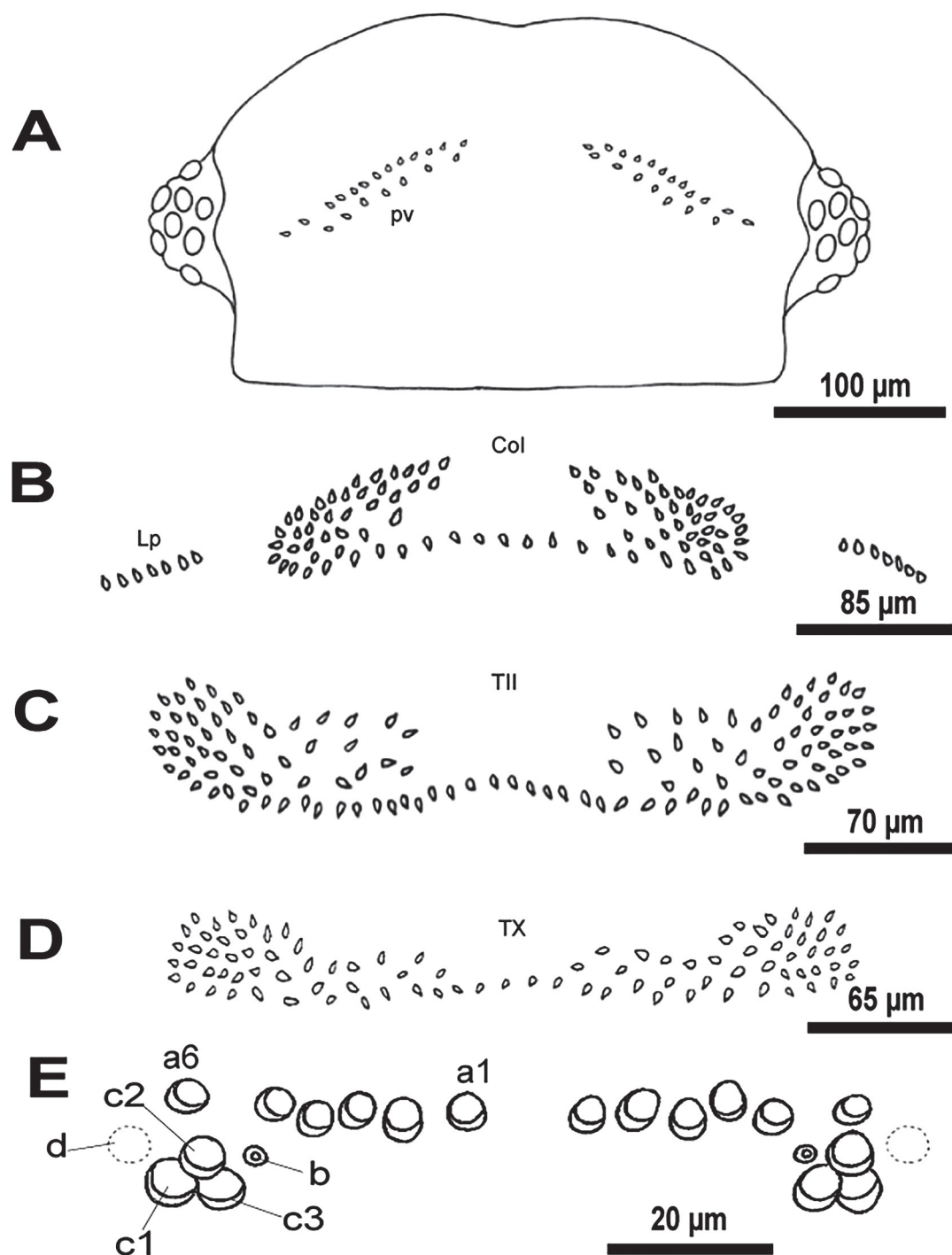


Fig. 5. Diagnostic morphological features of *Unixenus binhdinhensis* sp. nov., Holotype. **A**, head capsule showing eye pattern of eight ommatidia per side and posterior vertex trichome sockets (pv); **B**, trichome socket pattern on collum (Col) with lateral protuberances (Lp); **C**, trichome sockets on tergite II; **D**, trichome sockets on tergite X; **E**, Ornamental trichomes a1–a6, trichome b, three trichomes c, and the circular indentation d.

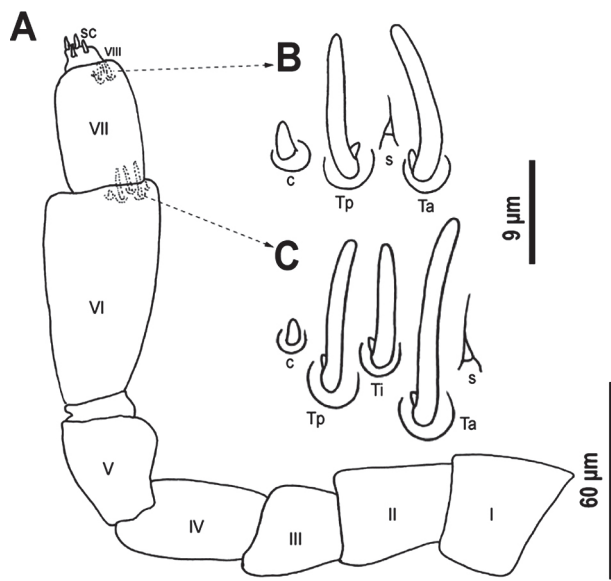


Fig. 6. Diagnostic morphological features of *Unixenus binhdinhensis* sp. nov., Holotype. **A**, left antenna showing eight antennomeres (I–VIII) and four sensory cones (sc); **B**, sensilla arrangement on antennomere VII, with a conical sensillum (C), thick bacilliform sensilla (T, posterior (Tp) and anterior (Ta)), and a setiform sensillum (S); **C**, sensilla on antennomere VI, with a conical sensillum (C), three thick bacilliform sensilla (T) including the intermediate sensillum (Ti) positioned distally, and a setiform sensillum (S).

process reaching about half the claw length, and a posterior lateral process exceeding half the claw length. Anterior setiform process equal to claw length. Lamellar process present (Fig. 7E).

Male sexual organs. A pair of penes present on coxae II (Fig. 7A); two pairs of coxal glands on coxae VIII and IX.

Caudal bundles. As in congeners (Huynh and Veenstra, 2021), the caudal bundles conform to the type I arrangement of Condé and Nguyen Duy-Jacquemin (2008). Caudal trichomes bear 2–4 backward hooks (Fig. 3I).

Telson. Dorsal ornamental trichome sockets symmetrically arranged on either side of the telson. Holotype with single row of six trichome *a* sockets per side (paratypes 5–8) varying in size. Each side also with one socket of trichome *b* and three large sockets of trichome *c* (c1–c3) with protruding bases; these three sockets in a ventroposterior triangular arrangement. A circular indentation *d* is present laterally, near the exterior side of trichome *c* group (Fig. 5E).

Etymology. The species name refers to Binh Dinh, the coastal region where this *Unixenus* species is most abundant. This area is characterised by extensive spiny leaved clumps grasslands occurring among rocky outcrops along the coastline between Quy Nhon to Tuy Hoa in the mid-central coastal region of Vietnam.

Remarks. *Unixenus binhdinhensis* sp. nov. shares

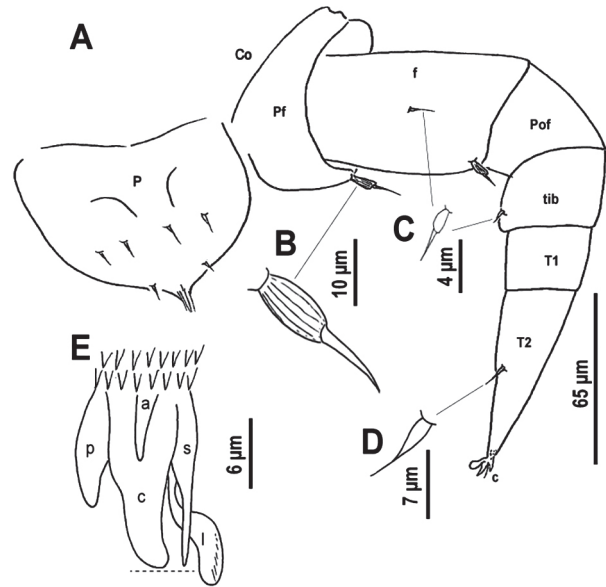


Fig. 7. Diagnostic morphological features of *Unixenus binhdinhensis* sp. nov., Holotype. **A**, left second leg showing penis (p) and seven segments: coxa (Co), prefemur (Pf), femur (f), postfemur (Pof), tibia (tib), tarsus I (T1), tarsus II (T2), and claw (C); **B**, bi-articulated setae with a ridged funicle on coxae, prefemurs, distal femurs, and posterior edge of the last sternite; **C**, small seta on the intermedio-posterior of femur and on tibia; **D**, setiform seta on the tarsus II; **E**, telotarsus–claw showing all processes: lateral (a = anterior, p = posterior), claw (c), lamella (l), and setiform process (s); a dotted line indicating the equal length of the claw and the setiform process.

features typical of *Unixenus*. In most congeners, antennomere VI bears three thick bacilliform sensilla arranged with a setiform sensillum positioned anteriorly between two thick bacilliform sensilla, and a posterior conical sensillum. In contrast, *U. binhdinhensis* sp. nov. differs from this pattern: the setiform sensillum is positioned anteriorly to the bacilliform sensillum cluster, and the intermediate bacilliform sensillum (Ti) is conspicuously positioned distally (Fig. 6C). This distinct configuration of sensilla on antennomere VI clearly differentiates the new species from all known congeners. Phylogenetic analyses further support its separation (Fig. 17), revealing a marked genetic divergence from other described species and confirming its status as a new member of the genus *Unixenus*.

Unixenus phanrangensis sp. nov.

Figs 4B, 9–11

Material examined. Holotype adult ♂ (IB-Myr 1046), Vietnam, Tra Cang, Thuan Nam District, 23 km south of Phan Rang City, Ninh Thuan Province (now Khanh Hoa Province), on the South-Central coast, (lat 11.463719°, long 108.920661°; elevation 48 m), grass bushes growing along the banks of the dried creek, 16 November 2024, leg. C. Huynh.

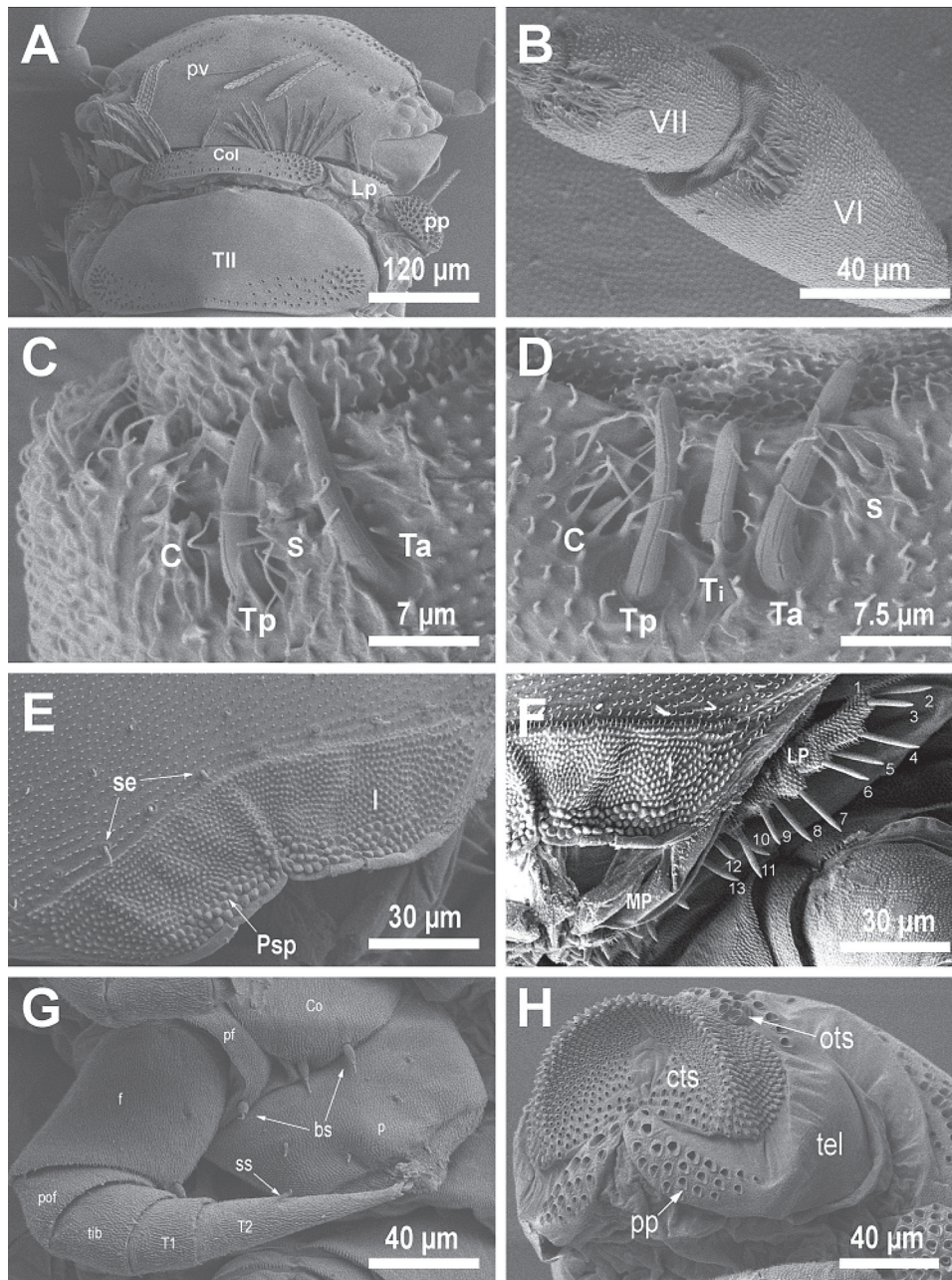


Fig. 8. SEM images of paratype, *Unixenus binhdinhensis* sp. nov.. **A**, head showing eight ommatidia per side, posterior vertex trichome sockets (pv), collum (Col) and tergite II; **B**, antennomeres VI–VII; **C–D**, sensilla arrangement on antennomeres VII (**C**) and VI (**D**); **E**, labrum (l) with papillae (Psp), posterior margin setae (se); **F**, 13 sensilla on lateral palp (LP) and the medial palp (MP) on the left gnathochilarium; **G**, right second leg with penis (p) and setae (bs: biarticulated setae with a ridged funicle) on coxa, prefemur, and distal of femur; **H**, caudal bundle structure with sockets in subadult stage showing caudal trichome sockets (cts), ornamental trichome sockets (ots), pleural projection (pp), and telson (tel).

Paratypes, two subadults ♀♀, one at stage VII with 12 leg pairs (used for SEM) and one at stage VI with 10 leg pairs (IB-Myr 1046) (Figs 1, 2C, 4B). All specimens were slide-mounted apart from the specimen used for SEM.

Diagnosis. Body dark brown, becoming lighter laterally. Antennomere VI with three thick bacilliform sensilla; one setiform sensillum positioned anteriorly between two of the bacilliform sensilla, and one conical sensillum posteriorly (Fig. 10A). Legs with biarticulated setae bearing a spine-ridged funicle (Fig. 10C). Telotarsus with the anterior setiform process longer than the claw (Fig. 10B).

Description. Holotype male body: 2.0 mm; paratype stadium VI: 1.2 mm; caudal bundle: 0.5 mm.

Colouration. Body dark brown dorsally, becoming lighter laterally; trichomes of the pleural projections and the caudal trichome bundle pale yellow (Fig. 4B).

Head. Posterior vertex trichomes arranged in two

oblique rows of sockets. The anterior row has larger sockets medially, decreasing in size toward both ends, and bears 11 sockets (L) and 12 (R). The posterior row comprises fewer sockets, with 4 (L) and 5 (R). A distinctly wider median gap separates the two rows, distinguishing this species from other three species (Figs 9A, 11A). Paratype (subadult, 10 legs stage) with 10 (L) and 11 (R) sockets on the anterior row, and the posterior row 4 (L) and 3 (R). Trichobothria, clypeo-labrum, gnathochilarium, antennomeres VI and VII as in Fig. 3. Except that posterior margin of the labrum has 11 short setae (Figs 10A, 11B).

Body. Tergites as described for the preceding species (Figs 9B–D). Except lateral protuberances bear 5 trichome sockets each side (Fig. 9B); paratype (subadult) with the same number of lateral sockets.

Legs. Segmentation and chaetotaxy as in the preceding species. Except coxae I–II bear 1–2 biarticulated setae with spine ridged funicle (Fig. 10C), coxae III–XIII bear 2–4 such setae.

Telotarsus. As in the preceding species, except the anterior setiform process exceeds the claw length (Figs 10B, 11C).

Caudal bundles and Male sexual organs. As in the preceding species.

Telson. Dorsal ornamental trichome sockets arranged in two uneven rows. Holotype, 9 trichome *a* sockets per side (paratype with 10 (Fig. 11D)), arranged in two rows; one socket of trichome *b*; three large sockets of trichome *c* (*c*1–*c*3); and a circular indentation *d* (Fig. 9E).

Etymology. The species name refers to Phan Rang, the coastal region where this *Unixenus* species was collected. This area is characterised by a dry climate and sandy coastal habitats in the southernmost part of the central coastal region of Vietnam.

Remarks. *Unixenus phanrangensis* sp. nov. shares the diagnostic features typical of *Unixenus*. The arrangement of sensilla on antennomere VI conforms to the generic pattern.

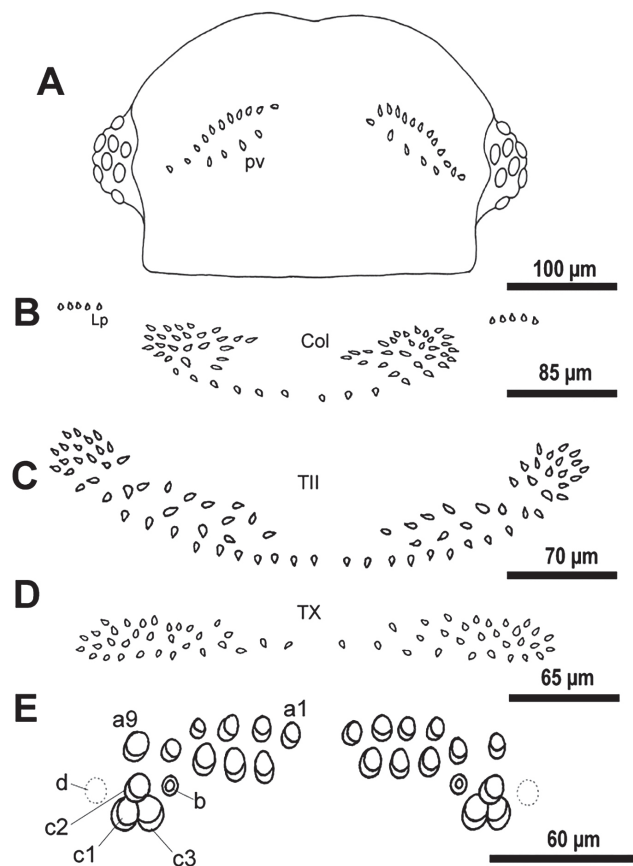


Fig. 9. Diagnostic morphological features of *Unixenus phanrangensis* sp. nov., Holotype. A, head capsule with eye pattern of eight ommatidia per side and posterior vertex trichome sockets (pv); B, trichome socket pattern on collum (Col) and lateral protuberances (Lp); C, trichome sockets on tergite II; D, trichome sockets on tergite X; E, Ornamental trichomes a1–a9, trichome *b*, three trichomes *c* and the circular indentation *d*.

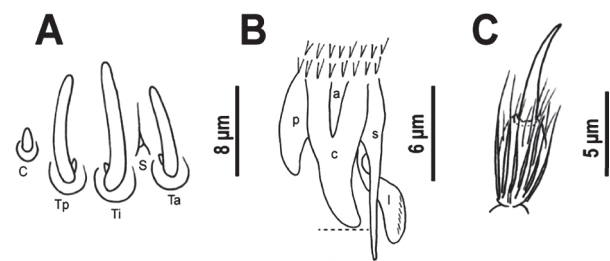


Fig. 10. Diagnostic morphological features of *Unixenus phanrangensis* sp. nov. and *Unixenus phuquyensis* sp. nov., A, sensilla on antennomere VI with three thick bacilliform sensilla (T) arranged transversely; B, telotarsus–claw with setiform process longer than claw indicated by dotted line; C, biarticulated setae with a spine ridged funicle on coxae, prefemurs, distal femurs, and posterior edge of last sternite.

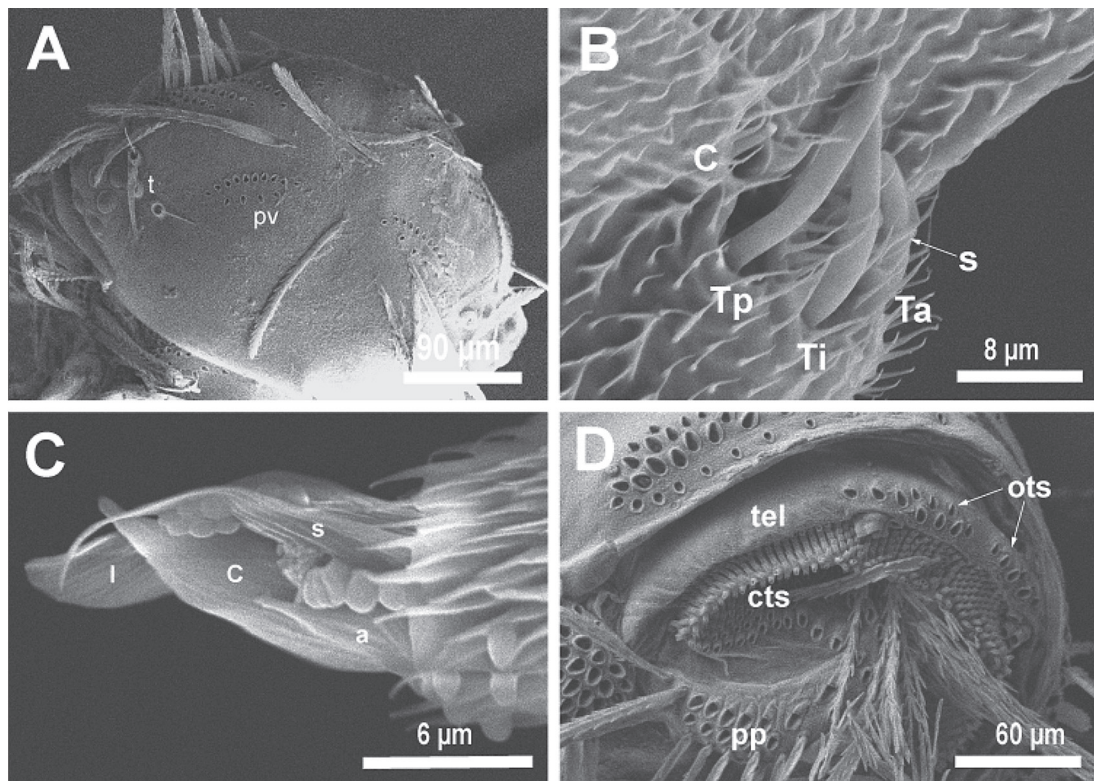


Fig. 11. SEM images of paratype (subadult, 12 legs pairs), *Unixenus phanrangensis* sp. nov., **A**, head with eye patterns and posterior vertex trichome sockets (pv); **B**, antennomeres VI with bacilliform sensilla; **C**, telotarsus-claw with processes; **D**, telson (tel) in subadult stage, showing ornamental trichome sockets (ots) and its caudal bundle trichome sockets (cts), and the pleural projection (pp).

Because this configuration is common in the genus, it is of limited value for distinguishing the new species from its congeners. However, the combination of colouration (Fig. 4B), body length, arrangement of ornamental trichome sockets (Fig. 9E), and the anterior setiform process of the telotarsus, which exceeds the claw length (Fig. 10B), differs from other species of *Unixenus*. These morphological characters clearly separate *U. phanrangensis* sp. nov. from its congeners. In addition, its genetic profile supports its recognition as a distinct species within the genus (Fig. 17).

***Unixenus lysonensis* sp. nov.**

Figs 4C, 12–14

Material examined. Holotype adult ♂ (IB-Myr 1047), Vietnam, Ly Son Islands (lat 15.384875°, long 109.132733°; elevation 108 m), from grass tussocks along the roadside. 4 February 2023, leg. C. Huynh. Paratypes (four adult ♀♀) collected with holotype (IB-Myr 1047). All specimens slide mounted. (Figs 1, 2D, 4C).

Diagnosis. Body light yellow brown. Antennomere VI with three thick bacilliform sensilla; one setiform sensillum positioned anteriorly between two of the bacilliform sensilla,

and one conical sensillum posteriorly (Fig. 13A). Leg setae biarticulated with a ridged funicle (Fig. 13C). Telotarsus with anterior setiform process equal to claw length (Fig. 13B).

Description. Holotype male body length 2.0 mm; paratypes 1.8–2.0 mm; caudal bundle 0.5 mm.

Colouration. Body light yellow brown; trichomes of the pleural projections darker brown; caudal trichome bundle dark silvery colour (Fig. 4C).

Head. Post vertex trichomes forming two rows of equal-sized trichome sockets; anterior and posterior rows slightly oblique, and close together. Anterior row with 15 sockets on both sides; posterior rows with 6 (L) and 7 (R) (Figs 12A, 14A). Paratypes show variation in vertex trichome socket counts: anterior rows with 10–16 sockets; posterior rows with 4–8. Trichobothria, clypeolabrum, gnathochilarium, antennomeres VI and VII as in the generic diagnosis (Fig. 3), except that the posterior margin of the labrum bears 11 short setae (paratypes with 10). (Figs 13A, 14B).

Body. Collum and tergites as described for the preceding species (Figs 12B–D). Lateral protuberances bear 6 trichome sockets each side (Fig. 12B); paratypes showed 5–6.

Legs. Segmentation and chaetotaxy as in the preceding species, except those coxae I–II bear 1–2 biarticulated setae

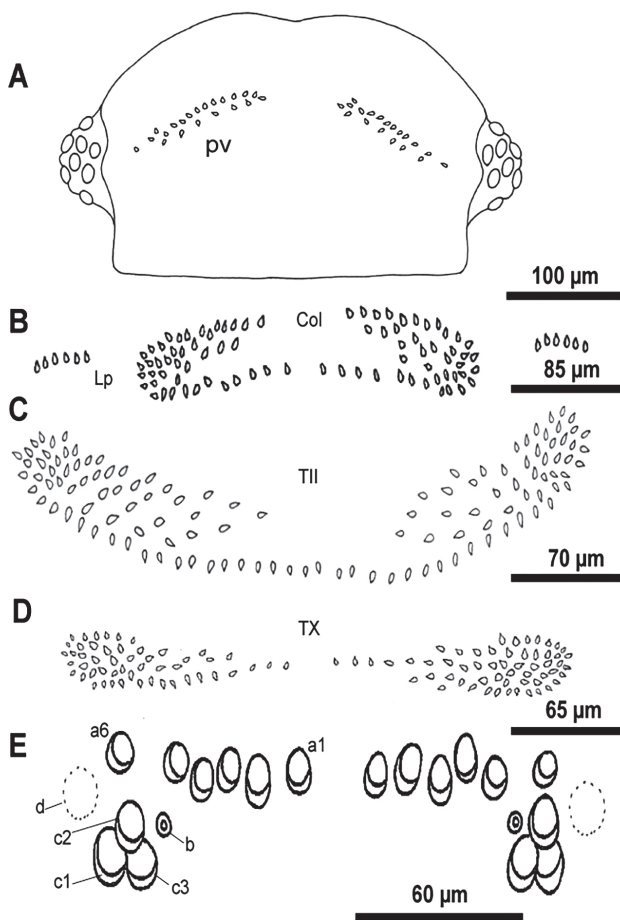


Fig. 12. Diagnostic morphological features of *Unixenus lysonensis* sp. nov., Holotype. **A**, head capsule with eye pattern of eight ommatidia per side and posterior vertex trichome sockets (pv); **B**, trichome socket pattern on collum (Col) and lateral protuberances (Lp); **C**, trichome sockets on tergite II; **D**, trichome sockets on tergite X; **E**, Ornamental trichomes a1–a6, trichome b, three trichomes c (C1, C2 and C3) and the circular indentation d.

with a ridged funicle (Fig. 13C), whereas coxae III–XIII bear 3–4 such setae.

Telotarsus. As in the preceding species, except that the anterior setiform process is equal in length to the claw (Figs 13B, 14D).

Caudal bundles and Male sexual organs. As in the preceding species.

Telson. As in *U. binhdinhensis* sp. nov., holotype with six trichome *a* sockets form a single row per side (paratypes with 5–7), one trichome *b* socket, three large trichome *c* sockets (c1–c3), and a circular indentation *d* (Fig. 12E).

Etymology. The species name refers to the Ly Son Islands, a volcanic island group located 30 km northeast of the Quang Ngai Province (now Kon Tum Province), off the mid-central coast of Vietnam (Fig. 1), where this *Unixenus* species

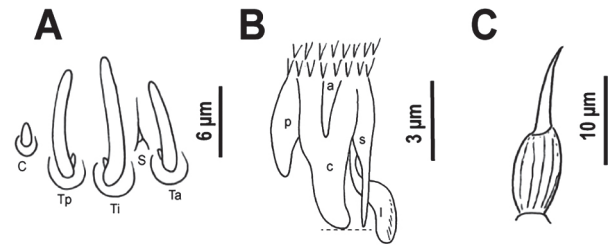


Fig. 13. Diagnostic morphological features of *Unixenus lysonensis* sp. nov., Holotype. **A**, sensilla on antennomere VI with three thick bacilliform sensilla arranged transversely; **B**, telotarsus–claw with setiform process equal the claw with a dotted line indicated; **C**, articulated setae with a ridged funicle on coxae, prefemurs, distal femurs, and posterior edge of last sternite.

was collected, located approximately 30 km offshore from Quang Ngai Province on the mid-central coast of Vietnam.

Remarks. *Unixenus lysonensis* sp. nov. shares the diagnostic characters typical of *Unixenus*. This similarity makes species identification challenging and complicates distinguishing this taxon from congeners. Despite these similarities, *U. lysonensis* sp. nov. can be reliably distinguished from other described species by a unique combination of characters, including the colouration of live specimens (Fig. 4C), the arrangement of posterior vertex trichome sockets (Fig. 12A), the structure of the leg setae (Fig. 13C), and the morphology of the telotarsus (Fig. 13B). In addition, molecular data clearly support its distinctiveness, further confirming its status as a separate species within the genus (Fig. 17).

Unixenus phuquyensis sp. nov.

Figs 4D, 10, 15, 16

Material examined. Holotype adult male ♂ (IB-Myr 1048), Vietnam, Phu Quy Island (lat 10.546719°, long 108.947353°; elevation 51 m), grass bushes growing along a hillside, 13 November 2024, leg. C. Huynh.

Paratypes (four adult ♀♀) (IB-Myr 1048) collected with the holotype. All specimens slide mounted. (Figs 1, 2E, F, 4D).

Diagnosis. Body light yellow brown, two darker bands laterally. Antennomere VI as in the generic diagnosis. Leg setae biarticulated with spine-ridged funicle (Figs 10C, 16G). Telotarsus with anterior setiform process surpassing claw length (Figs 10B, 16F).

Description. Holotype male body length 2.0 mm; paratypes 1.8–2.0 mm; caudal bundle 0.5 mm.

Colouration. Body light yellow brown; two darker bands laterally; caudal trichome bundle dark silvery colour (Fig. 4D).

Head. Post vertex trichomes as in the preceding species. Anterior row with 12 (L) and 11 (R); posterior row with 5

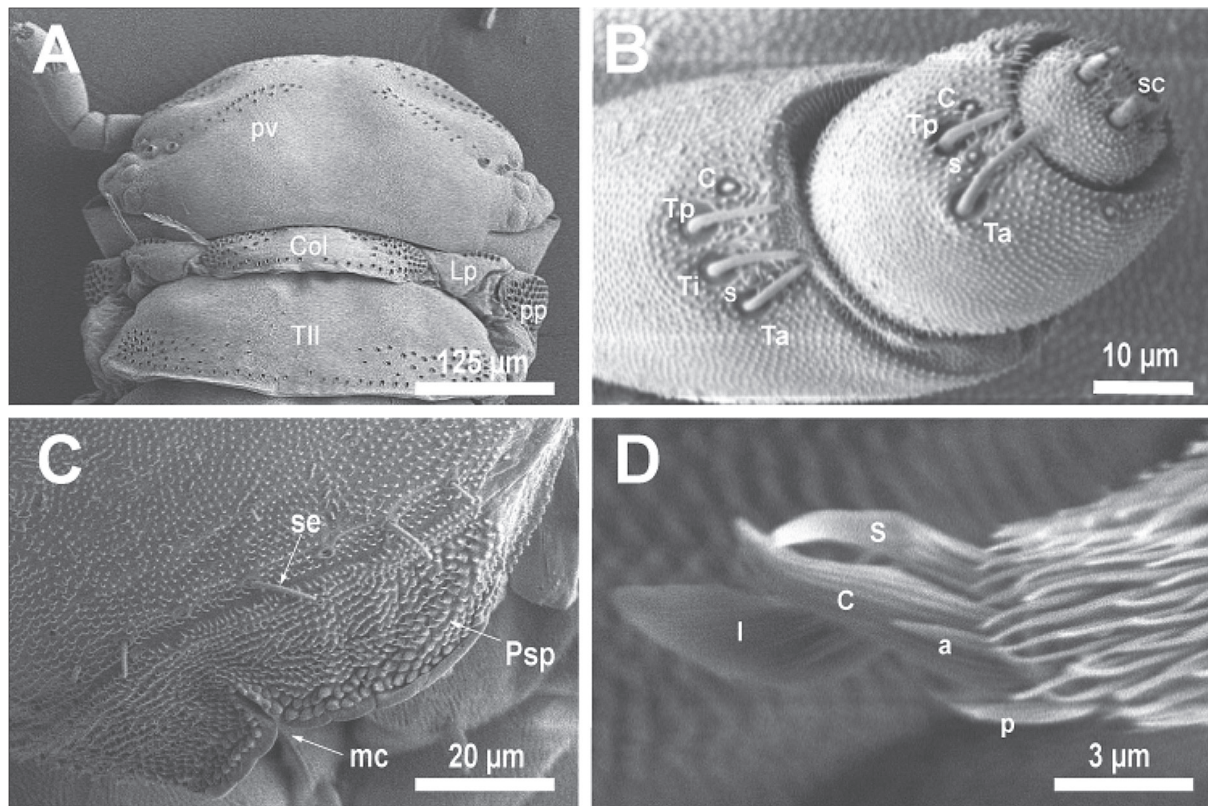


Fig. 14. SEM images of paratype, *Unixenus lysonensis* sp. nov.. **A**, head with eight ommatidia per side, posterior vertex trichome sockets (pv), collum (Col), lateral protuberances (Lp), and tergite II with pleural projection (pp); **B**, antennomeres VI–VII with sensilla; **C**, Labrum with papillae (Psp) on the surface, a median cleft (mc), and setae (se) along the posterior margin. **D**, Telotarsus-claw showing associated processes.

(L) and 6 (R) (Figs 15A, 16A). Paratypes showed variation in vertex trichome socket counts: anterior rows with 13–14 sockets; posterior rows with 6–9 sockets. Trichobothria, clypeolabrum, gnathochilarium, antennomeres VI and VII as in Figs 3, 10A, 16B. Except that the posterior margin of the labrum bears 10 short setae (paratypes with 10–14).

Body. Collum and tergites as in described for the preceding species. Lateral protuberance bearing 4 trichome sockets (R) and 5 (L); paratypes with 5–6 (Figs 15B–D).

Legs. Segmentation and chaetotaxy as in the preceding species, except those coxae I–II bear 1–2 biarticulated setae with a spine-ridged funicle (Fig. 10C), whereas coxae III–XIII bear 3–5 such setae.

Telotarsus. As in the preceding species, except the anterior setiform process surpasses the length of the claw (Figs 10B, 16F).

Caudal bundles and Male sexual organs. As in the preceding species.

Telson. As in *U. binhdinhensis* sp. nov., holotype with six trichome *a* sockets per side (paratypes with 5–7), one trichome *b* socket, three large trichome *c* sockets (c1–c3), and a circular indentation *d* (Figs 15E, 16H).

Etymology. The species is named after Phu Quy Island, an ancient volcanic island located approximately 100 km southeast of Phan Thiet City, Binh Thuan Province (now Lam Dong Province), off the southernmost part of the central coast of Vietnam (Fig. 1), where this *Unixenus* species was collected, located approximately 100 km southeast of Phan Thiet City, Binh Thuan Province, off the southernmost part of the central coast of Vietnam.

Remarks. *Unixenus phuquyensis* sp. nov. exhibits the diagnostic characters typical of *Unixenus*. Several morphological features, particularly antennal structure, tergal trichome socket arrangement, and telotarsal morphology, closely resemble those of the preceding species, most notably *U. phanrangensis* sp. nov., making morphological separation difficult. Minor differences are observed with respect to body colouration (Fig. 4D), claw morphology (Fig. 10B) and the structure of the leg setae (Fig. 10C); however, these characters alone provide limited evidence for confidently distinguishing this taxon based solely on morphology. Accordingly, molecular analysis plays a critical role in distinguishing *U. phuquyensis* sp. nov. This species genetic profile clearly supports its distinctiveness and confirms its placement as a separate species within the genus *Unixenus* (Fig. 17).

Phylogenetic Analysis

Sequences from four new *Unixenus* species: *U. binhdin-hensis* **sp. nov.**, *U. lysonensis* **sp. nov.**, *U. phanrangensis* **sp. nov.**, and *U. phuquyensis* **sp. nov.**, were compared with other penicillate millipede sequences available in GenBank (Table 1). Maximum likelihood analysis of the 18S dataset, based on 1000 bootstrap replicates, recovered a phylogenetic tree with bootstrap values indicated at the nodes. All four new species clustered within a well-supported clade containing other *Unixenus* taxa, confirming their placement within the genus and clear separation from other genera (Fig. 17A). A second maximum likelihood analysis based on the mitochondrial *COI* region likewise recovered a distinct *Unixenus* clade with strong bootstrap support (100%), including all sampled species. Within this clade, the four new species were clearly differentiated from one another, with moderate to high bootstrap support (>50%) for interspecific relationships (Fig. 17B). The combined results demonstrate fitting well between nuclear and mitochondrial markers, with 18S resolving genus-level relationships and *COI* providing finer resolution at the species level.

DISCUSSION

Morphological characters normally used to separate species within the genus *Unixenus* provided limited resolution in this study of four closely related species. Additional diagnostic characters were therefore used to assist in differentiating the new species. These included the colouration of live specimens, together with finer morphological features such as the arrangement of trichome sockets on the vertex and tergites, the pattern of ornamental trichome sockets, the structure of leg setae, and telotarsal morphology.

In addition, molecular approaches proved essential for

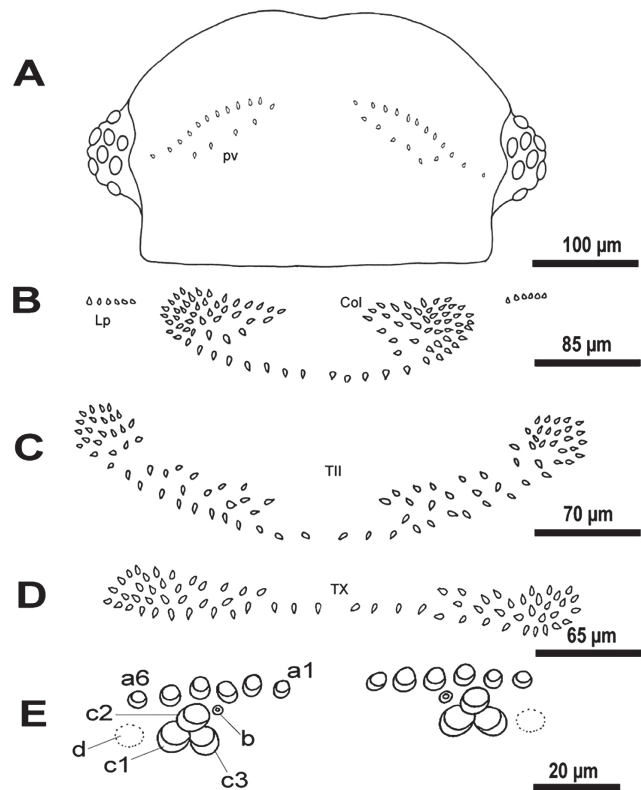


Fig. 15. Diagnostic morphological features of *Unixenus phuquyensis* **sp. nov.**, Holotype. **A**, head capsule with eye pattern of eight ommatidia per side and posterior vertex trichome sockets (pv); **B**, trichome socket pattern on collum (Col) and lateral protuberances (Lp); **C**, trichome sockets on tergite II; **D**, trichome sockets on tergite X; **E**, Ornamental trichomes a1–a6, trichome b, three trichomes c (C1, C2 and C3), and the circular indentation d.

Key to described species of *Unixenus* from Vietnam

- | | |
|--|--|
| 1. Leg setae biarticulated, funicle ridged (without spines) (Fig. 7B) | 2 |
| – Leg setae biarticulated, funicle bearing distinct spine-like ridges (Fig. 10C) | 3 |
| 2. Setiform sensillum positioned between bacilliform sensilla Ta and Ti (Fig. 13A) | <i>U. lysonensis</i> sp. nov. |
| – Setiform sensillum positioned anterior to bacilliform sensillum Ta (Fig. 6C) | <i>U. binhdin-hensis</i> sp. nov. |
| 3. Body length approximately 2.0 mm or less | 4 |
| – Body length exceeding 2.0 mm | 5 |
| 4. Body light yellow brown; pleural projections darker brown; caudal bundle trichomes dark silvery (Fig. 4D) | <i>U. phuquyensis</i> sp. nov. |
| – Body dark brown dorsally, lighter laterally; pleural projections and caudal bundle trichomes pale yellow (Fig. 4B) | <i>U. phanrangensis</i> sp. nov. |
| 5. Posterior claw process longer than half the length of the main claw | <i>U. intragramineus</i> Huynh and Veenstra 2018 (Vietnam) |
| – Posterior claw process shorter than half the length of the main claw | <i>U. moniqueae</i> Huynh and Veenstra 2020 (Vietnam) |

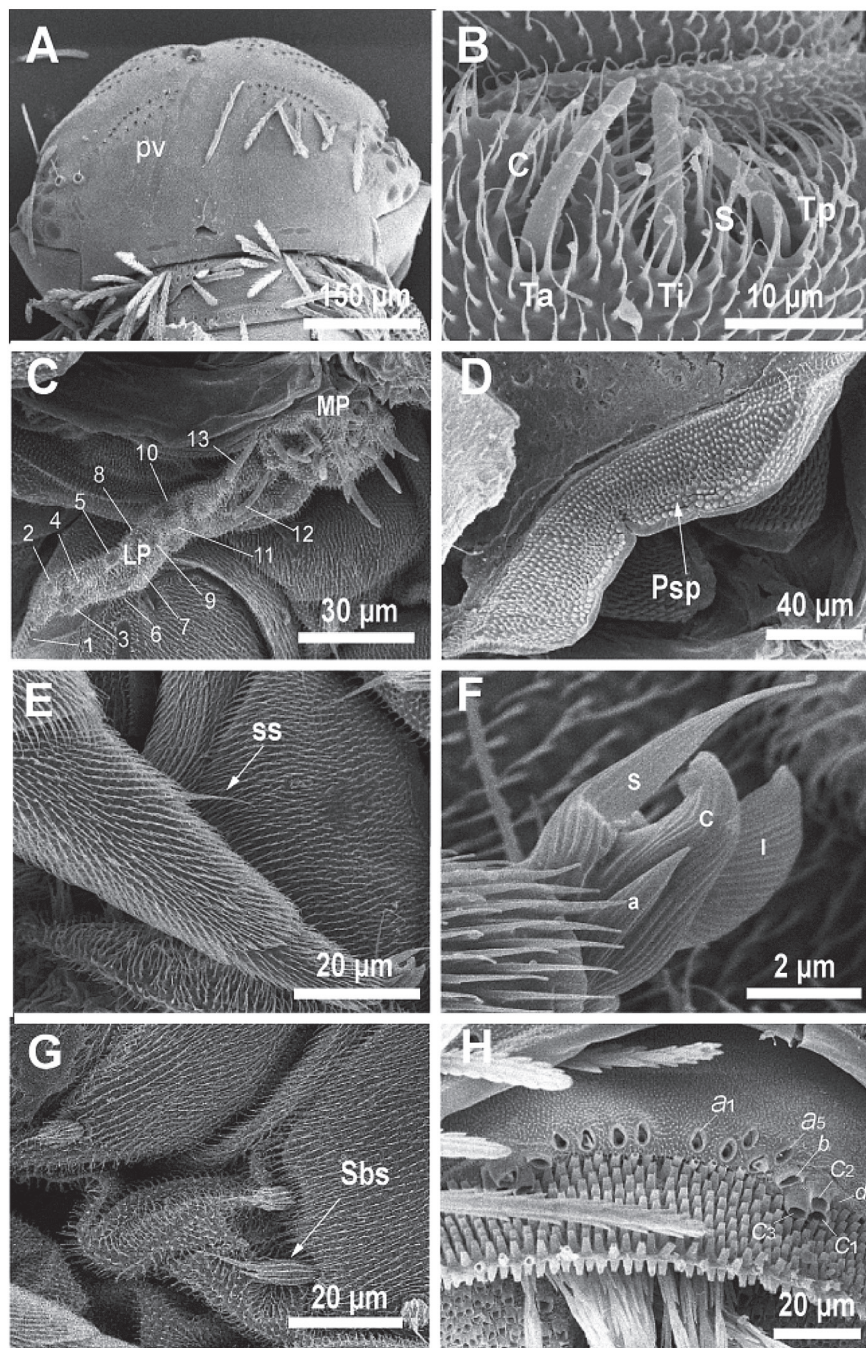


Fig. 16. SEM of paratype, *Unixenus phuquyensis* **sp. nov.** **A**, head showing eye patterns, posterior vertex trichome sockets (pv); **B**, antennomeres VI with sensilla; **C**, gnathochilarium with 13 sensilla; **D**, labrum with papillae; **E**, tarsus II with a setiform seta (ss); **F**, telotarsus–Claw with processes, setiform process (l) longer than the claw (C); **G**, biarticulated setae with spine ridged funicle; **H**, ornamental trichome sockets (arrows indicated the structures).

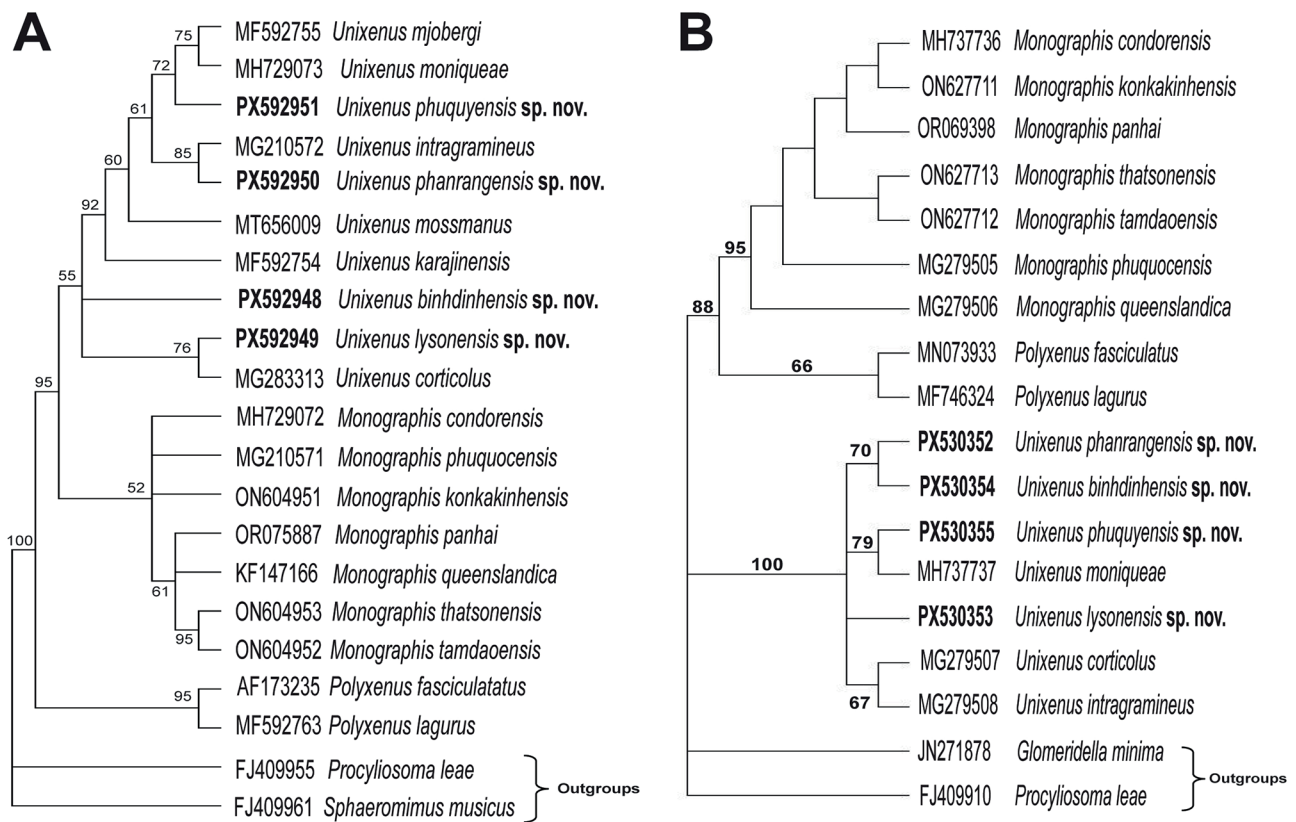


Fig. 17. Molecular phylogenetic trees reconstructed using the maximum likelihood method based on **A**, 18S rRNA and **B**, CO1 gene sequences of the four newly described *Unixenus* species and other penicillate millipedes retrieved from GenBank. Bootstrap support values (>50%) are shown above the branches.

resolving species boundaries. Phylogenetic analyses based on two gene regions, the nuclear 18S rRNA gene and the mitochondrial CO1 gene, provided complementary levels of resolution. The 18S marker effectively resolved relationships at the genus level but showed limited power in distinguishing closely related species. In contrast, the CO1 dataset provided clear genetic differentiation among the four taxa, supporting their recognition as distinct species.

Apart from differences in the colouration of live specimens, the four newly described *Unixenus* species share most key morphological characters and can therefore be regarded as cryptic species. They exhibit similar body lengths, comparable arrangements of bacilliform sensilla on antennomere VI, and closely matching patterns of tergal trichome sockets, making species identification based solely on external morphology difficult. Among these taxa, *U. binhdinhensis* **sp. nov.** is the only species showing a distinct sensilla arrangement on antennomere VI. In contrast, *U. phanrangensis* **sp. nov.**, *U. lysonensis* **sp. nov.**, and *U. phuquyensis* **sp. nov.** display largely overlapping character states, with the structure of leg setae and telotarsal morphology providing the most reliable morphological distinctions.

Taxonomic analysis reveals two geographically distinct

species groups. The first group comprises *U. binhdinhensis* **sp. nov.** from the mid-central coastal region and *U. lysonensis* **sp. nov.** from offshore islands within the same region, herein referred to as the northern group, in contrast with the southern group. These species share similar arrangements of tergal trichomes, biarticulated leg setae with a ridged funicle, and a telotarsal anterior setiform process equal in length to the claw, although *U. binhdinhensis* **sp. nov.** differs in the sensilla arrangement on antennomere VI.

The second group includes *U. phanrangensis* **sp. nov.** from the southernmost central coastal region and *U. phuquyensis* **sp. nov.** from a nearby offshore island. These species exhibit similar arrangements of tergal trichomes, biarticulated leg setae with a spine-ridged funicle, and an anterior setiform process exceeding the length of the claw. Their close geographic proximity and shared morphological features suggest a close evolutionary relationship.

These distributional patterns indicate recent evolutionary processes within *Unixenus*, with greater divergence apparent among the northern lineages. Overall, the taxonomic resolution of these four new *Unixenus* species requires careful assessment of subtle morphological differences supported by molecular evidence (Fig. 17). This study highlights the

importance of integrative taxonomy, incorporating molecular phylogenetics, in resolving cryptic diversity within morphologically conservative penicillate millipede lineages.

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