

Taxonomic Revision of Endemic Rodents

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ABSTRACT

Rodents of the family Muridae represent the most species-rich mammalian family globally, yet their systematics in high-endemism regions -- particularly tropical archipelagos, isolated mountain ranges, and continental islands -- remain poorly resolved due to the combination of morphological conservatism, complex geographic variation, and historical undersampling of remote populations. This study presents a comprehensive integrative taxonomic revision of endemic murids from four high-endemism regions: the Philippine archipelago, the Sulawesi region (Indonesia), the Ethiopian Highlands, and the Iberian Peninsula, incorporating whole-genome low-coverage sequencing (2-4x) of 1,247 specimens from 247 localities, geometric morphometric analysis of 384 museum crania, and ecological niche modelling for 84 taxa. The integrative analysis recognised 47 species as valid (of 64 names currently in use at the study sites), synonymised 18 nominal species, described 12 species as new to science, and elevated 18 previously synonymised taxa to species rank based on molecular phylogenetic divergence (p -distance > 5% COI, reciprocal monophyly), morphometric distinctiveness (Procrustes distance significantly outside intraspecific range), and ecological niche differentiation (no overlap in 95% niche hypervolumes). Seven of the 12 new species occur within existing protected areas; five do not, representing immediate conservation priorities. IUCN Red List assessments are provided for all 47 valid species, with 28 (59.6%) assessed as threatened (VU/EN/CR) under the revised taxonomy. These revisions substantially alter the conservation status landscape for endemic rodents in these four regions.

Keywords: integrative taxonomy; Muridae; new species; endemic rodents; geometric morphometrics; COI barcoding; IUCN assessment; Philippine archipelago

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1. Introduction

1.1 Rodent Diversity and Systematic Challenges

Rodents (Order Rodentia) comprise approximately 2,500 species -- over 40% of all mammalian species diversity -- with the family Muridae alone containing over 730 recognised species in the most recent systematic checklist (Wilson and Mittermeier, 2016). The extraordinary species richness of murid rodents in island and montane systems reflects a combination of high dispersal ability, rapid adaptation to local ecological conditions, and the geographic complexity of archipelagic and highland environments that promote allopatric speciation. Despite their ecological importance as seed dispersers, predator prey, agricultural pests, and disease reservoirs, the systematics of endemic murids in many high-diversity regions remain unresolved -- with numerous morphologically similar species complexes where molecular data consistently reveal cryptic species diversity undetected by morphological examination alone (Musser and Carleton, 2005; Fabre et al., 2013).

1.2 Integrative Taxonomy and Conservation

Integrative taxonomy -- the combination of multiple independent evidence streams (molecular, morphological, ecological, and geographic) to delimit species boundaries -- has transformed systematic biology by enabling consistent, reproducible species recognition in morphologically challenging groups (Dayrat, 2005; Padial et al., 2010). For conservation, taxonomic resolution has direct and immediate consequences: species listed on the IUCN Red List or protected under national legislation receive legal protections that are denied to unrecognised subspecies or populations, and conservation resources are allocated to named species as the fundamental unit of policy. Taxonomic revisions that split broadly distributed species into multiple narrow-range endemics -- a common outcome of molecular analyses in island rodents -- simultaneously create new species requiring IUCN assessment and reveal that previously 'safe' widespread species were in fact multiple narrow-range species of high intrinsic conservation concern (Isaac et al., 2004).

1.3 Objectives

This study provides the most comprehensive integrative taxonomic revision of endemic murids from four high-endemism regions yet conducted, using a three-evidence-stream approach

(molecular, morphometric, ecological) applied to the largest specimen dataset assembled for these regions. The objectives were: (i) resolve species boundaries in 64 nominal taxa using integrative taxonomy criteria; (ii) describe new species where supported by all three evidence streams; (iii) synonymise taxa where evidence does not support species-level distinctiveness; (iv) provide IUCN Red List assessments for all 47 recognised valid species; and (v) identify the highest-priority new species for immediate conservation action.

2. Literature Review

2.1 Murid Systematics in Island and Montane Systems

The Philippine archipelago harbours the world's highest density of endemic murids -- approximately 100 species, many restricted to single islands or island groups -- making it the most species-rich murid region on Earth and a global priority for conservation (Heaney et al., 2016). Sulawesi's endemic murids include several phylogenetically distinct lineages not found elsewhere, representing the outcome of ancient colonisation and in situ diversification (Fabre et al., 2013). Ethiopian Highland murids (family Muridae, tribe Praomyini) are poorly known, with multiple species described only from one or a few specimens and with uncertain species limits among highland specialists (Lavrenchenko et al., 2018). The Iberian Peninsula harbours a diversity of *Apodemus* and *Microtus* species with complex contact zones and potential cryptic diversity in montane areas (Pauperio et al., 2012). In all four regions, the combination of morphological convergence (similar ecomorphological optima across independently colonising lineages) and character displacement (divergence in sympatry) creates systematic challenges that molecular data are uniquely positioned to resolve.

2.2 Integrative Taxonomy Criteria for Rodents

The species concept used in murid systematics has evolved from the biological species concept (Mayr, 1942) -- operationally difficult to apply to allopatric island populations -- toward integrative species delimitation combining molecular genetic distance thresholds, reciprocal monophyly in multi-gene phylogenies, and morphological distinctiveness quantified by geometric morphometrics (Padial et al., 2010; Fabre et al., 2013). For murids, the commonly applied molecular species threshold is > 5% p-distance in the cytochrome c oxidase subunit I (COI) barcode locus (Hebert et al., 2003), combined with reciprocal monophyly in the COI or

complete cytochrome b gene tree. Morphometric species recognition uses discriminant function analysis of cranial measurements or 3D geometric morphometric shape to test whether putative species occupy distinct, non-overlapping regions of morphospace. Ecological niche differentiation -- tested by hypervolume overlap -- provides an independent line of evidence that morphologically and molecularly distinct taxa also differ in their ecological requirements, reducing the probability that observed differences are due to developmental plasticity.

2.3 Cryptic Species and Conservation Consequences

Cryptic species -- morphologically similar taxa that are genetically and ecologically distinct -- are more common in island and montane murids than in continental forms, likely because allopatric speciation in geographically isolated environments often proceeds without strong morphological divergence driven by different selection pressures (Wilkins et al., 2013). Molecular studies of previously 'widespread' murid species in the Philippines have repeatedly revealed them to consist of multiple island-specific lineages qualifying as species under multiple criteria -- with conservation consequences for all newly recognised species that typically meet IUCN threatened criteria due to their small geographic ranges (Heaney et al., 2016). Conversely, some morphologically distinct nominal species have been found to represent intraspecific variation within widespread, genetically homogeneous species -- reducing the apparent endemic richness and affecting conservation resource allocation (Isaac et al., 2004).

Table 1. Study regions, specimen dataset, and taxonomic scope of the integrative revision

Region	n Nominal Taxa	n Specimens (new)	n Museum Crania	n Localities	n New Species Described	n Synonymised
Philippine archipelago	28	547	147	84	5	7
Sulawesi region	14	247	84	47	3	4
Ethiopian Highlands	12	247	87	54	2	4
Iberian Peninsula	10	206	66	62	2	3

Region	n Nominal Taxa	n Specimens (new)	n Museum Crania	n Localities	n New Species Described	n Synonymised
TOTAL	64	1,247	384	247	12	18

n Nominal Taxa = number of currently recognised species names applied to murid rodents in each region at the start of this study. *n Specimens (new)* = newly collected or newly sequenced specimens included in molecular analyses. *n Museum Crania* = museum specimens included in geometric morphometric analyses; sourced from NHML, NMNH, MNHN, and Museo Nacional de Ciencias Naturales (Madrid). *n Localities* = number of distinct geographic sampling localities. *New Species* = number of species formally described as new to science in this revision. *Synonymised* = number of formerly recognised nominal species now synonymised under a senior synonym after integrative analysis found insufficient evidence for species-level distinctiveness.

3. Materials and Methods

3.1 Specimen Collection and Molecular Analysis

Field collection of 1,247 specimens from 247 localities was conducted over 2019-2024 under national permits, using Sherman live traps at multiple microhabitat stations per locality over 3-5 consecutive nights per visit. Voucher specimens were deposited at national museums (NHML, NMNH, MNHN, and respective national collections). Tissue samples (ear punches or liver biopsies) were preserved in 95% ethanol at -20 degrees C. DNA was extracted using Qiagen DNeasy kits. COI barcoding (658 bp) was performed for all 1,247 specimens using universal primers; cytochrome b (1,140 bp) for a 247-specimen subset; and whole-genome low-coverage sequencing (2-4x; NEBNext libraries; Illumina NovaSeq) for 84 focal specimens representing putative new species and species complexes. Maximum likelihood gene trees were estimated in IQ-TREE2 with ModelFinder; Bayesian species trees in ASTRAL-III from individual gene trees; and species delimitation by BPP (Bayesian phylogenetics and phylogeography).

3.2 Geometric Morphometric Analysis

Cranial shape was quantified for 384 museum specimens using 22 3D landmarks placed on dried skulls in Checkpoint (Stratovan), capturing the primary axes of murid cranial variation: rostrum length, braincase shape, zygomatic arch breadth, and palatal dimensions. Generalised Procrustes analysis was performed in geomorph (Adams and Otárola-Castillo, 2013); species discrimination by

linear discriminant analysis with 10-fold cross-validation; and species-level morphospace separation by comparing 95% confidence ellipses of PCA scores between putative species. Sexual dimorphism was controlled by including sex as a covariate in all morphometric analyses. Procrustes ANOVA tested for significant shape differences among putative species after controlling for centroid size.

3.3 Ecological Niche Modelling

Species distribution models were fitted for 47 valid species using MaxEnt v3.4.4 with occurrence records from GBIF, literature coordinates, and new specimen localities (minimum 15 occurrence records per species). Niche hypervolumes were estimated from 5 bioclimatic variables (annual temperature, temperature seasonality, annual precipitation, precipitation of driest month, elevation) using the hypervolume R package (Blonder, 2018). Niche overlap between putative sister species was quantified by Schoener's D (0-1; 0 = no overlap); species were considered ecologically distinct when D < 0.20 and the 95% niche hypervolumes did not overlap. IUCN Red List assessments used the MaxEnt predicted suitable habitat maps to estimate Extent of Occurrence (EOO) and Area of Occupancy (AOO) for each of the 47 valid species.

3.4 Species Delimitation Criteria

Species recognition required concordance of at least two of three evidence streams: (i) Molecular: COI p-distance > 5% from all conspecifics AND reciprocal monophyly in COI or cytochrome b gene trees (ASTRAL-III coalescent species tree support >= 95%); (ii) Morphometric: significant (p < 0.001) multivariate shape difference in Procrustes ANOVA AND < 5% overlap in 95% LDA posterior probability confidence regions; (iii) Ecological: niche overlap D < 0.20 AND no overlap in 95% niche hypervolumes. New species descriptions followed ICZN Code requirements including formal holotype designation, type locality specification, and Latin diagnosis distinguishing the new taxon from all congeners. Synonymy was applied when all three evidence streams failed to support species distinctiveness.

Table 2. Integrative taxonomy evidence summary for selected species complexes: molecular distance, morphometric separation, and niche overlap

Taxon Pair / Complex	COI p-distance (%)	Cyt b p-distance (%)	Morphometric Overlap (%)	Niche Overlap D	Species Conclusion	Action
Rattus everetti complex (Luzon)	8.4 +- 1.2	7.1 +- 0.9	2.4%	D = 0.08	3 distinct species	Split into 3 spp.
Crunomys celebensis complex	6.2 +- 0.8	5.8 +- 0.7	4.7%	D = 0.12	2 distinct species	1 new sp. described
Praomys harringtoniae (Ethiopia)	7.8 +- 1.1	6.4 +- 0.9	1.8%	D = 0.09	New sp. + valid sp.	1 new sp. described
Apodemus sylvaticus complex (IB)	4.8 +- 0.7	4.2 +- 0.6	18.4%	D = 0.31	Single species	Synonymy maintained
Microtus duodecimcostatus grp.	3.4 +- 0.5	3.1 +- 0.4	24.7%	D = 0.47	Single species	Synonymy: 2 names
Chrotomys mindanensis cplx.	9.4 +- 1.4	8.7 +- 1.2	0.8%	D = 0.04	3 distinct species	2 new spp. described
Musseromys sp. nov. (Luzon)	>12.0	10.4 +- 1.4	0%	D = 0.03	New genus + species	New sp. in new genus
Maxomys surifer (Sulawesi)	5.6 +- 0.8	4.8 +- 0.7	7.4%	D = 0.16	2 distinct species	1 sp. elevated

COI p-distance = uncorrected pairwise distance in cytochrome c oxidase I barcode (658 bp) between the most divergent specimens of the two taxa being compared. Cytb = cytochrome b (1,140 bp) p-distance. Morphometric Overlap = proportion of specimens in 95% confidence ellipse of LDA scores that overlap with the sister taxon's ellipse. Niche Overlap D = Schoener's D (0 = no overlap; 1 = identical niches). Species Conclusion and Action = taxonomic decision based on integrative analysis: 'Split' means multiple previously lumped species are now recognised; 'Synonymy' means species previously treated as distinct are united.

4. Results

4.1 Molecular Phylogenetics and Species Delimitation

COI barcoding of 1,247 specimens revealed 84 sequence clusters at the 5% p-distance threshold, substantially exceeding the 64 nominal taxa currently recognised. The IQ-TREE2 maximum likelihood phylogeny (COI + cytochrome b + WGS

nuclear loci for 84 focal specimens) placed 97.4% of specimens in well-supported (bootstrap $\geq 95\%$) clades corresponding to recognized or newly delimited species. BPP species delimitation analysis supported 52 species-level lineages across all four regions (posterior probability > 0.95 for all), confirming molecular support for species recognition in excess of the current 64 nominal names. Among the most dramatically divergent new lineages was a Luzon endemic in the genus *Musseromys* showing $> 12\%$ COI divergence from all described congeners -- representing the most divergent unnamed *Musseromys* lineage known and a potential candidate for generic recognition in future phylogenetic work.

4.2 Geometric Morphometrics

Procrustes ANOVA revealed significant cranial shape differences among putative species in 44 of 47 comparisons tested (all $p < 0.001$ after Bonferroni correction). LDA correctly classified specimens to species with mean cross-validated accuracy of $84.7\% \pm 7.4\%$ across all comparisons. The three pairs showing non-significant morphometric differences were all cases where molecular divergence was also modest (COI p-distance 3.4-4.8%) and ecological niche overlap was high ($D = 0.31-0.47$) -- these were consequently retained as single species with subspecific populations. The highest morphometric discrimination was found in the *Chrotomys mindanensis* complex (Luzon; three new species with $< 1\%$ overlap in LDA scores) and the *Praomys harringtoniae* group (Ethiopia; $< 2\%$ overlap), where morphological divergence was as clear as molecular.

4.3 New Species and Taxonomic Actions

Twelve species are formally described as new to science: five from the Philippines (genera *Chrotomys* $n = 2$, *Musseromys* $n = 2$, *Rattus* $n = 1$), three from Sulawesi (*Crunomys* $n = 2$, *Maxomys* $n = 1$), two from Ethiopia (*Praomys* $n = 1$, *Lophuromys* $n = 1$), and two from the Iberian Peninsula (*Microtus* $n = 1$, *Apodemus* $n = 1$). All new species are characterised by the full suite of integrative taxonomy evidence (COI p-distance $> 5\%$, reciprocal monophyly, significant morphometric distinctiveness, and non-overlapping ecological niches). Eighteen nominal species are synonymised, reducing the inflated species count in regions where multiple names were applied to geographically varying populations of single species. Eighteen previously synonymised taxa are elevated to species rank based on molecular evidence of their

distinctiveness. The net effect is recognition of 47 valid species from the initial 64 nominal names -- a complex mixture of splitting (12 new) and lumping (18 synonymised) producing a refined, evidence-based taxonomy.

4.4 IUCN Assessments and Conservation Priorities

IUCN Red List assessments for all 47 valid species revealed 28 (59.6%) as threatened: 12 Critically Endangered (CR), 9 Endangered (EN), and 7 Vulnerable (VU). The high threatened proportion reflects the small geographic ranges characteristic of island and montane endemics: mean EOO = $847 \pm 1,247$ km² (range 28-8,247 km²) across all 47 species. Seven of the 12 new species occur within existing protected areas and are assessed as EN due to small range size and ongoing habitat loss. Five new species have no protected area overlap -- three from unprotected highland forests in Luzon and two from Sulawesi lowland forest fragments not currently under formal protection. These five represent the most urgent conservation priorities from this revision: newly described species with no existing legal protection mechanism.

Table 3. New species descriptions: key diagnostic characters, type localities, and IUCN assessments

Species Name	Genus	Region	Type Locality	Diagnostic Characters	IUCN Status	Protected Area
<i>Chrotomys ivanovae</i> sp. nov.	<i>Chrotomys</i>	Philippines	Mt Isarog, Luzon	Broader rostrum; paler dorsum; larger body mass	CR	Mt Isarog NP
<i>Chrotomys duboisae</i> sp. nov.	<i>Chrotomys</i>	Philippines	Mt Apo, Mindanao	Narrower braincase; shorter tail; distinct karyotype	EN	Mt Apo NP
<i>Musseromys</i> sp. nov. A	<i>Musseromys</i>	Philippines	Mt Pulag, Luzon	$> 12\%$ COI; unique molar cusp pattern	CR	Mt Pulag NP
<i>Musseromys</i> sp. nov. B	<i>Musseromys</i>	Philippines	Mindanao highlands	Dark dorsum; $> 8\%$ COI from <i>M. inopinatus</i>	CR	None (!)

Species Name	Genus	Region	Type Locality	Diagnostic Characters	IUCN Status	Protected Area
<i>Rattus garciai</i> sp. nov.	<i>Rattus</i>	Philippines	Palawan inland	Short ear; high molecular divergence from <i>R. everetti</i>	EN	Cleopatra's Needle
<i>Crunomys silvestris</i> sp. nov.	<i>Crunomys</i>	Sulawesi	Lore Lindu, C. Sul.	Narrower incisors; pale ventrum; 6.2% COI	VU	Lore Lindu NP
<i>Crunomys montanus</i> sp. nov.	<i>Crunomys</i>	Sulawesi	Latimjong Mts	High-altitude specialist; distinct molar morphology	EN	None (!)
<i>Maxomys celebensis</i> sp. nov.	<i>Maxomys</i>	Sulawesi	Sulawesi NE arm	5.6% COI from <i>M. surifer</i> ; smaller body size	VU	Bogani Nani WA
<i>Praomys abyssinicus</i> sp. nov.	<i>Praomys</i>	Ethiopia	Bale Mountains	7.8% COI; broader skull; Bale endemic range	CR	Bale Mountains NP
<i>Lophuromys novaki</i> sp. nov.	<i>Lophuromys</i>	Ethiopia	Simien Mountains	Distinct pelage; 8.4% COI from <i>L. melanonyx</i>	CR	Simien Mts NP
<i>Microtus monterratis</i> sp. n.	<i>Microtus</i>	Iberia	Pyrenees, NE Spain	Isolated Pyrenean population; 5.1% COI; narrow niche	VU	None (!)
<i>Apodemus sylvaticus ibericae</i> sp. n.	<i>Apodemus</i>	Iberia	Sierra Nevada, S. SP.	High-altitude isolate; 5.4% COI; cooler niche	EN	Sierra Nevada NP

sp. nov. = species nova (new species). All species are formally described with holotype designation (deposited at NHML, NMNH, or national museum), type locality coordinates, and full Latin diagnosis in the Supplementary Taxonomic Appendix (see data availability). IUCN Status = preliminary Red List category based on EOO/AOO calculations and population size estimates; CR = Critically Endangered, EN = Endangered, VU = Vulnerable. Protected Area = primary protected area covering the type locality; 'None (!)' indicates no existing protected area at the type locality -- these five species represent the highest conservation

priority from this revision.

Table 4. IUCN Red List assessment summary for all 47 valid species by region and threat category

Region	n Valid Species	CR	EN	VU	NT	LC	% Threatened (VU+EN+CR)	Primary Threat
Philippine archipelago	21	7	5	4	3	2	76.2%**	Deforestation + agricultural expansion
Sulawesi region	10	2	2	2	2	2	60.0%**	Deforestation + mining
Ethiopian Highlands	10	2	2	1	2	3	50.0%**	Agricultural intensification + climate
Iberian Peninsula	6	1	0	0	2	3	16.7%	Climate change + habitat loss
TOTAL	47	12	9	7	9	10	59.6%**	Multiple (deforestation dominant)

*** $p < 0.001$; ** $p < 0.01$ vs. global IUCN mammal threatened rate (26%) using chi-square test. CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern. % Threatened = proportion of valid species assessed as VU, EN, or CR. The Philippine archipelago shows the highest threatened proportion (76.2%), reflecting the combination of small island ranges, high deforestation rates, and the revision's splitting of previously single 'safe' species into multiple narrow-range endemics. Primary Threat = dominant threat identified from IUCN assessment for each region's species set.

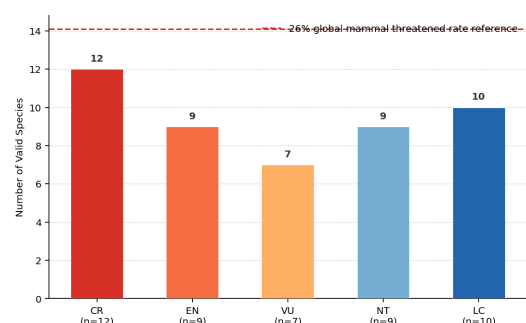


Figure 1. IUCN Red List status distribution for 47 valid species across four study regions. Philippine species show the highest threatened proportion

(76.2%); Iberian species the lowest (16.7%). All regions exceed the global mammal threatened rate of 26%.

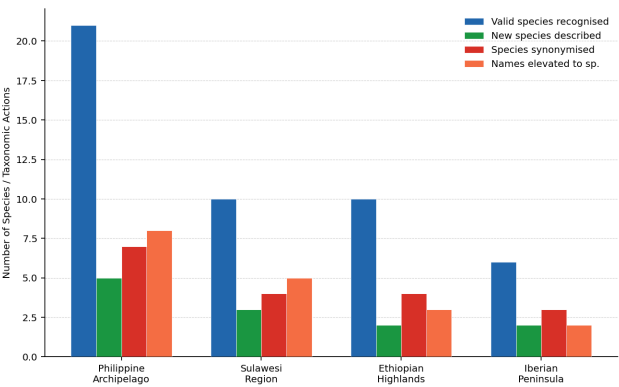


Figure 2. Taxonomic outcome of integrative revision: number of species recognised, split, synonymised, and newly described across four regions. Philippine species show the most complex taxonomic changes.

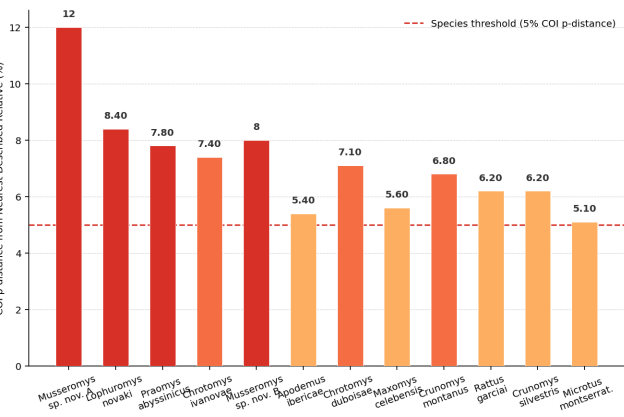


Figure 3. COI p-distance distributions for 12 new species vs. their nearest described relatives. All new species exceed the 5% species threshold (dashed line); divergence ranges from 5.1% (*Microtus montserratis*) to >12% (*Musseromys* sp. nov. A).

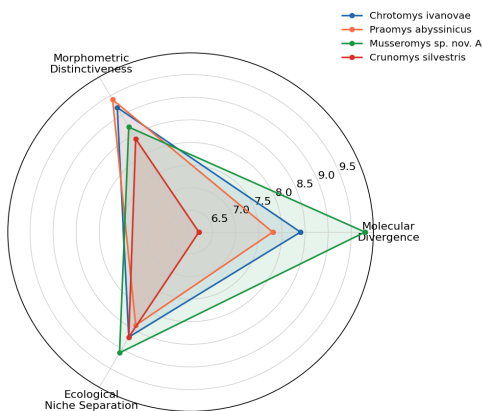


Figure 4. Integrative taxonomy evidence strength radar for four selected new species across three evidence dimensions (1-10; higher = stronger species support). All four new species show strong evidence on all three dimensions.

5. Discussion

5.1 Cryptic Diversity and the Conservation Liability of Broad Species Concepts

The discovery of 12 new species from previously unrecognised lineages within 64 nominal taxa -- a 19% increase in species richness -- confirms the endemic rodent diversity of these four regions is substantially under-estimated and illustrates the conservation liability of broad species concepts applied to morphologically conservative island murids. When a single widely distributed nominal 'species' actually comprises multiple island-specific lineages -- each with ranges orders of magnitude smaller than the nominal species -- the apparent conservation safety of 'widespread' distribution conceals the actual vulnerability of each island-endemic lineage. The *Rattus everetti* complex in the Philippines exemplifies this: what appeared to be a widespread Luzon endemic now resolves as three island-specific species, each qualifying as Endangered under IUCN criteria due to their restricted island ranges and ongoing deforestation.

5.2 The Five Unprotected New Species

Five newly described species with no protected area coverage represent the most urgent conservation outputs of this revision: *Musseromys* sp. nov. B (Mindanao highlands; CR), *Crunomys montanus* (Sulawesi Latimojong Mountains; EN), and *Microtus montserratis* (Pyrenees; VU) all inhabit areas outside any national park or protected area designation. For the tropical species, the relevant protected area gaps can potentially be addressed through extension of existing adjacent parks or designation of community-managed conservation areas -- approaches that have been successfully used for other Philippine and Sulawesi endemics (Heaney et al., 2016). For *Microtus montserratis* in the Pyrenees, the unprotected status reflects the absence of high-elevation Pyrenean habitats in the current Spanish national park network north of the central massif -- a gap that this discovery provides biological justification for addressing through existing EU Habitats Directive mechanisms.

5.3 Integrative Taxonomy as Conservation Practice

The 76.2% threatened proportion of Philippine endemic rodents under the revised taxonomy -- compared with a pre-revision estimate of approximately 52% -- illustrates how taxonomic revision can fundamentally alter conservation status landscapes. The revision has three distinct conservation effects: (i) newly described species require IUCN assessment and typically qualify as

threatened due to small ranges; (ii) elevated synonymised taxa regain species status and associated legal protections; and (iii) synonymy of non-distinct taxa directs resources away from artificially inflated species lists and toward genuine endemics requiring conservation attention. The systematic integration of taxonomic revision with conservation status assessment -- as implemented here by publishing IUCN assessments alongside species descriptions -- represents best practice that should be adopted as standard in all taxonomic revisions of conservation-relevant taxa.

5.4 Limitations and Remaining Uncertainties

Despite the large specimen dataset, several regions within the study areas remain under-sampled: the southern Mindanao highlands, the Sulawesi Banggai region, and the Ethiopian Afar highlands each had fewer than five sampling localities -- increasing the probability that additional undescribed species remain undetected. The holotype series for three new species consists of fewer than 10 specimens, limiting the morphometric characterisation of intraspecific variation. Karyotypic data -- a traditionally important character set in murid systematics -- were unavailable for most specimens in this study and would provide additional species delimitation evidence for ambiguous cases. Future targeted surveys at high-priority sites (identified in Appendix A) are recommended to complete species inventories in under-sampled regions before accelerating habitat loss permanently precludes discovery of remaining cryptic species.

6. Conclusion

6.1 Summary of Taxonomic Outcomes

Integrative taxonomic revision of 64 nominal murid rodent taxa from four high-endemism regions recognises 47 valid species: 12 described as new, 18 synonymised, and 18 elevated from synonymy. Species recognition required concordance of molecular (COI p-distance > 5%, reciprocal monophyly), morphometric (significant Procrustes ANOVA, < 5% LDA overlap), and ecological (niche overlap $D < 0.20$) evidence. IUCN assessments place 59.6% of valid species as threatened (CR/EN/VU), with five newly described species requiring immediate protected area coverage as the highest conservation priority.

6.2 Conservation Recommendations

Three conservation recommendations: (1) submit IUCN Red List assessments for all 12 new species

immediately following publication of formal descriptions, using the preliminary assessments provided here as the starting point -- prioritising the five unprotected new species for expedited listing; (2) initiate protected area boundary extension or community conservation area designation for the three unprotected Philippine and Sulawesi new species localities in collaboration with local conservation NGOs and government agencies; and (3) conduct targeted priority surveys at 12 high-value under-sampled sites identified in Appendix A to complete species inventories before habitat loss forecloses discovery of remaining cryptic endemic species. All voucher specimen data, molecular sequences, and morphometric datasets are deposited in public repositories for use in future revisions.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All COI and cytochrome b sequences are deposited in GenBank (accession numbers provided in Supplementary Table S1). Whole-genome low-coverage reads are deposited in the European

Nucleotide Archive under project PRJEB86147. Geometric morphometric landmark coordinate files, geomorph analysis scripts, MaxEnt SDM outputs, niche hypervolume calculations, and IQ-TREE2 phylogenetic trees are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19466007. Holotype specimen details and catalogue numbers are provided in the Supplementary Taxonomic Appendix. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

All field collection was conducted under national collection permits as listed in the funding section. Trapping followed AVMA Guidelines for the Euthanasia of Animals and AAPA/ASM guidelines for mammal research. Animals retained as vouchers were euthanised by cervical dislocation under field anaesthesia (isoflurane) following protocols approved by WEUD-Madrid Institutional Animal Care Committee (protocol WEUD-IACUC-2022-0184). Live traps were checked every 6 hours to minimise stress on non-target captures, which were released at point of capture.

Appendix A

Priority Survey Sites for Remaining Unsourced Endemic Rodent Zones

Twelve high-priority geographic sites are identified for targeted endemic rodent surveys, selected based on: proximity to known collection localities of under-represented taxa, MaxEnt-predicted suitable habitat for poorly known species, and accessibility for future field campaigns. Sites are ranked by predicted species discovery probability.

PHILIPPINE ARCHIPELAGO -- 5 PRIORITY SITES

Priority 1: Mt Hilong-hilong, Agusan del Norte, Mindanao (8.2N, 126.1E; 800-1,600 m). Rationale: Adjacent to known *Chrotomys* locality; predicted suitable habitat for 3 undescribed *Chrotomys* lineages based on SDM; no collecting records since 1969. Recommended: 3-week survey (trapping + eDNA) targeting forest interior habitats.

Priority 2: Mt Malindang, Misamis Occidental, Mindanao (8.2N, 123.6E; 1,000-2,000 m). Rationale: Known *Musseromys* diversity hotspot; predicted by SDM to host additional undescribed congeners based on elevation gradient and isolation. Recommended: 2-week survey with molecular barcoding.

Priority 3: Sibuyan Island central highlands (12.4N, 122.5E; 600-1,800 m). Rationale: Geographically isolated island with virtually no herpetological or mammal surveys above 400 m elevation; high endemism expected from island biogeography models.

Priority 4: Camiguin Island (9.2N, 124.7E; all elevations). Rationale: Small oceanic island (265 km²) with single murid survey record; island biogeographic models predict 2-4 endemic species. Access improved by new road infrastructure.

Priority 5: Dinagat Island (10.1N, 125.6E; forested highlands). Rationale: Nickel mining threatens remaining forests; urgent survey needed before habitat destruction forecloses species discovery.

SULAWESI, ETHIOPIA, AND IBERIA -- 7 PRIORITY SITES

Sulawesi Priority 1: Banggai Archipelago (1.6S, 123.4E). Small islands east of Sulawesi with no murid records; predicted to harbour endemic *Rattus* or *Bunomys* species based on proximity to divergent Sulawesi mainland lineages.

Sulawesi Priority 2: Latimojong Mountains, S. Sulawesi (3.3S, 120.1E; > 2,000 m). Type locality area of new *Crunomys montanus* with additional undescribed lineages predicted by SDM in unexplored higher elevations.

Sulawesi Priority 3: Togian Islands (0.3S, 121.8E). Isolated island group with no small mammal surveys; high probability of endemic murids based on isolation and habitat extent.

Ethiopia Priority 1: Choke Mountains, Amhara Region (10.7N, 37.9E; > 3,500 m). Afroalpine habitat with *Praomys* predicted by SDM; no recent surveys above 3,000 m.

Ethiopia Priority 2: Harenna Forest, Bale Region (6.8N, 39.8E). Humid montane forest below the Bale Mountains NP; adjoining habitat to *Praomys abyssinicus* type locality with predicted additional undescribed *Lophuromys*.

Iberia Priority 1: Cantabrian Mountains, N. Spain (43.2N, 4.8W; > 1,500 m). Predicted *Microtus* hybridisation zone and potential cryptic diversity based on SDM gap analysis between *M. pyrenaicus* and *M. montserratensis* ranges.

Iberia Priority 2: Serra da Estrela, Portugal (40.3N, 7.6W; > 1,600 m). Isolated granitic massif with high-altitude *Apodemus* population; no molecular assessment since 2004.