

Molecular and morphological systematics of the *Bunomys* division (Rodentia: Muridae), an endemic radiation on Sulawesi

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Abstract

Sulawesi is the largest, most topographically complex island in the Wallacean biogeographic zone, and it has a rich fauna of endemic small mammals, dominated by rodents of the family Muridae. Among murids, the *Bunomys* division is the most species-rich radiation on Sulawesi. In total, the division contains 11 genera and 32 species, five and 20 of which are endemic to Sulawesi. We combined a five-locus phylogeny and linear cranial morphology to better understand the taxonomy and local scales of endemism within the *Bunomys* division on Sulawesi. Phylogenetic analyses of mitochondrial and nuclear DNA placed *B. fratrorum* among other genera and inferred *Paruromys* as sister to the type species of *Taeromys* (*T. celebensis*). We resolve these issues by resurrecting *Frateromys*, a genus under which *B. fratrorum* was once placed, and returning *Paruromys dominator* to *Taeromys*. Within three species, *F. fratrorum*, *T. callitrichus*, and *T. taerae*, we recovered Pleistocene age divergences between populations sampled across the northern peninsula of Sulawesi; divergence between western and eastern populations of *F. fratrorum* may reflect the existence of two species.

KEY WORDS

local endemism, molecular phylogeny, Muridae, paraphyly, Sulawesi, systematics, taxonomy, Wallacea

1 | INTRODUCTION

Oceanic island systems are important models for the study of evolution because they provide replicated areas of speciation (Wallace, 1860, 1863; Whittaker & Fernández-Palacios, 2007). Speciation on islands has been studied both in the context of their isolation from other landmasses (e.g. Demos et al., 2016; Roberts et al., 2011) and the diversification of species within islands (e.g. Giarla et al., 2018; Kyriazis et al., 2017). Our understanding of the mechanisms of speciation in most taxa, however, is limited by inadequately resolved taxonomy and incomplete knowledge of geographic distributions at scales relevant to the speciation

process (Dufresnes et al., 2019; Eldridge et al., 2018; Feulner et al., 2006; Giarla et al., 2018; Shen et al., 2019).

At the interface of Asia and Australia, the island of Sulawesi is a prime natural laboratory for the study of biogeography and biodiversity (Carstensen et al., 2012; Lohman et al., 2011; Rosauer & Jetz, 2015; Whitten et al., 2012). It is the largest isolated island between Asia and Australia and has remained separated from other landmasses by deep ocean channels throughout the last 10 million years of its formation (Nugraha & Hall, 2018). The marine barriers that isolate Sulawesi are traced by Wallace's Line to the west and Weber's Line to the east. These lines are recognized as two of the sturkst biogeographic transitions on earth (Lohman

et al., 2011; Whitten et al., 2012). While the age and isolation of Sulawesi provide the primary mechanisms explaining the island's high endemism (Lohman et al., 2011), its complex geography has promoted within-island speciation in many animal clades (Eldridge et al., 2018; Evans et al., 1999, 2003; Evans, et al., 2003; Fooden, 1969; Giarla et al., 2018; Linkem et al., 2013; von Rintelen et al., 2014). Sulawesi's geography features a peculiar shape, consisting of a central core and four long peninsulas. The island's mountainous terrain holds 20 summits $>2,500$ m (Hall, 2011; Voris, 2000; Whitten et al., 2012). Across Sulawesi, seven areas of endemism (AoE) are largely defined by the four peninsulas and the central core, with the northern peninsula split into three AoEs (Figure 1). Several disparate taxonomic groups have species and divergent populations restricted to a single AoE (Evans et al., 2008; Evans, et al., 2003; Fooden, 1969). The prevalence of divergent lineages among these AoEs reflects

the importance of within-island speciation and shared mechanisms of isolation as a source of diversity on Sulawesi. Episodic marine incursion into the areas in the AoE boundaries, habitat variation associated with elevational gradients on the island's mountains and climatic variation near AoE boundaries may have fostered speciation and contributed to the shared patterns of endemism (Eldridge et al., 2018; Evans, et al., 2003; Giarla et al., 2018).

The northern peninsula of Sulawesi is the largest and most biogeographically complex peninsula on Sulawesi. For all but the last 1–2 Ma of its subaerial history, the northern peninsula was an island or island chain isolated from the rest of Sulawesi (Nugraha & Hall, 2018). Its complex geological history is reflected by its division into three areas of endemism (Figure 1; NE, NC, and NW AoEs) (Evans et al., 2008; Evans, et al., 2003). These AoEs are separated by the Gorontalo divide, a lowland area with relatively dry

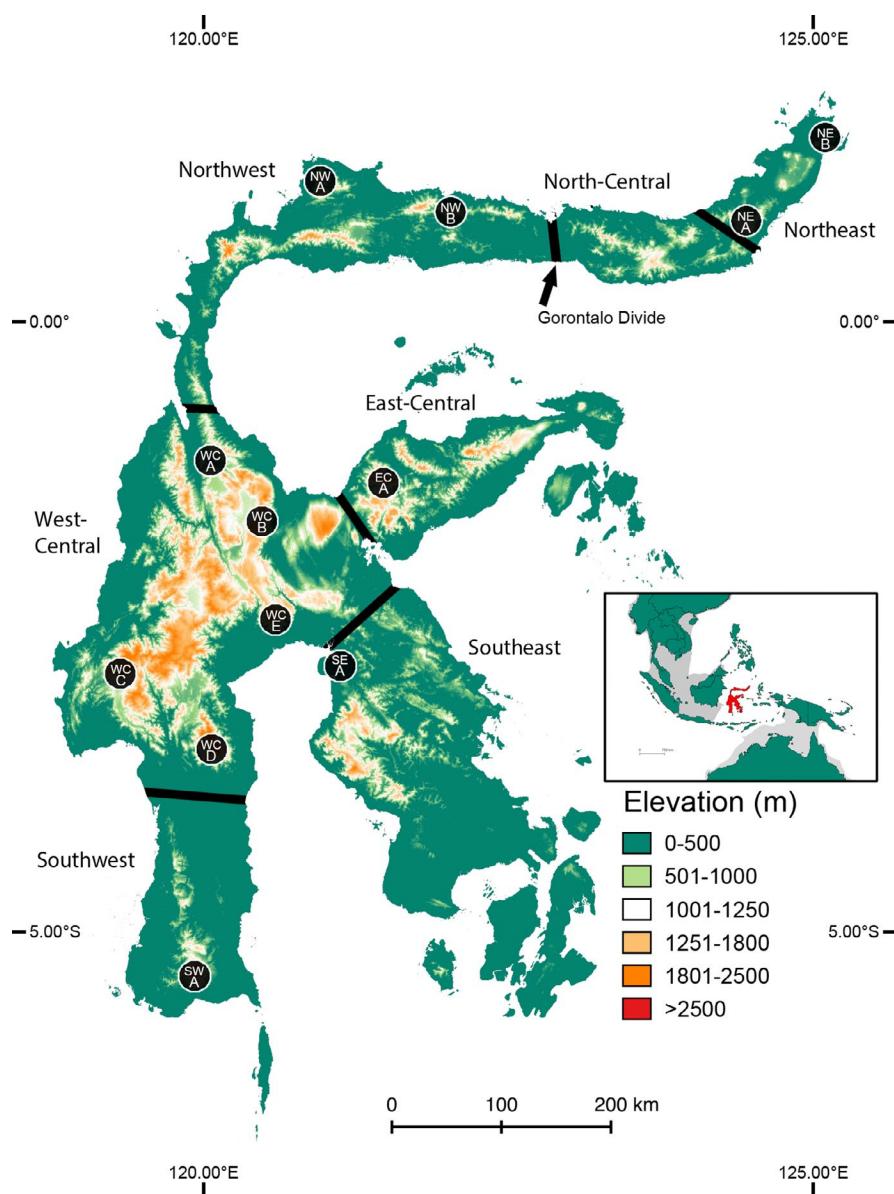


FIGURE 1 Map of Sulawesi showing Areas of Endemism (AoE; boundaries represented by black bars), the Gorontalo divide (black arrow), elevational variation and sampling localities for molecular analyses. The sampling localities were labelled with AoE abbreviation: WC (West-Central), SW (Southwest), SE (Southeast), EC (East-Central), NW (North-west) and NE (North-east) and a unique identification for sampling localities within each AoE region (see Table S1 for locality details). The inset shows the location of Sulawesi within the Indo-Australian Archipelago and the extent of land (grey polygon) during Pleistocene sea level low-stands (<120 m) [Colour figure can be viewed at wileyonlinelibrary.com]

habitat (Figure 1; Evans et al., 2008; Evans, et al., 2003) and a suture between two microplates that were ancient islands (Figure 1; Shekelle et al., 2017). Several studies in other taxa have identified the Gorontalo divide as the most substantial break in species and phylogeographic populations on the northern peninsula (Evans et al., 1999; Evans et al., 2003; Evans, et al., 2003; Shekelle et al., 2017; Walton et al., 1997). Indeed, a systematic study of murid rodents on Sulawesi considered the Gorontalo divide the most substantial biogeographic boundary on the island (Musser, 2014).

The Bunomys division (Rowe et al., 2019) comprises 11 described genera and 32 species and is one of the most diverse radiations of mammals in Wallacea (Fabre, Reeve, et al., 2018; Musser, 2014; Rowe et al., 2019). The division is represented by four species in the Lesser Sundas (genera *Komodomys* Musser and Boeadi, 1980; *Papagomys* Sody, 1941; *Paulamys* Musser, 1986; and *Rattus timorensis* Kitchener, Aplin and Boeadi, 1991), three species in the Philippines (genus *Bullimus* Mearns, 1905), four species on the Sunda shelf (genus *Sundamys* Musser & Newcomb, 1983), two species in the Maluku Islands (genus *Halmaheramys* Fabre et al., 2013) and 20 species on Sulawesi (genera *Bunomys* Thomas, 1910, *Eropeplus* Miller and Hollister, 1921, *Lenomys* Thomas, 1898; *Paruromys* Ellerman, 1954; and *Taeromys* Sody, 1941). Phylogenetic analyses suggest that the four Bunomys division species (genus *Sundamys*) that occur west of Wallace's Line on the Sunda Shelf are the result of secondary colonization from Wallacea (Rowe et al., 2019). All species in the Bunomys division evolved from a single Pliocene colonization of Sulawesi where they account for 20 of the 48 murid species recognized on the island (Rowe et al., 2019). On Sulawesi, the Bunomys division radiated into a diverse assemblage of ecomorphological forms found across the island from sea level to the highest sites that have been surveyed (~2,600 m). Their body size ranges from under 100 grams (e.g. *Bunomys chrysocomus* Hoffmann, 1887) to over 300 grams (e.g. *Lenomys meyeri* (Jentink, 1879)). The radiation includes terrestrial (e.g. *B. chrysocomus*), general (e.g. *Paruromys dominator*) and arboreal (e.g. *L. meyeri*) species (Musser, 2014; Nations et al., 2019). The genus *Bunomys* retained the generic body plan of terrestrial, medium-sized murids in the tribe Rattini, but includes species with omnivorous (*B. chrysocomus*), fungivorous (*B. karokophilus* Musser, 2014) and carnivorous (*B. prolatus* Musser, 1991, *B. toraja* Musser, Achmadi, Esslestyn and Rowe in Musser, 2014) diets (Musser, 2014). Other species are primarily herbivorous (*Taeromys callitrichus* (Jentink, 1879)) or frugivorous (*P. dominator* (Thomas, 1921), *Taeromys celebensis* and *T. hamatus* (Miller and Hollister, 1921)). The genera *Eropeplus* and *Lenomys* are large (>300 g), semi-arboreal, woolly rats with exceptionally large and complex molars that aligned them morphologically with the genera *Pithecheir* Cuvier, 1833 and *Lenothrix* Miller, 1903 of the

Sunda Shelf (Musser, 1981). Indeed, based on cranial and dental trait similarities, they were placed in the Pithecheir division (Aplin & Helgen, 2010; Carleton & Musser, 2005).

Although Sulawesian members of the Bunomys division are found across the island at all elevations that have been surveyed, only four species are distributed in more than two AoEs and 10 species are restricted to a single AoE (Musser, 2014). With eight recognized species, the genus *Bunomys* Thomas, 1910 is the most species-rich genus in the Bunomys division (Musser, 2014; Rowe et al., 2019). Two species of *Bunomys* (*B. chrysocomus* and *B. andrewsi* (Allen 1911)) are common and widespread across large areas of Sulawesi, including multiple AoEs and wide elevational ranges. Six species are restricted to a small portion of the island including one or two AoEs (Musser, 2014). One of the most geographically restricted is *B. fratrorum* (Thomas, 1896), which is known only from the eastern half of the northern peninsula of Sulawesi. The geographic pattern of endemism suggests that geographic isolation, especially on Sulawesi's peninsulas, may promote speciation. However, many new species of rats have been described from Sulawesi in recent years, including two species in the genus *Bunomys* (Esslestyn et al., 2012, 2015; Mortelliti et al., 2012; Rowe et al., 2014, 2016; Musser 2014). New geographic records often result in substantial changes to our knowledge of species' distributions (Achmadi et al., 2014). A recent revision of genus *Bunomys* reported that some species are known from few records or localities with substantial geographic gaps in sampling (Musser, 2014). Moreover, the monophyly of the genus *Bunomys* and species boundaries within it have not been tested with genetic data. Indeed, *B. fratrorum* was once treated as a separate genus, *Frateromys* Sody, 1941.

With the goals of better understanding the taxonomy, evolutionary relationships and geographic ranges of Sulawesi's Bunomys division members, we (a) conducted field surveys across the northern peninsula, (b) inferred phylogenetic relationships, (c) tested the monophyly of genera and (d) quantified morphological variation.

2 | MATERIALS AND METHODS

2.1 | Field survey

Across the northern peninsula, 15 species were recorded from previous surveys, but with substantial gaps west of the Gorontalo divide (Figure 1; compiled in Musser, 2014). From 2013 to 2016, we surveyed small mammals on two mountains west of the Gorontalo divide in the North-west AoE and two mountains east of the Gorontalo divide in the North-east AoE (Figure 1; Table 1). Our efforts included sampling: (a) around two camps on Mt. Dako (NW-A; 400 m and 1,600 m) from 1 to 16 March 2013; (b) around two camps on Mt.

TABLE 1 List of species collected from four mountains across the northern peninsula of Sulawesi, Indonesia

| Species | North-West AoE | | | | North-East AoE | | | | Nearby records 1895–2014 |
|--------------------------------|------------------------|--------------------------|-----------------------------|-------------------------------|-------------------------------|----------------------------|------------------------------------|---|-----------------------------|
| | Mt. Dako 2013 400 m | Mt. Dako 2013 1,600 m | Mt. Buliobuto 2014 425 m | Mt. Buliobuto 2014 1,300 m | Mt. Buliobuto 2014 1,300 m | Mt. Amhang 2016 1,500 m | Mt. Dua Saudara* 2016 < 1,000 m | | |
| <i>Bunomys fraterorum</i> | — | NR | — | — | — | + | + | — | — |
| <i>Bunomys chrysocomus</i> | + | — | + | — | + | — | — | + | + |
| <i>Echinothrix centrosa</i> | — | — | + | — | + | — | — | — | — |
| <i>Echinothrix leucana</i> | — | — | — | — | — | + | + | + | + |
| <i>Haeromys minahassae</i> | NR | — | NR | — | + | — | — | + | + |
| <i>Hyorhinomys stuempkei</i> | — | + | — | — | — | — | — | — | — |
| <i>Lenomys meyeri</i> | — | — | — | — | + | + | + | + | + |
| <i>Margaratomys beccarii</i> | — | — | — | — | — | — | — | + | + |
| <i>Maxomys musschenbroekii</i> | + | + | + | + | + | + | — | + | + |
| <i>Maxomys dollmani</i> | — | NR | — | — | — | — | — | — | — |
| <i>Maxomys helwaldi</i> | — | + | + | + | + | + | + | + | — |
| <i>Paromys dominator</i> | + | + | + | + | + | + | + | + | + |
| <i>Rattus facetus</i> | — | + | — | + | + | — | — | — | — |
| <i>Rattus hoffmanni</i> | + | + | + | — | + | — | — | + | + |
| <i>Rattus marmosurus</i> | — | — | — | — | — | + | + | + | + |
| <i>Rattus xanthurus</i> | — | — | — | — | — | + | + | + | + |
| <i>Taeromys taerae</i> | — | NR | — | — | — | — | — | — | — |
| <i>Taeromys callitrichus</i> | NR | — | NR | — | — | + | + | + | + |
| <i>Taeromys celebensis</i> | — | — | — | — | — | + | + | + | + |

NR represents new records for the AoE. Nearby records were based on Musser (2014).

The asterisk indicates samples obtained from local villagers.

Buliohuto (NW-B; 425 m and 1,300 m) from 16 January to 2 February 2014; (c) around one camp on Mt. Ambang (NE-A; 1,500 m) from 15 February to 2 March 2016; and (d) rats collected by villagers near the base of Mt. Dua Saudara (NE-B; <1,000 m). Specimens taken on the first three mountains were collected using a combination of victor rat traps and 20 L pitfalls. Trapping procedures followed the guidelines of the American Society of Mammalogists (Sikes et al., 2016; Sikes & Gannon, 2011), with approvals under ethic permits from Louisiana State University (Permit No. 13-020) and Museums Victoria (MVAEC 15002).

2.2 | Genetic sequencing

We obtained tissue samples from 14 of 18 described *Bunomys* division species on Sulawesi (Table S1). Tissue samples were not available for *Bunomys karokophilus*, *Taeromys arcuatus* (Tate and Archbold, 1935), *T. hamatus* or *T. microbullatus* (Tate and Archbold, 1935). We also included one undescribed genus and one undescribed species of *Taeromys* first published by Rowe et al. (2019). To these samples, we added published sequences from 12 additional *Bunomys* division species from the Lesser Sundas (*Papagomys*, *Komodomys* and *Rattus timorensis*), the Maluku islands (*Halmaheramys*), the Philippines (*Bullimus*) and the Sunda Shelf (*Sundamys*). We included *Rattus hoffmanni* Matschie, 1901, and *Rattus facetus* Miller and Hollister, 1921, as outgroups. We extracted DNA from tissue samples using a QIAextractor machine or a QIAGEN DNeasy blood and tissue kit. For each sample, we amplified and sequenced one mitochondrial DNA locus (cytochrome b) and fragments of four unlinked autosomal nuclear exons: exon 11 of breast cancer 1 (BRCA1); exon 1 of retinol-binding protein 3 (IRBP); the single exon of recombination activating gene 1 (RAG1); and exon 10 of growth hormone receptor (GHR). Amplification and sequencing followed the procedures of Rowe et al. (2019). All new sequences are available on GenBank with accession numbers (MW058816-MW059016; Table S1).

2.3 | Phylogenetic analyses

We aligned homologous sequences using MUSCLE 3.8.425 (Edgar, 2004) with default settings, inspected the resulting alignments manually with AliView 1.24 (Larsson, 2014) and then concatenated the alignments in Geneious 10.2.5. For phylogenetic analyses, we created two concatenated data sets, one consisting of all loci and the other with the mitochondrial gene removed. We estimated the best-fit model(s) of sequence evolution using ModelFinder (Kalyaanamoorthy et al., 2017) implemented in IQ-TREE 1.6.10 (Nguyen et al., 2015). For ModelFinder input, we used the all-locus data set divided by

codon position for each locus (i.e. maximum of 15 partitions). Searches were completed using the Bayesian Information Criterion (BIC) and greedy algorithm (Lanfear et al., 2012). Using the results from ModelFinder, we performed maximum likelihood analyses for each data set using IQ-TREE with 1,000 pseudo-replicates of ultrafast bootstrap approximation (UFBoot2) (Minh et al., 2013; Nguyen et al., 2015). To complement our bootstrap search, we performed SH likelihood-ratio tests (Shimodaira & Hasegawa, 1999) implemented in IQ-TREE using constrained trees with monophyletic genera *Bunomys* and *Taeromys*. The constrained trees were created using TreeGraph v2.15 (Stöver & Müller, 2010).

We used a secondary calibration approach with the all-locus data set in BEAST v2.5.1 (Bouckaert et al., 2014) to estimate the divergence times of the species and genera within the *Bunomys* division. We took a 3.45 Ma (95% HPD = 3.09–3.81 Ma) crown age for the *Bunomys* division from Rowe et al. (2019) set as a log-normal distribution for the BEAST2 prior as follows: Mean = 1.237, Standard Deviation = 0.0612, and offset = 0. In BEAUTi, we implemented the favoured partition schemes using the SSM 1.1.0 package on the all-locus data set for BEAST2 analyses (Table S2). We estimated the topology and used Bayesian strict-clock analyses in BEAST2 to estimate the divergence dates. Clock and substitution models were unlinked among partitions, but tree models were linked. For the tree priors, we applied the birth-death model with exponentially distributed birth and death rates (mean = 1; offset = 0). For our data set, which mixes species and populations, the birth-death model produced more consistent and precise results compared to other models supported by BEAST2 (e.g. Ritchie et al., 2017). Other priors remained in their default settings. We performed BEAST2 analyses with two independent MCMC runs of 10^8 generations each, with sampling every 10^4 generations. BEAST2 was run using the BEAGLE v3.1.0 algorithm using a GPU set at double precision floating point operation (Ayres et al., 2019). We checked convergence and appropriate ESS on Tracer 1.7.1 (Rambaut et al., 2018). We combined the two BEAST tree files from the two runs using LogCombiner v2.6.1. We created a maximum clade credibility phylogeny from the combined tree file set at 10 per cent burnin using TreeAnnotator 2.5.1 (Bouckaert et al., 2014).

2.4 | Morphological analyses

To characterize morphological differences among *Bunomys* division members, we examined and measured 264 specimens of 16 species from 34 localities across Sulawesi (Table S3). These specimens comprise seven of the eight named species of *Bunomys* and representatives of each of the four other *Bunomys* division genera endemic to Sulawesi including an undescribed genus (Rowe et al., 2019). All

specimens are deposited at Museums Victoria (NMV) in Melbourne, Louisiana State University Museum of Natural Science (LSUMZ) in Baton Rouge, the American Museum of Natural History (AMNH) in New York, the Field Museum of Natural History (FMNH) in Chicago, the National Museum of Natural History (USNM) in Washington D.C. or Museum Zoologicum Bogoriense (MZB) in Bogor.

We used a digital caliper (0.01 mm accuracy) to measure a standard set of 20 craniodental characters from each specimen following Musser and Heaney (1992). Measurements consisted of greatest length of skull (GLS), zygomatic breadth (ZB), length of nasal (LON), length of rostrum (LR), breadth of rostrum (BR), interorbital breadth (IB), breadth of zygomatic plate (BZP), breadth of braincase (BBC), height of braincase (HBC), postpalatal length (PPL), length of diastema (LD), length of bony palate (LBP), length of incisive foramina (LIF), breadth of incisive foramina (BIF), breadth of mesopterygoid fossa (BMF), length of bulla (LB), crown length of maxillary molar row (CLMM), alveolar breadth of first upper molar (BUM), breadth of upper incisor (BUI) and depth of upper incisor (DUI) (Figure S1). We included measurements from adult individuals only, which we identified by fully erupted upper third molars (M3) and fused basioccipital-basisphenoid sutures.

We used principal component analyses (PCA) of the correlation matrix on untransformed variables to examine craniodental variation among genera and species within the *Bunomys* division radiation on Sulawesi. These analyses were conducted in R (R Core Team, 2020) using ggplot2 for visualization (Wickham, 2016).

3 | RESULTS

3.1 | Field surveys

From 2013 to 2016, we documented 20 murid species from four northern peninsula mountains, consisting of 11 species from Mt. Dako (NW-A), 9 from Mt. Buliohuto (NW-B), 13 from Mt. Ambang (NE-A) and 7 from Mt. Dua Saudara (NE-B; Table 1). We collected specimens of *B. fratrorum* from Mt. Ambang and obtained the same species from Mt. Dua Saudara in the eastern half of the northern peninsula where the species was thought to be endemic. We also collected several individuals from Mt. Dako on the western end of the northern peninsula that appeared most similar to *B. fratrorum* in external characters. In addition, we also recorded *Taeromys taerae* and *T. callitrichus* outside their known ranges on Mt. Dako and Mt. Buliohuto, respectively (Table 1). We did not detect *Lenomys meyeri* or *Taeromys celebensis* from Mts. Dako or Buliohuto, but other studies have recorded them from nearby localities in the NW Area of Endemism (Musser, 2014; Table 1). Similarly, we did

not detect *Bunomys chrysocomus* or *Margaretamys beccarii* from Mts. Ambang or Dua Saudara, but other studies have recorded them from nearby localities in the NE Area of Endemism (Musser, 2014; Table 1).

3.2 | Phylogenetic relationships and divergence dates

The concatenated alignment of all loci contained 67 individuals, representing 43 species. Seven individuals from three species were represented by only the mitochondrial locus (see Figure 2). The data set is 5,349 base-pairs (bp) long with 8.9% missing data. The concatenated alignment of all nuclear genes contained 60 individuals, 4,544 bp and no missing data (see Table S2 for details). For the all-locus data set, the maximum likelihood (IQ-TREE) and Bayesian (BEAST2) analyses produced nearly identical topologies (Figure 2). Both supported a monophyletic radiation of genera on Sulawesi (*Bunomys*, *Eropeplus*, *Lenomys*, *Paruromys*, *Taeromys* and gen. et sp. n.) sister to *Halmaheramys* from the Maluku Islands, as reported previously (Rowe et al., 2019). The nuclear-only data set placed *Halmaheramys* sister to the genus *Bunomys* within the Sulawesi radiation, but with modest support (maximum likelihood bootstrap values (MLBV) = 80%). However, only two of the four nuclear loci were available for *Halmaheramys*. Within the Sulawesi radiation, the all-locus data set supported the earliest split between a clade containing all species of *Bunomys*, except *B. fratrorum* (Bayesian posterior probabilities (PP)=1; MLBV = 100%) and a clade containing all other genera and *B. fratrorum* (PP = 0.93; MLBV = 84%). The nuclear-only data also supported the placement of *B. fratrorum* with other genera, to the exclusion of other *Bunomys* (MLBV = 76%; Figure S2). While the support values for monophyly of this 'all other genera' clade were modest from both the all-locus and nuclear-only data sets, an SH test using the all-locus data set shows that a monophyletic *Bunomys* including *B. fratrorum* has a significantly lower likelihood (delta logL = 49.31, $p = .009$). Thus, the inclusion of *B. fratrorum* in *Bunomys* renders the genus polyphyletic. We estimated the divergence of *B. fratrorum* from other *Bunomys* circa 2.4 Ma in the Early Pleistocene (95% Highest Posterior Density (HPD)= 2.04–2.84 Ma; Figure 2). At the base of the 'all other genera' clade, we recovered five well-supported descendant lineages but without support for relationships among any of them. These included (a) a monotypic lineage representing an undescribed genus (Rowe et al., 2019), (b) *Eropeplus* + *Lenomys*, (c) *Bunomys fratrorum*, (d) *Taeromys celebensis* + *Paruromys dominator* and (e) all other *Taeromys*. The well-supported placement of *Paruromys* sister to *T. celebensis* (MLBV = 100%,

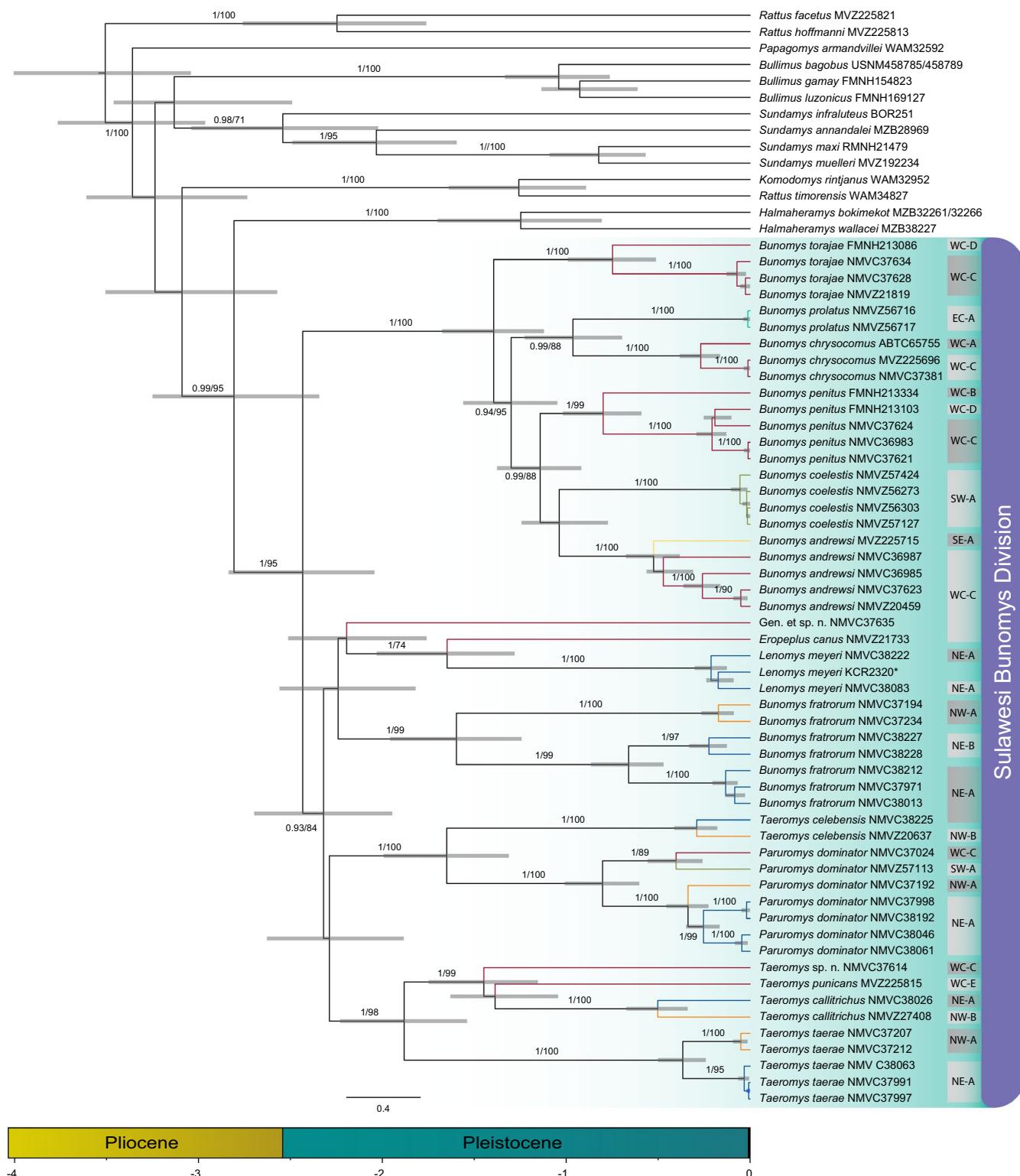


FIGURE 2 Fossil-calibrated Bayesian (BEAST2) phylogeny of the *Bunomys* division. Numbers at nodes indicate posterior probabilities (BEAST) followed by UFBoot2 bootstrap support (IQ-TREE). Only PP >90% and MLBV >70% are shown. Grey bars represent 95% HPD intervals for node ages. The populations of species across Sulawesi were labelled with specific geographic localities shown in Figure 1. The branch colours indicate AoE regions corresponding to the specific localities at the tips (see Table S1 for locality details). The asterisk indicates a sample obtained from a wildlife market [Colour figure can be viewed at wileyonlinelibrary.com]

PP = 1.0), the type species for the genus *Taeromys*, renders *Taeromys* paraphyletic. An SH test of a monophyletic *Taeromys* showed significantly lower likelihood

($\delta\text{L} = 127.35, p = <.0001$). This relationship also was well-supported by the nuclear-only data (MLBV = 99%; Figure S2). In contrast, the node uniting all *Taeromys*

and *P. dominator* was not well-supported by any analysis (MLBV = 39%, PP = 0.41).

Within species, Bayesian and maximum likelihood analyses of the all-locus data set revealed several examples of deep divergence and reciprocal monophyly among geographic localities. This was most notable in *B. fratrorum* where three reciprocally monophyletic clades were evident among sampling localities. The western northern peninsula population (NW AoE) from Mt. Dako (NW-A) diverged from the eastern northern peninsula populations (NE AoE) from Mts. Ambang (NE-A) and Dua Saudara (NE-B) circa 1.5 Ma in the Pleistocene (95% HPD = 1.24–1.96 Ma; Figure 2). We also recovered strong support for reciprocal monophyly of samples from Mt. Ambang ($n = 3$) and Mt. Dua Saudara ($n = 2$) with divergence circa 0.6 Ma (95% HPD = 0.47–0.87 Ma). Similarly, we inferred reciprocal monophyly for Mt. Dako and Mt. Ambang populations of *T. taerae*, but with divergence <0.5 Ma (95% HPD = 0.24–0.5 Ma). We recovered a similar divergence time circa 0.5 Ma (95% HPD = 0.34–0.67 Ma) between the individual samples of *T. callitrichus* from Mt. Buliohuto (NW-B) west of Gorontalo and Mt. Ambang (NE-A) east of Gorontalo.

Multiple divergent populations with ages, circa 0.7–0.8 Ma, were also evident within *B. penitus*, *B. torajae* and *P. dominator* sampled from other AoEs outside the northern peninsula (Figure 2).

3.3 | Variation in morphology

From our principal component analysis, we retained the first two axes, using the latent root criterion (McGarigal et al., 2013), as each had eigenvalues >1 . The first axis represented skull size and explained 86% of the variation, whereas PC2 explained 3.6% and contrasted rostrum and nasal length with skull width (Figure 3; Table 2). The genera *Bunomys*, *Lenomys*, *Taeromys* and *Paruromys* were clearly separated in morphospace. *Bunomys* (including *B. fratrorum*) was distinct from most other genera along PC1 except the larger species (*B. fratrorum*) overlapped with some specimens of the smaller species of *Taeromys* (*T. hamatus*, *T. taerae*) and with the gen. et sp. n. *Eropeplus* was completely encompassed by *Taeromys* in PC1 and PC2 space.

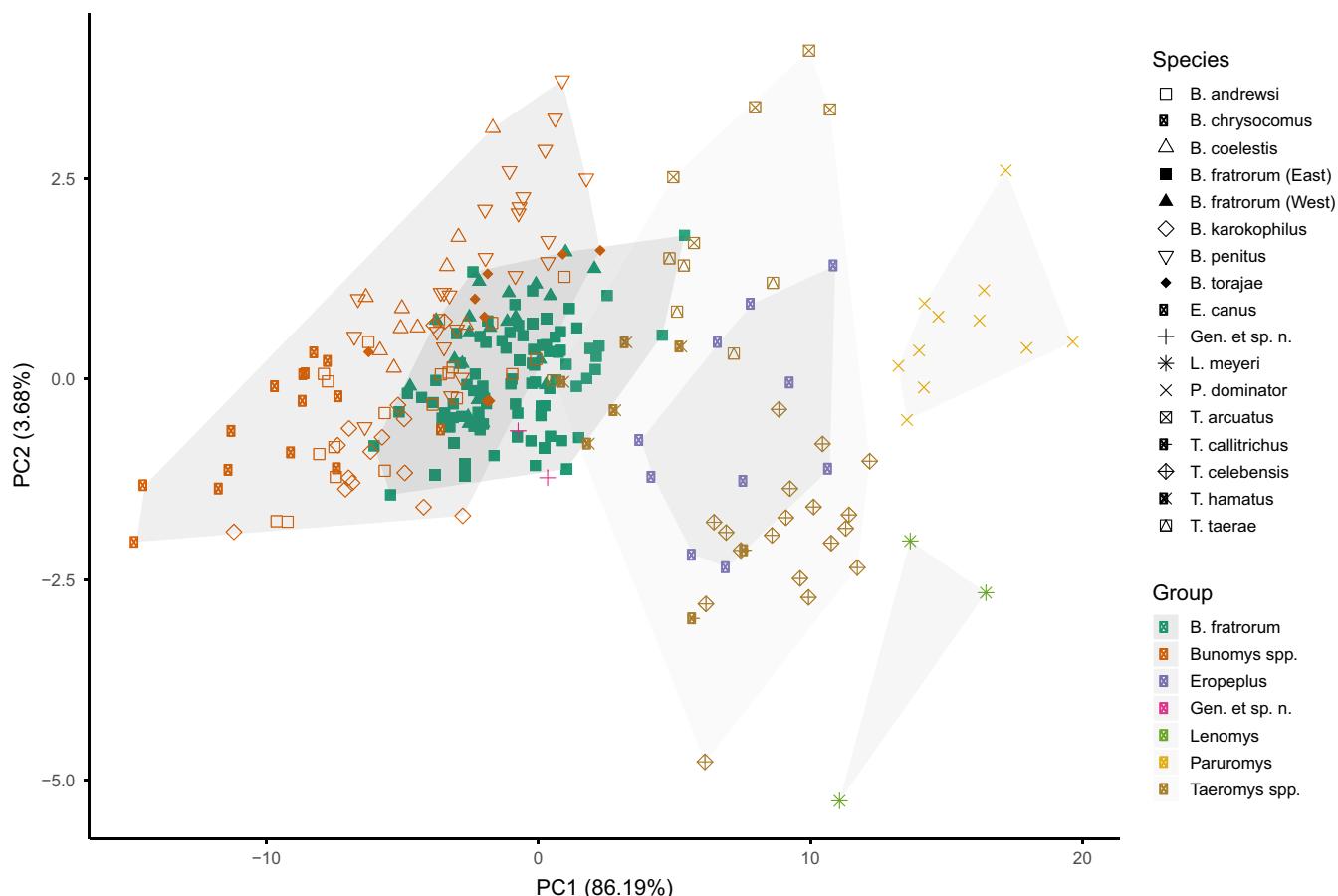


FIGURE 3 Principal component analyses (PCA) of linear craniodental measurements from species in the *Bunomys* division. Minimum polygons drawn around *Bunomys* (excluding *fratrorum*), *Bunomys fratrorum*, *Eropeplus*, gen. et sp. n., *Lenomys*, *Paruromys* and *Taeromys*. Loadings are provided in Table 2 [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Variable loadings, eigenvalues and percentage of variance for the principal component analyses. Variable abbreviations are defined in the ‘Materials and Methods’

| Variables | Principal components | |
|------------------------|----------------------|--------|
| | PC1 | PC2 |
| GLS | 0.711 | 0.055 |
| ZB | 0.357 | -0.386 |
| LON | 0.281 | 0.428 |
| LR | 0.175 | 0.674 |
| BR | 0.073 | 0.051 |
| IB | 0.042 | -0.011 |
| BZP | 0.142 | -0.089 |
| BBC | 0.195 | -0.300 |
| HBC | 0.126 | -0.196 |
| PPL | 0.247 | -0.131 |
| LD | 0.194 | 0.084 |
| LBP | 0.211 | -0.053 |
| LIF | 0.072 | 0.121 |
| BIF | 0.019 | -0.003 |
| BMF | 0.016 | -0.001 |
| LB | 0.056 | -0.074 |
| CLMM | 0.136 | -0.119 |
| BUM | 0.033 | -0.047 |
| BUI | 0.030 | -0.063 |
| DUI | 0.056 | -0.066 |
| Eigenvalue | 37.71 | 1.61 |
| Percentage of variance | 86.19 | 3.68 |

4 | DISCUSSION

Previous studies of Sulawesi vertebrates, including macaques (Evans et al., 1999; Evans et al., 2003; Evans, et al., 2003; Fooden, 1969), toads (Evans, et al., 2003) and spiny rats (Giarla et al., 2018) found that endemic species and phylogeographic lineages are structured by areas of endemism (AoEs) west and east of the Gorontalo divide on the northern peninsula of Sulawesi. Studies of other taxa (grasshoppers, Bridle et al., 2001; skinks, Linkem et al., 2013; and snails, von Rintelen et al., 2014), which did not find a strong break at the Gorontalo divide, also did not find support for AoEs in other parts of Sulawesi. Our recent surveys combined with previous records (Musser, 2014) of murid rodents across the northern peninsula supported the endemism of six species west or east of the Gorontalo divide. These combined records show that *Echinothrix leucura*, *Rattus marmosurus* and *R. xanthurus* are only found east of Gorontalo. In contrast, the closest relatives of these species are only found west of the Gorontalo divide (*R. facetus* for *R. marmosurus* and *R. xanthurus* and *E. centrosa* for *E. leucura*). Our surveys of

Mts. Dako and Buliohuto provided the first records of four species of murids from the NW AoE, between Gorontalo and the central core of Sulawesi. Two of these species, *Taeromys callitrichus* and *Haeromys minahassae*, were previously recorded from east of the Gorontalo divide and from the central core of Sulawesi, but not the NW AoE in between (Table 1; Carleton & Musser, 2005; Musser, 2014). Two other species, *Bunomys fratrorum* and *Taeromys taerae*, were thought to be endemic to areas east of the Gorontalo divide.

While our surveys indicated a range extension for *B. fratrorum*, *T. callitrichus* and *T. taerae* across the northern peninsula that appears to undermine the importance of the Gorontalo divide as a biogeographic boundary, our phylogenetic analyses found deep divergence between populations of *B. fratrorum* and modest divergence between populations of *T. callitrichus* and *T. taerae* on either side of the divide. The divergence of *B. fratrorum* populations from west and east of the divide was nearly as deep as the divergence among all other species of *Bunomys*. Even among the two eastern-most populations (Mts. Ambang and Dua Saudara), we recovered reciprocal monophyly but with modest divergence, less than any species pair in our data. The divergence of *T. callitrichus* and *T. taerae* populations from either side of the Gorontalo divide was similarly more recent than between species pairs. However, reciprocal monophyly for *T. taerae* samples suggests that populations have been evolving independently for a long time (only 1 sample per population was available for *T. callitrichus*). Therefore, our results are consistent with biogeographic boundaries on the northern peninsula isolating incipient populations and species in the early to late Pleistocene (Evans, et al., 2003; Nugraha & Hall, 2018).

We also observed divergent populations within other species sampled across Sulawesi but not consistently associated with AoEs. After *Bunomys fratrorum*, the next deepest divergences within species are evident in *B. penitus*, *B. torajae* and *P. dominator*, each with comparable crown ages. In *P. dominator*, reciprocal monophyly is evident between samples from the northern peninsula (NW and NE AoEs) and from the rest of Sulawesi (WC and SW AoEs), which is represented by the boundary between the WC and NW AoEs. This boundary is associated with the history of the northern peninsula as a separate island until ~1 Ma (Nugraha & Hall, 2018). In contrast to *P. dominator*, the comparable divergences within the two *Bunomys* spp. occur entirely within the WC AoE. For *B. penitus*, the divergence occurs between the single sample from Mt. Rorekatimbo (WC-A) in the north-east part of the West-Central AoE and the remaining samples, which are from the southwest part of the West-Central AoE (WC-C, WC-D). In *B. torajae*, divergence occurs between these same two localities (WC-C, WC-D), which are the only localities where this species is recorded. Based on a wider sampling of Murinae, but less complete sampling of the *Bunomys* division, we previously reported these WC-D samples as *Bunomys* sp. n.

(Rowe et al., 2019). In the current phylogeographic context of this study, these populations appear to have geographic variation comparable to other currently recognized species on Sulawesi. In contrast, *Taeromys* sp. n. (also reported in Rowe et al., 2019) is deeply divergent from other species of *Taeromys* sampled in this study.

In addition to revealing divergence of populations across Sulawesi, our phylogenetic analyses rendered the genus *Bunomys* polyphyletic by inclusion of *B. fratrorum*, which is nested among other *Bunomys* division genera. *Bunomys coelestis* and *B. fratrorum* were the first two species of *Bunomys* described (Thomas, 1896), and both were originally placed in *Mus*. The genus *Bunomys* was later proposed by Thomas (1910) for *B. coelestis*, a SW AoE endemic. *Bunomys* was later moved to *Rattus* (Ellerman, 1941). However, *Rattus* has long been an unnatural grouping of difficult-to-place species (e.g. Ellerman, 1941; Tate, 1936). The elevation of *R. fratrorum* to *Frateromys fratrorum* (Sody, 1941) was just one of a dozen genera proposed by Sody to resolve the now well-supported view that *Rattus* (sensu Carleton & Musser, 2005; Ellerman, 1941; Tate, 1936) ‘constitutes a heterogeneous group’ (see *R. timorensis* in this study; Rowe et al., 2019; Thomson et al., 2018). Since their first descriptions, the genera *Mus*, *Bunomys* (Musser, 1981, 2014; Tate, 1936; Thomas, 1910), *Rattus* (Ellerman, 1941; Tate, 1936) and *Frateromys* (Sody, 1941) have applied at various times to species currently in the genus *Bunomys*. However, for nearly forty years now, the genus *Bunomys* has remained stable (Musser, 1981), with addition only of newly described species from Sulawesi (Musser, 1991, 2014). However, our phylogenetic analyses show that *Bunomys*, as currently defined, constitutes a heterogeneous and polyphyletic taxon. We also argue that the stability of the genus in common taxonomic usage warrants recognizing *Bunomys* as used by Thomas, 1910 and not the brief mention of *Bunomys* as a possible name for the tooth of an undescribed rodent found in a cave in Madagascar (Grandidier, 1905, p. 50). Here, we repair the monophyly of *Bunomys* by resurrecting the available generic name *Frateromys* for *B. fratrorum*, as proposed by Sody (1941).

Our phylogenetic analyses also rendered *Taeromys* paraphyletic with *Paruromys dominator* sister to *T. celebensis*. *Paruromys dominator* was originally described as a *Rattus* (Thomas, 1921), and *Taeromys celebensis* was described as *Mus celebensis* (Gray, 1867). The genus *Taeromys* was subsequently introduced by Sody to help resolve the heterogeneous group that was *Rattus* (Sody, 1941). Sody (1941) gave *T. celebensis* as the type species and included *T. dominator* in this new genus. Later, *T. dominator* was returned to *Rattus* using the subgenus *Paruromys* (Laurie & Hill, 1954). Musser and Newcomb (1983) then elevated *Paruromys* to genus. This arrangement was maintained by subsequent studies without molecular phylogenetic data (Carleton & Musser, 2005;

Musser, 1984, 2014). *Paruromys dominator* and *T. celebensis* share similar features of skins, skulls and teeth and are often confused in collections (Musser, 2014; Musser & Newcomb, 1983). Given the sister relationship of *P. dominator* to the type species of *Taeromys*, we transfer *Paruromys dominator* back into *Taeromys*. However, the monophyly of our revised *Taeromys* was not well-supported in our analysis with low support values at the node uniting all sampled *Taeromys*. Further phylogenetic studies are needed to determine whether *Taeromys* is indeed monophyletic. The genus name *Arcuomys* Sody, 1941, is available but applies to *T. arcuatus*, one of three named species of *Taeromys* not in our data set.

In contrast to the genetic data, standard cranial measurements used widely in murine taxonomy (Balete et al., 2007; Fabre, Fitriana et al., 2018; Heaney et al., 2011; Helgen, 2003; Musser & Heaney, 1992; Rickart et al., 2005; Rowe et al., 2014;) were much less effective at defining generic boundaries. Using phenotypic characters to distinguish generic boundaries among species of Murinae, particularly among members of Tribe Rattini (sensu Rowe et al., 2019), has been a challenge for more than a century. Many murines were described first under *Mus* Linnaeus, 1758, later transferred to *Rattus* Fischer, 1803, and ultimately transferred to a distinct genus (e.g. *Niviventer* Marshall, 1976). While *Frateromys fratrorum* was at the upper limits of genus *Bunomys* on PC1, they were completely subsumed in PC2 and overlapped other large-bodied *Bunomys* on PC1 (see also Musser, 2014). However, these same cranial data could discriminate genus *Bunomys*, excluding *F. fratrorum*, from all other *Bunomys* division genera by combinations of PCs 1 and 2 (Figure 3). In contrast to *Bunomys* and *Frateromys*, *Paruromys*, which we transfer to *Taeromys*, is completely separated from all other *Taeromys* along PC1. *Paruromys* is also separated from its sister lineage, *T. celebensis*, on PC2, whereas *T. celebensis* overlaps other species of *Taeromys* and the genus *Eropeplus*. Thus, the quantitative cranial morphological data mislead the inference of generic boundaries both by recovering overlap among distantly related lineages (i.e. *Bunomys* and *Frateromys*) and by recovering morphological divergence in closely related phylogenetic lineages (i.e. *T. celebensis* and *P. dominator*). These patterns show that evolution of size diversity is not particularly informative for understanding relationships and that quantitative traits capture relatively limited differences in cranial shape.

This study joins other recent discoveries based on new field surveys over the last ten years that demonstrate the need for new collections to address our incomplete understanding of murid taxonomy and geographic distributions on Sulawesi (Esselstyn et al., 2012, 2015; Mortelliti et al., 2012; Musser, 2014; Rowe et al., 2014, 2016). The *Bunomys* division is the most diverse radiation of murid rodents on

Sulawesi. While the taxonomy of the genus *Bunomys* was reviewed recently (Musser, 2014), our addition of molecular phylogenetic data shows that many taxonomic issues remain unresolved, including within *Bunomys* and other genera within the *Bunomys* division. The complex topography and geography of Sulawesi are likely to have facilitated within-island speciation in many groups of organisms, but they also make documenting the island's many species and their geographic distributions a substantial challenge (Esselstyn et al., 2012, 2015; Mortelliti et al., 2012; Rowe et al., 2014, 2016).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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