# Supplemental Results

## On UCEs as loci for phylogenetic inference

Ultra-conserved elements (UCEs) have proven increasingly popular and useful as loci for phylogenomic analyses across a range of taxonomic levels and time scales (Crawford et al. 2012; McCormack et al. 2012; Faircloth et al. 2013; McCormack et al. 2013; Jarvis et al. 2014; Blaimer et al. 2015; Meiklejohn et al. 2016; Alexander et al. 2017; Burress et al. 2018; Bossert et al. 2019; Oliveros et al. 2019; Quattrini et al. 2020; Alda et al. 2021) (McClean et al., 2022; Smith et al., 2013). UCEs are typically collected using bait capture and targeted enrichment approaches, harvested from whole genomes as we have done, or a combination of the two. This is driven by both their ready application to non-model organisms and museum specimens (Bi et al. 2013; Faircloth 2017; Zhang et al. 2019), their possession of desirable characters for use in phylogenetic reconstruction (Faircloth et al. 2012; McCormack et al. 2012), and their subsequent ability to provide resolutions to previously intractable nodes (Faircloth et al. 2013; Blaimer et al. 2015; Alda et al. 2021). However, both the function of UCEs and the influence of selection upon them remain poorly understood (Bejerano et al. 2004; Katzman et al. 2007). Rates of molecular evolution may also vary within UCE loci (Tagliacollo and Lanfear 2018) and phylogenetic reconstructions using UCEs (and other phylogenomic markers) can be confounded by gene tree discordance driven by processes such as incomplete lineage sorting and introgression (Jeffroy et al. 2006; Degnan and Rosenberg 2009; Meiklejohn et al. 2016; Chan et al. 2020; Alda et al. 2021).

While UCEs are generally treated as non-coding and independent, they may not be evenly distributed throughout the genome (McCole et al. 2018) and may overlap the same genes (Van Dam et al. 2021). Merging UCEs that overlap genes can increase topological support but has limited impact on the topology recovered (Van Dam et al. 2021). When available, filtering by phylogenetic signal and noise (Gilbert et al. 2018) can also lead to better supported estimates of tree topology, as can allele phasing of SNPs derived from UCE loci (Andermann et al. 2019; McLean et al. 2022). However, as we notice in our reconstructions and as has been observed elsewhere with multiple phylogenomic markers (Reddy et al. 2017; Chan et al. 2020; Minh et al. 2020a; Vanderpool et al. 2020), bootstraps are a poor indicator of support for the correct topology when using phylogenomic data. We estimated high approximated bootstrap values across all nodes in our species tree (Fig. 1), even for nodes which conflict with previously inferred topologies for these species (Fig. S1) and show elevated gene tree discordance (Fig. S2).

UCEs have recently seen increased use in dating analyses and best practices continue to be developed (Blaimer et al. 2015; Branstetter et al. 2017; Bossert et al. 2019; Oliveros et al. 2019; Quattrini et al. 2020). Critically, the scale of UCE datasets can make popular methods of divergence time estimation computationally intractable, while gene tree discordance and substitution rate heterogeneity complicate the selection of appropriate models (Van Dam et al. 2017; Tagliacollo and Lanfear 2018). One strategy to overcome these issues is the selection of a set of loci with model-appropriate properties including clock-like behaviour and low gene tree discordance, as described by the SortaDate software package (Smith et al. 2018). Such gene filtering approaches have been suggested as best practice (Walker et al. 2019) and SortaDate specifically has been used in a range of phylogenomic analyses across multiple taxonomic groups (Lind et al. 2019; Del Cortona et al. 2020; Quattrini et al. 2020; Shee et al. 2020; Koenen et al. 2021), though some researchers have found gene filtering has a limited impact on estimated divergence times but increases the associated variance (Oliveros et al. 2019; McGowen et al. 2020).

Least-squares dating purports vastly reduced computation time with similar accuracy (To et al. 2016) to comparable dating methods implemented in software such as BEAST (Drummond et al. 2006) and r8s (Sanderson 2003). It appears to be robust to topological error (To et al. 2016) and substitution rate heterozygosity between lineages (To et al. 2016; Tong et al. 2018). While developed for dating of rapidly evolving viruses (To et al. 2016), it has seen use in eukaryotes (Yue et al. 2017; Anijalg et al. 2018; Brüniche–Olsen et al. 2018; Tong et al. 2018; Thomas et al. 2019). Given the known rapid evolution of substitution rate in rodents (Douzery et al., 2003), our concerns with tree topology, and its tractability, it is likely appropriate for our dataset of filtered UCE loci.

## Eliminating possible sources of error in reconstruction of the rodent phylogeny

Given the unexpected placement of the two *Apodemus* species and *R. soricoides* recovered in the inferred species tree (Fig. 1, Fig. S1), we attempted to systematically account for sources of error in both the data itself and the methodology employed. We first note that the two *Apodemus* species are represented by chromosome level assemblies obtained by different research groups, while for *R. soricoides* we present a novel chromosome level assembly (see Table 1). Their unexpected taxonomic placement would therefore appear not to be an artifact of assembly quality.

The mislabeling of taxa at any step of data processing could lead to mislabeled species trees, leading us to incorrectly conclude the placement of some species. To check for mislabeling, we took a random sample of 100 UCE loci that we extracted from every species and used BLAST (Altschul et al. 1990) to align them to the original whole genomes. In the case of introduced mislabeling, we would expect UCE loci for one species to align best to a different species. However, every BLASTed locus aligned to the expected species. Sequences are also unlikely to be paralogs, as putative paralogs are removed by lastz (Harris 2007) as part of the standard PHYLUCE pipeline (Faircloth 2016).

As noted in Table 1, not all UCE loci were successfully extracted for every taxa ranging between 2223 for *Apodemus speciosus* to the full set of 2645 for *Mus musculus*. While ML reconstruction methods like those employed in IQ-TREE 2 (Minh et al. 2020b) and the gene-tree coalescent methods in ASTRAL-III (Zhang et al. 2018) are generally robust to missing data even with moderate incomplete lineage sorting (Chernomor et al. 2016; Xi et al. 2016), this is dependent on missing data being randomly distributed and sufficiently many genes being sampled (Sanderson et al. 2010; Xi et al. 2016). To assess the impact of missing data, we reran the same concatenated species tree reconstruction in IQ-TREE 2 (Minh et al. 2020b) on a set of 1600 UCE loci that are present in all 18 of our taxa of interest. The topology of the resulting species tree was identical to the one inferred when using all loci, meaning that our results are not biased by missing data.

In order to investigate other sources of error in sequence data that may have been transmitted into the phylogenetic analyses, we used TreeShrink (Mirarab et al. 2014) to identify abnormally long branch lengths among the gene trees and remove erroneous taxa (default parameters). Each taxon was cut from between 5 and 126 gene trees. The filtered gene trees were used to construct a consensus phylogeny with ASTRAL-III (Zhang et al. 2018) as in the Methods and returned the same topology. Further, we used the R (R Core Team 2021) package Rogue (Smith, 2021) to identify rogue taxa – those with a variable position across trees because of conflict among their data that can confound consensus tree construction (Wilkinson 1994; Kearney 2002; Wilkinson 2003) – in our dataset. If the removal of a taxon from a set of inferred trees – such as those obtained from bootstrapping or from sampling a Bayesian posterior probability – leads to increased information content in the resulting consensus tree, it is marked as rogue. When applied to a set of 100 bootstrap trees generated in IQ-TREE 2 (Minh et al. 2020b), Rogue did not detect any rogue taxa. This comports with the high estimated bootstrap support (Fig. 1) for our tree and supports the notion that bootstrapping methods will fail to evidence the true topology when it is obscured by gene tree discordance (see Discussion).

While Rogue (Smith, 2021) is intended for summarizing sets of trees that have previously been inferred, we also applied it to our estimated UCE trees. In principle, this is equivalent to filtering the data prior to inference by removing taxa that behave in a “rogue-like” fashion. We identified three rogue taxa from UCE trees: *Rhynchomys soricoides*, *Rhabdomys dilectus*, and *Grammomys dolichurus*. We then realigned and filtered our UCE loci without the three putative rogue taxa and repeated our species tree estimations as described in the Methods (Fig. S12). Because *R. soricoides* is a key taxon in our dataset for comparing our inferred groupings with previously inferred trees, its removal makes it difficult to discern the effects of these rogue taxa. These three taxa do not collectively represent the most discordant nodes in our species trees (Fig. S2), and whether their identification as rogue taxa indicates a problem with the underlying data or is informative about their biology is unclear.

Next, using IQ-TREE 2 (Minh et al. 2020b), we performed a constrained tree search to force the topology to match the relationships recovered by previous work (Schenk et al. 2013) (Fig. S1). However, the tree inferred from the unconstrained search (Fig. 1) significantly outperformed the constrained tree (Table S1), suggesting that the UCE loci in our dataset genuinely better support this alternative topology.

We also constructed phylogenetic networks (Fig. S11) with the SNaQ estimation method (Solis-Lemus and Ane 2016) within PhyloNetworks (Solis-Lemus et al. 2017; Bastide et al. 2018). Phylogenetic networks allow reticulation points to be formed between two branches, which may represent common important biological events that are known to confound phylogenetic inference, including incomplete lineage sorting and introgression (Maddison 1997; Barton 2001; Mallet 2007; Kubatko 2009; Hibbins and Hahn 2022). The initial network topology with zero hybrid edges matched that of the coalescent species tree (Fig. 1). Adding one hybrid edge produces an overall topology that is instead consistent with the concatenated tree, with the hybrid edge suggesting introgression from *Arvicanthis niloticus* into the other Arvicanthini. Adding a second hybrid edge suggests introgression from the Praomyini into *Mus musculus* and joins *Rhynchomys soricoides* into a clade with *Grammomys dolichurus* and *Rhabdomys dilectus*.

## Divergence time discussion

When estimating divergence times on our inferred species trees, the Eumuroidea root (A) is placed at 24.27 Ma, which is concordant with the reconstruction of Schenk et al. (2013). The range between minimum and maximum reconstructed age is wide, overlapping both the maximum first appearance and estimated divergence time for the clade as described by Steppan and Schenk (2017). The estimated date for Muridae (B) of 22.33 Ma likewise has a wide range, and appears to be approximately 2 (Schenk et al. 2013), 6 (Chevret and Dobigny 2005), or 7 (Steppan and Schenk 2017) million years older than other estimates. It aligns well with the estimated age of the clade recovered by Aghová et al. (2018) and, with some variance for the dating method used, the supermatrix derived mammalian tree of Meredith et al. (2011) but, as with other nodes, is much younger than was estimated by Hedges et al. (2015). The time of separation of Otomyini and Arvicanthi (P) (paraphyly of Arvicanthi notwithstanding, though see Fig. S3 for a time tree inferred without *Arvicanthis niloticus* and *Rhabdomys dilectus* that recovers a similar divergence time) is in general agreement with Lecompte et al. (2008), Schenk et al. (2013), and Aghová et al. (2018) at 8.17 Ma. Despite using a comparatively young calibration range for the *Rattus* group (Q) our results suggest the clade is possibly even younger given it is reconstructed at the minimum end of the assigned calibration (2.4 Ma), though this may better reflect an internal divergence within *Rattus* sensu lato than the origin of the group. We also reconstruct the origins of the Praomyini (K, 4.88 Ma) as approximately 0.5-1 Ma younger than other estimates (Lecompte et al. 2008; Schenk et al. 2013; Aghova et al. 2018), though these older estimates overlap our confidence intervals and Schenk et al. (2013) recover a close median age of 5.1 Ma. Nicolas et al. (2021) have recently estimated the Praomyini to have diversified even earlier (7.1 Ma). Within the Murini (M), our divergence of 3.55 Ma for *M. caroli* (N) followed by the separation of *M. musculus* and *M. spretus* (O, 1.58 Ma) is very similar to estimates by Suzuki et al. (2004).

## Species tree summary

Phylogenomic datasets represent a wealth of opportunity to better understand taxonomic relationships, but their size and complexity can make them challenging to use and prone to introducing error (Young & Gillung, 2020; Zhang et al, 2019). As our analyses are based on the available whole genomes of murid rodents, we are inevitably limited in our taxon sampling. Coalescent methods such as ASTRAL-III (Zhang et al., 2018) appear to be resilient to analyses on a small number of taxa (Song et al., 2012; Xi et al., 2015), though adding taxa to a dataset is well understood to improve phylogenetic resolution in general (see Bravo et al., 2019 and citations therein for a discussion). In contrast, adding more genomic data rather than taxa can, counterintuitively, lead to increased support for erroneous topologies (Kumar et al., 2012; Roycroft et al., 2019). It remains to be seen therefore the degree to which the topologies we recover are the result of taxon sampling versus underlying properties of the data, although the extent of gene tree discordance we observe remains striking. Ultimately, choice of data and the models used may matter more than taxon sampling (Reddy et al., 2017), though knowing which data to choose a priori remains an unsolved problem.

Here, we have leveraged the resources of the model organisms the house mouse (*Mus musculus*) and brown rat (*Rattus norvegicus*) along with new genomes from 8 closely related species and eight previously sequenced rodent genomes to understand the systematics of murine rodents and causes and consequences of phylogenetic discordance along the murine genome. Our genomes begin to fill the gap in sampling of murine rodents which, despite their outstanding diversity and speciousness, have relatively few whole genomes sequenced and help to place these important model systems in an evolutionary context and provide us with the resources to study the landscape of phylogenetic discordance along the chromosome.

# Supplemental Figure legends

**Figure S1**: Murine topology previously inferred by Steppan and Schenk, 2017 (left), compared to our topology inferred from concatenated UCE loci (Right; Fig. 1). Lines between the two phylogenies indicate conflicting relationships among the Apodemini, Otomyini, and Hydromyini. Figure generated with the cophyloplot() function in the R package ape (Paradis and Schliep, 2019).

**Figure S2**: ASTRAL-III species tree with internal branch lengths in coalescent units such that shorter branches indicate greater discordance. Branch labels indicate quadripartition support. Final normalized quartet score is 0.81, *i.e.*, 81% of quartet trees induced by the gene trees are represented in the species tree.

**Figure S3**:Gene-concordance factors (gCF) and site-concordance factors (sCF) for each branch in the concatenated species tree. Note that the lowest possible value for sCF is approximately 30, while gCF can be as low as 0.

**Figure S4**: Discordance at nodes on the ASTRAL species tree established using the PhyParts package (Smith et al., 2015). The number of gene trees that support the shown species tree at each node is given above each branch and is represented by the blue portion of the pie chart. The number of gene trees that show a supported conflict with the gene tree is below the branch and is represented in pie charts by green (the most common conflicting partition) and red (all other supported conflicts). The grey section of the pie charts show conflicting gene trees with no support.

**Figure S5**: Time-calibrated version of the concatenated species tree estimated without putatively rogue taxa (*Rhynchomys soricoides*, *Rhabdomys dilectus*, and *Grammomys dolichurus*). Node age confidence intervals are shown as blue bars. Axis on the bottom represents time in millions of years before present. Calibrations are described in Tables 2 and S2. Node C was used as a fixed calibration,

**Figure S6**: The number of variable and informative sites from 165,409 10kb windows from alignments of seven taxa to the mouse reference (mm10) coordinate system. A variable site is defined as any site with more than one allele. An informative site is defined as any site with at least two alleles present in at least two taxa. Average number of variable sites: 1187.8. Average number of informative sites: 401.0.

**Figure S7**: Measures of phylogenetic similarity and decay on the X chromosome. A) The log fit to the mean of distributions of tree distances between windows at increasing genomic distance (10kb steps). B) The same, but on a log scale with a linear fit. C) The genomic distance between windows at which tree distance becomes random for 100 replicates of random window selection. D) The slopes of the correlation between genomic distance and tree distance from panel B represent the rate at which tree similarity decays across the chromosome.

**Figure S8**: Dotplot of whole genome alignment between mouse (mm10) and rat (rnor6) genomes.

**Figure S9**: Summary of the whole genome alignment between mouse and rat. A) The distribution of aligned block sizes. B) The distribution of the total number of aligned bases for each range of block sizes. C) The distribution of inter-block distances relative to mouse (left) and rat (coordinates) for all blocks shorter than 20 kb. Dashed lines represent average distance between two alignment blocks and are labeled with said average.

**Figure S10**: Distributions of recombination rate across 19 mouse autosomes and the X chromosome estimated in 5Mb windows. Each line segment represents a single aligned block between the two genomes.

**Figure S11**: Phylogenetic networks for 18 rodent species. Hmax indicates the maximum permitted number of hybrid edges. Hmax of 3 or higher leads to reticulations that conflict with rooting the tree to *Phodopus sungorus* and are therefore excluded. When hmax=0 (-Ploglik = 20422.547) we recover the same topology as the coalescent species tree (Fig. 1B). For hmax=1 (-Ploglik = 20422.547), the overall topology is instead consistent with the concatenated tree but introduces a hybrid edge that suggests a low level of introgression from *Arvicanthis niloticus* into the other Arvicanthini. While the topology is still in conflict with the generally accepted relationships within Muridae ((Steppan and Schenk 2017); Fig. S1), the signal of the relationship between the Arvicanthini is recovered by the hybrid edge. For hmax=2 (-Ploglik = 12726.4) an additional hybrid edge suggesting introgression from the Praomyini into *Mus musculus* is recovered.

**Figure S12**: Species trees generated after the removal of the putative rogue taxa (*Rhynchomys soricoides*, *Rhabdomys dilectus*, and *Grammomys dolichurus*) from sequence data. A) Maximum likelihood tree from concatenation of all UCE alignments. Branch lengths are in units of substitutions per site and node labels indicate approximated bootstrap and SH-aLRT values. B) Quartet-based species tree inferred from individual UCE trees. Internal branch lengths are in coalescent units such that shorter branches indicate greater discordance. Branch labels indicate quadripartition support. Final normalized quartet score is 0.92, i.e. 92% of quartet trees induced by the gene trees are represented in the species tree.

# Supplemental Tables

### Table S1: Results of tree topology tests from IQ-TREE2 (Minh et al., 2020) comparing the original species tree shown in Figure 2A (Free) with a second tree of constrained topology (Constrained) such that the relationships between the Otomyini, Arvicanthi, Apodemini, Murini, and Praomyini are forced to match those shown in Supplementary Figure 1. Both trees were generated using the same set of filtered alignments, but best fit models were recalculated using ModelFinder (Kalyaanamoorthy et al., 2017). Tree: Tested topology. logL: Maximum likelihood. deltaL: Difference in logL from maximal logL. bp-RELL: bootstrap proportion using RELL method (Kishino et al. 1990). p-KH: p-value of one sided Kishino-Hasegawa test (1989). p-SH: p-value of Shimodaira-Hasegawa test (2000). c-ELW: Expected Likelihood Weight (Strimmer & Rambaut 2002). p-AU: p-value of approximately unbiased (AU) test (Shimodaira, 2002). Plus signs (+) indicate a topology was not rejected, while minus signs (-) indicate the topology was significantly excluded. Despite the constrained topology matching the expected relationships, there is clearly better support for the alternative topologies in Figure 2 when using UCE loci.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Tree** | **logL** | **deltaL** | **bp-RELL** | **p-KH** | **p-SH** | **c-ELW** | **p-AU** |
| Free | -36730176.13 | 0 | 1 + | 1 + | 1 + | 1 + | 1 + |
| Constrained | -37160286.86 | 4.3011x105 | 0 - | 0 - | 0 - | 0 - | 2.64x10-77 - |

### Table S2: The estimated age of each node in Figure 1. Nodes with an asterisk (\*) indicate those used in calibration, as in Table 2. Node C was used as the fixed calibration (see Methods: Divergence time estimation). Minimum and maximum ages are the lowest and highest values respectively at each node across the three estimated time trees.

|  |  |  |
| --- | --- | --- |
| Node | Estimated Age (mya) | Min/Max Age (mya) |
| A | 24.27 | 19.59/29.64 |
| B | 22.33 | 18.01/28 |
| C\* | 13.08 | 12.1/14.05 |
| D | 11.9 | 10.39/14.05 |
| E | 11.45 | 9.73/13.67 |
| F\* | 5.96 | 5.3/7.2 |
| G | 8.38 | 7.08/10.39 |
| H | 8.28 | 7/10.3 |
| I | 5.64 | 4.14/7.77 |
| J | 7.39 | 6.36/9.07 |
| K | 4.88 | 3.86/6.35 |
| L | 4.05 | 3.06/5.31 |
| M\* | 5.59 | 5.3/7.2 |
| N | 3.55 | 2.68/5.1 |
| O | 1.58 | 1.09/2.32 |
| P | 8.17 | 6.06/10.84 |
| Q\* | 2.4 | 2.4/3.59 |

# Jon: Need clarification

Diagram, schematic

Description automatically generated

**Supplementary Figure 2:** Maximum likelihood species trees generated in IQ-TREE2 (Minh et al., 2020) from concatenated UCE loci as described in methods. Here, individual taxa with unexpected placement have been removed from the analysis: *Apodemus speciosus* (2A), *Apodemus sylvaticus* (2B), *Rhynchomys soricoides* (2C), and all three of these taxa (2D). Compared to Figure 2 in the manuscript, which was generated on a full set of taxa we see that 2A recovered the same overall topology. In 2B, *Apodemus speciosus* still diverges after *Otomys typus* and *Arvicanthis niloticus*, but *Rhynchomys soricoides* now diverges after *Grammomys dolichurus* and *Rhabdomys dilectus* rather than before. Removing *Rhynchomys soricoides*, as in 2C, causes a dramatic shift in topology, splitting the *Mus* group. In 2D we recover a topology more aligned with expectation (Supplementary Figure 1), though the Arvincanthini remain paraphyletic.

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