Figure 2. A time-calibrated, family-level phylogeny of rodents, showing the masseter muscle character states of extant and fossil taxa as well as the probability of each state at ancestral nodes based on the ordered ARD model. Character states correspond to masseter architecture shown in figure 1. Numbers at nodes indicate bootstrap support less than 100 and letters at nodes correspond to fossil constraints from table 1. 'Pli.' denotes the Pliocene epoch and 'Pl' denotes the Pleistocene epoch on the timeline. Outgroups *Ochotona princeps* and *Oryctolagus cuniculus* were pruned out prior to stochastic character mapping analysis.

Ctenohystrica, but with varying bootstrap support (BS: 100, 79, 66, respectively; figure 2; electronic supplementary material, figure S1). Further supporting this conclusion, our bipartition frequency analysis revealed that an order of magnitude more gene trees were consistent with a sister relationship between Sciuromorpha and Ctenohystrica versus the two alternative topologies (table 2). For relationships within the mouse-related clade, the concatenated and ASTRAL trees identify a sister relationship between Castorimorpha and Myomorpha (BS = 84, 99, respectively), while ASTRID supports Castorimorpha and Anomaluromorpha as sisters (BS = 78). More gene trees were topologically consistent with the latter than the former (table 2). Importantly, none of our analyses recovered a sister relationship between the two mouse-related suborders with hystricomorphous taxa (Anomaluromorpha and Myomorpha). Our per-locus site-likelihood analysis resulted in low magnitude ΔlnL values and did not show a pattern of a few loci or clusters of loci driving support for particular relationships at either node of interest (figure 3).

TreePL produced an ultrametric tree with divergence dates broadly comparable with previous studies [86,87] and

inferred a divergence date at an unconstrained node for Aplodontidae and Sciuridae at 31 Mya, consistent with the appearance of the first definitive squirrel [88]. We therefore consider this temporal framework suitable for stochastic character mapping. The ARD model had the highest AIC score in both ordered and unordered comparisons (table 3). When we compared the unordered and ordered ARD models, the ordered model had substantially higher support (table 3). Stochastic character mapping using the ordered ARD model estimated an average of: 5.9 transitions from protrogomorphy to hystricomorphy and 1.2 transitions from hystricomorphy back to protrogomorphy, 2.5 transitions from protrogomorphy to sciuromorphy and 1.2 transitions from hystricomorphy to myomorphy, but none in the reverse of these directions; and no transition between hystricomorphy and sciuromorphy or sciuromorphy and myomorphy.

4. Discussion

Our well-supported inference of a Ctenohystrica−Sciuromorpha clade is concordant with previous work which removed