

Title:

Evolution: the evolutionary rat race in New Guinea and Australia

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Summary (40 words):

A new molecular phylogeny of a remarkable radiation of New Guinean and Australian rodents indicates multiple transitions between biomes and biogeographical regions within the group, and suggests that a key role was played by the geological history of New Guinea.

Main text:

Australia, New Guinea and neighbouring islands (collectively Sahul) are well known for their marsupials and monotremes, but they also support a diverse and unique rodent fauna of more than 170 species that collectively span a remarkable range of sizes and ecologies^{1,2}. The Sahul rodents all belong to the subfamily Murinae (mice and rats), and comprise two distinct radiations^{3,4}: the ecologically diverse “Old Endemics” (>150 extant species in at least 36 genera, comprising part of the tribe Hydromyini), and the more conservative “New Endemics” (>20 species, all within the genus *Rattus*). In a new paper in *Current Biology*, Roycroft et al.⁵ use the power of comparative genomics to confidently resolve the evolutionary relationships of modern hydromyine species from Sahul, and use the resultant phylogeny to identify the major trends that have shaped the diversification of this successful and fascinating clade.

The broad outline of hydromyine evolution in Sahul has been known for some time. The fossil record indicates that crown murine rodents had begun to diversify in mainland Asia prior to 11 Ma⁶, and it has long been accepted that the ancestor of the Sahul hydromyins arrived from the north, either from the Sunda region or the Philippines⁷. Hydromyins must have reached the Australian continent by ~3.6 Ma at the latest, based on the age of the oldest known fossils³. After their arrival, hydromyins radiated into a wide range of ecological niches in Sahul (Figure 1), with extant species including semi-aquatic (e.g. *Hydromys*), arboreal (e.g. *Pogonomys*), and desert (e.g. *Notomys*, *Zyzomys*) forms^{1,2}. However, a detailed understanding of the evolution of Sahul hydromyins has been hampered by the absence of a comprehensive, well-resolved phylogeny that densely samples all major lineages.

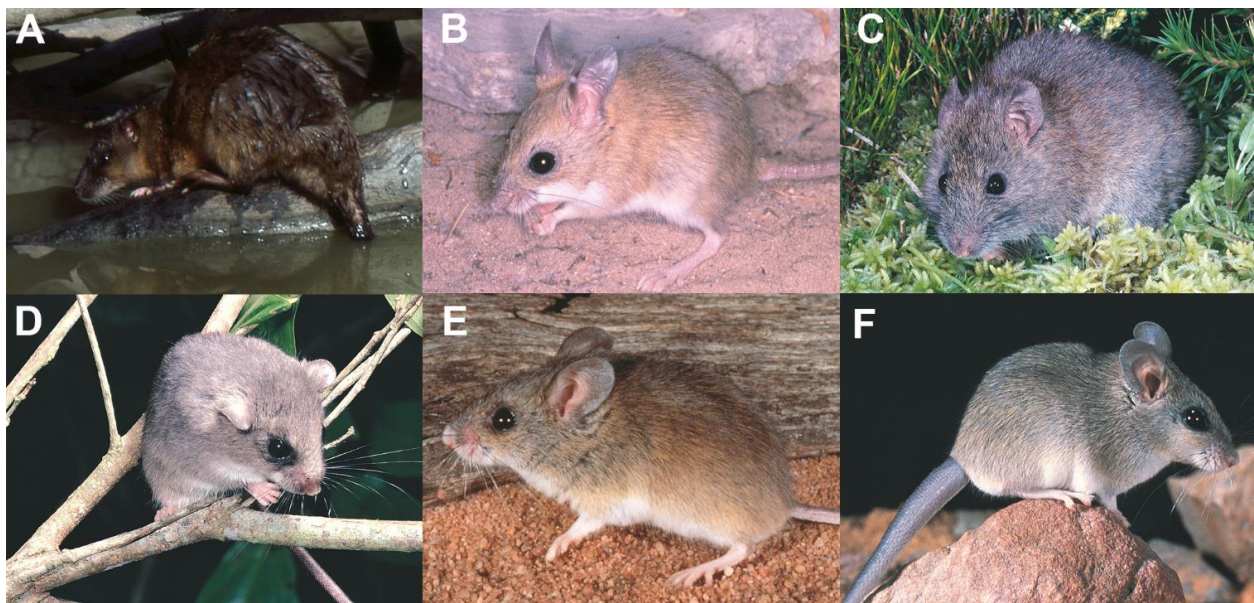


Figure 1. Examples of the ecological diversity of modern Sahul hydromyins. A) The rakali or Australian water-rat, *Hydromys chrysogaster* (Photographer: Robert W.G. Jenkins; Copyright: Australian Museum). **B)** The spinifex hopping-mouse, *Notomys alexis* (Photographer: W.G. Breed; Copyright: Australian Museum). **C)** The broad-toothed rat, *Mastacomys fuscus* (Photographer: G.A. Hoye; Copyright: Australian Museum). **D)** The prehensile-tailed rat, *Pogonomys mollipilosus* (Photographer: Hans & Judy

Beste; Copyright: Australian Museum). **E**) The Piliga mouse, *Pseudomys pilligaensis* (Photographer: Dick Whitford; Copyright: Australian Museum). **F**) The common rock rat, *Zyzomys argurus* (Photographer: Hans & Judy Beste; Copyright: Australian Museum).

This gap has been filled by Roycroft et al.⁵, who generated a new dataset of over one million base pairs of DNA sequence data from ~1200 genes, sampled from 120 of the 154 currently recognised Sahul hydromyini species. Importantly the authors were able to obtain sequence data from museum skins of multiple species that are recently extinct or known from only a handful of specimens, some collected over a century ago, building on their previous work⁸. Their phylogenetic analyses are largely congruent with previous molecular studies⁸⁻¹⁰, but several key nodes are confidently resolved for the first time, and it seems that only a few relationships within the Sahul radiation remain uncertain. Their preferred phylogeny indicates the presence of seven major lineages that vary markedly in taxonomic and ecological richness, from the *Coccymys* lineage, with only a single genus (*Coccymys*) and four described species (of which two were sampled by Roycroft et al.) to the Uromys and Pseudomys Divisions, each with over 40 species in multiple, ecologically disparate genera. They also reveal that the taxonomy of Hydromyini is in need of revision, with evidence that several genera, as currently recognised, are not monophyletic and that (perhaps unsurprisingly) species diversity within the clade is currently underestimated. Roycroft et al.'s phylogeny will be an invaluable guide to future taxonomic revisions.

Roycroft et al. were also able to estimate divergence times within Hydromyini using a molecular clock analysis, which suggests that the common ancestor of the radiation reached Sahul between 9.3 and 8.1 Ma. Among mammals, murine rodents appear to be particularly adept overwater dispersers, and they are the only terrestrial mammals to have successfully dispersed

to some isolated landmasses¹¹. Recent geological reconstructions indicate that there was little or no emergent land in the region corresponding to modern New Guinea until <10 Ma^{12,13}, and so an earlier dispersal may simply not have been possible. Intriguingly, ancestral state reconstructions on the dated phylogeny suggest that Sahul hydromyins were restricted to highland forest biomes in New Guinea for the first 3.5 Ma of the clade's history. Roycroft et al. (2022) propose that this changed following major geological uplift of New Guinea, starting ~5 Ma, which led to an increase in the amount of emergent land, reducing the distance between New Guinea and nearby landmasses (including continental Australia) and also facilitating the spread of lowland forest and savanna biomes in New Guinea. Hydromymin lineages that subsequently evolved to occupy these biomes in New Guinea may therefore have been "preadapted" to similar biomes present in the north of the Australian continent.

From ~5 Ma onwards, the evolutionary history of hydromyins appears to have been highly complex, with multiple transitions between biogeographical areas and biomes. However, Roycroft et al. (2022) uncover some intriguing patterns within this complexity. Notably, there appear to have been only two transitions directly from mesic to arid biomes by hydromyins, although there is evidence of a further four from savanna to arid. By contrast, transitions from arid to mesic appear to have been much more common, with six such transitions identified by Roycroft et al. (2022). This is of interest given the apparent failure of the other radiation of Sahul murines, the "New Endemics", to evolve to successfully occupy arid habitats since their arrival in Australia, which occurred >280 ka based on fossil evidence¹⁴, and potentially 1 Ma or earlier, based on molecular clock estimates¹⁵; the "New Endemics" have remained largely restricted to mesic environments despite high diversification rates¹⁵. Thus, successful adaptation to arid biomes appears "difficult" for murines, as it is for small mammals in general (particularly those that are not specialist burrowers), presumably due to the difficulty of maintaining successful thermoregulation and water balance in such harsh environments¹⁶.

Dispersals amongst landmasses between Australia, New Guinea and adjacent islands seem to have been frequent, with the direction of dispersal typically (but not always) reconstructed as being from Australia and New Guinea to islands, rather than vice versa, congruent with the predictions of island biogeography, which state that successful colonisations are more likely to be the result of dispersals from larger to smaller landmasses. However, the true biogeographical history of Hydromyini is likely to have been considerably more complex than this, for two main reasons. Firstly, the fossil record indicates that certain hydromyini lineages that are currently restricted to New Guinea once occurred in Australia^{3,14}. Particularly relevant here is evidence for a major faunal turnover event in northern Australia, with a transition from mesic to more xeric environments that saw the apparent local extinction of multiple mammalian lineages (including several hydromyins) that still survive in New Guinea^{14,17}; at least some typically “New Guinean” taxa present in northern Australia today may be comparatively recent immigrants¹⁷. Secondly, major oscillations in sea level during the Pliocene and particularly the Pleistocene would have caused marked changes in the amount of emergent land on the Sahul shelf; indeed, for multiple periods during the Pleistocene, Australia, New Guinea and at least some adjacent islands (e.g. the Aru Islands) would have formed a single, continuous landmass, connected by thousands of square kilometres of emergent land in what is now the Arafura Sea^{3,4,18}. These islands may therefore represent a refugia for hydromyini lineages that were once much more widespread but that have gone extinct elsewhere as sea levels have risen. Untangling this complexity, with repeated formation and severing of connections between areas that may have lasted only a few thousand years in each case, may be beyond current biogeographical models, particularly as molecular phylogenies typically only sample extant or recent extinct lineages.

Nevertheless, Roycroft et al.’s is a major achievement in advancing our understanding of a fascinating and successful clade; for the first time we have a robust phylogeny of the Sahul hydromyins, and a significantly improved understanding of the multiple complex geographic and

ecological transitions that have shaped their evolutionary history. There are obvious and intriguing avenues for extending this work. Direct incorporation of fossil taxa will allow more robust inference of the biogeographical and diversification dynamics of hydromyins. However, the available fossil evidence is extremely fragmentary, and many highly significant specimens remain to be formally described¹⁴ or even studied in detail³. As whole genomes for hydromyins become available, meanwhile, there is an exciting opportunity to identify the molecular basis for key adaptive traits¹⁹, for example those associated with adaptations to arid environments. The fact that there have been multiple transitions to the same biomes and ecological niches within Hydromyini, as revealed by Roycroft et al., means that it should be possible to determine to what extent similar ecological adaptations are underpinned by similar molecular changes in different lineages. Finally, Roycroft et al.'s study adds to evidence from multiple other clades²⁰ supporting New Guinea's status as a unique "evolutionary laboratory" that has generated astonishingly diverse terrestrial vertebrate and invertebrate faunas in a variety of biomes within only a few million years, with a major driver of this being the dynamic, and still incompletely understood, geology of the island.

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