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Convergent evolution of aquatic foraging in a new genus and species (Rodentia: Muridae) from Sulawesi Island, Indonesia

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Abstract

The island of Sulawesi, in Indonesia, lies at the crossroads of the Indo-Australian Archipelago and has remained isolated from the Asian (Sunda) and Australian (Sahul) continental shelves for at least the last 10 million years. Of the 50 native species of rodents on Sulawesi, all are endemic and represent the evolution of a variety of ecological and morphological forms within the Muridae and Sciuridae. Carnivorous rodents have evolved, perhaps independently, in Muridae from the Philippines, Sulawesi, and Sahul, but semi-aquatic murids are only known from Sahul. Here we describe a new genus and species of insectivorous water rat from Sulawesi. Phylogenetic analyses demonstrate that it is related to the shrew rats of Sulawesi and represents an origin of aquatic carnivory that is independent from the evolution of water rats on Sahul. Many areas of Sulawesi have not been surveyed systematically and current lists of mammal species are likely to dramatically underestimate actual diversity.

Key words: Indo-Pacific, Mammalia, molecular phylogeny, molecular systematics, Murinae, shrew rats, taxonomy, water rats

Introduction

The Indo-Australian Archipelago is a major area of biogeographic interchange (Lohman *et al.* 2011) and of significant interest to evolutionary biologists because it provides numerous systems for testing the effects of climatic variation, geological evolution, and isolation on the processes of diversification and community assembly (Heaney 1986; Evans *et al.* 2003; Brown *et al.* 2013). The region encompasses the Asian (Sunda) and Australian (Sahul) continental shelves as well as oceanic archipelagos (Philippines, Wallacea) that have never been connected by land to any continent. The island of Sulawesi is the largest landmass between the Sunda and Sahul shelves and was not connected to either during low sea stands of the last 10 million years (Scotese *et al.* 1988; Hall 1998, 2012; Rohling *et al.* 1998; Voris 2000). The combination of a large, topographically complex island that has remained isolated by water barriers, yet is proximally located between two continental landmasses has produced high levels of endemism and a unique mixture of Australian and Asian lineages.

Rodents of the family Muridae comprise over 30% of known mammal species on Sulawesi (Musser & Carleton 2005; Musser *et al.* 2010; Esselstyn *et al.* 2012; Mortelliti *et al.* 2012; Musser 2014). All of the island's murid species are endemic, as are 11 of the 14 murid genera, highlighting the degree to which the rats and mice of Sulawesi represent an endemic radiation. This diversity includes a wide range of eco-morphological forms that have been recapitulated in other, independent radiations of murid rodents (Rowe *et al.* 2008). Examples of this recapitulation include the carnivorous (we use 'carnivorous' to describe animals that primarily eat Metazoans; we consider 'invertebrate-eating' and 'insectivory' to represent nested subcategories of carnivory) rodents of the Philippines (e.g. *Chrotomys*, *Rhynchomys*, *Soricomys*; Musser 1982; Jansa *et al.* 2006) and New Guinea (e.g. *Pseudohydromys*; Jackson & Woolley 1993; Flannery 1995; Helgen & Helgen 2009). On New Guinea, some carnivorous rodents are semi-aquatic, and known commonly as water rats (e.g. *Baiyankamys*, *Crossomys*,

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type specimen. Richard Marchant of Museum Victoria identified prey items in the mouth and stomach of the type specimen. We are grateful to Sandy Ingleby of the Australian Museum, Robert Voss and Eileen Westwig of the American Museum of Natural History, and William Stanley of the Field Museum of Natural History for access to comparative specimens. Tissues for new sequences reported in this study were loaned kindly from the Field Museum of Natural History, the South Australian Museum, the Carnegie Museum of Natural History, the Museum of Vertebrate Zoology, Museum Victoria, the University of Kansas Natural History Museum, and the Royal Ontario Museum. Sean Maher assisted with making figure 1. We thank Kris Helgen and James Patton for constructive comments on an earlier version of the manuscript. This research was funded by the National Science Foundation (OISE-0965856 and DEB-1343517), National Geographic Society (9025-11), and the Australia and Pacific Science Foundation (12-6).

References

Barnett, A.A. (1997) The ecology and natural history of a fishing mouse *Chibchanomys* spec. nov. (Ichthyomyini: muridae) from the Andes of Southern Ecuador. *Zeitschrift fur Saugetierkunde*, 62, 43–52.

Brown, R.M., Siler, C.D., Oliveros, C.H., Esselstyn, J.A., Diesmos, A.C., Hosner, P.A., Linkem, C.W., Barley, A.J., Oaks, J.R., Sanguila, M.B., Welton, L.J., Blackburn, D.C., Moyle, R.G., Peterson, A.T. & Alcala, A.C. (2013) Evolutionary processes of diversification in a model island archipelago. *Annual Review of Ecology, Evolution, and Systematics,* 44, 411–435. http://dx.doi.org/10.1146/annurev-ecolsys-110411-160323

Cannon, C.H., Summers, M., Harting, J.R. & Kessler, P.J. (2007) Developing conservation priorities based on forest type, condition, and threats in a poorly known ecoregion: Sulawesi, Indonesia. *Biotropica*, 39, 747–759. http://dx.doi.org/10.1111/j.1744-7429.2007.00323.x

Esselstyn, J.A., Achmadi, A.S. & Rowe, K.C. (2012) Evolutionary novelty in a rat with no molars. *Biology Letters*, 8, 990–993. http://dx.doi.org/10.1098/rsbl.2012.0574

Evans, B.J., Supriatna, J., Andayani, N., Setiadi, M.I., Cannatella, D.C. & Melnick, D.J. (2003) Monkeys and toads define areas of endemism on Sulawesi. *Evolution*, 57, 1436–1443. http://dx.doi.org/10.1111/j.0014-3820.2003.tb00350.x

Flannery, T.F. (1995) *Mammals of New Guinea* Revised and updated edition. Comstock/Cornell, Ithaca, 568 pp.

Geoffroy, E. (1804) Mémoire sur un nouveau genre de mammifères nommé Hydromis. *Bulletin de la Société Philomatique*, 3, 253–254.

Gordon, R.G. (2005) Ethnologue: Languages of the World (Online Version). Dallas, Texas. Available from: https://www.ethnologue.com (28 February 2014).

Gray, J.E. (1867) Notes on the variegated or yellow-tailed rats of Australasia. *Proceedings of the Zoological Society of London*, 1867, 597–600.

Hall, R. (1998) The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. *In*: Hall, R. & Holloway, J.D., (Eds.), *Biogeography and geological evolution of SE Asia*. Backhuys Publishers, Leiden, pp. 99–131. http://dx.doi.org/10.1002/mmnz.20000760119

Hall, R. (2012) Late Jurassic–Cenozoic reconstructions of the Indonesian region and the Indian Ocean. *Tectonophysics*, 570, 1–41. http://dx.doi.org/10.1016/j.tecto.2012.04.021

Heaney, L.R. (1986) Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. *Biological Journal of the Linnean Society*, 28, 127–165. http://dx.doi.org/10.1111/j.1095-8312.1986.tb01752.x

Helgen, K.M. (2005) The amphibious murines of New Guinea (Rodentia, Muridae): the generic status of *Baiyankamys* and description of a new species of *Hydromys*. *Zootaxa*, 913, 1–20.

Helgen, K.M. & Helgen, L.E. (2009) Chapter 8. Biodiversity and biogeography of the moss-mice of New Guinea: A taxonomic revision of *Pseudohydromys* (Muridae: Murinae). *Bulletin of the American Museum of Natural History*, 331, 230–313. http://dx.doi.org/10.1206/582-8.1

Hinton, M.A.C. (1943) Preliminary diagnoses of five new murine rodents from New Guinea. *Annals and Magazine of Natural History*, 11, 552–557. http://dx.doi.org/10.1080/03745481.1943.9728040

Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17, 754–755. http://dx.doi.org/10.1093/bioinformatics/17.8.754

Jackson, K.L. & Woolley, P.A. (1993) The diet of five species of New Guinean rodents. *Science in New Guinea*, 19, 77–86.

Jansa, S.A., Barker, F.K. & Heaney, L.R. (2006) The pattern and timing of diversification of Philippine endemic rodents: evidence from mitochondrial and nuclear gene sequences. *Systematic Biology*, 55, 73–88.

Kerbis Peterhans, J.C. & Patterson, B.D. (1995) The Ethiopian water mouse *Nilopegamys* Osgood, with comments on semi-aquatic adaptations in African Muridae. *Zoological Journal of the Linnean Society*, 113, 329–349.

http://dx.doi.org/10.1111/j.1096-3642.1995.tb00937.x
Lanfear, R., Calcott, B., Ho, S.Y. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701. http://dx.doi.org/10.1093/molbev/mss020
Lohman, D.J., de Bruyn, M., Page, T., von Rintelen, K., Hall, R., Ng, P.K., Shih, H.T., Carvalho, G.R. & von Rintelen, T. (2011) Biogeography of the Indo-Australian archipelago. *Annual Review of Ecology, Evolution, and Systematics*, 42, 205–226. http://dx.doi.org/10.1146/annurev-ecolsys-102710-145001
Maddison, D.R. & Maddison, W.P. (2003) *MacClade*, version 4.06. *Sinauer, Sunderland, Massachusetts, USA*. http://dx.doi.org/10.1002/evan.1360030112
Majnep, I.S. & Bulmer, R. (1990) Kalam hunting traditions. *In*: *Working papers in Anthropology, Archaeology, Linguistics, and Maori Studies*. University of Auckland, Auckland, pp. 86–91.
Merker, S., Driller, C., Perwitasari-Farajallah, D., Pamungkas, J. & Zischler, H. (2009) Elucidating geological and biological processes underlying the diversification of Sulawesi tarsiers. *Proceedings of the National Academy of Sciences*, 106, 8459–8464. http://dx.doi.org/10.1073/pnas.0900319106
Mattson, R.A. (1996) *An introduction to the aquatic insects of North America*. *Journal of the North American Benthological Society*, 15 (3), pp. 401–403.
Miller, G.S. & Hollister, N. (1921) Descriptions of sixteen new murine rodents from Celebes. *Proceedings of the Biological Society of Washington*, 34, 67–76.
Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *In*: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, pp. 1–8. http://dx.doi.org/10.1109/gce.2010.5676129
Mortelliti, A., Castiglia, R., Amori, G., Maryanto, I. & Musser, G.G. (2012) A new species of *Margaretamys* (Rodentia: Muridae: Murinae: Rattini) from Pegunungan Mekongga, southeastern Sulawesi, Indonesia. *Tropical Zoology*, 25, 74–107. http://dx.doi.org/10.1080/03946975.2012.696439
Musser, G.G. (1969) Results of the Archbold Expeditions. No. 91. A new genus and species of murid rodent from Celebes, with a discussion of its relationships. *American Museum Novitates*, 2384, 1–41.
Musser, G.G. (1981) Results of the Archbold expedition. No. 105. Notes on systematics of Indo-Malayan murid rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. *Bulletin of the American Museum of Natural History*, 168, 229–334.
Musser, G.G. (1982) Results of the Archbold expedition. No. 110. *Crunomys* and the small-bodied shrew rats native to the Philippine Islands and Sulawesi (Celebes). *Bulletin of the American Museum of Natural History*, 174, 1–95.
Musser, G.G. (1991) Sulawesi rodents: Descriptions of new species of *Bunomys* and *Maxomys* (Muridae, Murinae). *American Museum Novitates*, 3001, 1–41.
Musser, G.G. (in press) A systematic review of Sulawesi *Bunomys* (Muridae, Murinae) with the description of two new species. *Bulletin of the American Museum of Natural History.*
Musser, G.G. & Piik, E. (1982) A new species of *Hydromys* (Muridae) from western New Guinea (Irian Jaya). *Zoologische Mededelingen*, 56, 153–166.
Musser, G.G. & Durden, L.A. (2002) Sulawesi rodents: description of a new genus and species of Murinae (Muridae, Rodentia) and its parasitic new species of sucking louse (Insecta, Anoplura). *American Museum Novitates*, 3368, 1–50. http://dx.doi.org/10.1206/0003-0082(2002)368<0001:srdoan>2.0.co;2
Musser, G.G., Durden, L.A., Holden, M.E. & Light, J.E. (2010) Systematic review of endemic Sulawesi squirrels (Rodentia, Sciuridae), with descriptions of new species of associated sucking lice (Insecta, Anoplura), and phylogenetic and zoogeographic assessments of sciurid lice. *Bulletin of the American Museum of Natural History*, 339, 1–260. http://dx.doi.org/10.1206/695.1
Musser, G.G. & Heaney, L.R. (1992) Philippine rodents: definitions of *Tarsomys* and *Limnomys* plus a preliminary assessment of phylogenetic patterns among native Philippine murines (Murinae, Muridae). *Bulletin of the American Museum of Natural History*, 211, 1–138. http://dx.doi.org/10.2307/1382414
Olsen, P.D. (2008) Water Rat. *In*: Van Dyck, S. and Strahan, R. (Eds.), *The Mammals of Australia. 3rd Edition*. Reed New Holland, Sydney, pp. 662–664.
Rohling, E.J., Fenton, M., Jorissen, F.J., Bertrand, G., Ganssen, G & Caulet, J.P. (1998) Magnitude of sea level lowstands of the last 500,000 years. *Nature*, 394, 162–165. http://dx.doi.org/10.1038/28134
Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574. http://dx.doi.org/10.1093/bioinformatics/btg180
Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
Rowe, K.C., Reno, M.L., Richmond, D.M., Adkins, R.M. & Steppan, S.J. (2008) Pliocene colonization and adaptive radiations

in Australia and New Guinea (Sahul): Multilocus systematics of the old endemic rodents (Muroidea: Murinae). *Molecular Phylogenetics and Evolution*, 47, 84–101.
http://dx.doi.org/10.1016/j.ympev.2008.01.001
Rowe, K.C., Aplin, K.P., Baverstock, P.R. & Moritz, C. (2011) Recent and rapid speciation with limited morphological disparity in the genus *Rattus*. *Systematic Biology*, 60, 188–203.
Scotese, C.R., Gahagan, L.M. & Larson, R.L. (1988) Plate tectonic reconstructions of the Cretaceous and Cenozoic ocean basins. *Tectonophysics*, 155, 27–48.
http://dx.doi.org/10.1016/0040-1951(88)90259-4
Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
http://dx.doi.org/10.1093/bioinformatics/btl446
Thomas, O. (1907) On three new mammals from British New Guinea. *Annals and Magazine of Natural History*, 7, 70–74.
http://dx.doi.org/10.1080/00222930709487303
Veron, G., Patterson, B.D. & Reeves, R. (2008) Global diversity of mammals (Mammalia) in freshwater. *Hydrobiologia*, 595, 607–617.
http://dx.doi.org/10.1007/s10750-007-9122-1
Voris, H.K. (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, 27, 1153–1167.
http://dx.doi.org/10.1046/j.1365-2699.2000.00489.x
Voss, R.S. (1988) Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. *Bulletin of the American Museum of Natural History* 188, 260–493.

APPENDIX A. Specimens examined.

Baiyankamys shawmayeri: AM M8661
Crossomys moncktoni: AM M14163, AM M15454, AM M8652, AM M9543
Echiothrix leucura: AMNH 101243, AMNH 153013, AMNH 225680, AMNH 225685, MZB 27875
Hydromys hussoni: AM M18627
Hydryomys chrysogaster: NMV C25843, NMV C26872, NMV C32103, NMV C32104
Melasmothrix naso: FMNH 213284, FMNH 213447, FMNH 213448, NMV C37064
Parahydromys asper: AM M14164, AM M15370, AM M9541
Paucidentomys vermidax: FMNH 213102, MZB 35001
Sommeromys macrorhinos: AMNH 226956, MZB 34758, MZB 34903, NMV C37074
Tateomys macrocercus: FMNH 213450, NMV C37080, NMV C37081
Tateomys rhinogradoides: FMNH 213338, FMNH 213434, NMV C37082, NMV C37083