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Caecilita Wake & Donnelly, 2010 (Amphibia: Gymnophiona) is not lungless: implications for taxonomy and for understanding the evolution of lunglessness

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Abstract

According to current understanding, five lineages of amphibians, but no other tetrapods, are secondarily lungless and are believed to rely exclusively on cutaneous gas exchange. One explanation of the evolutionary loss of lungs interprets lunglessness as an adaptation to reduce buoyancy in fast-flowing aquatic environments, reasoning that excessive buoyancy in such an environment would cause organisms being swept away. While not uncontroversial, this hypothesis provides a plausible potential explanation of the evolution of lunglessness in four of the five lungless amphibian lineages. The exception is the most recently reported lungless lineage, the newly described Guyanan caecilian genus and species *Caecilita iwokramae* Wake & Donnelly, 2010, which is inconsistent with the reduced disadvantageous buoyancy hypothesis by virtue of it seemingly being terrestrial and having a terrestrial ancestry. Re-examination of the previously only known specimen of *C. iwokramae* and of recently collected additional material reveal that this species possesses a reasonably well-developed right lung and is a species of the pre-existing caecilian genus *Microcaecilia* Taylor, 1968. We therefore place *Caecilita* in the synonymy of *Microcaecilia*, and re-evaluate the plausibility of the reduced disadvantageous buoyancy hypothesis as a general explanation of the evolution of lunglessness.

Key words: amphibian, *Atretochoana,* buoyancy, Guyana, lunglessness

Introduction

Lungs are an ancestral feature of Tetrapoda and are almost ubiquitous among living tetrapods. Secondary lunglessness is a rare condition that is currently considered to have evolved independently five times within amphibians, twice in caecilians, twice in salamanders and once in frogs (Hutchison, 2008; Wake & Donnelly, 2010), but nowhere else within the tetrapods. Explanations of the evolution of this unusual condition have mostly suggested that lunglessness is or was an adaptation to life in fast-flowing waters where pulmonary buoyancy, and concomitant difficulty in maintaining position, could be positively disadvantageous (e.g., Wilder & Dunn, 1920; Wilkinson & Nussbaum, 1997; Bickford *et al*., 2008). This is a plausible, if controversial, explanation of lunglessness in amphibians (Hutchison, 2008) with the clear exception of lunglessness in the recently discovered monotypic caecilian genus *Caecilita*. *Caecilita iwokramae* Wake & Donnelly, 2010 appears to be a small terrestrial species belonging to a family of entirely terrestrial, directly developing caecilians (Wilkinson *et al*., 2011). As such, its reported lunglessness cannot be readily explained by reference to an aquatic lifestyle and *Caecilita iwokramae* therefore represents the greatest empirical challenge to the generality of the reduced disadvantageous buoyancy (RDB) hypothesis for the origin of lunglessness in amphibians.

Caecilita iwokramae was described on the basis of a single specimen from the Iwokrama Rainforest in Guyana. It was reported to lack lungs, pulmonary arteries and veins, and have sealed internal and external nostrils. Sealed external nostrils have not been found in any other tetrapod and, together with the other unusual features, were used to justify recognition of the new monotypic genus *Caecilita*. However, our re-examination of the type

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The inaccurate claims of lunglessness and of other associated internal and external morphological features of the holotype of *Caecilita iwokramae* are surprising. Whereas the apertures in the external and internal nares are difficult, but by no means impossible, to discern with light microscopy, the lung is well-developed, readily located in the expected anatomical position, and receives a readily discerned arterial supply. Our conflicting observations demonstrate that observation reports in comparative anatomy can sometimes be misleading. Given its rarity, the discovery of any additional independent instance of amphibian lunglessness is important and any claim to have done so is substantial. We recommend, in addition to attempting thorough documentation, investigators making surprising and substantial morphological discoveries should seek opportunities to have their basic observations corroborated by independent observers, particularly when the observations challenge a widely accepted general explanation for some class of naturally occurring phenomena.

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References

Beachy, C.K. & Bruce, R.C. (1992) Lunglessness in plethodontid salamanders is consistent with the hypothesis of a mountain stream origin: a response to Ruben and Boucot. *American Naturalist*, 139, 839–847. http://dx.doi.org/10.1086/285360

Bickford, D., Iskandar, D. & Barlian, A. (2008) A lungless frog discovered in Borneo. *Current Biology*, 18, R374–R375. http://dx.doi.org/10.1016/j.cub.2008.03.010

Bruce, R.C., Beachy, C.K., Lenzo, P.G. Pronych, S.I. & Wassersug, R.J. (1994) Effects of lung reduction on rheotactic performance in amphibian larvae. *Journal of Experimental Zoology*, 268, 377–380. http://dx.doi.org/10.1002/jez.1402680506

Gower, D.J., Doherty-Bone, T.M., Loader, S.P., Wilkinson, M., Kouete, T.M., Tapley, B., Orton, F., Daniel, O.Z., Wynne, F., Flach, E., Müller, H., Menegon, M., Stephen, I., Browne, R.K., Fisher, M.C., Cunningham, A.A. & Garner, T.W.J. (2013) *Batrachochytrium dendrobatidis* infection and lethal chytridiomycosis in caecilian amphibians (Gymnophiona), *EcoHealth*, 10, 173–178. http://dx.doi.org/10.1007/s10393-013-0831-9

Hoogmoed, M.S., Maciel, A.O. & Coragem, J.T. (2011) Discovery of the largest lungless tetrapod, *Atretochoana eiselti* (Taylor, 1968) (Amphibia: Gymnophiona: Typhlonectidae), in its natural habitat in Brazilian Amazonia. *Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais*, 6, 241–262.

Hutchison, V.H. (2008) Amphibians: lungs' lift lost. *Current Biol*ogy, 18, R392–R393. http://dx.doi.org/10.1016/j.cub.2008.03.006

Limaye, A. (2006) *Drishti - Volume Exploration and Presentation Tool*. Poster presentation. Vis 2006, Baltimore.

Nussbaum, R.A. & Wilkinson, M. (1995) A new genus of lungless tetrapod: a radically divergent caecilian (Amphibia: Gymnophiona). *Proceedings of the Royal Society B*, 261, 331–335. http://dx.doi.org/10.1098/rspb.1995.0155

Reagan, N.L. & Verrell, P.A. (1991) The evolution of plethodontid salamanders: did terrestrial mating facilitate lunglessness? *American Naturalist*, 138, 1307–1313. http://dx.doi.org/10.1086/285288

Ruben, J.A. & Boucot, A.J. (1989) The origin of the lungless salamanders (Amphibia: Plethodontidae). *American Naturalist*, 134, 161–169. http://dx.doi.org/10.1086/284973

Ruben, J.A., Reagan, N.L., Verrell, P.A. & Boucot, A.J. (1993) Plethodontid salamander origins: a response to Beachy and Bruce. *American Naturalist*, 142, 1038–1049.
http://dx.doi.org/10.1086/285590

Wake, M.H. & Donnelly, M.A. (2010) A new lungless caecilian (Amphibia: Gymnophiona) from Guyana. *Proceedings of the Royal Society B*, 277, 915–922.
http://dx.doi.org/10.1098/rspb.2009.1662

Wilder, I.W. & Dunn, E.R. (1920) The correlation of lunglessness in salamanders with a mountain brook habitat. *Copeia*, 1920, 63–68.

Wilkinson, M. (1989) On the status of *Nectocaecilia fasciata* Taylor, with a discussion of the phylogeny of the Typhlonectidae (Amphibia: Gymnophiona). *Herpetologica*, 45, 23–36.

Wilkinson, M. & Nussbaum, R.A. (1997) Comparative morphology and evolution of the lungless caecilian *Atretochoana eiselti* (Taylor) (Amphibia: Gymnophiona: Typhlonectidae). *Biological Journal of the Linnean Society*, 62, 39–109.
http://dx.doi.org/10.1111/j.1095-8312.1997.tb01616.x

Wilkinson, M. & Nussbaum, R.A. (2006) Caecilian phylogeny and classification. *In*: Exbrayat, J.-M. (Ed.), *Reproductive biology and phylogeny of Gymnophiona*. Science Publishers Inc, Enfield, Jersey, Plymouth, pp. 39–78.

Wilkinson, M., O'Connor, A. & Nussbaum, R.A. (2013) Taxonomic status of the neotropical caecilian genera *Brasilotyphlus* Taylor, 1968, *Microcaecilia* Taylor, 1968 and *Parvicaecilia* Taylor, 1968 (Amphibia: Gymnophiona: Siphonopidae). *Occasional Papers of the Museum of Zoology, University of Michigan*, 744, 1–12.

Wilkinson, M., San Mauro, D., Sherratt, E. & Gower, D.J. (2011) A nine-family classification of caecilian amphibians. *Zootaxa* 2874, 41–64.