Zootaxa 4004 (1): 001–075
www.mapress.com/zootaxa/

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.4004.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:BCAD1EAC-7DE9-4981-9E7B-11D041DE56AF

ZOOTAXA

4004

Phylogenetic systematics of egg-brooding frogs (Anura: Hemiphractidae) and the evolution of direct development

SANTIAGO CASTROVIEJO-FISHER[1,2,9], JOSÉ M. PADIAL[3], IGNACIO DE LA RIVA[4], JOSÉ P. POMBAL, JR.[5], HELIO R. DA SILVA[6], FERNANDO J. M. ROJAS-RUNJAIC[1,7], ESTEBAN MEDINA-MÉNDEZ[8] & DARREL R. FROST[2]

[1]*Lab. de Sistemática de Vertebrados, Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Av. Ipiranga 6681, Porto Alegre, RS 90619-900, Brazil*
[2]*Division of Vertebrate Zoology (Herpetology), American Museum of Natural History, New York, NY 10024, USA*
[3]*Section of Amphibians and Reptiles, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA 15213, USA*
[4]*Department of Biodiversity and Evolutionary Biology, Museo Nacional de Ciencias Naturales-CSIC, C/ José Gutiérrez Abascal 2, 28006 Madrid, Spain*
[5]*Departamento de Vertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, Rio de Janeiro, RJ 20940-040, Brazil*
[6]*Instituto de Biologia, Universidade Federal Rural do Rio de Janeiro, Caixa postal 74524, Seropedica, RJ 23897-970, Brazil*
[7]*Museo de Historia Natural La Salle, Fundación La Salle de Ciencias Naturales, Caracas 1010-A, Venezuela*
[8]*Instituto de Genética, Edif. M1-304, Departamento de Ciencias Biológicas, Universidad de los Andes, Carrera 1E No. 18A–10, A.A. 4976, Bogotá, Colombia.*
[9]*Corresponding author. E-mail: castroviejo.fisher@gmail.com*

Magnolia Press
Auckland, New Zealand

Accepted by V. Orrico: 12 May 2015; published: 20 Aug. 2015

SANTIAGO CASTROVIEJO-FISHER, JOSÉ M. PADIAL, IGNACIO DE LA RIVA, JOSÉ P. POMBAL, JR., HELIO R. DA SILVA, FERNANDO J. M. ROJAS-RUNJAIC, ESTEBAN MEDINA-MÉNDEZ & DARREL R. FROST

Phylogenetic systematics of egg-brooding frogs (Anura: Hemiphractidae) and the evolution of direct development

(*Zootaxa* 4004)

75 pp.; 30 cm.

20 Aug. 2015

ISBN 978-1-77557-771-3 (paperback)

ISBN 978-1-77557-772-0 (Online edition)

FIRST PUBLISHED IN 2015 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: zootaxa@mapress.com

http://www.mapress.com/zootaxa/

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of contents

Abstract . . . 3
Introduction . . . 4
Material and methods . . . 8
Results . . . 12
Discussion . . . 15
Systematics . . . 20
Family: Hemiphractidae Peters, 1862 . . . 20
Subfamily: Cryptobatrachinae Frost *et al*., 2006 . . . 20
Genus: *Cryptobatrachus* Ruthven, 1916 . . . 21
Genus: *Flectonotus* Miranda-Ribeiro, 1926 . . . 22
Subfamily: Hemiphractinae Peters, 1862 . . . 23
Genus: *Fritziana* Mello-Leitão, 1937 . . . 23
Genus: *Gastrotheca* Fitzinger, 1843 . . . 24
Gastrotheca fissipes species group . . . 26
Gastrotheca longipes species group . . . 27
Gastrotheca marsupiata species group . . . 27
Gastrotheca microdiscus species group . . . 27
Genus: *Stefania* Rivero, 1968 . . . 28
Genus: *Hemiphractus* Wagler, 1828 . . . 28
Acknowledgements . . . 30
References . . . 30
Author contributions . . . 42
Author note . . . 42
Appendix 1 . . . 43
Appendix 2 . . . 61
Appendix 3 . . . 64
Appendix 4 . . . 65
Appendix 5 . . . 67

Abstract

Egg-brooding frogs (Hemiphractidae) are a group of 105 currently recognized Neotropical species, with a remarkable diversity of developmental modes, from direct development to free-living and exotrophic tadpoles. Females carry their eggs on the back and embryos have unique bell-shaped gills. We inferred the evolutionary relationships of these frogs and used the resulting phylogeny to review their taxonomy and test hypotheses on the evolution of developmental modes and bell-shaped gills. Our inferences relied on a total evidence parsimony analysis of DNA sequences of up to 20 mitochondrial and nuclear genes (analyzed under tree-alignment), and 51 phenotypic characters sampled for 83% of currently valid hemiphractid species. Our analyses rendered a well-resolved phylogeny, with both Hemiphractidae (sister of Athesphatanura) and its six recognized genera being monophyletic. We also inferred novel intergeneric relationships [((*Cryptobatrachus*, *Flectonotus*), (*Stefania*, (*Fritziana*, (*Hemiphractus*, *Gastrotheca*))))], the non-monophyly of all species groups previously proposed within *Gastrotheca* and *Stefania*, and the existence of several putative new species within *Fritziana* and *Hemiphractus*. Contrary to previous hypotheses, our results support the most recent common ancestor of hemiphractids as a direct-developer. Free-living aquatic tadpoles apparently evolved from direct-developing ancestors three to eight times. Embryos of the sister taxa *Cryptobatrachus* and *Flectonotus* share a pair of single gills derived from branchial arch I, while embryos of the clade including the other four genera have two pairs of gills derived from branchial arches I and II respectively. Furthermore, in *Gastrotheca* the fusion of the two pairs of gills is a putative synapomorphy. We propose a revised taxonomy concordant with our optimal topologies.

Key words: *Cryptobatrachus*, *Flectonotus*, *Fritziana*, *Gastrotheca*, gills, *Hemiphractus*, Neotropics, parsimony, *Stefania,* taxonomy, total evidence, tree-alignment