

Duellman, W. E. 2015. **Marsupial frogs: *Gastrotheca* & allied genera; with osteology** by Linda Trueb. x + 407 pp. Johns Hopkins University Press, Baltimore, Maryland.

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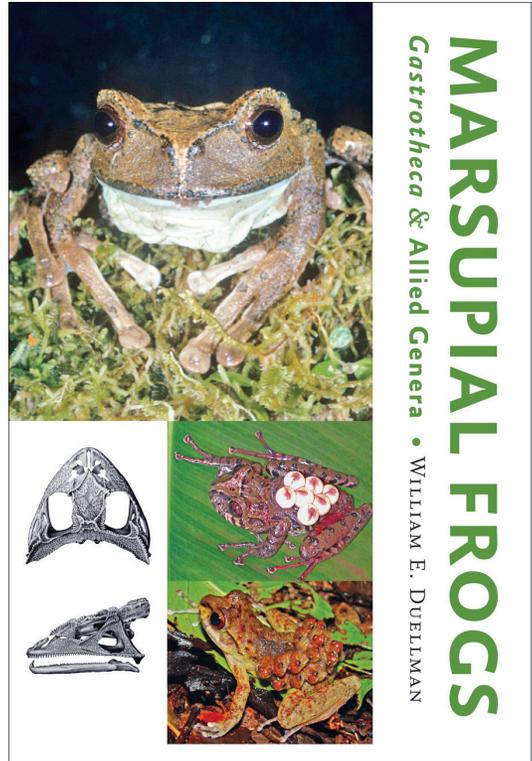
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I was a lucky eavesdropper on a decade of Bill Duellman's 50-year conversation with marsupial frogs. On my first trip to South America he introduced this 23 year-old to several species. I remember well collecting *Gastrotheca riobambae* in the city of Quito, carefully pulling *Gastrotheca ochoai* from spiny bromeliads on hot and dry mountainside in southern Peru, and following the eyeshine of an *Amphignathodon guentheri* high in a tree across a seemingly impassable stream in Ecuador.

Marsupial frogs (Hemiphractidae, six genera, 104 species) are a fascinating clade in which females brood developing embryos on the dorsum in modes ranging from simple adherence to the dorsum, to a closed dorsal pouch, to pouches within the body cavity behind the peritoneal layer. Amazingly, in some species females give birth to feeding tadpoles and in others to froglets. Species range from Panama to Bolivia and southeast Brazil, inhabiting a variety of habitats and elevations including rainforest, mesic forest, cloud forest, montane scrub, elfin forest, páramo, and puna, from sea level to 4360 m (see Chapter 8). They inhabit both pristine and disturbed areas—*G. riobambae* can be heard calling in Quito. The *Gastrotheca* clade (68 species), only 30my old, has evolved to occupy a wide variety of niches, living under rocks and logs, on low vegetation, terrestrial and arboreal bromeliads, and unreachable forest canopy.

Marsupial Frogs is a true systematic monograph, an increasingly under-appreciated mode of publication. Every species of *Gastrotheca* has a photograph or drawing, as do almost all of the other hemiphractid species.



Duellman used specimens and data from 78 institutions; this depth of coverage is increasingly rare, as most taxonomic treatments tend to focus only on a few collections. Despite being a monograph, the introductory chapters are easy reading, concisely informative, and will be interesting to a diverse audience.

High-quality images of live frogs were contributed by many colleagues. The production values are high, although I noted a few typos and inconsistencies (Guiana Shield vs Guyana Shield). On page 27, *Gastrotheca* is said to include 69 species, but 67 on page 117. I counted 68 in the Table of Contents.

Following the Introduction (Chapter 1), which includes materials and methods, two chapters on phylogeny frame the remainder of the book: the history of the phylogenetic placement of Hemiphractidae within frogs

(Chapter 2) and a phylogeny and taxonomy of Hemiphractidae (Chapter 3).

The first phylogenies of marsupial frogs, based on mitochondrial ribosomal genes, found that the placement of *Gastrotheca* and *Cryptobatrachus* rendered Hylidae polyphyletic (Ruvinsky and Maxson 1996, Darst and Cannatella 2004), but with poor support. Unfortunately, these preliminary trees led to the extreme partitioning of the Hylidae into four families (Amphignathodontidae, Cryptobatrachidae, Hemiphractidae, and Hylidae). Analyses of more complete data and taxon sampling have shown that Amphignathodontidae, Cryptobatrachidae, Hemiphractidae form a clade, for which the valid name is Hemiphractidae (Wiens *et al.* 2007).

Duellman provides an expanded molecular phylogeny of 77 species of hemiphractids (Chapter 3), which is enhanced with an overview of reproductive mode and distribution of the major lineages. It sets the stage for chapters on the genera of hemiphractids (Chapter 9) and species accounts for eight subgenera (four of them new) of *Gastrotheca* (Chapters 10–12). It is notable that Chapter 3 begins “Herein I present a hypothesis ...” (p. 22), acknowledging that his phylogeny is not the final word.

His use of subgenera merits a mention, especially given the current practice of excessive splitting genera into more genera, rather than using infra-generic taxa. Although Duellman has argued against using the subgenus rank (Duellman 1977), his rationale was avoiding the confusion caused by the International Code of Zoological Nomenclature, under which the same name (e.g., *Gastrotheca*) might be used simultaneously as subgenus or genus rank. Here he favors the use of infra-generic taxon names. This taxonomy indicates a trend toward classification based on an increasingly tree-like hierarchy that provides more phylogenetic information than do simple lists. Unfortunately, tree-thinking has not yet fully transformed the practices of taxonomists, to their detriment.

A series of chapters (4–8) treats specialized topics. Chapter 5 is a mosaic of chromosomes, muscle variation, and vocalization, and coverage of each of these topics is cursory. It would have been interesting to reinterpret the evolution of chromosomes (Fig. 6.2) in light of the new phylogeny. In contrast, the Reproductive Biology chapter (Chapter 7) is data-rich, and one can tell that this is what Duellman enjoys writing. Chapter 6 describes external morphology and includes much useful information about collecting such data. Duellman’s treatment of biogeography (Chapter 8) is concise, presenting a chronogram and narrative of the historical biogeography. Images of the many habitats of hemiphractids are a nice addition.

The osteology chapter (Chapter 4) deserves special note, as it was written by Linda Trueb. The skull illustrations are exquisite, and moreover, character state variation among and within subgenera is described. This chapter is a good introduction for neophytes tackling frog osteology. A combined phylogeny based on DNA and morphology (Fig. 4.11) using species of *Gastrotheca* is compared to the DNA-only tree, but the source of the morphological data is not clear; perhaps it is from Mendelson *et al.* (2000). Support values, as well as branch lengths for the combined tree (Fig. 4.11) are lacking. Thus, it is difficult to make general conclusions about the evolution of morphology. The taxon names on the phylogeny are misaligned, so I would guess that Trueb did not execute these illustrations.

The taxonomic accounts (Chapters 9–12) are thorough, following a model that Duellman has used for decades. I would have liked to see georeferenced localities as part of the supplementary material. Nonetheless, the locality information on the maps will be useful for revising the shape files on the IUCN Red List of Threatened Species website (maps.iucnredlist.org) using actual data.

I noted discrepancies between Duellman’s dot maps and the Red List polygons. In most cases the polygons considerably exceeded the

distribution indicated by Duellman's maps, suggesting over-extrapolation by the Red List based on undocumented information. In other cases the expected overlap between the polygons and the localities on Duellman's maps is minimal. My survey of a few species indicates that these discrepancies cannot be explained away by the assessment date (~2004) of the Red List relative to the publication of this book. In some cases the Red List is inaccurate. For example, the type-locality of *G. lateonota* is El Tambo, which is southwest of Huancabamba, Peru (Fig. 12.22), but the Red List plots the type-locality as directly west of Huancabamba, about 60km from the type-locality. Similarly, as noted by the Red List and by Duellman, the only known locality of *G. williamsoni* is San Esteban, Venezuela. However, the Red List map shows a small irregular polygon that does not include San Esteban, and the polygon is drawn on the wrong side (south) of the Coastal Range.

Duellman reports the reproductive mode for each species, a key evolutionary feature of the clade. However, if information is missing, the condition is imputed based on that in close relatives. Unfortunately, the extrapolation then is transferred to the phylogeny (Fig. 3.1), without notation that the character state is actually missing. Clearly, this practice will mislead data miners.

"Integrative taxonomy" is indeed a buzzword (3180 hits for the phrase on Google Scholar), and a young taxonomist might have the impression that use of multiple data sources is new. But consider the following:

"A thoroughly trained systematist today must have at least a speaking acquaintance with morphology, developmental biology, cytogenetics, biochemistry, behavior, ecology, and biogeography, and be thoroughly grounded in systematic theory and practice, as well as diverse computational methods. In addition, he or she must have a working knowledge of a group of organisms and of the geography of the region of the earth inhabited by those organisms."

One could imagine reading this in any paper on integrative taxonomy, but Duellman wrote this 30 years ago (Duellman 1985: 759) reflecting his long and forward-looking perspective on our field.

Bill's larger efforts have been either regionally focused taxonomic treatments—hylid frogs of Middle America (Duellman 1970) and Terrarana of Peru (Duellman and Lehr 2009), analyses of herp communities at Santa Cecilia (Duellman 1978), and Cusco Amazonico (Duellman 2005), and a textbook (Duellman and Trueb 1986). This outstanding volume is the result of the longest enduring of Duellman's research projects; add it to your bookshelf! I'm saving space for one more after this one.

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