



The auditory region of *Brachycephalus* and its bearing on the monophyly of the genus (Anura: Brachycephalidae)

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Abstract

We surveyed the morphology of the auditory region of members of the anuran genus *Brachycephalus*. The sample included seven of the eleven known species; in addition, *Brachycephalus ephippium* and *B. vertebralis* were each represented by several specimens from different localities. All species lack a tympanum, tympanic annulus, stapes, and Eustachian tube. However, the operculum and the *m. opercularis* remain. The large operculum bears a robust process for the *m. opercularis* and covers most of the fenestra ovalis. The auditory apparatus of *Brachycephalus* is distinguished by the large size and the orientation of the fenestra ovalis, which faces posterior, rather than lateral. The morphology of these structures is compared to those of other minute brachycephalid frogs considered to be close relatives of *Brachycephalus*, and the importance of these characters as evidence of the monophyly of the genus is discussed. We also discuss the importance of other morphological features cited to support close relationships among small-sized brachycephalids, and consider the role of miniaturization in generating convergent pattern of loss of morphological features.

Key words: digit reduction, middle ear, miniaturization, ostia pharyngea, *tympanic annulus*, stapes, systematics

Introduction

In perhaps no other group of tetrapods has the evolution of small size resulted in so many apparently convergent losses and/or reductions of osteological elements as has occurred among extant amphibians (Alberch 1980; Alberch and Alberch 1981; Alberch and Gale 1985; Trueb and Alberch 1985; Yeh 2002). In anurans, the effects of miniaturization (Hanken and Wake 1993) are noticeable in parts of the skull (Trueb and Alberch 1985, Yeh 2002), fingers, and toes (Alberch and Gale 1985, Estrada and Hedges 1996). Occasionally, reduction and absence of elements have confused anuran systematists; there are different interpretations of relationships of minute species depending upon whether an absence has been treated as a convergent character or homologous loss. Such is the case of several of the smallest Neotropical anurans—members of the genera *Atelopus*, *Brachycephalus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella*—the taxonomic relationships of which have been debated for decades (e.g., MacDiarmid 1971). More recently, this debate also grew to include *Euparkerella* (Izecksohn 1988) and *Truebella* (Graybeal and Cannatella 1995).

The recent application of DNA-sequence data for large numbers of lissamphibian taxa has produced new schemes of relationships, which seemingly are independent of the effects of morphological convergences resulting from the process of miniaturization (Darst and Cannatella 2004; Frost *et al.* 2006). Among the many new clades (and proposed taxonomic rearrangements), both analyses revealed *Brachycephalus* to be nested