BREVIORA

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TREE HOLES TO TRASH: UNIQUE UPSIDE-DOWN TERRESTRIAL SPAWNING, AGONISTIC INTERACTIONS, COMPLEX MATING CALLS, AND UNNATURAL BREEDING ALTERATIONS IN *MINERVARYA CHARLESDARWINI* (ANURA, DICROGLOSSIDAE)

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ABSTRACT. Anuran amphibians exhibit the greatest diversity of reproductive modes among tetrapod vertebrates. The Andamanese Charles Darwin's frog, *Minervarya charlesdarwini*, is the only species of the family Dicroglossidae that is known to naturally deposit eggs in water-filled cavities of tree holes or buttresses, where they then undergo exotrophic development. We describe the reproductive behavior in this species that involves a unique combination of traits: (1) Males produce complex advertisement calls comprising at least three different call types, in addition to a type of aggressive call. (2) Unpaired males exhibit agonistic interactions with each other and with mated pairs. (3) Mate selection, amplexus, and oviposition take place inside water-filled cavities. (4) During axillary amplexus, mating pairs synchronously switch between head-up and head-down positions above and below the water surface using both forward and backward movements. (5) At the time of egg laying, amplectant pairs are in an upside-down position on the cavity walls with their bodies completely outside the water. (6) Eggs are deposited over multiple bouts on the inner walls of the cavities and terrestrially above the water surface. Upside-down spawning in *M. charlesdarwini* is a unique trait among phytotelm-breeding terrestrial frogs. The combination of terrestrial oviposition sites in water-filled phytotelmata and the upside-down egg-laying posture is a novel report for the family Dicroglossidae and perhaps all anurans. This specialized behavior is also likely derived for a species that is embedded in a group of largely aquatic-breeding minervaryan frogs. Although *M. charlesdarwini* appears to be an obligate phytotelm breeder, individuals were often observed breeding inside cylindrical, water-filled plastic sapling bags in

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