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## I. INTRODUCTION

In the biological world, sound signalling is an efficient means of communication, propagating quickly over long distances even in obstructed or dark environments without leaving trails (Bradbury & Vehrencamp, 1998). Acoustic communication has evolved only in vertebrates and in some groups of arthropods, perhaps because the emission and reception of sound waves requires specialized structures. Mammals, birds, amphibians and even fishes are known to communicate using sound (Bradbury & Vehrencamp, 1998; Hauser, 1996; Ladich & Collin, 2006; Marler & Slabbekoorn, 2004; Narins *et al.*, 2006; Sebeok, 1965). Among these groups of vertebrates, there is great diversity of emitted acoustic signals and of the information transmitted. Conversely, most animals belonging to the four main lineages usually described as reptiles (turtles, tuatara, squamates and crocodylians) are relatively silent: snakes are only sensitive to low-frequency sounds (below 1 kHz) and few species produce sounds (Young, 2003); lizards favour visual or chemical communication channels (Cooper *et al.*, 2002; Zuri & Bull, 2000) and rarely vocalize (Frankenberg, 1982); and turtles limit their sound emissions to coitus (Galeotti, Pellitteri & Fasola, 2004). Only the 23 extant species of crocodylians emit vocalizations, some with a repertoire of auditory signals which occur in a variety of contexts (Britton, 2001; Campbell, 1973; Garrick, Lang & Herzog, 1982; Herzog & Burghardt, 1977). Living reptiles are not monophyletic, having pursued independent evolutionary trajectories since the Triassic (Carroll, 1982; Meyer & Zardoya, 2003; Shine, 2005; Martin, 2008); crocodylians belong Archosauria, which also includes birds, pterosaurs and dinosaurs (Fig. 1). Acoustic communication is thus a trait shared by all modern archosaurs. It is also likely that, based on inferences from fossilized dinosaur nests with eggs and juveniles in associations with adults (Coombs, 1982; Meng *et al.*, 2004; Norell *et al.*, 1995; Tullberg, Ah-King & Temrin, 2002; Varricchio *et al.*, 1997), and from the presence of anatomical features thought to be involved in sound emission,

such as the hollow crest of some hadrosaurs (Hopson, 1975; Weishampel, 1981), acoustic communication might also have been present in other archosaur groups (Fig. 1). A comparison of crocodylian and bird bioacoustics may thus shed light on the behaviour of these long extinct animals.

The acoustic signals of crocodylians play a major role in the first stages of life, particularly in interactions between juveniles and adults (Campbell, 1973), as well as later during courtship and territorial defence (Garrick *et al.*, 1982). Despite the presumed importance of sound signals in crocodylians, the acoustic structure of vocalizations, their mode of production, how auditory information is processed in the brain, and the precise role of acoustic signals in their behaviour remain poorly understood or unknown. One purpose of this review is to stimulate research on crocodylian acoustic communication.

This review attempts to summarize current understanding of crocodylian acoustic communication, including sound production and reception. We make frequent comparisons to birds although we do not review bird acoustic communication in detail, this having been covered previously by others (e.g. Marler & Slabbekoorn, 2004). Throughout we emphasize research questions critical to advancing our understanding of crocodylian bioacoustics.

## II. CROCODYLIAN VOCALIZATIONS: A VARIETY OF SIGNALS WITH UNCERTAIN ROLES

Due to the absence of detailed study, classifying crocodylian vocalizations is not easy. In birds, it is usual to distinguish between songs and calls. Songs are typically more or less complex series of different notes and are typically used in a reproductive context (mate attraction and/or territorial interaction). All birds do not sing songs whereas calls are produced by most species, by both sexes and during the whole life. The repertoire of calls depends on the species, ranging from a few to a very large number (Marler &