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SHORT COMMUNICATION

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Dark gaping - presumed independent origin for a remarkable warning signal in four Neotropical snake species

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Mouth gaping is a widespread warning signal displayed by a great number of vertebrate species, from fish to mammals (Tickell, 1984; Brantley et al., 1994; Moon-Fanelli, 2011; Toledo et al., 2011). This behaviour is widespread among reptiles, especially among lizards and snakes (Hertz et al., 1982; Bramble et al., 1984; Greene, 1988; Combrink et al., 2016). In snakes, it usually is an effective warning signal, as cornered snakes may easily strike at, and even bite the potential predator (e.g. Sazima, 2000). However, some species mouth gape as a bluff and do not bite the opponent (Greene, 1988). In several colubroid snake lineages this mouth gaping may be either a pre-bite phase such as a threat, or a bluff (Greene, 1988; Martins et al., 2008). Mouth gaping is likely enough to discourage the attack of some but not all predators. Consequently, it is often a step within a more complex behavioural repertoire (e.g. Burghardt & Greene, 1988; Marques & Sazima, 2004). In addition, such behaviour may be complemented by other signals, such as tongue hanging, hissing, or teeth displaying (Burghardt & Greene, 1988) which possibly emphasise the threat posture.

Here we briefly describe and illustrate the mouth gaping behaviour in four species of Neotropical snakes that have dark oral lining, which indicates that this feature likely increases the threat signal of this display. Furthermore we present a simplified phylogenetic tree to show the distribution of mouth gaping among related snake lineages.

We gathered the data used herein during photography sessions of *Leptophis ahaetulla*, *Oxybelis aeneus*, *Chlorosoma laticeps* and *Tomodon dorsatus* individuals. We elicited this defensive behaviour by approaching our hand and occasionally gently touching the body of the snake. Mouth gaping is already recorded for *L. ahaetulla*, *O. aeneus*, and *T. dorsatus* (Greene, 1988; Martins et al., 2008; Marques et al., 2019) but until recently there was no information about this behaviour in *C. laticeps*. This latter snake is known only from the type specimen and a few preserved ones (Zaher et al., 2008). While handling an individual collected in the Atlantic Forest at the Sooretama Reserve in the state of Espírito Santo, we took a picture of mouth gaping by *C. laticeps* and presented it in a field guide (Marques et al., 2019). A simplified phylogenetic tree based on Zaher et al. (2009), Grazziotin et al. (2012), Jadin et al. (2014, 2019), Klaczko et al. (2014), Montigelli et al. (2019), and Albuquerque et al. (2022) was used to show the distribution of dark gape behaviour among related lineages of Neotropical snakes.

All four species cited below displayed a sigmoid (S-shaped) posture of the anterior portion of the body, gaped the mouths with head facing our hand, and stayed in this posture for a few seconds (Fig. 1). The simplified phylogenetic tree (Fig. 2) shows that dark gape arose independently, appearing in two lineages of Colubridae and Dipsadidae. All species reported here show a darkening of the inner portion of the mouth with almost black mucosa, except *L. ahaetulla*, in which the dark pigmentation surrounds the larynx and trachea. However, in this latter species, the dark lining is restricted to a few individuals, the remaining ones having light mouth lining.

Among colubrid snakes, mouth gaping is a widespread defensive behaviour, with the great majority of species displaying light oral mucosa (Greene, 1988). Light coloured mouth lining occurs in snakes phylogenetically related to *Leptophis* and *Oxybelis* with its sister group *Chironius* (Martins et al., 2008). The presence of light or dark pigment in the oral mucosa of *L. ahaetulla* together with the fact that related species have light oral mucosa and display mouth gaping suggests that the acquisition of dark pigment is evolutionarily more recent than this defensive gaping. Thus, it is possible that dark pigment in *Leptophis* evolved to enhance the warning effect of mouth gaping. A similar scenario (warning enhancement) could have occurred among *O. aeneus*, as related snakes that display mouth gaping (e.g., all *Chironius* species and most individuals of *Leptophis*) have light oral mucosa. The congener, *O. fulgidus*, displays mouth gaping but has no dark pigments in the oral mucosa (Mendes et al., 2019), which indicates that the dark mucosa in *O. aeneus* is likely a derived character that appeared after mouth gaping evolved as a warning signal.

Among dipsadid snakes, the independent origin of mouth gaping associated with blackish oral mucosa is even more evident when considering the phylogenetic relationships among the species within this clade. Mouth gaping appears to be uncommon among dipsadid species (Greene, 1988; Martins et al., 2008). There is no record of this defensive behaviour among the great majority of *Philodryas* species and *Xenoxybelis*, which are closely related to *Chlorosoma*. An exception is *P. aestiva*, which was recorded mouth gaping while attacked by birds in the wild (Banci et al., 2018). However, this latter species has light oral mucosa similar to its congeners and *Xenoxybelis*. *Chlorosoma* includes three species, *C. dunupyana*, *C. laticeps* and *C. viridissimum* (Melo-Sampaio et al., 2021). The last two species are green and both

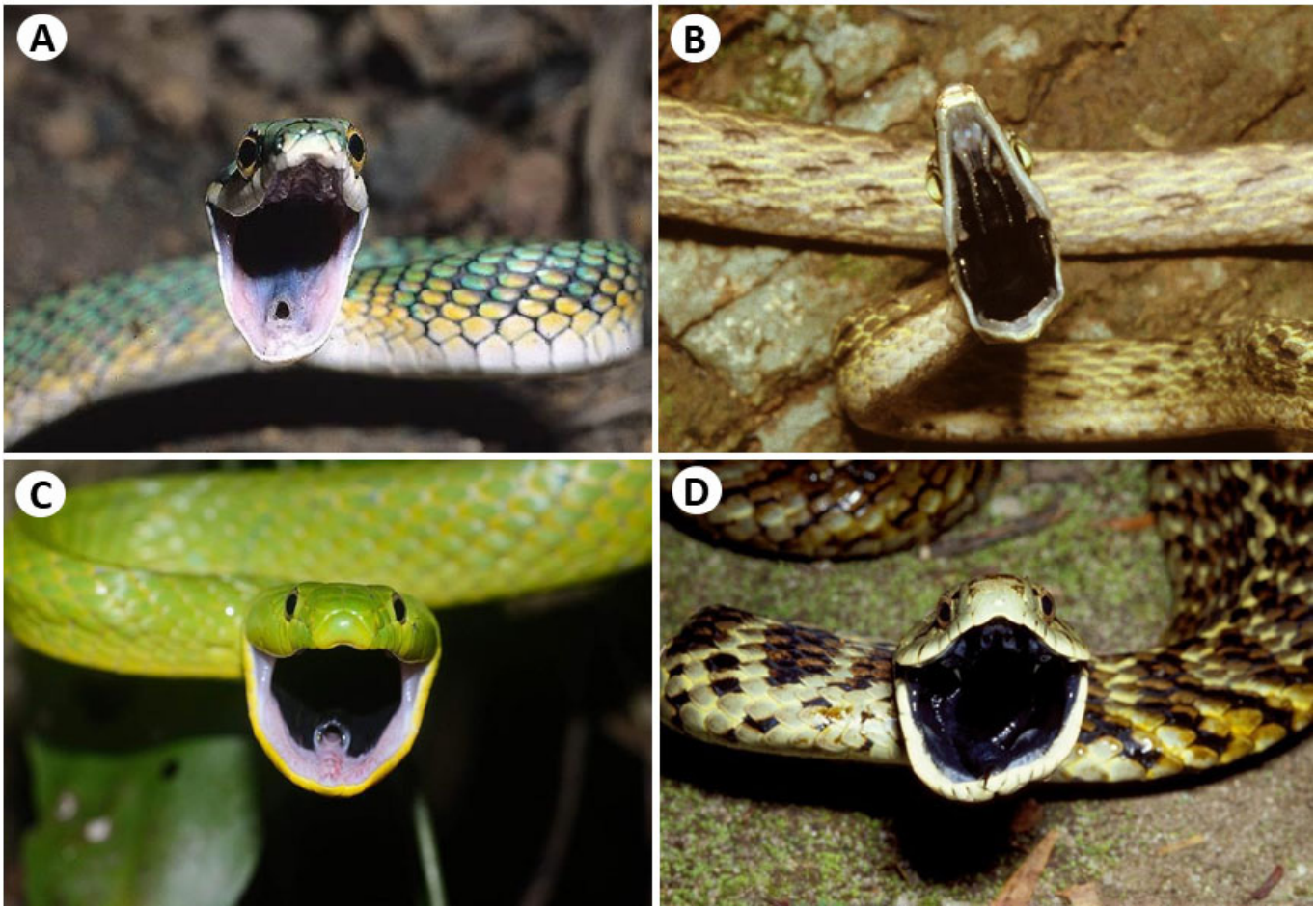

Figure 1. Dark mouth gaping and S-shaped posture recorded for - **A.** *Leptophis ahaetulla*, **B.** *Oxybelis aeneus*, **C.** *Chlorosoma laticeps*, and **D.** *Tomodon dorsatus*

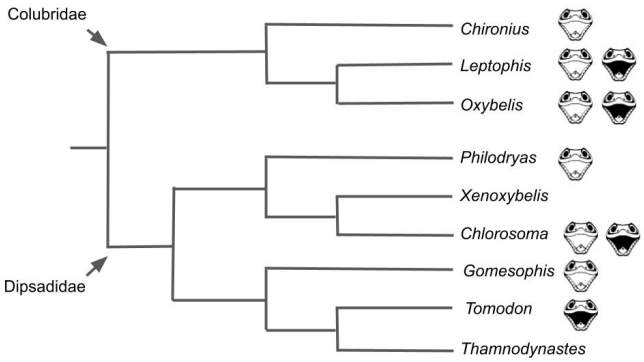

Figure 2. Simplified phylogenetic tree showing the position of the genera in which mouth gaping is recorded including those with light and dark mouth lining. Constructed trees based on phylogenies published in Zaher et al. (2009), Grazziotin et al. (2012), Jadin et al. (2014, 2019), Klaczko et al. (2014), Montigelli et al. (2019), and Albuquerque et al. (2022).

display lateral compression of the body, S-coil posture and mouth gaping (Marques et al., 1999, this study) but only *C. laticeps* has a dark oral mucosa. Thus, dark mucosa appears to be a derived condition in *C. laticeps*, as it is absent in other *Chlorosoma* and all related *Philodryas* and *Xenoxybelis* species (Zaher et al., 2008; Arredondo et al., 2020).

Tomodon dorsatus, which belongs in the Tachymenini, shares the dark oral mucosa and gaping display with other congeners (Harvey & Muñoz, 2004) and *Calamodontophis*, apparently a sister genus (Franco et al., 2006). The other two related genera in the Tachymenini, *Gomesophis* and *Thamnodynastes*, have light oral mucosa and at least the first displays mouth gaping (Menezes, 2017). Thus, the dark mouth lining and mouth gaping display appear to have arisen at least once (*Tomodon* + *Calamodontophis*) within this snake lineage.

The relationship between mouth gaping and dark oral mucosa is not restricted to these Neotropical species, as snakes from other lineages and other regions of the world gape with a dark mouth as well. Two unrelated examples are the North American rough green snake *Opheodrys aestiva* (Colubridae) and the African black mamba *Dendroaspis polylepis* (Elapidae) (Pitman, 1965; Walley & Plummer, 2000; Muller et al., 2012), which supports the suggestion that the black mouth lining is a feature that increases the warning signal of mouth gaping in snakes.

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