

The nucho-dorsal glands of Asian natricine snakes: Correlated evolution among diet, morphology, antipredator behavior, and defensive chemistry

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For animals with complex defensive systems, natural selection should favor morphological, ecological, behavioral, and physiological traits that function effectively together. A Japanese natricine snake, *Rhabdophis tigrinus*, possesses unusual defensive organs known as nuchal glands, which consist of a series of paired organs embedded under the skin of the neck. These glands contain bufadienolides, a group of cardiotoxic steroids, which are sequestered from the skin toxins of toads consumed as prey. To use these toxic chemicals effectively to deter predation, the snake performs peculiar antipredator displays, such as neck arch and neck butting. We investigated how these correlated traits -- the glands, antipredator behaviors, sequestered prey toxins, and diet -- have evolved. Sixteen snake species possess similar organs, which are collectively called as nucho-dorsal glands. According to classical taxonomy based on morphological characters, the nucho-dorsal glands are observed in three nominal genera. In two of those genera, glands are found in some species but not in others. Our molecular phylogenetic analysis revealed that secondarily loss of the glands has occurred at least once, and probably several times. Furthermore, it is likely that the distribution of the glands along the body (on only neck region or on the full length of the body) also exhibits homoplasy or reversal. In accordance with the loss or extension of the glands, unique antipredator displays also seem to have been lost or modified. A clade consisting of several species has shifted its primary prey from anurans (including toads) to earthworms. This dietary change seems to be related to changes in the chemical composition of the glandular fluid and possibly to the loss or extension of the glands. These results support the correlated evolution of related traits associated with the nucho-dorsal gland system.