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Review

The diversity and evolution of anuran skin peptides

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Amphibians exhibit various, characteristic adaptations related to their "incomplete" shift from the aquatic to the terrestrial habitat. In particular, the integument was subject to a number of specialized modifications during the evolution of these animals. In this review, we place special emphasis on endogenous host-defence skin peptides from the cuteanous granular glands anuran amphibians (frogs and toads). The overview on the two broad groups of neuroactive and antimicrobial peptides (AMPs) goes beyond a simple itemization in that we provide a new perspective into the evolution and function of anuran AMPs. Briefly, these cationic, amphipathic and α-helical peptides are traditionally viewed as being part of the innate immune system, protecting the moist skin against invading microorganisms through their cytolytic action. However, the complete record of anuran species investigated to date suggests that AMPs are distributed sporadically (i.e., non-universally) across Anura. Together with the intriguing observation that virtually all anurans known to produce neuropeptides in their granular glands also co-secrete cytolytic peptides, we call the traditional role for AMPs as being purely antimicrobial into question and present an alternative scenario. We hypothesize AMPs to assist neuroactive peptides in their antipredator role through their cytolytic action increasing the delivery of the latter to the endocrine and nervous system of the predator. Thus, AMPs are more accurately viewed as cytolysins and their contribution to the immune system is better regarded as an accessory benefit.

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"The amphibian skin may be regarded as an enormous storehouse of biogenic amines and active polypeptides. Indeed, no other vertebrate or invertebrate tissue can compare with amphibian cutaneous tissue in regard to variety and concentration of these active compounds."

Roseghini, Erspamer, Endean, 1976

Introduction

Extant amphibians (Lissamphibia) represent the modern descendants of the most ancient tetrapod group, where some well-known members of the amphibian stem group from the Devonian, such as *Ichthyostega*, present some of the first fossil records of terrestrial vertebrates [207]. With a distribution across all continents except Antarctica, lissamphibians are remarkably diverse. Despite the transition from the aquatic environment to a more hostile terrestrial life, lissamphibians have adapted to various habitats ranging from Arctic tundra to arid deserts, and to altitudes ranging from sea level to elevations of 5000 m [80]. Frogs and toads (Anura), in particular, cover the entire width of these habitats. A total of 7302 amphibian species have been described for the three monophyletic amphibian orders, with 88% of these being anurans (Fig. 1) [92].

The shift to terrestriality was associated with drastic changes, particularly many physiological challenges, including maintenance of water balance, readjustment of respiration in response to altered oxygen saturation, and higher fluctuations of the daily environmental temperature. Accordingly, lissamphibians show many characteristic evolutionary adaptations in their morphological and physiological traits, ones that have been conserved throughout the group. Thus, among the most important adaptations for lissamphibians involve those of the skin, which evolved numerous adaptive characters to overcome the radically modified environmental conditions and related physiological issues.

As the immediate interface with the environment, the skin needs to protect the animal from the harmful impacts stated above. Unlike other terrestrial vertebrates (Amniota), lissamphibians lack integumental structures to minimize water loss or facilitate thermoregulation (e.g., scales, feathers, or hair). Instead, the more permeable nature of the amphibian skin increases the risk of desiccation as well as the undesired influx of hostile constituents. Indeed, the latter constitutes a major, current threat with growing environmental pollution caused by human agriculture and industry leading to the recent worldwide phenomenon of amphibian decline. Nevertheless, the amphibian integument is an exquisitely adapted and highly specialized organ that supports physiological functions (e.g., respiration, osmoregulation, thermoregulation) as well as phenotypical color modification by means of chromatophores. The latter may be the result of antipredator adaptations that manifest themselves in different ways, ranging from the inconspicuous appearance of leaf litter frogs (mimicry) to the eye-catching aposemantic coloration signaling highly toxic animals (e.g., Dendrobatidae).

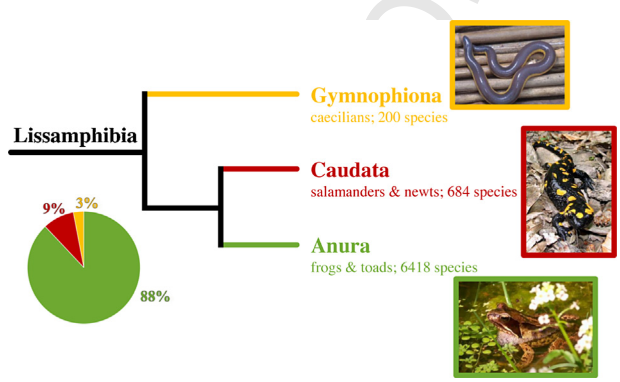

Fig. 1. The three orders of Lissamphibia with the number of species in each. Photos taken from www.amphibiaweb.org.

The amphibian skin is particularly characterized by its remarkable cutaneous exocrine apparatus with numerous granular (serous) and mucous glands [80,254]. These glands are dispersed largely at the dorsum of the animals and communicate directly with the external surface by means of secretory ducts. Whereas the mucous glands constitutively release discrete amounts of mucopolysaccharides to maintain the moist nature of the skin, the discharge of the granular secretions with their venomous and noxious compounds is inducible through various stimuli, one of which is stress (e.g., predatory attack). In addition, clusters of granular glands in exposed parts of the body with high concentrations of venom, called macroglands (e.g., parotoids and inguinal glands), have evolved in several species and reflect an improved defensive mechanism. Interestingly, there are growing indications about intra-individual variation of secretory products between the different granular gland types [120,144], observations that further underpin the remarkable plasticity and adaptive value of the cutaneous organ system in amphibians.

It has been hypothesized that the cutaneous glands of the first amphibians initially maintained homeostasis by producing and releasing key endogenous regulatory molecules as an adaptation to the new terrestrial environmental conditions (e.g., Na^{+}–K^{+} ATPase for sodium and water homeostasis) [73]. Various bioactive substances, such as biogenic amines and neuroactive peptides, which act as hormones, neurotransmitters and neuromodulators [17,83] are still being found in the skin of extant amphibians, particularly in anurans, and have counterparts that occur naturally in the central and peripheral nervous system as well as in the gastrointestinal tract of these animals and other vertebrates (e.g., serotonin, bradykinin). However, given that the amounts of anuran skin amines and peptides often exceed the effective, physiological threshold required for optimal functioning in a regulatory role, it was further hypothesized that the compounds were secondarily recruited for a dose-dependent chemical defence against potential predators [73]. This development, in turn, gave rise to a variety of venomous compounds that are stored in the specialized granular glands, also known as the poison glands.

Although the focus of this review is on the frog skin host-defence peptides, the chemical defence of amphibians goes beyond

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