Skin Derivatives in Vertebrate Ontogeny and Phylogeny

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Received June 24, 2008

Abstract—The skin of vertebrates has numerous and diverse derivatives, either located within the epithelial sheet itself (glands) or extending above its surface (teeth, scales, feathers, hairs, etc.). Many of them have a modular structure and constitute structural–functional units. Ontogenetically, all skin derivatives are of ectomesodermal origin, and their morphogenesis is subject to metabolic control, heterochronies (divergence in the timing of origination and development), and regulation by means of tissue interactions and molecular signaling via similar pathways. The diversification (origination of morphological diversity) of skin derivatives within the same morphological type is explained by the development of new generations of ectomesodermal structures separated by heterochronies and regulated by changes in the gradients of molecular signaling pathways under the influence of environmental factors. Evolutionary relationships between the majority of skin derivatives are obscure, except for teeth and glands associated with sensory organs that have evolved together with these organs. Apparently, many vertebrate skin derivatives (scales, feathers, hairs, and glands) originated as novelties at nodal stages of phylogeny and subsequently evolved convergently or in parallel.

DOI: 10.1134/S1062359009020101

INTRODUCTION

The problem of origination and diversification of skin derivatives in vertebrates is still a challenge to zoologists. The main difficulty in solving it is that, in contrast to the situation with other organ systems (musculoskeletal, nervous, excretory, etc.), it is hardly possible to trace evolutionary relationships between the derivatives characteristic of representatives of different classes. Moreover, numerous cases of parallelism and convergence make identification of the general trend of their evolution even more difficult. The discussion of the problem is accompanied by the advancement of numerous hypotheses and conjectures that cannot yet clarify the evolutionary scenario concerning the origination, morphogenesis, diversification, and homology or historical divergence of these structures. This is due to the scarcity of relevant paleontological, embryological, and comparative morphological data. Views on evolutionary transformations of skin derivatives based on their morphology are largely contradictory, since they are not supported by factual data on the initial and transitional forms of these derivatives, induction of their morphogenesis, differences in the biochemical composition of tentative homologous structures, etc. Many of them have the typical drawback noted by Matveev (1932): they are based on the analysis of morphological structures in a direct consecutive series of extant forms, but this approach does not allow their evolutionary relationships to be revealed, since comparisons are made not between ancestors and descendants but rather between definitive forms representing terminals of lateral branches of the phylogenetic tree.

Attempts to discuss the problem with regard to comparative morphological, biochemical, molecular biological, and tissue engineering data show that such a comprehensive approach holds much promise for solving it (Chuong and Homberger, 2003; Wu et al., 2004; Chernova, 2006, 2008a, 2008b; Fuchs, 2007).

This article deals with only a few aspects of the problem, with attention being paid to (1) skin derivatives as modular structures, (2) ways to resolve antagonism between the glandular and supporting functions of the skin, (3) morphogenesis of skin derivatives and heterochronies, (4) convergence and parallelism as trends in the evolution of skin derivatives, (5) hypotheses concerning evolutionary relationships between the skin derivatives, and (6) substantiation of the “generative concept” of the origination and diversification of skin derivatives. The analysis is based on the most recent results of research in comparative anatomy, developmental biology, molecular biology, and tissue engineering, as well as on our generalizations of empirical data and original long-term studies on the morphology of feathers, hairs, and glands in more than 100 bird species and 400 mammal species (Sokolov et al., 1988a, 1994; Sokolov and Chernova, 1994a, 1994b, 2001; Chernova, 1996, 2006, 2008a, 2008b; Chernova and Tselikova, 2004; Shabadash and Chernova, 2006; etc.).

The integument epithelium of chordates underwent major transformations in the course of phylogeny, changing from a monolayer sheet of uniform nonkeratinized cells capable of secretion (in Acrania and Tunicata) to a multilayer stratified epithelium, either nonkeratinized (in cyclostomes and fishes, with a few exceptions)
or keratinized partially (in amphibians) or completely (in amniotes). The skin is an exclusive evolutionary acquirement of vertebrates, and it should be discriminated from the integuments of other animals. The skin consists of two tissues differing in origin, namely, the epithelial and connective tissue layers separated by a basal membrane. The surface epidermis is of ectodermal origin, while the underlying derma is a mesodermal derivative developing on account of the somite dermatome. These layers exert reciprocal influences on each other when forming different derivatives during ontogeny. The emergence of vertebrates on land, the main historical event in their phylogeny, was reflected in the development of two basic types of the cover epithelium, essentially aquatic and terrestrial, with the transitional amphibiotic or ichthyoid type (Chernova, 2008b).

Skin derivatives are numerous and diverse. They can be divided into appendages, or structures extending above the skin surface, and glands, which lie within the skin. However, this division is obviously tentative. For example, hair and feather follicles lie in the dermal or even hypodermal layer, with only the keratinous shaft of these structures protruding outward. Glands lie within the skin but often have accompanying skin or keratinous protrusions. The same applies to keratinization. Scales, feathers, and hairs are keratinous structures, whereas glands are not keratinized. However, the follicles of feathers and hairs are not subject to keratinization and remain capable of regeneration, while the ducts of many glands are keratinized.

The presence of glands is a characteristic feature of the skin of vertebrates and chordates in general. Although the skin of reptiles and birds is traditionally considered nonglandular, it does contain specialized structures analogous to glands. Skin glands are capable of production and release of secretions synthesized by glandulocytes (glandular cells). They are conventionally separated into common glands (CGs) and specific glands (SGs), which differ in numbers, topography, structure, the composition and amount of secretion, and biological significance.

Some trends in the evolutionary development of integuments can be noted in the phylogeny of vertebrates. They are as follows: (1) gradual thickening of the cover epithelium and its differentiation into special cells, layers, and structures; (2) maintenance of similar structure and omnipotence of the germinative epidermal layer, which gives rise to all other skin structures, including glands; (3) similar differentiation of glandular structures into CGs and SGs in all vertebrate classes; (4) gradual improvement of morphophysiological coordination between the structure of the secretory gland region and the mode of its secretory activity; (5) multifunctionality of the skin cover and its glandular apparatus, with their different functions being in a dynamical equilibrium and offering examples of antagonism, substitution, or mutual complementation; (6) functional analogy between the glands of different vertebrates, which is due to their various morphological modifications; (7) specific features of skin morphology and functions acquired as adaptations to environmental conditions; and (8) the absence of evolutionary succession between skin glands that have evolved in different classes of Vertebrates.

Skin derivatives as modular structures. Skin derivatives may be considered in terms of methodological approaches aimed at systematizing data on the morphological diversity of structures in a complex organ, such as structural histology (Savostiyanov, 2005), the concept of structural–functional units (Khrushchev and Brodsky, 1961; Terskikh et al., 2003), or a theory of modular structure of the organisms and their organs (Marfenin, 1999; Notov, 1999; Savostiyanov, 2005). Feathers, nails, hairs, horns, as well as fish scales and animal epithelial tissues are classified as modular objects. The reason for identifying structural–functional units within an intricately functioning organ is that such an organ is always heterogeneous and the properties of its compartments may vary widely (but within limits of the norm), whereas the properties of its structural–functional unit are much more stable and different variations do not affect the principles of its organization (unless in pathological cases). For example, we consider that a structural–functional unit of a hepatoid SG is its individual lobe with a system of secretory ducts, accessory structures (the hair, hair funnel, and cistern in which the secretion accumulates and “matures”), and associated apocrine and sebaceous glands (together with the hepatoid SG, they form combined lobes and ducts). This complex provides for the synthesis, maturation, and release of the complete hepatoid gland secretion, supplementing it with additional protein or glycoprotein, lipids, and melanin.

The hair follicle complex is also an example of structural–functional unit. In addition to the follicle itself, it includes the connective tissue envelope, dermal papilla, glands, muscles, vessels, nerves, epidermal hair funnel, and hair shaft.

Glands also demonstrate the modular type of organization, which is known to pertain to systems with a modular structure, sustainable growth, and cyclic morphogenesis. Glandular fields may be classified as discrete modular objects, since they consist of CGs—equivalent, interchangeable elements showing relatively loose connections with one another. On the other hand, SGs consisting of indispensable, strongly interconnected elements and firmly integrated compact organs are examples of unitary objects.

Ways to resolve antagonism between the glandular and supporting functions of the skin. Skin keratinization accompanied by degeneration of epithelial cells (keratinocytes and corneocytes) and the secretory capacity of glandulocytes are in antagonism to each other. This antagonism can be resolved by means of (1) spatial segregation or (2) heterochronies of anlagen and their derivatives in the course of development or (3)