VI. THE COMPARATIVE ANATOMY OF THE SKIN AND THE EXOSKELETON

A. GENERAL CONSIDERATIONS ON THE SKELETON

The term *skeleton* includes all of the hardened portions of the bodies of animals. The skeleton of the invertebrates is commonly external, forming a hard covering inclosing the body, while that of the vertebrates is both external and internal. In invertebrates, further, the skeleton is a lifeless secretion, containing no cells, whereas the vertebrate skeleton is almost invariably cellular, either being composed entirely of hardened cells or consisting of cells and intercellular products. There are two distinct kinds of skeleton in vertebrates, different in origin and function: (1) the external skeleton, or *exoskeleton*, derived from the skin, and forming a covering and protective layer on the outside of the body; (2) the internal skeleton, or *endoskeleton*, derived chiefly from the inner wall of the epimere, and constituting a support and framework for the body and a place of attachment of the voluntary muscles.

B. THE STRUCTURE OF THE SKIN

Since the exoskeleton is derived from the skin, the structure of the skin must first be understood. The skin occurs only in vertebrates and may be defined as a surface covering easily separable from the underlying muscular layer of the body wall. Study of the development of the skin and of its microscopic structure (Fig. 18) reveals that it consists of two distinct parts: an outer layer, the *epidermis*, composed of *epithelial cells*, and derived from the *ectoderm* of the embryo; and an inner layer, the *dermis*, *corium*, or *cutis*, composed of *connective tissue* and formed from the mesenchyme of the *dermatome*, which in turn comes from the epimere (Fig. 16).

1. Conditions in the lower chordates.—In *Amphioxus* and the tunicates a skin is lacking. The surface is clothed with a one-layered epidermis similar to the embryonic ectoderm; this is underlain by connective tissue corresponding to the vertebrate dermis. An exoskeleton is lacking, but tunicates are inclosed in a "tunic" secreted by the epidermis. This is a thick gelatinous layer composed chiefly of cellulose and containing loose wandering cells.

2. The vertebrate skin.—The epidermis of vertebrates differs from that of all other animals. It is a *stratified* epithelium, composed of several to many layers of cells, produced by proliferation from the original single layer (Fig. 18). It usually contains *one-celled glands* (Fig. 19) or is invaginated into the dermis as *many-celled glands* (Fig. 18)—hollow or solid, flask-shaped or tubular bodies opening to the surface. The dermis characteristically consists of white, fibrous connective tissue of loose irregular or of dense parallel fibers.

3. The skin of aquatic vertebrates.—In aquatic vertebrates (cyclostomes, fishes, tailed amphibians) the relatively thin epidermis contains numerous mucous gland cells (Fig. 19), whose secretion keeps the skin moist and slimy; otherwise its cells are much alike throughout. The dermis usually presents a loose layer next to the epidermis and a compact layer below (Fig. 19).

4. The skin of land vertebrates, exemplified by the frog.—The secretion of mucus is, in general, an insufficient protection for land vertebrates. Instead, the outer layers of the epidermis undergo *keratinization*, i.e., flattening and hardening into a *horny* stratum (Fig. 18) which is shed continuously in small bits or at intervals as a whole (constituting a molt) and is replenished continuously by proliferation from below. Multicellular glands replace the unicellular glands of aquatic forms.

As an example of the skin of a land vertebrate, a cross-section of the frog's skin may be examined. Identify the following parts:

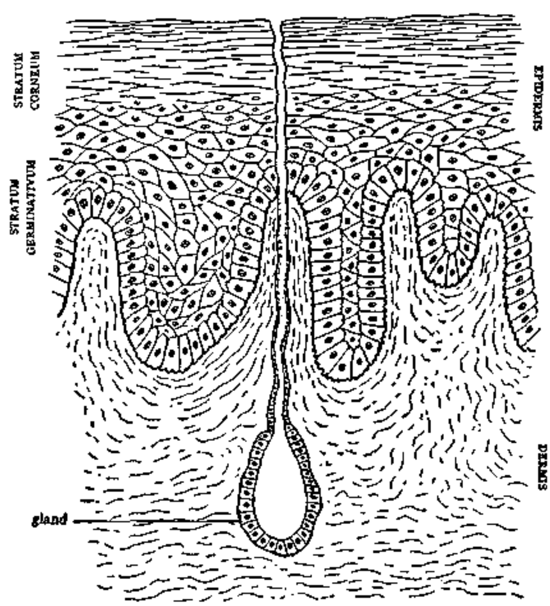

Fig. 18.—Diagrammatic cross-section through the amniote skin, based on mammals.

a) Epidermis: The outer part of the skin, the epidermis, consists of several layers of epithelial cells. The outermost layers are thin, flattened, and keratinized, i.e., converted into a dead, hard, horny material, protecting against drying. This keratinized stratum is termed the *stratum corneum*. Beneath the stratum corneum the cells gradually change from a flattened to a rounded and finally to a columnar shape. These lowermost layers of rounded to columnar cells constitute the *stratum germinativum* (also called *stratum mucosum*, *profundum*, and *malpighii*).[1] In the frog's skin these layers are not sharply demarcated. The lowermost or basal layer of the stratum germinativum, consisting of tall columnar cells, is the active portion of the epidermis and continuously proliferates cells which are pushed outward, become flat and horny, and finally form part of the stratum corneum, which thus is constantly renewed from below to compensate for surface shedding.

b) Dermis or corium: The dermis is the inner part of the skin, consisting of fibrous connective tissue (Fig. 19). In the frog and other lower vertebrates

[1] In many books only the lowermost row of cells is called stratum germinativum or malpighii, since this row is the active proliferating part of the epidermis. This, however, makes it necessary to invent some other name for the layers between this row and the stratum corneum. It seems best, to the author, to call the whole epidermis below the stratum corneum stratum germinativum; and, where necessary, the lowermost row can be called basal layer of the stratum germinativum.

the dermis next the epidermis consists of loose open connective tissue (*stratum laxum*) and deeper down of layers of dense, parallel, wavy fibers (*stratum compactum*). In addition to the connective tissue fibers the dermis contains: *pigment cells*, dark, irregular branching cells just beneath the epidermis; the *cutaneous glands*, flask-shaped bodies composed of epithelial cells and opening on the surface by a narrowed *neck;* and columns containing smooth muscle cells, blood vessels, and nerves, ascending through the dermis. Of these structures, the most conspicuous are the cutaneous glands, really parts of the stratum germinativum, invaginated into the loose portion of the dermis. They produce mucous and other protective secretions.

Draw a small portion of the skin to show the parts named above.

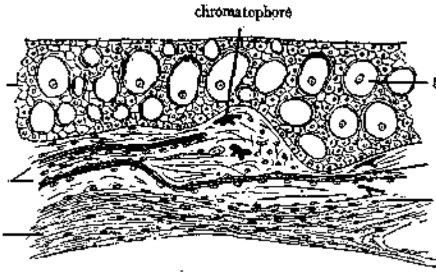

FIG. 19.—Section through the skin of a fish showing unicellular mucous glands in the epidermis (after Klaatsch, 1890). Note loose and compact strata of the dermis and location of scales in the former.

5. The amniote skin.—The amniote skin in correlation with land life has a well-developed stratum corneum, except in the cetaceans, where only a thin, imperfectly keratinized layer is present. Keratinization reaches its height in the reptiles, where among snakes and lizards the stratum corneum is shed *in toto* periodically as a *molt*, preceded by the formation of a new stratum corneum beneath. The skin of birds is notably thin and delicate. There is a paucity of cutaneous glands among reptiles and birds; the most constantly present type is the uropygial gland of birds, opening on a prominent papilla in front of the tail stump (p. 52). The thick skin of mammals has a deep stratum corneum, separated from the stratum germinativum by two thin layers—the transparent *stratum lucidum* and the granular *stratum granulosum.* The mammalian stratum germinativum is characterized by the scalloping of its under surface caused by dermal projections, called *papillae*, which carry blood vessels to the epidermis. The dermis of amniotes generally lacks distinct stratification into loose and compact layers. Leather consists of dermis which has undergone a tanning process.

The mammalian skin is particularly rich in number and types of glands except in Cetacea and Sirenia. Besides various kinds of glands localized in particular regions or limited to particular groups of mammals, there are generally present three types of cutaneous glands: *sebaceous, sweat,* and *mammary* or *milk* glands. The sebaceous or oil glands are solid epidermal ingrowths, usually but not necessarily associated with hair follicles, which secrete an oily substance for lubricating the skin and hairs and protecting against water.[2] The sweat glands are long, hollow tubular glands, usually more or less coiled, which secrete the sweat as a means

[2] The "pores" of the skin so frequently mentioned in advertisements of cosmetics are really the openings of the sebaceous glands; there are no pores through the skin.

of lowering body temperature. The mammary glands are histologically similar to sweat glands, and both are presumably derived from a common type of hollow tubular gland.[3]

The milk glands of monotremes form a pair of oval masses, each composed of numerous lobules, in turn made of branching tubular glands. Each lobule opens directly on the flat surface, in common with a hair follicle; and the numerous milk pores thus occupy paired, oval milk areas on the abdomen. Teats are lacking.[4] Among other mammals the number of milk glands is diminished, and they are clustered about elevations, the *nipples* or *teats*, of which up to twenty-five may be present. At the base of each teat the mammary glands, especially when swollen during lactation, may cause a rounded elevation, the *mamma* or *breast*. Although possibly there were originally in marsupials four rows of teats (producing median teats by fusion of members of the inner rows), the teats in all placental mammals are arranged in two longitudinal rows or derived from such by loss. Loss from different levels explains why the remaining teats may have any position on the ventral surface, as pectoral, abdominal, inguinal, etc. Reduction to a single pair of nipples is seen in man, horse, elephant, sheep, etc. Occurrence of extra nipples is probably a throwback to an ancestral condition. In embryology each row of nipples appears on a longitudinal elevated ridge termed the *milk ridge*, which can be regarded as derived by elongation of the oval milk areas of monotremes. In the milk ridge each nipple begins as an epidermal thickening (Fig. 20*A*) which sinks inward and proliferates the milk glands, and in some forms also sprouts evanescent hair follicles, hairs, and sebaceous glands (Fig. 20*C*), probably a reminiscence of the monotreme condition. In most placental mammals a papilla forms and everts as the nipple, forming an *eversion* type of nipple (Fig. 20*E*). In some mammals, however, notably the ungulates, the nipple arises chiefly by elevation of the adjacent skin, so-called *proliferation* nipples (Fig. 20*H*).[5] The human nipple is intermediate between these extremes.

The marsupial pouch of marsupials probably has no relation to the mammae or teats of placental mammals. It is lacking in the most primitive marsupials and therefore has evolved within the group. The work of Bresslau (1920) indicates that in higher marsupials each teat was sunk in a pocket and that the marsupium arose by fusion of these pockets.

6. Color.—Color in vertebrates is vested in the skin and is caused either by pigment or by structures capable of diffracting light. The pigment may occur as diffuse substance or as granules, or may be located in special branched cells, called *chromatophores*. Epidermal pigment is usually of the diffuse or granular type, whereas dermal pigment is nearly always inside chromatophores, which typically form a layer just beneath the epidermis. Chromatophores are of three general sorts: *melanophores*, containing *melanin*, a brown to black protein pigment; *xanthophores* or *lipophores*, containing yellow to red fatty pigment; and *guanophores* or *iridocytes*, filled with crystals of guanine, which reflect or refract light and produce white, silvery, metallic, or iridescent colors. The pigment can wander to various extents along the branches of the chromatophores or can aggregate into a central ball, so that various shades of color result. Chromatophores are characteristic of fishes, amphibians, and reptiles. The col-

[3] The view originating with Gegenbaur, and widely copied, that the milk glands of monotremes are modified sweat glands and those of other mammals are modified sebaceous glands is untenable; all mammary glands are of the sweat-gland type.

[4] Although it is commonly stated that the milk exudes upon the coarse hairs of the milk areas and is licked from these hairs by the young, it appears that no one has ever actually witnessed the manner of nursing of monotreme babies.

[5] The idea of true and false teats must be abandoned. The ungulate teat is not, as formerly supposed, formed wholly from adjacent skin and hence is not a false teat; as Fig. 20 shows, only its outer surface is so formed; the lumen is really the termination of the milk glands.

ors and color patterns of these groups result from fixed arrangements of the various kinds of chromatophores in definite locations. Thus the green color of frogs is caused by a blue diffraction of the guanophores seen through a layer of yellow xanthophores. Black spots represent aggregations of melanophores. Many of these forms exhibit striking color changes with reference to day and night, background, or physiological state. Such color change results from pigment migrations in the chromatophores, rearrangements of the chromatophores, and sometimes changes in the number of chromatophores, and is usually controlled by hormones mediated through the nervous system, although in some cases nerves may act directly to

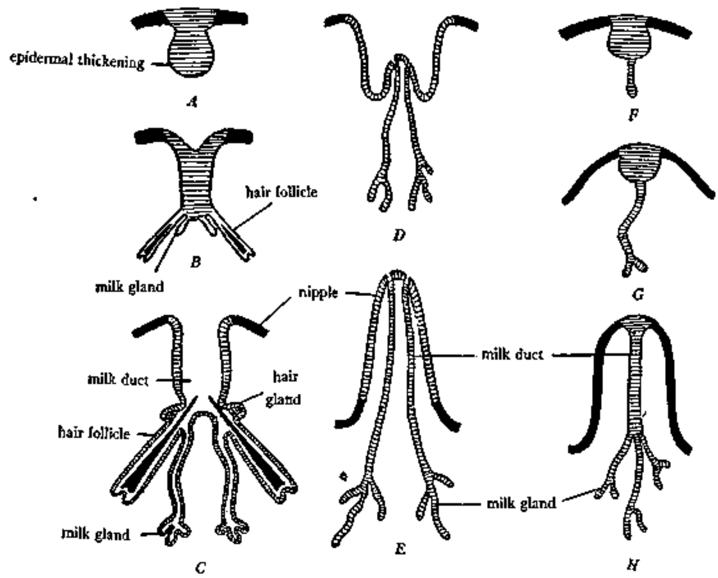

FIG. 20.—Types of mammalian nipples (based on Bresslau, 1920); derivatives of nipple primordium crosshatched, adjacent skin black. *A*, nipple primordium formed as epidermal ingrowth; *B*, primordium sprouting hair follicles and milk glands; *C*, primitive nipple, with hair follicles, milk glands, and sebaceous (hair) glands opening into milk duct; *D*, first stage in the formation of an eversion nipple (hair follicles and sebaceous glands have degenerated); *E*, eversion nipple complete, nipple formed wholly of epidermis of original primordium; *F*, early stage of ungulate nipple; *G*, later stage; *H*, final stage of ungulate nipple; the nipple is formed of adjacent skin, and its lumen is the milk duct, as in the case of other nipples.

disperse or concentrate the pigment granules. The colors of birds and mammals consist chiefly of diffuse or granular pigment in the feathers and hairs, which get them from pigment cells during development; but pigment also occurs in the epidermal cells, and dermal chromatophores may be present. The different skin colors of man are vested in epidermal pigment granules. Colors produced by physical means—e.g., diffraction of light by fine parallel striations—are not uncommon in feathers. Thus the iridescent blue or green wing patch (speculum) seen in the wings of male ducks is physically produced.

C. GENERAL REMARKS ON THE EXOSKELETON

The exoskeleton is derived from the skin by hardening processes in epidermis or dermis or both. Exoskeleton derived from the epidermis is spoken of as *epidermal;* it is produced by the activity of the stratum germinativum