Symmetry and Asymmetry of Configuration and Structure of Vertebrate Skin

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Abstract—The use of vertebrate skin in biosymmetrics, in particular, its configuration, thickness, and spatial structure of the dermal stroma is considered. The theories explaining the ordered arrangement and structure of skin as a result of morphogenesis (Turing, 1952; Gierer and Meinhardt, 1972; Belintsev, 1991) are reviewed. The study of quantitative aspects of bilateral symmetry is considered within the framework of (1) coefficients of symmetry and asymmetry, which provide estimates of symmetry; (2) extent of asymmetry of the curve of normal distribution (Gaussian curve), the inflection of which shows the mean of a sample. The use of these methods for statistical analysis is illustrated by particular examples.

INTRODUCTION

The phenomenon of symmetry and asymmetry forms one of fundamental problems of natural sciences, which is considered in all fields of sciences and engineering as a specific phenomenon connected with proportionality, ordering, similarity, and similar properties, providing integral perception of objects. Within the framework of biological sciences, these morphological categories have a dialectic character; they are typical of living matter at all organization levels. Their relationships provide not only harmonic forms of self-organizing systems, but also functional rationality, which frequently has an adaptive character. These patterns are investigated by biosymmetrics, which developed as a separate branch of scientific knowledge. It should be noted that, at present, biosymmetrics does not has a systematized set of examples of symmetry and asymmetry of vertebrate integument nor its derivatives. This emphasizes scientific novelty and practical significance of the present study, which provides biosymmetrics with particular examples in the field of zoological dermatology and shows an opportunity of application of certain general theoretical concepts as essentially universal.

When considering the symmetry of living things, it should be noted that it is of relative rather than absolute character, that is, respective parts of animals are not strictly identical in connection with topographical, species, age, geographical, physiological, and individual variation. In this respect, the identity of structures involved in comparisons should be taken as approximate. Note that the skin is an ectosomatic organ, which has the same symmetry types as the entire organism. Ectosomatic symmetry of the skin is manifested not only in "stiffened" symmetry of anatomy and histology, but also functional dynamic aspect, which is caused by adaptation to varying conditions (for example, molting in mammals or synchronization of replacement in the plumage of birds). Some knowledge in the field of skin symmetry are required in industrial activity (see below).

The purpose of the present study is to provide systematized data chosen in the field of symmetry and asymmetry of integument, which will serve in the further for theoretical judgements and generalization. The study is based on both original results and various published data required for the formation of integral insight in the resolution of our questions.

THEORIES EXPLAINING THE MORPHOGENESIS AND SYMMETRY OF INTEGUMENT AND ITS DERIVATIVES

To date, formalized models treating the morphogenesis of integument and its appendages and intended for understanding the basis of symmetrical arrangement of skin derivatives and ornamentation have been elaborated. It is known that the symmetry of skin and its derivatives is based on the mechanisms of self-organization of living systems, which have already undergone serious mathematical analysis. The symmetry of skin appendages results from the morphogenesis, which is based on (1) the reaction–diffusive model for the formation of biological patterns (Turing, 1952), (2) the activator–inhibitor model supplementing it (Gierer and Meinhardt, 1972), and (3) the

mechanochemical model of activity of epidermal cells (Belintsev, 1991).

The first model was presented by Turing (1952) in the fundamental paper *Chemical basis of morphogenesis:* spatial control of morphogenetic activity of cells is performed by molecular agents (morphogenes) and cell patterns are formed displaying the results and image of self-organizing chemical prepatterns (Belintsev, 1991). The model describes behavior of two substances which are designated *P* and *S; S* inhibits concentration of *P*. If *S* diffuses faster than *P,* in view of Turing's equation, concentration of *P* is described by a wavy curve with sharp peaks. The model predicts the areas of high and low concentration of a number of substances. At the point when concentration of certain substance exceeds a threshold, cells receive a signal to start directional differentiation. The model implies a compensatory character of activity of substances, which is observed in an increase in the amplitude of wave of one chemical substance combined with synchronous suppression of waves of the other (Gilbert, 1995). It is evident that, according to this model, activity of melanocytes producing melanin in the skin gives rise to regular color effects, such as stripes or spots. It has been established that stripes result from diverging waves and spots are evidence of disturbance in the autowave process, which result in the formation of domains in the shape of relatively loose mosaic (coloration of snakes and giraffe) or usual cluster structure with fuzzy boundaries. Monochromatic coloration is evidence of the absence of this process (Mazurov, 2008).

The Turing's model provided further success in mathematical reconstruction of morphogenesis. In particular, it is possible to explain specific patterns of coloration and surface skin layers by the second model (Gierer and Meinhardt, 1972; Meinhardt, 2008). The authors proposed that this model is based on the activator–inhibitor process, so that the activator initiates the formation of a certain derivative and the inhibitor hinders it, providing the alternating character of the development of skin appendages.

In the monograph *Physical Bases of Biological Morphogenesis,* Belintsev (1991) proposed mechanochemical treatment of the appearance of regular patterns of skin appendages, such as hair, glands, scales, and feathers. The author provided mathematical proof of mechanical interaction of the epidermis and dermis, which result in the appearance of regularly arranged skin appendages, in particular, a hexagonal grid of feather follicles. From this point of view, the integument is regarded as a model cellular layer, which is linked in each point with underlying elastic substrate; the presence of additional elastic connections influences the mechanical balance of the layer. According to the model of Gierer–Meinhardt, spaces between germs of skin derivatives, which are centers of morphological activation, are caused by the presence of inhibition fields interfering with the formation of epi-

dermal placode in the "sphere of influence" of these fields, which Belintsev explained by the presence of tangential tension (Belintsev, 1991).

At present, the models for skin derivatives are developed by means of computer graphics; computer simulation of macro- and micropatterns of skin with preassigned parameters are performed, introducing the elements of control of determined biosystems, which allow visual two- and three-dimensional reconstruction of the main morphogenetic stages, providing reliable recognition of the processes occurring at different stages pre- and postnatal ontogeny (Streit and Heidrich, 2002; Jiang et al., 2004).

SYMMETRY OF THE MAIN PARAMETERS OF INTEGUMENT

Integument configuration. The skin removed from an animal shows symmetrical arrangement of the right and left parts due to bilateral symmetry of the body. The extent of symmetry varies. In some cases, the skin outlines on the right and left sides are almost identical; in others, they distinctly differ possibly because of certain anatomical, physiological, and technological features (for example, because of different methods of skinning).

Skin thickness. Bilateral symmetry is manifested in quantitative characteristics of morphological properties. For example, the skin thickness in a particular topographic point of the right body side is approximately identical to that of the left side. This feature is of great physiological importance. (1) Elements of morphometric adaptation of a particular topographic site of the body, which performs certain function, are distinct and, hence, mirror reflection of physical properties has a similar function. This is true of the skin thickness, quantitative relationships of its layers, qualitative properties of the structure of the epidermis and collagenic stroma, which have characteristic arrangement of connective tissue elements in each topographic region. (2) Skins of some animals are used in tanning industry; raw materials are picked up to form parcels based on the skin thickness, which determines the production target of future leather. Skins are frequently subject to shabracking, that is, cut into particular topographical sites in view of known patterns of changes in physical properties of the skin (primarily its thickness), which then undergoes respective industrial processing.

Surface skin ornamentation. The papillary pattern (ornamentation of skin ridges on the volar and plantar surfaces and nasolabial planum) shows bilateral symmetry, chirality. Spirally twisted epidermal ridges are also observed on the scale of teleostean fishes (Dgebuadze and Chernova, 2009).

The significance of dermatoglyphics (and also prints of language of the person and a nasolabial plate of large horned livestock) for individual identification is well known (ornamentation differs even in monozy-

gotic twins) (Commins, 1946; Montagna, 1962). In humans, 40−60% of fingerprints are spirals or double loops (Gladkova, 1966). The same pattern may be observed on all digits. In digits of the left hand the spiral usually curves clockwise, while on the right hand, they curve predominantly counterclockwise. This example also displays bilateral asymmetry of patterns; in particular, in right-handed persons, whorls are more frequent on the right hand, while in lefthanders, on the left hand.

It is noteworthy that just symmetrically located structures determine the general habitus and species-specific traits, while asymmetry is characteristic of individual features. That is why, in criminalistics, facial composites are rarely felicitous, because they are strictly symmetrical, while individuality is most pronounced in the asymmetry of particular features; for example, it may well be that one eyebrow is raised, one mouth corner is lowered, the nose is crooked, one ear is somewhat protruding, etc., while their counterparts are not.

Merea is grain ornamentation on the skin surface deprived of epidermis, which is formed by both roughness of the dermal relief and skin derivatives (scales, scutes, osteoderms, feather and hair follicles, etc.) enclosed in the dermal layer. It is not only species-specific, but also provides leather with aesthetic properties in the case of industrial use of this rawstock. As the skin is curried after removal of the epidermis, the dermis surface remains rough, forming specific merea ornamentation. Merea usually forms a more or less symmetrical pattern on the skin due to certain arrangement of derivatives.

The merea of shark and teleostean skin shows bidimensional symmetry due to the arrangement of scales, which overlap each other imbricately, with the craniocaudally directed scale flows. The ray skin has granular structures covering the dorsal body region (Figs. 1a−1c); however, in the fin region, the skin merea is almost smooth and skin is thinner. In addition, the natural surface of skin may have light round spots. In some ray species, the center of the dorsal region has one largest bone grain symmetrical relative to the right and left body sides, which is used with effect in production activity (Figs. 1b, 1c). Merea skin of ganoid fishes (sturgeon, starred sturgeon, white sturgeon, etc.) has symmetrically positioned rows of rhombic bone scutes, the number of which depends on fish species. After currying, the merea of teleostean fishes looks like a regular grid formed of depressions of scale pouches.

The skin of toads is rich in glands scattered over the entire body. Therefore, its merea is rich in small chaotically arranged vesicular structures, only two of which (largest, flattened, lengthened oval) are in place of poisonous parotid glands, positioned symmetrically posterior to the eyes (Lyapustin and Fomenko, 2010). The entire set of vesicles forms a distinct circle in the dorsal region (Fig. 1d).
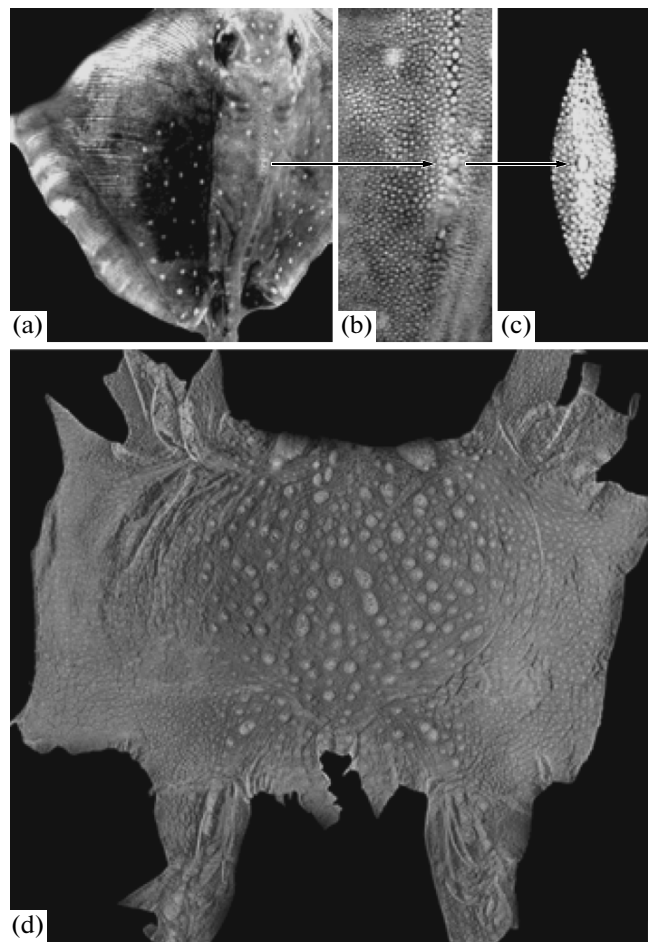

Fig. 1. Merea of a ray (a−c) and toad (d): (a) general appearance of the dorsal area, with granular surface; (b) the largest grain located just in the center of skin; (c) special character of finishing operations, emphasizing a grain on the leather; (d) distinct symmetrically positioned parotids.

In addition to horny scales, the skin of crocodiles has a new type of symmetrically positioned derivatives, osteoderms, which ossify in the course of postnatal ontogeny to form a protective skeleton on the dorsal body region.

The skin of snakes shows a bidimensional symmetry in the arrangement of regular horny scales, which sometimes had distinctive geometrical structures in particular topographical sites. Scales of the dorsal region usually form a hexagonal pattern (Figs. 2a, 2b).

The skin of birds is characterized by predominantly hexagonal (Figs. 2c, 2d), tetragonal, or chevron (wedge-shaped) arrangement of feather follicles, which form the skin merea. This arrangement is of great physiological importance, because it correlates with the character of innervation and attachment of antagonistic muscles, which provide high-grade flight in flying forms. The general arrangement of pterylae (feather tracts) and apteria on the avian body is species-specific character and bilaterally symmetrical. To
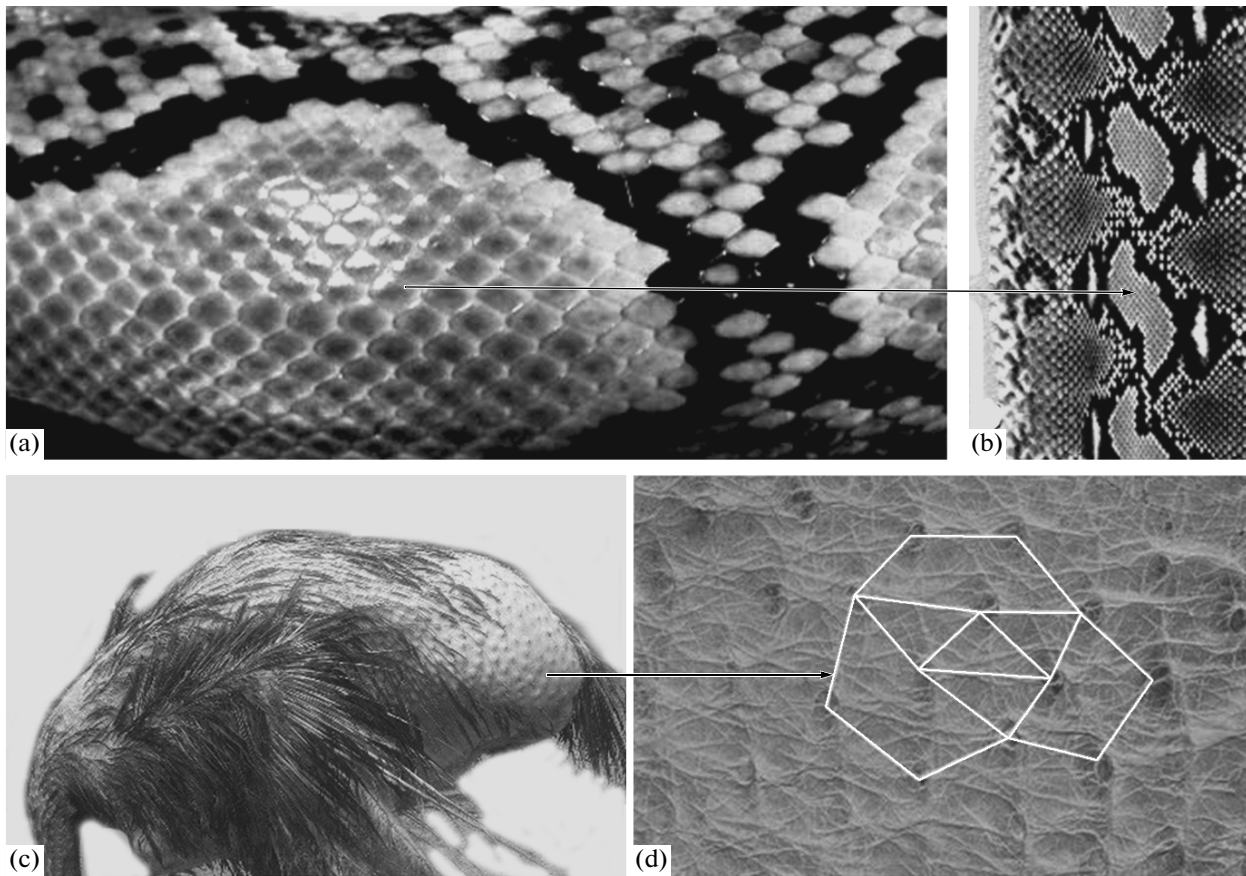
Fig. 2. Skin of the reticulated python (a, b) and African ostrich (c, d): (a) hexagonal pattern of scale arrangement; (b) merea of unstained leather; (c) naked site of female skin, with a distinct "diamond" zone with feather follicles; (d) leather merea, with white lines indicating hexagonal arrangement of feather follicles.

date, the formation of hexagonal grid has been investigated using the example of domestic chicken from the point of view of developmental biology (Gilbert, 1995). It has been established that the formation of strictly determined arrangement of feather follicles begins as early as days 5—6 of embryonic development, when accumulations of dermal cells are formed in certain sites of the dermal layer where feather germ will subsequently be formed. It has been shown that the points of accumulation arise in the shape of ordered tracts and feather rudiments appear almost simultaneously with the others. In neighboring tracts, the points of cell accumulation are displaced, providing the arrangement of the sites in staggered rows. The ectoderm has an effect on the position of mesenchyma accumulated in certain places and induces the formation of feathers (Gilbert, 1995).

Examples are provided by some other histological structures of birds with hexagonal arrangement. In particular, the study of fine architecture of green unfledged skin projections of *Philepitta castanea* (Eurylaimidae, Passeriformes), which is endemic to Madagascar Island, has shown that parallel collagen fibrils form a distinct hexagonal pattern in cross section (Prum and Torres, 2003).

The integument of mammals covered with hair is distinguished by more smoothed merea, which is only formed of uneven sites, depressions, and folds of natural ornamentation of the papillary dermis layer, which in distinctly seen by unaided eye in some species (for example, elephant).

SYMMETRY IN ARCHITECTONICS OF THE COLLAGENIC STROMA OF INTEGUMENT

The collagenic stroma of skin, which is morphologically composed of dermis, is a distinctly determined architecture of collagen fibers arranged in fascicles, suggesting the presence of certain elements of symmetry in the structure of the dermal layer. Histological study of architectonics of the collagenic stroma in different vertebrate classes is of certain interest; it provides an insight into structural patterns of interlacing fascicles of collagen fibers, which are connected with morphological symmetry.
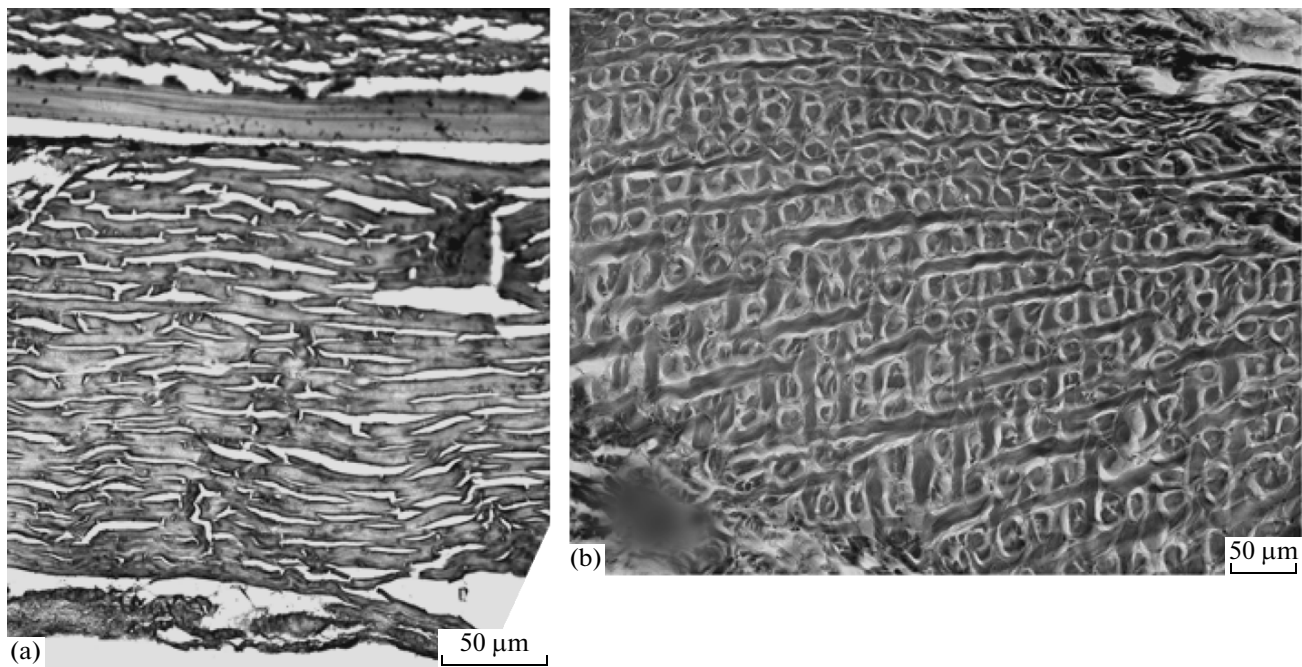
Fig. 3. Metameric structure of the collagenic stroma of integument: (a) rainbow trout, arcuate type of interlacing fascicles of collagen fibers of the stroma in the profound layer of the dermis, and (b) Java mouse deer, structure of the dermal layer of the sacrum in adult male. Sagittal sections. Staining according to Van Gizon. Microphotograph, ×400; 30.

Fishes. The fish skin has a strictly determined arrangement of fascicles of collagen fibers, which is required for locomotion. The superficial dermal layer is formed of a set of rather thin in parallel fascicles of collagen fibers, while the profound dermal layer, which plays an important biomechanical role, is more complex in structure. In the three-dimensional space, longitudinal fascicles of collagen fibers form a laminate structure of the dermis, which is added by thicker perpendicular fascicles of collagen fibers, which play a supporting role. Longitudinal fascicles of collagen fibers are wavy and horizontally oriented. Transverse sections (bidimensional space) show a special arcuate type of interlacing; combination of longitudinal and transverse fascicles of collagen fibers forms original segments in the shape of arches. This shape is caused by the treelike character of transverse fascicles; they are turned to the upper part of the profound dermal layer as a tree crown and collagen fibers extending along the roof of the profound dermal layer are connected to the neighboring "crown" of transverse fascicles. This dermal structure is only one variant of interlacing. Longitudinal and transverse fascicles of collagen fibers of the profound dermal layer are frequently beam-type in structure, so that their fascicles show an orthogonal folding. This type of interlacing is also characteristic of many teleostean species (Kiladze and Chernova, 2012). Both interlacing types periodically repeat within one histological section, suggesting metameric symmetry of architectonics of the collagenic stroma of fish skin (Fig. 3a).

Birds. In the three-dimensional space, the collagenic stroma in the skin of the African ostrich shows overlapping alternating longitudinal and transverse fascicles of collagen pierced by more massive perpendicular fascicles (Kiladze and Chernova, 2010).

Mammals. The collagenic stroma of mammal skin is formed by interlacing connective tissue components of different types, depending on the topographic site. In particular, the skin of cattle shows interlacing collagen fibers of three main types, rhomboid, looped, and horizontal wavy (Kaspar'yants et al., 1977). It is evident that the rhomboid type of fascicle interlacing is most regular and symmetrical; this allows the skin to resist a significant biomechanical load and provides high physicomechanical properties of skins in raw material and a semi-finished product. The looped type is distinguished by variously directed fascicles of collagen fibers, which form loop connection of fascicles due to branching and bends. The horizontal wavy type is divided into three subtypes, depending on the amplitude of fascicles folding according to the type of harmonic fluctuations: horizontal, normal, and vertical (Kaye, 1930).

The collagenic stroma of the dermal layer follows the patterns of rotatory and ornamental symmetry. For example, males of all age groups of the Java mouse-deer *Tragulus javanicus*, beginning from prenatal embryo, fascicles of collagen fibers in the skin of the sacrum are regularly arranged, crossing at a right angle to each other; this provides mechanical durability of this layer, which is necessary for dwelling in coarse

bush and combat (Fig. 3b) (Sokolov et al., 1994). In some other ungulates which fiercely struggle, with the head of a contender attacking the sacrum to establish the hierarchical status, the dermis shows the same structure (Sokolov, 1973). This universal three-dimensional principle of the construction of mechanically strong structures is also observed in other skin derivatives, for example, in thick skin of the African ostrich (Kiladze and Chernova, 2011) and the fibrillar layer of teleostean scales, in which fascicles of collagen fibers are positioned as in the layers of plywood (Dgebuadze and Chernova, 2009).

Both hips of horses have special oval skin sites, the middle layer of which is distinguished by a high density of architectonics of diagonally positioned fascicles of collagen fibers, which have a glassy aggregate state characteristic of cartilaginous tissue. In practical application, they are named "spiegel" (from the German mirror) (Kaspar'yants et al., 1977; Khludeev and Gordienko, 2008). Skins of boar and hog also have significant thickenings of the dermis due to cartilaginous outgrowths, which are positioned symmetrically in the scapular and shoulder regions (Khludeev, 1977).

Within the framework of structural histology, Savost'yanov (2005, 2012) has developed the concept of the spatial organization of epithelia, which involves the ides of an independent organization level of living matter, the histione as an intermediate link between cells and tissues. This theory treats the tissue is polymerization of particular modules, histiones. It is evident that the theoretical basis of this concept is expedient to apply to the collagenic stroma of the skin, which has a laminate−modular architectonics of folding connective tissue components. We believe that the recognition of efficient topological models reflecting structural organization of the dermis requires thorough empirical work based on extensive histological reconstructions. In the future, this information on the dermal stroma of vertebrates will serve for creation of a new classification of dermis architectonics.

Morphogenesis. It is possible to explain the regular arrangement of fascicles of collagen fibers in the skin by features of mechanical activity of cells during morphogenesis. This statement is corroborated experimentally. In the experiment, fibroblasts were initially attached to a thin rubber film and, taking off its surface within an individual cell, the film was simultaneously stretched within several centimeters around the cell (Harris et al., 1980, 1981). In tissue culture, active fibroblasts differentiate collagenic gel into clots of cells and compressions between them, with subsequent formation of directed cords of collagen fibers just in places of compression (Harris et al., 1984). It is evident that this morphogenetic mechanism explains the appearance of spatially regular patterns of the collagenic stroma of vertebrates.

STATISTICAL ESTIMATION OF SYMMETRY AND ASYMMETRY OF EMPIRICAL DISTRIBUTIONS OF MORPHOMETRIC PARAMETERS OF INTEGUMENT

In the theory of statistics, a technique for determination of symmetry and asymmetry of graphic interpretation of distribution of combined morphometric data is developed; in this respect, the estimate of asymmetry of normal distribution is most important.

The Gaussian curve, which reflects the essence of normal distribution, is a bell-shaped curve with one point of inflection, which reflects the mean value of a character. In this case, the mean value restored based on the point of inflection is the center of symmetry of the sample and the maximum and minimum values of the sample are approximately equidistant from the mean. At the same time, we rather frequently face the problem of estimation of asymmetry of a theoretical distribution; for this purpose, it is necessary to calculate the coefficient of asymmetry, which reflects the extent of remoteness of the mean value (peak in the Gaussian curve) from the modal interval. If the coefficient of asymmetry is equal to zero ($As = 0$), the Gaussian curve is absolutely symmetrical; however, this case rather rare. When dealing with a natural data set, it is usually possible to recognize either right-hand (positive in sign) or left-hand asymmetry (negative in sign). Right-hand asymmetry has a more flattened side in the right part relative to the center of distribution and, in the case of left-hand asymmetry, it is in the left part (Lakin, 1990). Asymmetry (As) is calculated as follows:

$$As = \frac{\mu_3}{\sigma^3} = \left. \frac{\sum_{i=1}^{k} f_i(x_i - \bar{x})^3}{n} \right/ \sigma^3,$$

where μ_3 is the central moment of the third order;

σ^3 is mean square deviation;

f_i is the number of variants (frequency), with $i = 1, ..., k$;

x_i is i-th variant, with $i = 1, ..., k$;

$\bar{x}$ is the mean of a parameter;

n is sample size (Lakin, 1990).

Let us illustrate this, using the distribution of the epidermis thickness in males and females of the African ostrich as an example. Thus, males show a significant right-hand asymmetry manifested in a rather sharp right displacement of the point of inflection of the curve (the mean thickness M = 79.7500 μm) relative to the modal interval (the mode of thickness Mo = 46.8750 μm). The coefficient of asymmetry $As = +1.6513$, that is, the prevalence of specimens of the left part of the sample; the "tail of the curve" (the term used by Rokitsky, 1973) extends to the right. Discussing the curve of the epidermis thickness in females, it
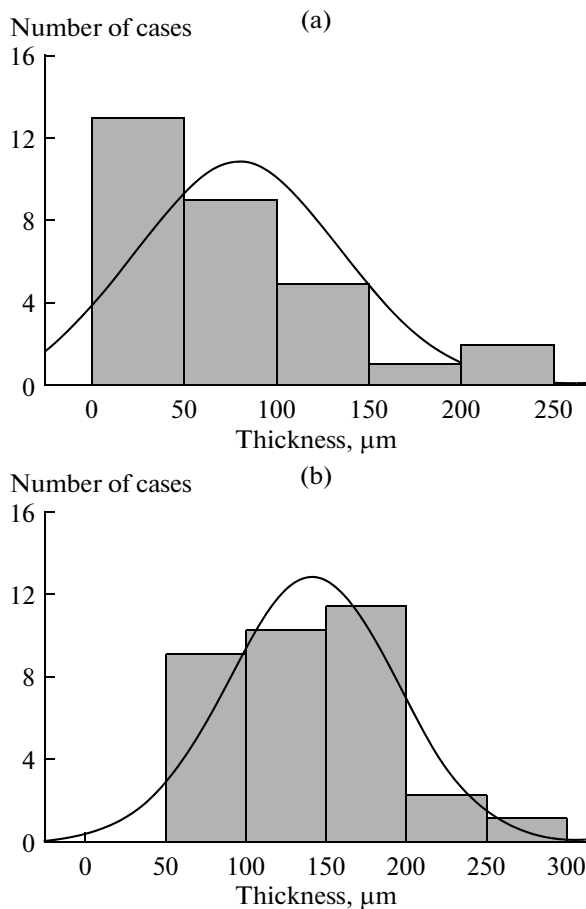
Fig. 4. Empirical distribution of the epidermis thickness of the neck in the African ostrich, combined with the curve of normal distribution: (a) males and (b) females ($n = 30$).

should be noted that they show a much more symmetrical distribution closer approaching the normal distribution (Fig. 4); in particular, the coefficient of asymmetry also shows a right-hand character, $As = +0.3251$, that is, less than 0.2 that of males. At the same time, the mode of the epidermis thickness $Mo = 187.5000$ μm and the mean $M = 143.5417$ μm, i.e., differ considerably.

Thus, statistical patterns manifested in the graphic form as the law of normal distribution are expedient to test for asymmetry to determine the shift of the curve center from the modal interval of the sample.

CONCLUSIONS

In summary, it should be noted that the problem of symmetry and asymmetry is, on the one hand, a subject of philosophy, which attracts attention of researchers in the field of synergetic approach, and, on the other hand, an object of research of fields of sciences that deal with particular forms of symmetry and asymmetry typical of the object in question. In the present study, we were intended to revise variants of skin symmetry.

We believe that the symmetry of integument coating animals is tightly connected with the body shape and the dominant type of symmetry characteristic of topography, contour, and physical properties of skin is bilateral symmetry, which means approximate identity of the right and left sides, reflecting the extent of asymmetry. The symmetry of merea is caused primarily by the arrangement of derivatives, which form a regular symmetrical pattern. It is established that the collagenic stroma is also adapted to habitats; at the same time, morphologically, the dermis of many vertebrates displays a regular pattern of interlacing fascicles of collagen fibers, which form symmetrical connective tissue structures. The study of quantitative aspects of bilateral symmetry is proposed to perform within the framework of coefficients of symmetry and asymmetry, which provide the estimates of symmetry of particular objects. Statistical estimation of symmetry within a sample is observed in the extent of asymmetry of the curve of normal distribution, whose point of inflection reflects the mean value of the sample. The theories explaining morphogenesis and symmetry of skin appendages (Turing, Gierer, Meinhardt, Belintsev) are considered. At present, these works are a subject of biomathematics and computer modeling.

We hope that the above data related to symmetry and asymmetry of vertebrate skin will give rise to wide discussions of results within the framework of biosymmetrics and will be useful for practical work of light industry.

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