EVIDENCE OF INHERENT SPONTANEOUS POLARIZATION IN THE METAZOAN INTEGUMENT EPITHELIA

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ABSTRACT The live integument epithelia of the metazoa have an inherent spontaneous polarization (an inherent permanent electric dipole moment) of corresponding direction perpendicular to the integument surface. The existence of the inherent polarization was proved by their temperature dependence, i.e., by the pyroelectric (PE) effect. Quantitative PE measurements were carried out on a number of integument epithelia of vertebrates and invertebrates (*a*) in vivo, (*b*) on fresh epidermis preparations, and (*c*) on dead, air-dried epidermis specimens of the same species. The demonstrated spontaneous polarization is not dependent on the living state and not caused by a potential difference between the outer and inner integument surface. Dead, dry epidermis samples (potential difference <0.01 mV) as well as dead, dry integument appendages (bristles, hairs), and dead cuticles (of arthropoda, annelida, nematoda) showed an inherent dipole moment of the same orientation as the live epidermis. The findings reveal a relationship between the direction (vector) of inherent spontaneous polarization and that of growth (morphogenesis) in the animal epidermis, their appendages, and cuticles. We conclude (*a*) that the inherent spontaneous polarization is present in live individual epithelial cells of the metazoan integument, and (*b*) that this physical property is related to the structural and functional cell polarity of integument epithelia and possibly of other epithelia.

INTRODUCTION

Previous experiments have shown the live insect integument (1) and the epidermis of live human skin (2) to have inherent spontaneous polarization (a permanent electric dipole moment) perpendicular to the outer integument surface. Inherent spontaneous polarization was also demonstrated in numerous tissues of man, animals, and plants (3, 4). The present work was undertaken to determine (*a*) whether this physical property obeys a natural law in the animal integument epithelia, and, if so, (*b*) whether this property may be expected in individual epithelial cells and could be related to their structural and functional cell polarity.

SPONTANEOUS POLARIZATION AND PYROELECTRIC BEHAVIOR

Prerequisites for spontaneous polarization in biological (as well as in nonbiological) materials are (*a*) the presence of a permanent electric dipole moment in the elementary components (e.g., molecules, structural unit cells), and (*b*) spontaneous parallel alignment of these dipole moments so that all positive dipole ends point in one direction and all negative ends in the opposite direction. Such a parallel alignment of elementary permanent dipole moments is termed "spontaneous polarization" in physics because it occurs spontaneously, that is, without the action of external fields or forces. In this state of the molecular order, the material concerned has a permanent electric dipole moment on the microscopic and macroscopic levels (5, 6).

Numerous chemical materials of the organisms, e.g., certain fiber proteins and lipids, have rodlike or prism-shaped molecules with a permanent electric dipole moment along their longitudinal molecular axis. In addition, many structures of organisms have a spontaneous parallel alignment of such rodlike or prism-shaped polar molecules. Thus, the necessary preconditions for spontaneous polarization do not only exist in pyroelectric (PE) crystals, PE ceramics, and PE polymers (like polyvinylidene fluoride, PVF_2), but also in certain structures of organisms (4).

The existence of inherent spontaneous polarization (an inherent permanent electric dipole moment) cannot be proved under static conditions because the bound charges on the surface can be compensated for by the flow of free charges within the polar material or in the surrounding medium; there is usually masking of the inherent polarization. The actual presence of the physical property can be proved quantitatively with the aid of the PE effect (5, 6), which is the change of the spontaneous polarization by a change of temperature. Structures of the organisms in which inherent spontaneous polarization is hidden thus show PE properties with suitable physical measuring methods.

Fast temperature change is generated most effectively by a rapidly changing light intensity absorbed in the body (Fig. 1). Light, of every possible wavelength that is absorbed in a body, produces heating, in the body and in

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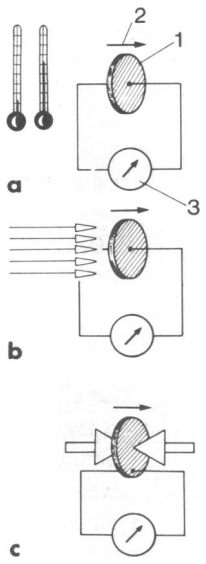

FIGURE 1 Pyroelectric (PE) and piezoelectric (PZE) measuring methods, shown schematically. *1* represents a PE sample (tourmaline disk) with its inherent polar axis (*2*). (*a*) If the sample is subject to a temperature change (heating or cooling), the flow of electric charges caused by the PE effect can be measured (*3*) as a current or a voltage response by means of a load resistance (not included in the figure). (*b*) The PE effect can be measured to a higher degree of accuracy if the temperature change occurs through absorption by the sample of a square radiation (light) pulse. This corresponds to the radiant heating method used in the present investigation. (*c*) The same specimen can also be used to demonstrate a PZE effect if subjected to a uniaxial pressure pulse, because all PE materials, without exception, also have PZE properties.

PE materials. This heating causes a change of its inherent spontaneous polarization, and thus a measurable PE effect. Red light or infrared (IR) light is mostly used to exclude additional photoelectric effects. Spontaneous polarization in biological structures and in nonbiological PE materials is present along an axis. In tissues, it occurs mostly along their physiological longitudinal axis, which frequently coincides with the direction of growth (4).

Quantitatively, the PE effect can be measured by the current generated in an external circuit of low electrical impedance compared to the sample itself. It is significant that the size of the PE effect does not correspond to the absolute temperature change (e.g., in degrees centigrade), but to the rapidity with which the temperature change takes effect, i.e., it is dependent on the factor dT/dt (T = temperature, t = time). The quicker the heating or cooling take effect, the greater is the effect (5, 6).

The PE current response produces a characteristic voltage/time behavior for the voltage across the external load resulting from its dependence on the factor dT/dt (Fig. 2). Moreover, it is significant that the PE effect is polar; on inversion of the specimen between the electrodes, the electric sign of the PE signal is inverted (Fig. 2 *c*), in contrast to photoelectric or thermoelectric signals, which do not change their sign on inversion of the specimen (Figs. 2 *a, b*).

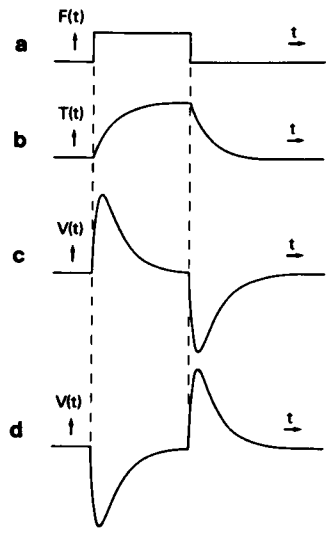

FIGURE 2 Voltage/timecourse of (*a*) a photoelectric signal (photodiode), (*b*) a thermoelectric signal (thermocouple), and (*c*) a PE signal (tourmaline disk). Traces of transient recorder; experimental apparatus (see Fig. 4). The PE voltage response depends on dT/dt (T, temperature; t, time) and changes its electric sign (*c, d*) if the PE sample is inverted between its measuring electrodes. This change of sign is caused by the inherent polar texture of PE materials and is one of the distinctive features of a PE response.

MATERIALS AND METHODS

Materials and Preparation

Table I provides a list of the animals investigated and measurements performed.

In Vivo Investigations. The measurements were carried out in a Faraday cage. A measuring electrode and a reference electrode were applied to the integument surface. Both electrodes (area, 10 mm^2) consisted of 5 μl water-suspended colloidal graphite held in place with adhesive rings (1). The graphite layer (thickness, ~30 μm) dried within a few minutes. The electrodes were connected using fine wires glued to the graphite surface with silver paste. For the in vivo measurements, we used the radiant heating method.

Preparation. Vertebrate skin specimens (area, ~2 cm^2) were prepared from (*a*) intact skin (epidermis plus corium), and (*b*) thin epidermal or corium layers (thickness, 40–95 μm). Invertebrate integument specimens (area, ~2 cm^2) had a thickness of 50–120 μm. The specimens were attached with their inner (or outer) surfaces to the grounded electrode in a shielded sample chamber (Fig. 3). The front electrode was identical to that used for the in vivo measurements. Fresh specimens were examined within 1 h after the start of their preparation. The PE measurements on integument specimens were carried out using the radiant and dielectric heating methods. Some samples of the investigated species were kept for 3 mo in the open air (20°C, 40–55% atmospheric moisture) for the measurements to be repeated in a dead, air-dried condition.

Pyroelectric Methods. A number of measuring methods have been developed for demonstrating the presence or absence of PE effect, two of which were used in the present investigation.

Radiant Heating Method. The principle of this method is shown in Fig. 1 *b*. A light pulse absorbed in the sample causes a rise in

TABLE I
INVESTIGATED ANIMALS AND CONDUCTED PE MEASUREMENTS

Genus species	Order	PE measurements		
		In vivo	Fresh preparations	Dead, dry specimens
Vertebrata				
Mus musculus (albino naked mouse)	Mammalia	+	+	+
Gallus domesticus (chicken)	Aves	+	+	+
Lacerta agilis (lizard)	Reptilia	+	+	+
Rana esculenta (frog)	Amphibia	+	+	+
Anguilla anguilla (eel)	Teleostei	+	+	+
Invertebrata				
Periplaneta americana (cockroach)	Arthropoda	+	+	+
Astacus astacus (crayfish)	Arthropoda	+	+	+
Lumbricus terrestris (earworm)	Annelida	—	+	+
Unio pictorum (painter's mussel)	Mollusca	—	+	—
Helix pomatia (edible snail)	Mollusca	—	+	—
Ascaris lumbricoides (mawworm)	Nematoda	—	+	+

temperature, T, of the sample and changes the sample's inherent polarization, if a polar material is present. This causes a voltage response of PE character (Fig. 2 *c*). A diagram of the complete experimental apparatus is given in Fig. 4.

A xenon lamp (450 W) was used as the light source. The light intensity, F_o, was measured for each row of trials using a PE radiometer (Laser Precision model RK-5100; Laser Precision Corp., Utica, NY), covering the wavelength range 250–1,600 nm. The light intensity reaching the sample was ~2 W/cm^2. The necessary square form of the radiation signal was obtained by using a rotating disk containing various cutouts, together with an electronic photoshutter (Prontor, Wildbad, West Germany). The purpose of the disk was to ensure that the rise time of the light impulses was as small as possible. For each voltage curve, $V(t)$, drawn with an oscilloscope (Tektronix 5103 N; Tektronix, Inc., Beaverton, OR) or a digital transient recorder (Nicolet Explorer III; Nicolet Instrument Corp., Madison, WI), the following parameters were determined: initial slope k of the PE voltage response; peak voltage, V_p; electrical time constant, τ_e; thermal time constant, τ_T. The output of the transient recorder was fed to an XY-recorder for easier quantitative evaluation on paper. The PE nature of the voltage responses was established by using the analysis of Simhony and Shaulov (8–10). Care was taken to avoid experimental errors. Photoelectric effects were excluded by an edge filter RG 695 (Jenaer Glaswerke Schott and Gen., Mainz, West Germany) in the course of the light beam, which suppressed wavelengths shorter than 695 nm. Thermal, non-PE effects were largely eliminated by short heating times (mostly 1 to 50 ms). Nonuniform heating effects could be diminished by using very thin samples. For further details see References 10, 1.

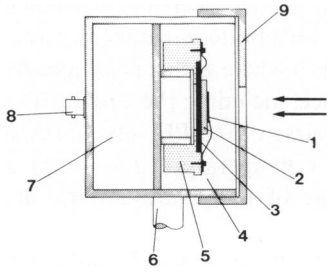

FIGURE 3 Sample chamber. *1*, Radiation receiving electrode; *2*, sample (e.g., skin preparation); *3*, gilded copper disk (grounded electrode, heat sink); *4*, front part of chamber; *5*, Teflon sample holder containing grounded electrode; *6*, tripod; *7*, rear part of chamber containing preamplifier with output (*8*); *9*, lid with window.

Dielectric Heating Method. A modified version of the method for determining the PE coefficient (11) was used for additional measurements on integument preparations. Electroded specimens were applied to the ground electrode (3, in Fig. 3) of the sample holder and heated for a short period (100–500 ms) by applying radio-frequency pulses (10–20 MHz; 50–100 mV). Polar materials (e.g., the synthetic PE polymer polyvinylidene fluoride, PVF_2, [12]) investigated with this method showed voltage responses with a characteristic PE voltage/

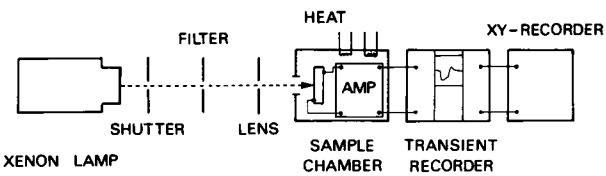

FIGURE 4 Experimental apparatus of the radiant heating method (Fig. 1 *b*).

timecourse. When the polar sample was inverted between the measuring electrodes, the electric sign of the voltage responses changed. This method volume heats the sample, largely eliminating heat gradients within the sample and thus the tertiary PE effect.

RESULTS

Evidence for PE Behavior of Live Metazoan Integument Epithelia

The investigated species of the vertebrates and invertebrates (altogether more than 3,000 PE measurements) showed, without exception, analogous PE properties of their integument epithelia. The outer integument surface of vertebrates and invertebrates responded to rapid changes of temperature with measurable voltage signals (Figs. 5–7). The electric sign of the voltage responses of the outer surface was negative on heating and positive on cooling.

The in vivo measurements have shown differences of the peak voltage V_p (8–10) of the integument responses between individuals of the same species and also between different integument areas for the same individual. But there were no fundamental differences in the physical characteristics of vertebrates and invertebrates (Figs. 5–7). The epidermis of live human skin (2) was no exception compared with the other vertebrates. The PE behavior of the metazoan integument epithelia thus conforms with a natural law. With the inner surface of the integument epithelia (integument preparations), the electrical signs of the voltage responses to thermal stimuli were opposite to those of the outer surface. Thus the integument epithelia (epidermis) are polar.

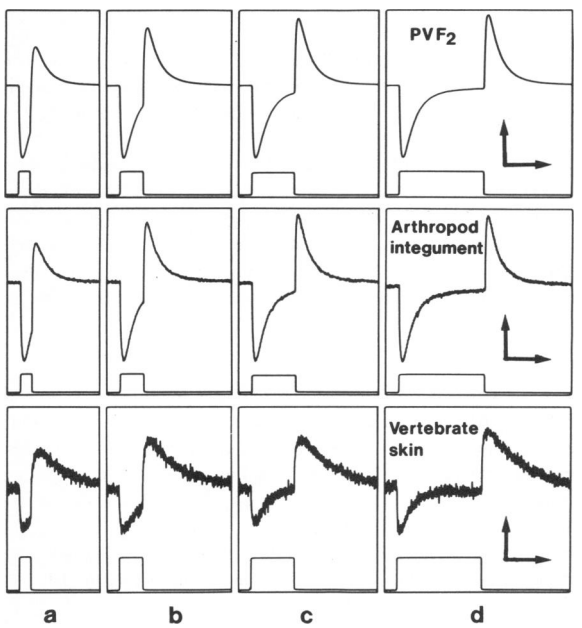

FIGURE 5 PE voltage responses to square light pulses (radiant heating method) of (*a*) 60 ms, (*b*) 120 ms, (*c*) 250 ms, and (*d*) 500 ms duration. PVF_2 = polyvinylidene fluoride, vert. 200 mV/div; arthropod (cockroach) integument specimen, vert. 25 mV/div; vertebrate (mouse) skin specimen, vert. 1 mV/div. Upper trace, PE responses (trace of transient recorder) lower trace, photodiode signals of the absorbed radiation. The negative slope of the PE signals corresponds to an increase of temperature. Integument samples, PE signals of the outer surface. The analogous voltage/timecourses of the PE responses of a nonbiological polar material (PVF_2) and of animal skin are shown.

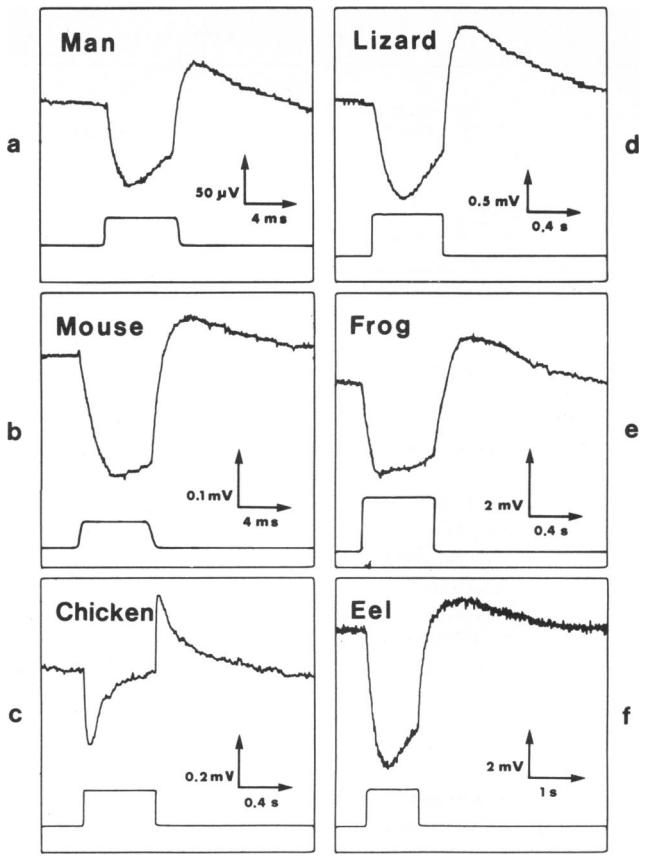

FIGURE 6 PE voltage responses of the epidermis of different vertebrates. In vivo measurements were taken using the radiant heating method. The upper trace shows epidermis response (trace of transient recorder); the lower trace shows photodiode signal of absorbed light pulse. The negative slope of the PE responses corresponds to an increase of temperature. Measuring values are indicated.

In the vertebrate skin the polar properties were localized in the epidermis; the polar axis was oriented perpendicular to the integument surface. The corium of the vertebrate skin showed no polar properties perpendicular to the skin surface. The invertebrate integument, having no corium at all, was polar as a whole with a polar axis from the outer to the inner surface, including the cuticle, if one existed. The voltage/timecourse of the PE voltage responses depended on dT/dt (T = temperature, t = time) and not on the absolute change of temperature (e.g., in degrees centigrade).

Additional proof of the PE nature of the voltage responses was as follows: interference filter measurements (see 1, 2) showed that the effects were independent of the wavelength of light, but were linearly dependent on the absorbed light intensity, F_o, controlled by a PE radiometer. Thus the effect was thermal (PE) and not a photo effect.

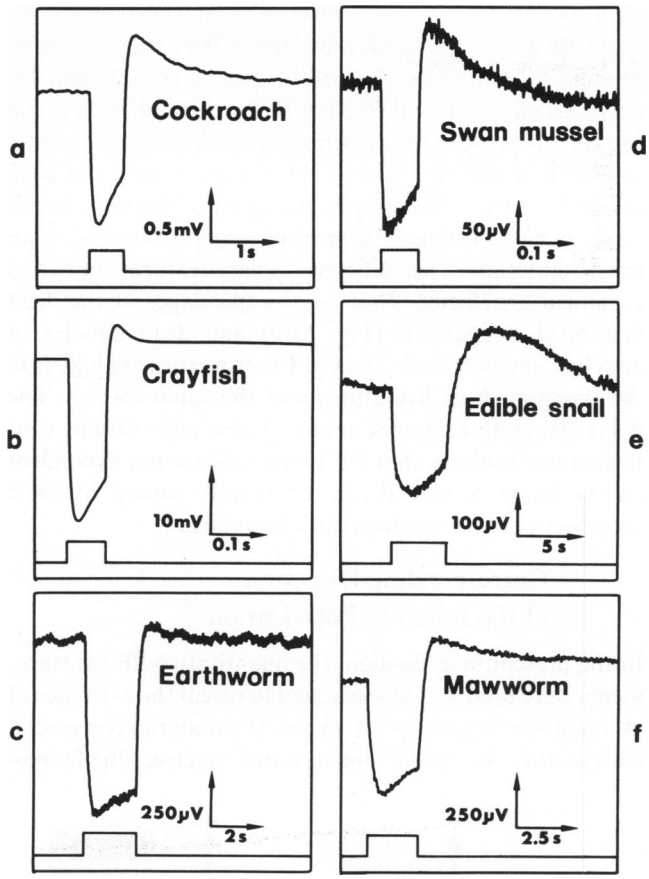

FIGURE 7 PE voltage responses of the integument of different invertebrates. Measurements were taken on fresh preparations using the radiant heating method. The upper trace shows skin response (outer surface); the lower trace shows photodiode signal of absorbed light pulse. The negative slope of the PE responses correspond to an increase of temperature. Measuring values are indicated.

Edge filter measurements (although not as conclusive as interference filter measurements) attested the PE nature of the voltage responses (Fig. 8). The trace of the voltage response of integument epithelia to a single square radiation signal was in agreement with the points calculated for the course of a theoretical PE voltage response according to references 8–10 (see also 1, 2). The analogy of the voltage/timecourse of responses of (*a*) integument epithelia, and (*b*) nonbiological materials with known PE properties (like polyvinylidene fluoride, PVF_2) under the same experimental conditions was convincing (Fig. 5). Like all known PE materials, the integument epithelia of the metazoa examined in the present investigation showed pronounced piezoelectric (PZE) properties. The facts will be described in a separate paper dealing with the sensory functions of the metazoan integument epithelia.

PE Behavior of the Dead Metazoan Epidermis

The PE behavior of live integument epithelia and of fresh (almost live) integument preparations showed no essential

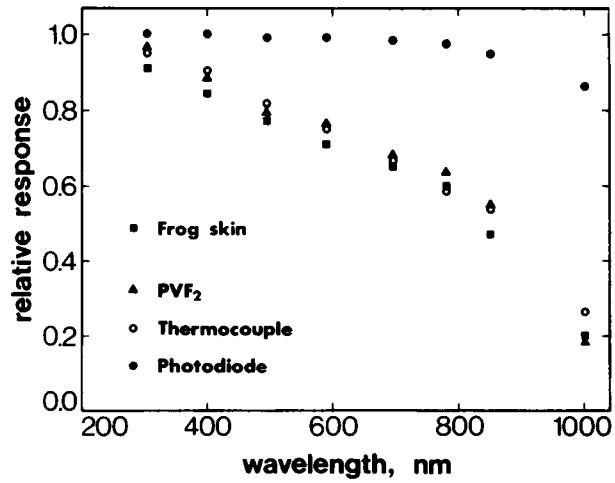

FIGURE 8 Edge filter measurements on frog skin. Measurements were taken on fresh preparations using the radiant heating method. The electrical response (relative to that with unfiltered light) for each material is plotted vs the 50% transmission points of the filters. The voltage responses of the skin correspond to those of the PE polymer polyvinylidene fluoride (PVF_2) and of a copper-constantan thermocouple and are different from those of the photodiode. The skin responses are caused by a temperature change (PE effect) and thus are not photoeffects.

differences; an inherent potential difference between the outer and inner epidermis surfaces was measurable (40–260 mV). In dead, air-dried (and more than three months old) integument specimens where the potential difference had decreased nearly to zero (<0.01 mV), pronounced PE (and PZE) properties were still measurable; the voltage/timecourse of the responses was analogous and the direc-

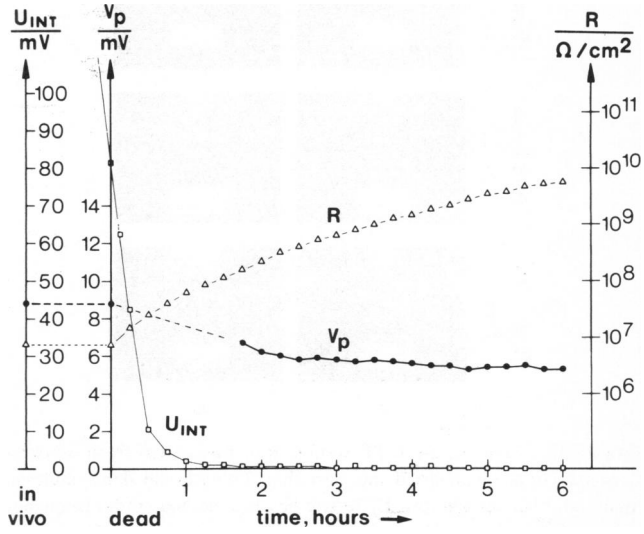

FIGURE 9 Comparative measurements of the PE voltage response and the potential difference in the integument of *Periplaneta americana* (cockroach) live and in dead, air-dried condition. The potential difference U_{int} (in vivo, 265 mV) drops after the animal's death (dead, 82 mV) and reaches 0 ~2 h later. The PE peak voltage value V_p (8–10) decreases slightly during the drying process of the integument, but remains constant afterwards, while the integument resistance, R, reaches a saturation value.

tion of the inherent polar axis had remained constant (Figs. 9, 10). During drying of the epidermis specimens, the PE peak voltage, V_p, slowly decreased, and in a few hours (or after several days) it reached a nearly constant value, which was measurable as long as the polar texture of the epidermis remained intact. The measurements have shown that the PE behavior is not dependent on the living state and is not caused by potential differences.

PE Behavior of Dead Epidermal Appendages and Cuticles

Keratin structures of the vertebrate integument (hair, feather, horn, bill, claw) were found to have PE properties with the direction of their inherent polar axis corresponding with that of the epidermis from which they had been produced. In all cases, the positive pole of the inherent PE polarization was found to point in the distal direction and the negative pole in the proximal direction (Fig. 11) (under condition of cooling). Keratin structures, which had been stored for several decades in zoological collections in the form of dried specimens, showed no major differences from fresh material. The inherent polar texture thus had remained unaffected. Epidermal appendages of the dead arthropod integument (Fig. 11 *g*) and dead cuticles of annelida and nematoda showed PE properties analogous to the integument of live animals of the same species. The polar structure remained intact. These observations confirmed our findings that PE properties are not dependent on the living state and are not mainly caused by ionic transport or other bioelectrical phenomena.

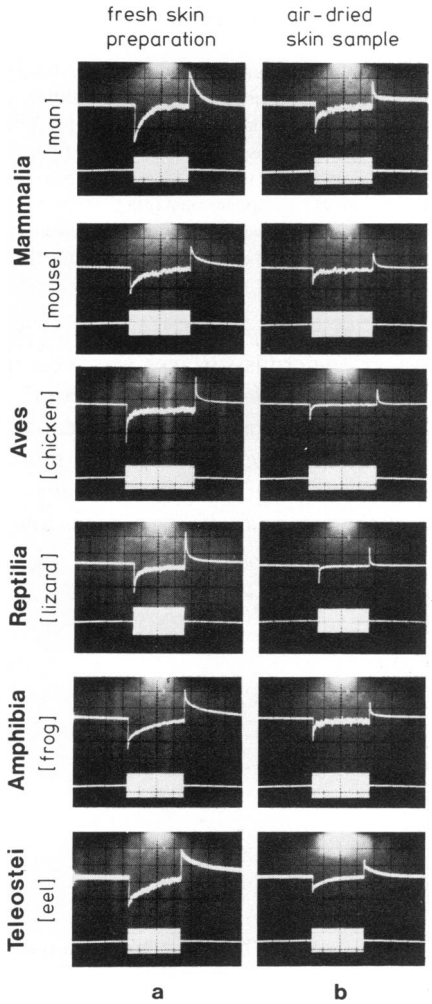

FIGURE 10 Comparison of PE voltage responses of (*a*) fresh preparations and (*b*) dead, air-dried and more than 3 months old skin samples of man and other vertebrates. Dielectric heating method (radio frequency pulses of 8 to 25 MHz and 280 to 500 ms duration). Qualitative measurements were taken. The upper beam shows skin responses (outer surface); the lower beam shows radio frequency signals. The potential difference of the fresh preparations was 65 to 240 mV; the potential difference of the dry samples was less than 0.01 mV. The examinations in (*a*) and (*b*) were carried out on the same sample of each individual. It is shown that dead, air-dried skin samples (potential difference near zero) retain PE properties, but the PE responses are smaller than in fresh preparations.

Corresponding Direction of the Inherent Polarization

In the present investigation, the quantitative PE measurements were used as a physical tool to reveal the existence of inherent spontaneous polarization. If a material possesses a temperature-dependent spontaneous electric dipole mo-

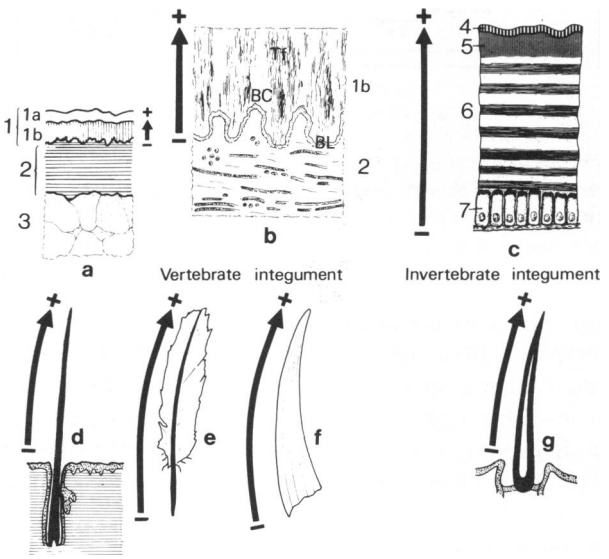

FIGURE 11 Relationship between inherent spontaneous polarization and morphological polarity in animal integument structures; drawn schematically. (*a, b*) Spontaneous polarization (arrows) of human epidermis. (*a*) General draft (×30); (*b*) enlarged details of the dermal-epidermal junction (×30,000); *1*, epidermis with stratum corneum (*1a*) and stratum germinativum (*1b*); *2*, dermis (corium); *3*, subcutis; *Tf*, keratin filaments (tonofilaments) oriented perpendicular to the dermal-epidermal junction; *BC*, basal cells (keratinocytes); *BL*, basal lamina. Arrows show the orientation of the polar axis of the epidermis (upon cooling). See, e.g., Figs. 4–9 and 4–14 in Ref. 19. (*c*) Spontaneous polarization (arrow) of insect integument (cockroach); *4*, cuticulin layer; *5*, inner epicuticle; *6*, procuticle; *7*, epidermal cells. (*d–f*) Appendages of vertebrate epidermis; (*d*) hair; (*e*) feather, (*f*) symbol for claw, horn, or bill; (*g*) appendage (bristle) of insect integument. The growth process invariably occurs with the positive pole of inherent polarization in front.

ment, it is pyroelectric. The orientation of the PE axis corresponded in the integument epithelia of the investigated metazoa (Figs. 5–7) under comparable experimental conditions. Therefore, the direction (the vector) of the inherent spontaneous polarization corresponded in the live epidermis of the investigated metazoa. Our additional measurements on the appendages and cuticles of the vertebrate and invertebrate skin have shown that these structures also have inherent spontaneous polarization of the same direction as the live metazoan integument epithelia, which produced them (Fig. 11).

DISCUSSION

Relationship Between Cell Polarity and Inherent Spontaneous Polarization

Individual epithelial cells are structurally and functionally polarized; an imaginary line passing through the centrosome (and possibly the Golgi apparatus) and the center of the nucleus defines the axis of cell polarity (13) (Fig. 12 *c*). Epithelian cell polarity is best recognized in simple epithelia; these consist of a single continuous layer of parallel oriented cells of the same type. Such simple epithelia are present in the integument of numerous invertebrates. Our measurements have shown that in the invertebrate integument (e.g., of the swan mussel, Fig. 7 *d*) there is spontaneous polarization perpendicular to the outer surface. We assume that individual cells of such invertebrate integument epithelia possess spontaneous polarization of the same direction as the invertebrate integument as a whole (Figs. 12 *b, c*). The axis of the inherent spontaneous polarization coincides with the imaginary axis of the structural/functional cell polarity.

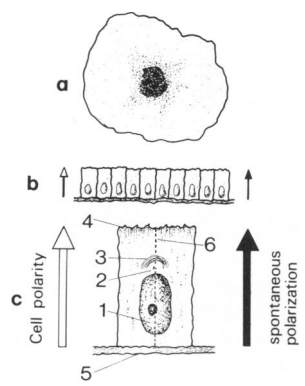

FIGURE 12 Directions of spontaneous polarization (dark arrows) and structural/functional cell polarity (white arrows) of integument epithelia; drawn schematically. (*a*) Single layer of a simple epithelium (cell culture); the direction of inherent polarization and cell polarity are perpendicular to the surface of the cell layer; (*b, c*) inherent spontaneous polarization and cell polarity of the single layer in (*a*) shown at different magnifications. *1*, Nucleus; *2*, centrosome; *3*, Golgi apparatus; *4*, free surface, *5*, basement membrane, *6*, imaginary line of polar cell axis passing through centrosome (and Golgi apparatus) and center of the nucleus.

The cell polarity is less obvious in stratified integument epithelia, especially in the vertebrate epidermis. We presume that the inherent spontaneous polarization of vertebrate epidermis is mostly localized in the basal cell layer and possibly in some of the suprabasal cell layers of the stratum germinativum. The keratin filaments in the basal cell layer (e.g., of human skin) perpendicular to the dermal-epidermal junction (Fig. 11 *b*) support this assumption, because keratin fibers have a strong dipole moment along their longitudinal axes (4, 14). We assume that not only epithelial cells with the function of protection possess inherent spontaneous polarization perpendicular to their free surface, but also those specialized for other physiological functions, in particular for sensory reception, secretion, and absorption. Further experiments using quantitative PE methods to clarify these questions are in preparation.

Relationship Between Direction of Growth and Direction of Inherent Spontaneous Polarization

The longitudinal growth of animal and plant structures investigated so far occurs toward the positive pole of their inherent spontaneous polarization (4). Irrespective of whether collagen, keratin, chitin, or plant structures were examined, the longitudinal growth invariably occurred with the positive pole in front (4).

Martin described PE behavior and a polar longitudinal axis of corresponding orientation in human and animal hair (14). These observations are confirmed by our measurements on the vertebrate and invertebrate integument and on their appendages (e.g., bristles, hairs). Toward the distal end (tip) of these structures, which is also the direction of growth, the electric charges were always positive, but always negative toward the basal end (under condition of cooling). The inherent spontaneous polarization of the vertebrate and invertebrate epidermis corresponds with the above observations. The outer epidermal surface (according to the direction of growth, the distal end) becomes positive and the inner surface (the basal end) becomes negative while cooling (Figs. 11 *b, c*). On a molecular level, these data can be explained by the fact that during the growth process linear structural elements with a permanent electric dipole moment along their longitudinal axis become oriented in such a way that the positive pole of their dipole moment points in the direction of growth.

Linear structural elements that occur in all organic cells and that play an important part in maintaining their structural polarity and in the polar division processes of cells (mitosis) are the microtubules. They were suspected of being the polar units mostly responsible for the polar direction of growth in organic structures (4). Recent investigations (e.g., 15–18) have shown that the microtubules are polar along their longitudinal axis, that a head-to-tail aggregation of polar subunits takes place, and that

their growth occurs only at the end oriented distally to their nucleation center. This fast-growing end is called the "plus end." We suggest (*a*) that the microtubules possess a permanent electric dipole moment along their longitudinal axis (like keratin or collagen molecules [4]), and (*b*) that the parallel aggregation of microtubules in individual cells of epithelia (and very possibly of other tissues) is related to their inherent spontaneous polarization and to their direction of growth.

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