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Helen T Ghiradella and Michael W Butler

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REVIEW

Many variations on a few themes: a broader look at development of iridescent scales (and feathers)

Helen T. Ghiradella[1,*] **and Michael W. Butler**[2]

[1] *Department of Biological Sciences, University at Albany, State University of New York,*
1400 Washington Avenue, Albany, NY 12222, USA
[2] *School of Life Sciences, Arizona State University, PO Box 874601, Tempe, AZ 85287, USA*

Iridescent structures are some of the most visually stunning phenomena in biological organisms. Insects and birds have in common the display of such colours in their non-living investiture, the scales and bristles in insects and the feathers in birds. The biological mechanisms underlying the formation of these structures, at least in insects, appear quite conservative in that the same architect, the eukaryotic cell, can produce not only the iridescent structure but, with some tweaking of the genome, other structures as well, a fact that may be of particular interest to materials scientists and industrial parties seeking to biomimic these forms. Here, we review two examples, one on the cellular and the other on the subcellular level of this developmental flexibility in insects. We then go on to review what is known about iridescent feather development in birds. We suggest that, in view of the increasing evidence that genes and pathways are conserved among taxa, the work on insects may perhaps suggest perspectives or directions of potential use in the study of birds.

Keywords: cuticle; development; feather; insect; iridescent structures; smooth endoplasmic reticulum

1. INTRODUCTION

Insects and birds are among the most conspicuously iridescent creatures and their colour-producing systems have long been studied (see Kinoshita & Yoshioka (2005*a*,*b*) for fine and detailed reviews of the optics of various biological and other iridescent systems). In insects, the same epidermal cell type that can under some conditions produce a scale or bristle (developmentally these are essentially the same structures) can, under other conditions, produce a line of other structures, including a mechanoreceptor bristle or even a *chordotonal organ*, the transducing element of an insect ear. On a subcellular level, the cell's smooth endoplasmic reticulum (SER) that appears to control the formation of some of the photonic reflectors in certain iridescent scales (*vide infra*) also controls within other cells a host of other cellular functions that may range from lipid assembly to some forms of bioluminescence. Given the increasing evidence for conservation of genes and developmental pathways among the taxa (Carroll *et al.* 2001), perhaps this concordance is not surprising, but we believe that this 'developmental flexibility' perspective is important in that it may imply possible applicability of scale developmental mechanisms to the study of feather development and, further, development of biomimetic and commercial replicates. Let us start with consideration of scale structure and development in insects.

2. STRUCTURAL COLOURS IN INSECTS

In order to mimic successfully biologically produced iridescent (and other) systems, we must know what we are dealing with. In this section, we consider the underlying architect of most, if not all, these complex, effective and beautiful systems in insects. This is the insect epidermal cell, and, in particular, one of its internal channel systems, the SER.

It is this cell that secretes the non-living *cuticle* that defines so much of insect biology. The cuticle is a polymeric construction that can be precisely tailored with respect to such material properties as chemical composition, fibril orientation and elastic properties (Neville 1993). It is highly likely that the great variety of iridescent (and other) structures we see in insects and elsewhere are manifestations of variations in a relatively few 'standard' developmental pathways within these

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*Author for correspondence (hghff@albany.edu).

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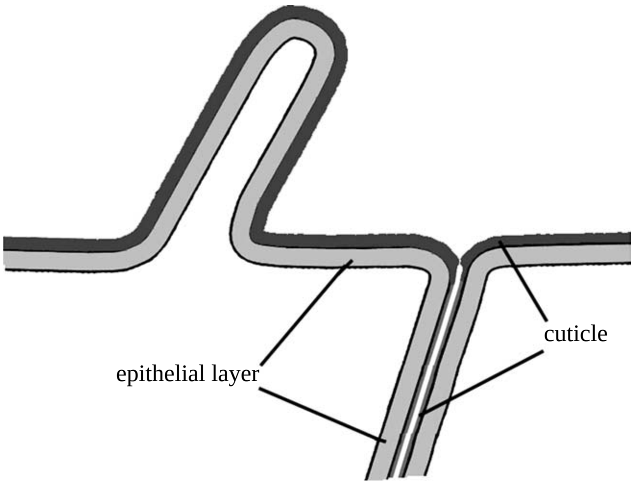

Figure 1. Abstracted view of a piece of an insect body wall. The epidermal layer and its associated cuticle may be thought of as a kind of body stocking that covers all topologically external surfaces: it may evaginate (left) to form wings, appendages or other external projections, or it may invaginate (right) to form the tracheal system, inner lining of the gut or of other geographically internal but topologically external surfaces.

cells. To illustrate the point, we consider just two of a host of possible examples. The first is the development of certain mechanoreceptors that are very different in form, but which, together with iridescent bristles and scales, all derive from the progeny of single epidermal cells. The second is on the subcellular level and involves the SER, which is apparently central to any of several different cellular processes (including the formation of some iridescent scale structures), depending on the specific cell and its function (*vide infra*; in the following discussion, we are letting the figure captions carry many of the structural details).

The insect body wall consists of a single layer of epidermal cells and their associated cuticle. It may be thought of as a 'body stocking' (figure 1) that lines all topologically external surfaces. Both external and internal structures may be quite complex in time as well as in space; during its lifetime, each epidermal cell may have to build a structure, control its function and then take it down and/or remodel it in preparation for a moult. And in addition to building cuticular structures, the epidermal cell may have to secrete wax, cement and/or glandular products (see Neville (1975) for a comprehensive review of the biology and chemistry of insect cuticle).

Figure 2 presents a diagrammatic view of a more or less standard section of cuticle, together with a few of the many modifications that may be associated with such. Figure 3 focuses on the external investiture, the scales and/or bristles, which are similarly variable in their structural capabilities. Any of the numerous parts of a standard scale or bristle may be modified to produce a structural colour or for other functions (Ghiradella 1998*a*). Scales and iridescent bristles are usually not innervated, but interestingly they are part of a cell lineage that may give rise to any of a host of sensor types: bristle mechanoreceptors (of which lepidopteran non-innervated scales and bristles may be considered simplified derivatives), stretch receptors, thermal receptors and sound receptors, in particular a group referred to as *chordotonal organs* (for reviews see Keil 1997, 1998; Held 2002; Lai & Orgogozo 2004; Yack 2004; Kernan 2007). Here, we will focus on two very different and yet closely related types, the mechanosensory bristle and the chordotonal organ.

The bristles are among the 'external' receptors that lie on or project above the cuticular surface, while the chordotonal organs, though homologous, have essentially sunk below the body wall. To form one of these systems, an epidermal cell gets a signal to transform into a *sense organ precursor* (SOP) cell. It then undergoes a series of stereotyped divisions (figure 4) whose progeny have well-defined roles in the resulting bristle or scale (see Held (2002) for a detailed review of the molecular events controlling the details of the process) or the chordotonal organ.

Figure 4 shows the SOP divisions and figure 5*a*–*c* the nature of the resulting progeny. One daughter cell divides further to produce the bristle- and socket-forming cells. The other divides to produce the sensory neuron, a sheath cell that secretes a sheath around the outer (ciliated) segment of the neuronal dendrite and possibly a glial or ligament or other cell. Figure 5*a* shows the cellular makeup of a typical bristle mechanoreceptor. Figure 5*b* shows a non-innervated bristle: in this case, only one of the two daughter cells from the first SOP division is likely to continue development and the structure has only the bristle and the socket.

Figure 5*c* shows diagrammatically an insect chordotonal organ. The defining characteristic is the *scolops*, a complex structure consisting of a cap and several connected rods (figure 6). The scolops is believed to stiffen or otherwise support the dendrite outer segment (DOS), presumably a requirement for effective transduction of the stimulus by the dendrite. The homology of the attachment cell seems at present still unresolved—it may be either to the scale or to the socket cell—while the so-called *scolopale* cell is considered homologous to the sheath cell. The latter secretes the (extracellular) cap that is homologous to the sheath (Chung *et al.* 2001; Lai & Orgogozo 2004).

Figure 6 presents a more detailed view of the scolopalial region of a moth ear chordotonal organ. Besides the cap, the scolops contains within the scolopale cell a ring of rods that consist largely of actin (Wolfrum 1990). Thus, we have a structure made by a combination of extra- and intracellular reinforcing elements. Actin bundles actually play a huge variety of roles in biological pattern formation, including helping shape the external sculpting of developing bristles and scales (Overton 1966; figure 7).

As mentioned above, the mechanosensory bristle and the chordotonal organ are only two of a group of different sensors that differentiate from epidermal SOPs. Their homology is not in doubt; indeed overexpression of a particular gene, *cut*, is known to transform what would otherwise be a bristle to a chordotonal organ (Merritt 1997). Not only are these mechanosensors related, but they also show up in different places on the same animal, which may also be carrying iridescent bristles and scales. It therefore seems risky to use the morphology and development of

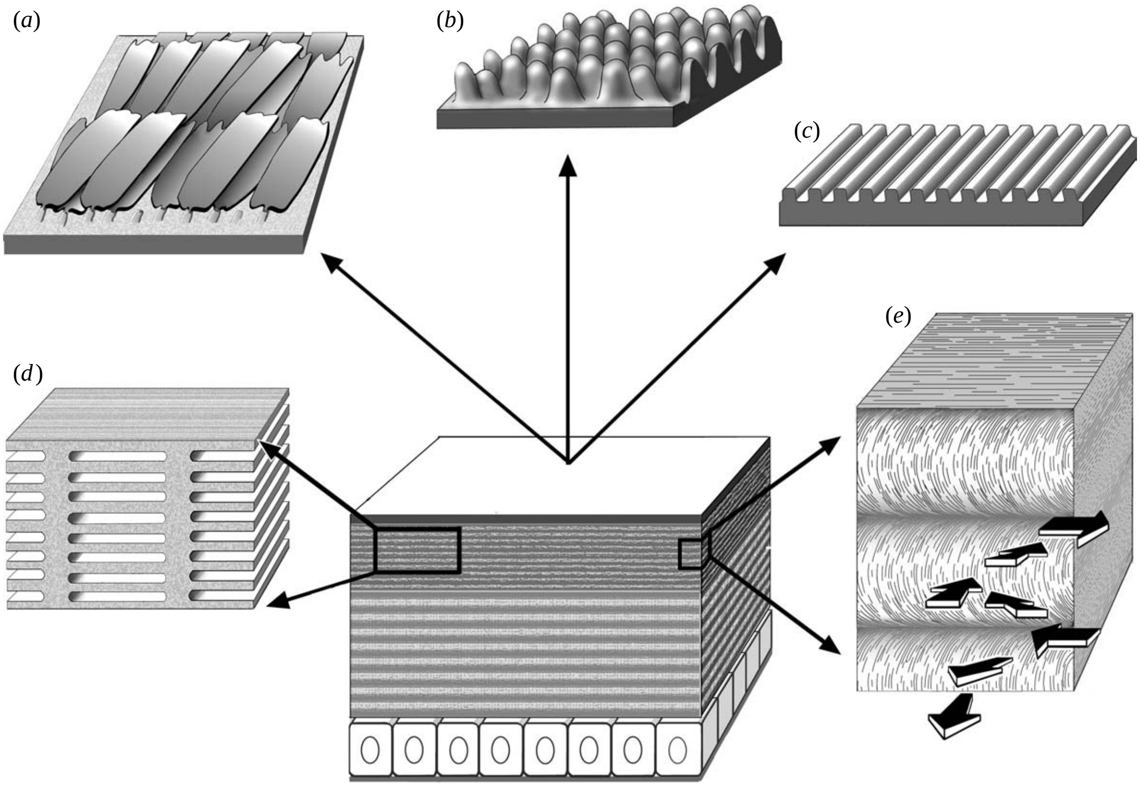

Figure 2. The insect's epidermal layer (bottom, centre) secretes the cuticle sequentially, starting with the outermost layer, the *epicuticle* and continuing with the inner layers. Of these, the outer ones may be cross linked (forming the *exocuticle*—darker region); the non-cross-linked regions are referred to as the *endocuticle*. The epi- and/or exocuticles may be modified in any of several ways to produce an optical effect: (*a*) the surface may be clothed in scales and/or bristles, each in its socket (two empty sockets are shown); (*b*) the surface may be thrown into a field of 'corneal nipples' that serve as the impedance-matching devices that enhance the harvesting of light and/or reduce surface reflection; (*c*) the surface may be sculpted into a diffraction grating; (*d*) part of the exocuticle may be formed into plates that form a thin film interference stack; (*e*) the exocuticle may tune its cholesteric liquid crystal helicoids (precessing arrows) to produce a visible colour. (Reproduced with permission from Ghiradella (2003).)

any of these closely related structures as a basis for defining evolutionary relationships among them, as many workers in the field have tended to do.

At the subcellular level, the SER is generally known to be involved in synthesis of lipids and in detoxification of various substances by the cell. It apparently has several other functions as well. It may be involved in storing and then releasing the nuclear membrane components during cell division (Anderson & Hetzer 2008). In skeletal muscle cells (figure 8), it is elaborated into the so-called *sarcoplasmic reticulum* (SR) that wraps around the contractile fibrils and reversibly releases calcium into the contractile machinery (Vogel 2001). For a large muscle cell to contract as a unit, the excitation resulting from events at the synapse must reach deep into the cell; for this, the cell membrane invaginates in long finger-shaped processes, the *t-tubules*, which carry the excitation into the interior of the fibre. The t-tubules and SR abut closely on each other in structures referred to as 'triads' (vertebrates) or 'dyads' (invertebrates), so that the excitation effectively launches calcium release and muscle contraction.

The SER in the muscle cells is generally only moderately reticulated, but, in other systems, it appears to be able to form virtually 'crystalline' networks (Argyros *et al.* 2002; Almsherqui *et al.* 2006; Michielsen & Stavenga 2008). Further, these structures form relatively easily by low-affinity protein interactions between protein domains on opposing membranes (Snapp *et al.* 2003; Hu *et al.* 2008). At least three of these highly formed SER systems share with the muscle SR a close association with what are essentially cell membrane t-tubules. The first of these is directly relevant to our interest here in those iridescent scales that have internal lamellae or three-dimensional photonic crystals. Figure 9 presents a view of part of a developmental stage of one of the latter. The SER forms a lattice; sleeves of cell membrane weave in through this template and form an 'inverted' lattice (a lattice within the lattice) within which cuticle may be secreted, as always extracellularly (see Ghiradella (1998*a*) for a general review of scale structure and development). Apparently, these SER systems are also quite labile and can switch easily between lattice and laminar structures (Snapp *et al.* 2003; Almsherqui *et al.* 2006), which may explain why at least one lycaenid butterfly has blue scales with internal films on the wing obverse and green scales with three-dimensional photonic crystals on the wing reverse (Kertész *et al.* 2006).

A second SER/t-tubule equivalent (in this case SER/microvillus) appears in some insect wax glands (Locke 1998), not surprising in view of the SER involvement in lipid production in cells in general. The third such system is perhaps more surprising; it involves the multicellular 'scales' of annelid worms of the family Polynoidae. These animals bear large dorsal

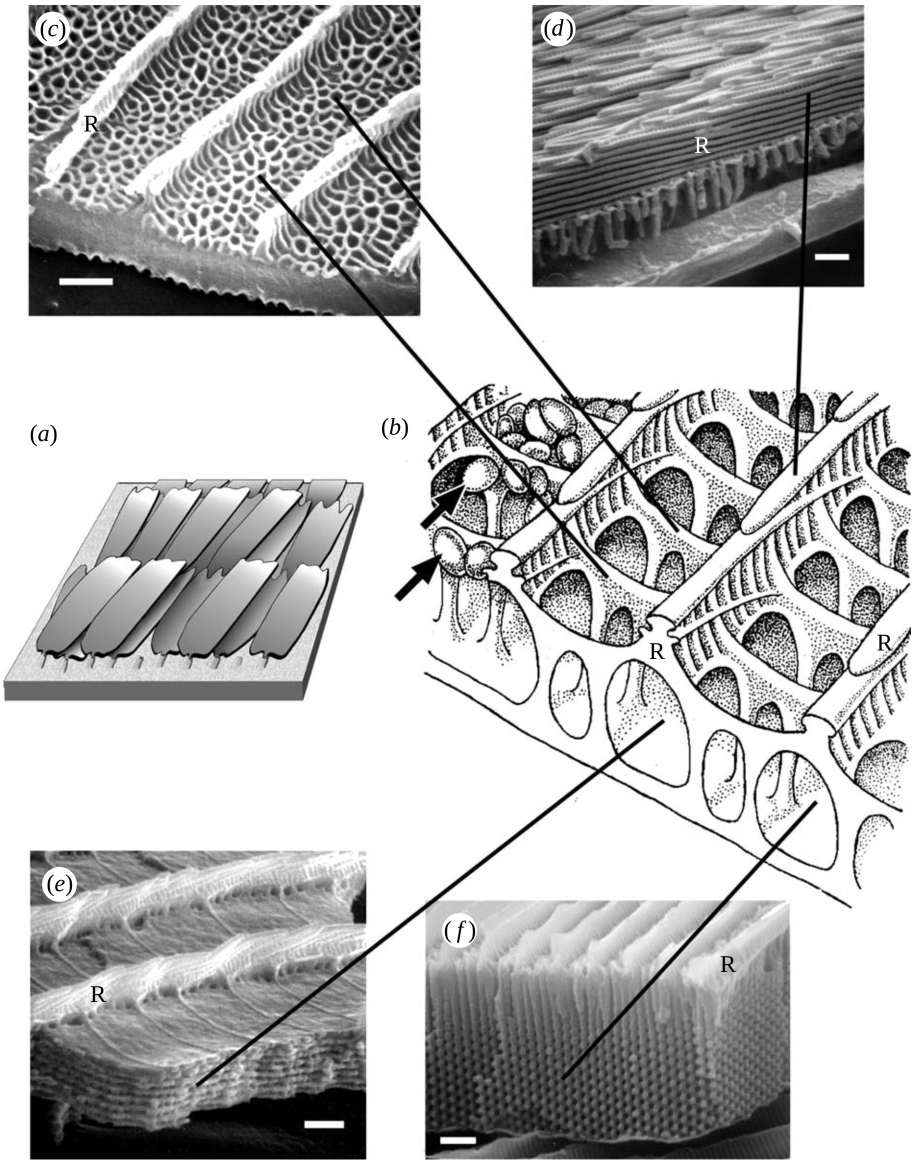

Figure 3. Scales and bristles (essentially the same structures) seem particularly versatile in developing optical architecture. (*a*) As in figure 2, a view of a piece of wing and its investiture of scales. (*b*) An ultrastructural view of a generic scale fragment. The scale is essentially a flattened sac; its upper layer is typically sculpted into a series of longitudinal *ridges* (R) that are joined at intervals by transverse *crossribs*. Ridges and crossribs together frame a series of windows into the scale interior, usually empty except for pillars that join the upper and lower scale surfaces and, in pierid butterflies, pigment beads (two dark arrows) that may scatter, absorb or otherwise control the reflection of selected wavelengths of light (Giraldo & Stavenga 2008). Any of these structures may be modified to produce an optical effect. For example, the crossribs may elaborate and the windows fill in (*c*) to produce a series of 'alveoli', essentially a two-dimensional photonic crystal that is part of a remarkable optical system (Vukusic & Hooper 2005); the ridges may be elaborated into (*d*) or the scale interior filled with (*e*) stacks of thin films that serve as complex quarter-wave thin film systems, or the scale interior may fill (*f*) with what are essentially biological three-dimensional photonic crystals. All scale bars = 1 μm. (Reproduced with permission from Ghiradella (2003).)

plates (scales) that they may shed when they are disturbed. The scales are bioluminescent and produce repeated flashes, presumably to distract a potential predator. The luminescent cells bear crystalloids of smooth ER ('photosomes'), which have dyadic associations with the cell membrane, and it is these that produce the light (Bassot & Nicolas 1988). Interestingly, similar (but non-luminescent) crystalloids appear in the eyes of these animals and some of their non-bioluminescent relatives (Bassot & Nicolas 1978). Note that *Aphrodite*, an annelid whose strikingly iridescent bristles contain two-dimensional photonic crystals (Parker *et al.* 2001) belongs to the same family of annelids.

This set of studies now adds bioluminescence to the range of SER functions. The relationship may be more extensive than we now realize: the lanterns of our North American fireflies are derived from fat body (see Ghiradella (1998*b*) for a review of firefly lantern structure), and, while the luminescent *photocytes* do not display well-developed internal membrane systems, they are packed with *peroxisomes*, organelles typically implicated in cellular handling of reactive oxygen species. The peroxisomes hold the flash reactants and

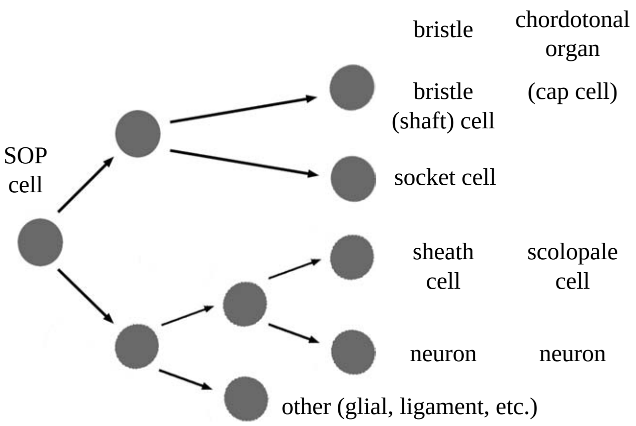

Figure 4. An epidermal cell gets a signal to differentiate into a SOP cell and proceeds through a series of stereotyped divisions whose products depend on what type the sensor is to be. Here, we are only considering two types, bristle mechanoreceptors and chordotonal organs (figure 5*a–c*). In a bristle mechanoreceptor, the progeny of one of the first daughter cells go on to make a bristle (or scale) cell (the *trichogen*) and a socket cell (*tormogen*) which in turn make their respective structures. The progeny of the other daughter cell become the neuron and the sheath cell (*thecogen*), the latter of which latter secretes a non-living sheath around the DOS, and possibly some additional cells as well. In chordotonal organs, the sheath cell is called a scolopale cell and has a variety of functions (figure 5*c*). (After Kernan (2007).)

ultimately produce the light. Unlike such other cellular organelles as mitochondria, centrioles and chloroplasts, peroxisomes have neither their own DNA nor other clear evidence for symbiotic origin in cells. Hoepfener *et al.* (2005) present evidence that they are derived from the cellular SER (but see de Duve 2007).

The above accounting adds up to at least seven, possibly eight, different processes mediated or controlled by the smooth ER and undoubtedly more remain to be discovered. This multiplicity of capacity may also hold true for other cellular organelles. A few general statements about the insect systems can be put forward at this point.

(i) Given the cell's control of the characteristics of its polymer products, we may need to understand the development of these products, as well as their structural deployment, before we can produce similar or equivalent products.

(ii) Biologically produced constructions may include both intra- and extracellular contributions joined together (as in the scolopes) to produce a more complicated structure. This may reflect both possibilities and limitations in the material composition of the structures.

(iii) Throughout the literature, there have been and continue to be attempts by different authors to use the details of scale structure as a way of defining evolutionary relationships for the species involved. We cannot support this view. Given the great developmental malleability of these systems, the apparent ease with which they can flip from one state to another, the existence of many variants at any of many levels, and the coexistence of the different forms on the same animal, there is no way we can realistically arrange them in terms of evolutionary 'progress'. Throwbacks exist and cells carry in them current and not-so-current fabrication directions which can switch roles in different tissues and different species. To emphasize our main point, the eukaryotic cell is multifunctional and multipotent, and we believe that we need to remember this in any interpretation of development and generation of form.

(iv) Many of these systems appear to be 'self-assembly' systems: precursor conditions are laid down and chemical forces and physical processes (elastic buckling, surface tension and the like) complete the pattern formation. The systems are fluid in time as well as space: it is not always clear whether a given structure represents a final operational goal, temporary scaffolding or a manifestation of a change in function as the cell enters a different life stage as, for example, in preparation for a moult.

The ultimate question must be where the control for these processes resides. In the genes, perhaps, but, with the increasing pace of modern developmental research, our hitherto rather mechanistic notion of gene structure and function is giving rise to a picture of a disturbingly fluid system of development in which the control of gene expression (and probably evolution) proceeds on many levels at the same time. Because insect iridescent systems, in particular, are so distinctive, so varied and must be 'written in stone' to preserve their optical functions, their study may well help us to understand some of these special developmental processes.

Let us now review what is known about the iridescent systems in birds that are also well known for their iridescent coloration. While the structures that contribute to the production to this iridescence are fairly well defined (Prum 2006), the developmental mechanisms responsible for them are just beginning to be quantitatively explored. The three main proposed mechanisms involve the deposition of one or more layers of keratin over melanin, a careful organization of melanocytes and keratinocytes within the developing barbule, or possibly self-assembly of keratin (Prum 2006).

3. DEVELOPMENT OF IRIDESCENT STRUCTURES IN FEATHERS

Iridescent structures in feathers are typically produced with either laminar or crystal-like nanostructures located in the barbules (Prum 2006). Laminar structures that can result in glossy, black iridescence rely on a single layer of keratin above a layer of melanin (e.g. satin bowerbirds, *Ptilonorhynchus violaceus minor*; Doucet *et al.* 2006) or multiple layers of keratin and melanin (e.g. European starlings, *Sturnus vulgaris*; Cuthill *et al.* 1999), wherein the interfaces between both air and keratin or keratin and melanin create iridescence (Doucet *et al.* 2006). Crystal-like nanostructures, such as those found in the peacock's tail (Zi *et al.* 2003), use ordered arrays of

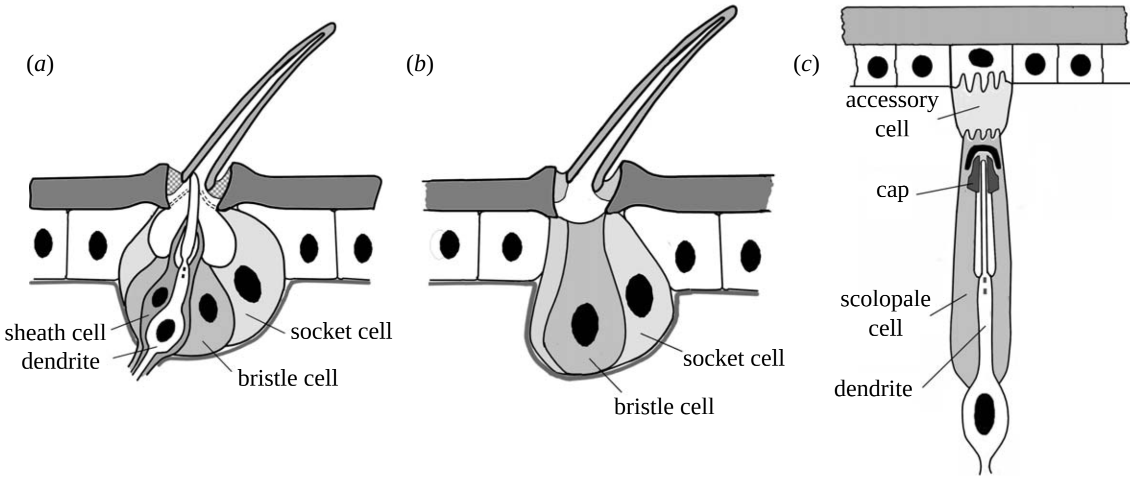

Figure 5. (*a*) Progeny of a SOP cell in a typical bristle mechanoreceptor. Bristle cell and socket cell have formed their respective structures and then drawn back, while the sheath cell has secreted the sheath around the DOS. The sheath is believed to enclose a sealed lymph space within which the ion fluxes may be controlled and held separately from those in the general haemolymph. (After Keil (1998).) (*b*) A non-innervated bristle or scale expresses only one daughter cell from the first SOP division, hence only the bristle and socket are formed. (*c*) A diagrammatic representation of a chordotonal organ such as may be found in certain insect ears (and reflecting the authors' current interpretation of the structure). The dendrite DOS is no longer involved with a bristle and socket, but the sheath cell (now called a 'scolopale' cell) extends around the dendrite, and the sheath is reduced to an extracellular cap holding the distal end of the cilium. The homology of the attachment cell seems unclear, being referred to by some authors as the socket cell and by others as the bristle cell.

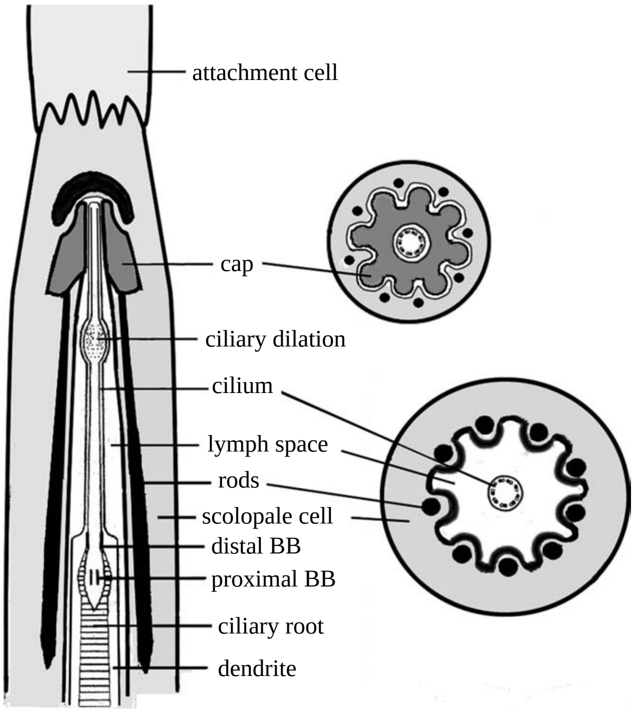

Figure 6. A closer look, in longitudinal and cross sections, at the DOS region of the chordotonal organ as shown in figure 5*c*. The cilium typically has along its length a dilation not found in external mechanosensors. The *scolops*, the structural complication that looks designed to brace or support the DOS, consists of the extracellular cap and a series of rods within the scolopale cell; the rods are composed largely of actin (Wolfrum 1990). The cap is highly indented and protrusions of the scolopale cell with their enclosed rods fit into the slots. The cilium appears firmly plugged into the cap central channel. (BB, basal body; ciliary region after Yack (2004).)

keratin, melanin and air, which give rise to coherent scattering of light waves. While the development of both laminar and crystal-like nanostructures has not been extensively studied, here we summarize possible developmental pathways in the context of general feather development.

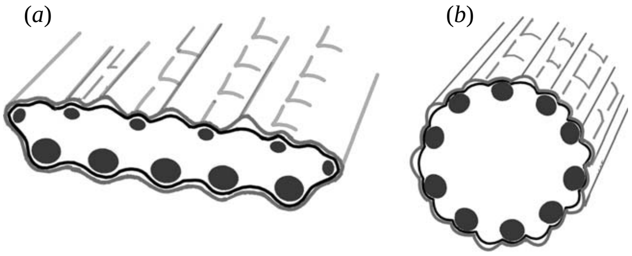

Figure 7. Highly diagrammatic views of a developing scale (*a*) and bristle (*b*). Both are characterized by rings of temporary actin bundles (similar to those in the scolopale cell) within the trichogen; these bundles are important in siting the surface ridges and through them the rest of the architecture. The bundle asymmetry is greater in developing scales than in bristles; in the latter case, at least, this asymmetry appears to affect the degree of curvature of the bristles (Tilney & DeRosier 2005), although the pronounced asymmetry in the scale bundles does not seem correlated with scale curvature.

Laminar nanostructures require one or more layers of keratin and melanin, in which the melanin can act as a poor mirror (Yin *et al.* 2006). The cellular control regarding the regular deposition of melanin within keratin layers has not been extensively studied. However, melanocytes near the follicle will produce melanosomes, melanin-producing organelles (Marks & Seabra 2001), which can then deposit melanin in the keratinocytes, which give rise to the feather filament (Yu *et al.* 2004). As the feather develops, keratin polymerizes and the melanin from the melanosomes is incorporated into the developing feather (Prum & Williamson 2002). How the melanin is arranged on the nanoscale, however, is still unknown. This is

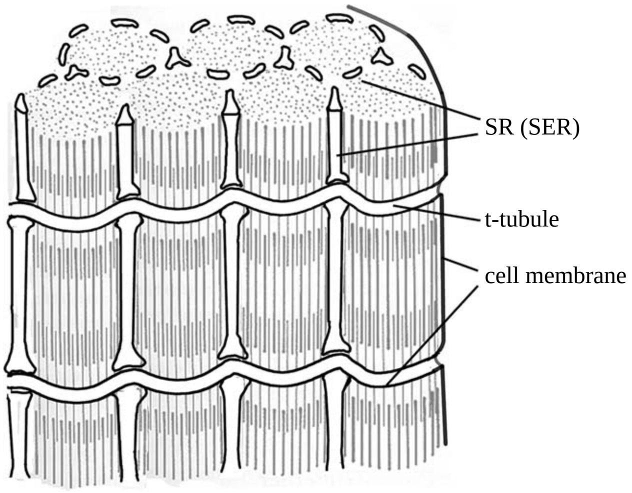

Figure 8. A system well known to cell physiologists: for skeletal muscle to contract as a unit, the excitation from activity at the synapse must be carried deep into the fibre, which action occurs through the agency of the t-tubules, finger-like invaginations of the cell membrane. The muscle's extensive and reticulated SER (or SR in the case of muscle) associates closely with the t-tubules and shuttles calcium into the contractile machinery in response to the excitation. (With permission from Vogel (2001).)

a fundamental problem regarding the development of laminar structures in feathers, as it is this step that produces the iridescence phenomenon. However, rearrangement of melanin granules among closely related blackbird (Icteridae) species does produce iridescent structures from a matte-black common ancestor (Shawkey *et al.* 2006). The application of new techniques, including genetic (e.g. Kerje *et al.* 2004) or molecular (e.g. Harris *et al.* 2005), in such a comparative context may be an appropriate avenue for future research.

Keratin is a fibrous protein typified by sulphur content (Meyers *et al.* 2008). While the self-assembly characteristics of α-keratin, typically found in mammals (Meyers *et al.* 2008), have been explored (e.g. Yamada *et al.* 2002), experimental assessment of self-assembly characteristics of β-keratin, typically found in reptiles and birds (Meyers *et al.* 2008), has been limited to questions regarding use of superheated feather waste from the poultry industry (Yin *et al.* 2007). Furthermore, recent research regarding the properties of α-keratin has shown that membrane templating, rather than self-assembly, may be responsible for the formation of intermediate keratin filaments (Norlén 2006). Since precise ordering of melanin granules, keratin and air is necessary to produce iridescent structures, the developmental process must demand a certain level of order. While observations of self-assembled copolymer blocks resemble patterns of spongy medullary β-keratin (Prum 2006), it seems unlikely that iridescent colours arise solely from such mechanisms, although self-assembly may be an important component (Prum 2006). Research from both the fields of materials properties and cell biology is necessary to characterize the developmental mechanisms of iridescent feather structures.

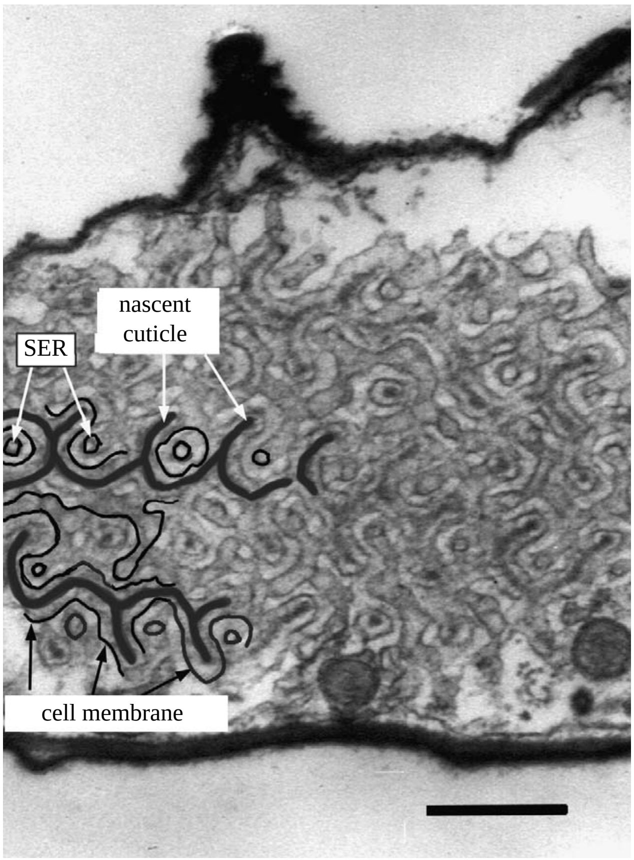

Figure 9. Another example of SER/cell membrane interaction, in this case in the development of the three-dimensional photonic crystals found in butterfly scales (figure 3*f*). The SER forms a lattice-like structure within which the sleeves of cell membrane are interwoven to form an inverse lattice. The cuticle that will form the photonic crystal can then be secreted (extracellularly, as usual) within the sleeves of membrane. Despite fixation, sections rarely catch perfect longitudinal or transverse views of these developing structures, hence the rather messy appearance of the image. Scale bar, 0.5 μm.

4. CONCLUSION

As we have seen, there is a wide variation in research regarding the development of iridescent coloration in biological contexts. While insects have been heavily investigated, it is perhaps time to extend this investigation more generally to non-living investiture and the complex forms it can take. With an increased understanding of the developmental mechanisms responsible for iridescence in feathers added to that in insect cuticle, we may be able to add to an already impressive list of biomimetic substrates modelled after avian and insect iridescent coloration. For example, a circular stair-like colloidal film was created to mimic the colours of the peacock tail feather (Cong & Cao 2004). Also, there is an 'interference pearl pigment' that consists of mica flakes coated by a TiO_2 film, the thickness of which is adjusted to the thin film interference condition (Kinoshita & Yoshioka 2005*a*). Finally, Saito *et al.* (2004) describe a process wherein they fabricated a substrate to mimic the brilliant structural blue of the *Morpho* butterfly out of inorganic materials, using a process that may be extended to mimic other colours.

More research in the developmental processes in nature will hopefully provide material scientists with a broader array of tools with which to synthesize iridescent colours in man-made substrates.

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