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PERSPECTIVES

EVOLUTION

Beyond the rainbow

Dinosaur color vision may have been key to the evolution of bird feathers

By **Marie-Claire Koschowitz,[1,2] Christian Fischer,[2] and Martin Sander[1,3]**

Once believed to be a diagnostic feature of birds, feathers are now known to have evolved in dinosaurs well before the first birds. In birds, feathers serve several functions: Down feathers insulate the body, whereas planar or pennaceous feathers are necessary for flight, communication, camouflage, and brooding (see the first figure). What was their original function in nonavian dinosaurs? Based on a specimen of *Archaeopteryx* that preserves a spectacular plumage of pennaceous feathers, Foth *et al.* (*1*) recently hypothesized that pennaceous feathers did not evolve for flight but for display. Together with insights into body size evolution in dinosaurs along the line to birds (*2*) and the discovery of protofeathers in early dinosaurs (*3*), these results contribute to an emerging understanding of why pennaceous feathers may have been superior to filamentous protofeathers.

Protofeathers presumably evolved in early dinosaurs (see the second figure) (*4*). Their main function must have been to insulate, because an increase in growth rate was facilitated by a faster metabolism early

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Vulturine guineafowl (*Acryllium vulturinum*) plumage. Structural colors like blue and violet are displayed in concert with intricate, high-resolution ornamentation. The close-up shows a specimen in the collection of the Museum Alexander Koenig. The full-size bird is from the Zoological Museum of the University of Göttingen.

PHOTO CREDITS: CHRISTIAN FISCHER (GUINEA FOWL) AND GEORG OLESCHINSKI (CLOSE-UP)

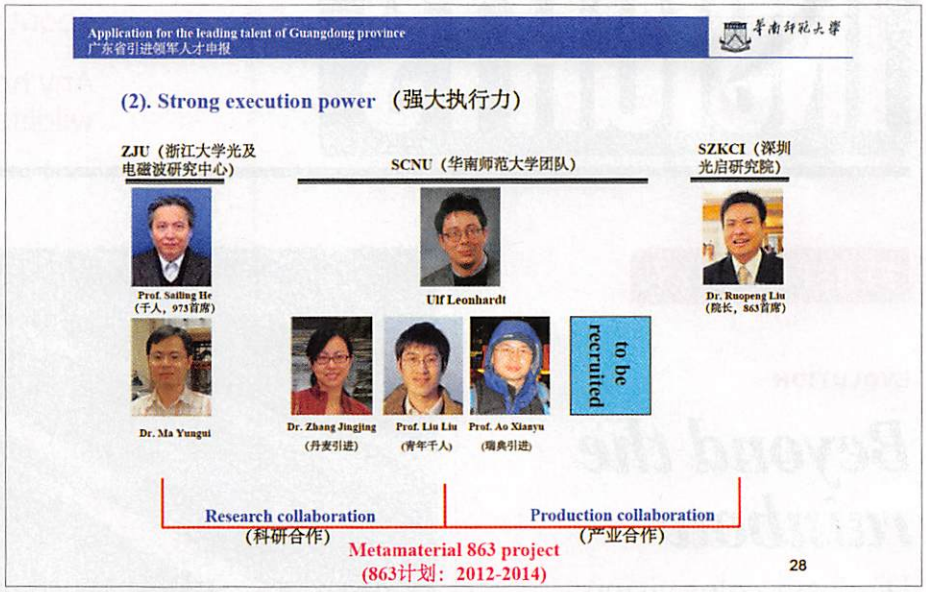
arguing that the mathematical tools of transformation optics are applicable to designing better absorbers. Ao also says that the work on absorbers was included in the Leading Talent proposal to satisfy a requirement to produce something that could be commercialized. "Otherwise, there is no chance to get this project approved at all," Ao says. "Leonhardt knew this reason quite well and agreed to this from the draft preparation to the final presentation."

Leonhardt insists he never saw a draft. When he began to have concerns, he e-mailed administrators for both programs, along with officials at the Ministry of Science and Technology; the Chinese Academy of Sciences; the Central Commission for Discipline Inspection, the Communist Party's anticorruption watchdog; and the National Natural Science Foundation of China. None responded directly to him, he says.

Representatives of the Leading Talent program reached by phone by *Science* declined to discuss the details of Leonhardt's grant, which was canceled on 9 October. The State Administration of Foreign Experts Affairs (SAFEA), which administers the Thousand Talents program for the Organization Department, did not respond to repeated interview requests.

Interviews with other foreign Thousand Talents recipients suggest that ignorance of award conditions is common. For example, Geoff Gadd, a geomicrobiologist at the University of Dundee in the United Kingdom, who has a part-time award for work at the Xinjiang Institute of Ecology and Geography in Urumqi, wrote *Science* that he has not received a resettlement subsidy or any information about the program in English. "I am not sure who administers the grant," Gadd wrote. "I received no details about this kind of thing." Fuel cell expert Subhash Singhal, a fellow emeritus at the Pacific Northwest National Laboratory in Richland, Washington, says he had a similar experience at the China University of Mining and Technology in Beijing, where he received a short-term Thousand Talents award: "[With] the grant process, I had absolutely no idea what they were doing or how they were doing it." His host institution's lack of transparency about award money issued in his name would probably deter him from returning to China, he says.

Several grant recipients say that the program has proven fruitful, and they were keen to renew the terms of their stay in China. "The networking is going to be long-term huge for me," says Michael Arnold, who received a Thousand Talents grant to work at the Kunming Institute of Zoology. "I can just see ripples going out through the rest of my career." But even those who were happy



A PowerPoint presentation prepared to accompany Leonhardt's Leading Talent grant application depicts a research team that he says didn't exist.

with their experience were not clued in to grant administration. Four out of the five researchers interviewed by *Science* say that they did not receive a resettlement subsidy. Foster says he received no money at all; his university in China paid for his accommodation, but he did not earn a salary and says he "didn't claim" a subsidy.

CCG's Wang concedes that the program has had growing pains. "There could be problems, there could be fake [scholars], there could be scandals." But he maintains, "The general picture and the message they're sending to attract talent is good."

WHEN ASKED ABOUT Leonhardt's allegations, other foreign scientists who work with Sailing He profess disbelief. Sune Svanberg says he and his wife felt "very appreciated" at COER: "We never felt that anything was different from what was said. I'm just astonished that something like this would develop."

Sailing He and others insist the dispute boils down to a personality conflict. They note that Leonhardt sued the University of St. Andrews in 2013 over pay for vacation days he never took. Leonhardt responds that his claim was justified, and he won compensation for most of the days he contested. (The University of St. Andrews declined to comment, citing privacy laws.)

Leonhardt and Silberg never returned to China for the second year of their 5-year terms. For months, they tried through lawyers to figure out what exactly had happened with the grant money due to Leonhardt, while attempting to terminate their contracts. Last December, COER still hoped to woo Leonhardt back; in an e-mail, Sailing He offered him a sum equal to the amount spent on the disputed equipment for "whatever equipment you tell SCNU to buy." Leonhardt refused. COER terminated their contracts in June.

COER now argues that Leonhardt was not in Guangzhou for the amount of time agreed upon in his contract, that he tried to abuse his travel funds while at SCNU, and that "he did not show any interest or intent in either building a lab or a research group," Li wrote in an e-mail. "Introducing [Leonhardt] to South China Normal University was the biggest mistake of my academic career," says Sailing He, who recently proposed to SAFEA that the Thousand Talents program dole out the resettlement subsidy over the course of a grant, rather than provide a lump sum up front.

Early last month, COER sent *Science* Leonhardt's Thousand Talents application, which Leonhardt had tried in vain to obtain through his lawyers. The date on the application—18 August 2011—predates his initial trip to Guangzhou to discuss the award. The document, in Chinese, describes research on Casimir forces, which Leonhardt says he didn't suggest until a year after the application was purportedly submitted.

Leonhardt suspects the document is a fake. COER acknowledges it doctored the date because it submitted the application after the deadline passed, but the center maintains that its researchers prepared the document at Leonhardt's request as a "personal favor." In an e-mail to *Science*, Li explained it this way: "We were just passively helping him." ■

With reporting by Adrian Cho.

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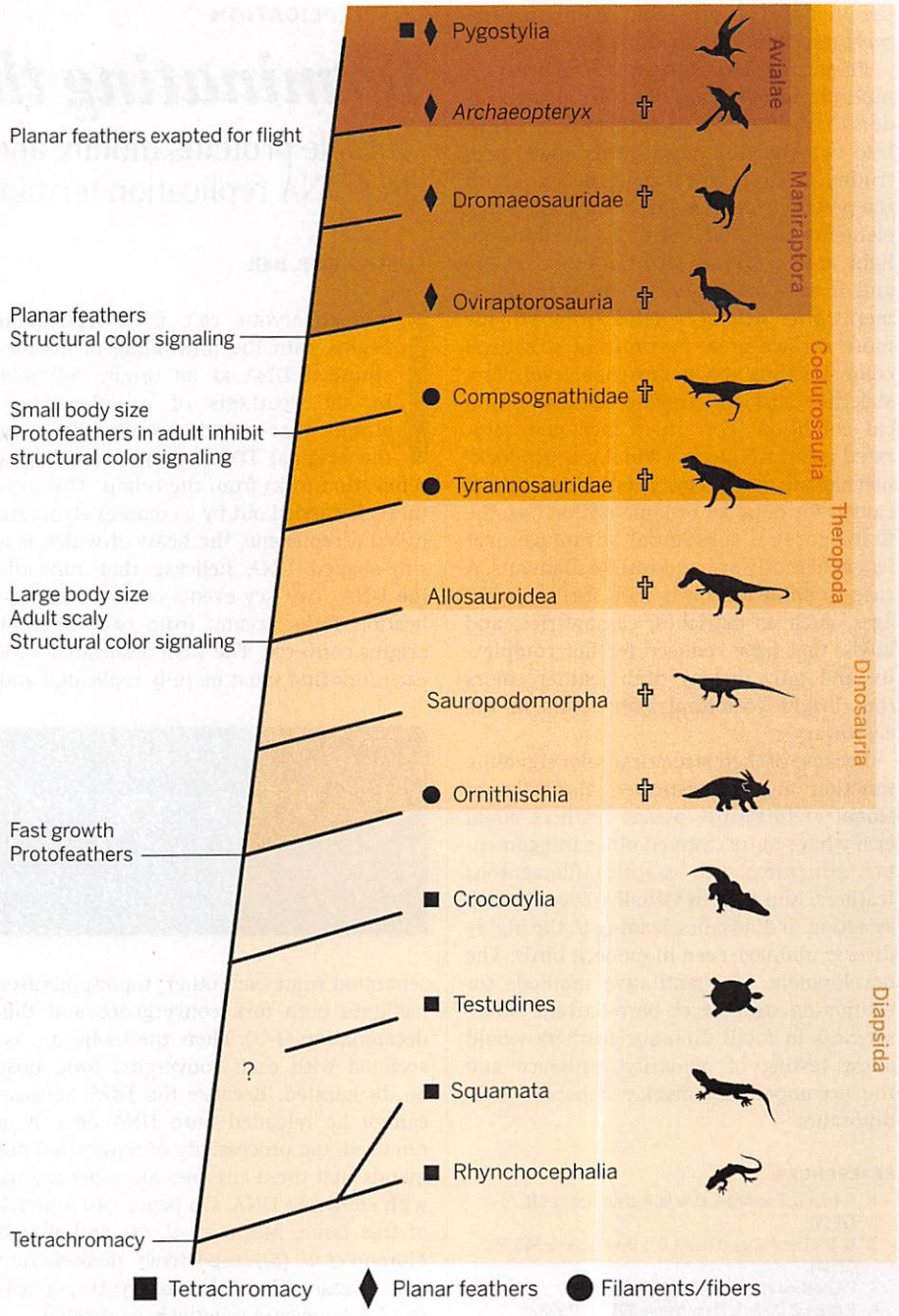
in dinosaur evolution (*5*). A faster metabolism necessitates body insulation because without an insulated skin, metabolic energy would be lost as heat instead of being available for growth. This is particularly true for small- to medium-sized animals such as early dinosaurs and their juveniles because of their poor ratio of body volume to body surface. A recent study (*2*) suggests that body size decreased much faster in the bird stem lineage than in other dinosaurs. For fast-growing, presumably warm-blooded animals (*5*), such miniaturization would only have been possible with sufficient body insulation.

However, protofeathers came at a price: the loss of structural color signaling capabilities. Structural color signaling is limited in a body cover of flexible hairlike structures such as the filamentous feathers of some birds. The display of structural colors (including iridescence, vivid blues and greens, and ultraviolet reflection) requires the precise arrangement of light-scattering elements at nanometer scales (*6*–*8*). In modern bird feathers, these elements consist of keratin, air, and melanosome-based nanostructures (*7*), producing iridescence and saturated color displays that are central to communication and sexual selection (see the first figure) (*9*).

Like every signaling system, structural color signaling involves a receiver: the eye of the (nonhuman) beholder. This raises the question of the visual capabilities of dinosaurs. Differentiated color vision, much superior to that of humans and other mammals (*10*), is known from virtually all extant reptiles (see the second figure) and in many taxa includes ultraviolet vision. Phylogenetic inference suggests that dinosaurs were endowed with the highly differentiated color vision of birds (*11*, *12*), termed "tetrachromacy" (the ability to discriminate hues ranging from ultraviolet to turquoise via a fourth, short-wavelength receptive cone cell; the other three cone cell types are sensitive to blue, green, and red). Tetrachromacy is a basal characteristic of land vertebrates and widely found in other vertebrates and invertebrates (*6*, *10*).

In addition to protofeathers, several nonavian maniraptoran dinosaurs independently evolved pennaceous feathers that clearly did not serve in flight (*13*, *14*). Pennaceous feathers may have been the solution to the evolutionary trade-off faced by these dinosaurs between insulation by protofeathers (*4*), increased metabolic rate (*5*), and miniaturization (*2*) on the one hand, and the loss of structural color signaling caused by protofeathers on the other. Instructive parallels can be found in early mammalian evolution, when fur starts to appear in the fossil record.



Color vision and feather evolution. Extant lizards, tuatara (Rhynchocephalia), turtles, crocodiles, and birds possess four cone cell types (tetrachromacy), enabling highly differentiated color vision that presumably was also present in dinosaurs. Protofeathers probably evolved in early dinosaurs for insulation and preceded planar feathers in coelurosaurians. Planar feathers, in turn, preceded flight or gliding. Miniaturization along the bird stem line led to a trade-off between color display and insulation, which could have been solved by the evolution of planar feathers serving both functions.

Here, coloration depends on the absence or presence of pigments ranging from reddish brown to black. Lacking a coherent surface, fur did not allow directed light scattering and severely impaired structural color display. Nocturnal activity patterns and body size reduction once again mandated body insulation, but sophisticated color perception and signaling lost their importance at night and differentiated color vision was lost (*15*).

It appears that in advanced maniraptoran dinosaurs, this trade-off was solved through the evolution of a new type of skin outgrowth that served insulation and display needs at the same time: the planar feather. Planar feathers would have covered up and partially replaced the filamentous protofeathers, thus leading to the evolution of contour feathers (the smooth feathers that form the outer covering of

the plumage), as preserved in the *Archaeopteryx* specimen studied in (*1*).

Planar feathers consist of a network of multiple interlocking branches of two orders (barbs and barbules) that are arranged into two sheetlike vanes horizontally protruding from a central shaft. Because both the precise arrangement of light scattering elements and the optimal exposition to light are mandatory for structural colors and iridescence, flattened branching filaments offer several benefits. They provide more surface area, maximizing structural color signaling at a macroscopic level. Also, sheetlike surfaces provide optimal physical conditions for iridescence and saturated color production. Finally, a "zip-lock" mechanism created by barbules generates a canvas for detailed ornamentation (see the first figure), a substantial advantage over less coherently ordered furlike filaments. A case in point are birds with furlike plumages, such as ostriches, cassowaries, and kiwis, that have reduced feather complexity and only display drab feather colors (but bright structural skin colors in the cassowary).

Because of their structural color signaling function and sophisticated three-dimensional architecture, planar feathers could easily have outperformed other integumentary structures such as scales, filamentous feathers, and hair in visually driven sexual selection in dinosaurs, leading to the highly diverse plumage seen in modern birds. The development of quantitative methods for estimating degrees of barb-barbule adhesiveness in fossil dinosaur feathers would allow testing of planarity resilience and the accompanying display capabilities in dinosaurs.

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DNA REPLICATION

Terminating the replisome

Multiple proteins modify and dismantle a key enzyme after DNA replication terminates

By **Stephen P. Bell**

In a eukaryotic cell, DNA replication begins with the unwinding of double-stranded DNA at an origin, followed by the synthesis of complementary strands that grow bidirectionally along the original DNA strands (forming a replication fork) from the origin. This synthesis is carried out by a complex structure called a replisome, the heart of which is a ring-shaped DNA helicase that unwinds the DNA. Two key events occur when replication forks arising from two different origins converge. The DNA associated with each fork first must be fully replicated and

separated from each other; topoisomerases facilitate both fork convergence and this decatenation (*1*–*3*). Then, the replisome associated with each converging fork must be dismantled. Because the DNA helicase cannot be reloaded onto DNA once it is removed, the processivity of replication demands that these enzymes associate tightly with substrate DNA. On pages 440 and 477 of this issue, Maric *et al.* (*4*) and Priego Moreno *et al.* (*5*), respectively, demonstrate that disassembly of the eukaryotic replicative DNA helicase is actively controlled.

In eukaryotic cells, loading and activation of the replicative DNA helicase are temporally separated to ensure that no origin reinitiates during the cell division cycle. Helicase loading occurs during the G_1 phase of the cell cycle, resulting in a dimer of the hexameric ring-shaped mini-chromosome maintenance (MCM) 2-7 helicase encircling the origin DNA (*6*). Upon entry into S phase, two helicase-activating proteins—cell division cycle 45 (Cdc45) and go-ichi-ni-san (GINS)—are recruited to each Mcm2-7 hexamer, forming the active replicative helicase, the Cdc45-Mcm2-7-GINS (CMG) complex (*7*). DNA unwinding at the origin results in the active CMG complex encircling the single-stranded "leading-strand" DNA template. The CMG complex forms the foundation upon which the DNA polymerases and other replisome proteins assemble. The resulting replisome replicates the associated DNA until it encounters another replisome and terminates replication. Although the proteins and events involved in eukaryotic helicase loading and activation have been intensively studied, how the replisome is disassembled upon replication termination has been unknown.

Maric *et al.* and Priego Moreno *et al.* gained their first insights into replication termination by studying ubiquitylation of the replisome. Each group discovered that a specific Mcm2-7 subunit (Mcm7) is modified by a chain of ubiquitin proteins (polyubiquitylated), with lysine 48 (K48) linkages between ubiquitins. This modification was only observed under conditions that allowed replication to be completed. Prevention of CMG formation, treatment with replication inhibitors, or blocking replication termination prevented Mcm7 ubiquitylation. Blocking Mcm7 ubiquitylation caused replication defects consistent with inhibition of replication termination (*5*). A member of the Skp1-Cullin-F-box (SCF) family of ubiquitin ligases mediates the observed Mcm7 ubiquitylation, and in budding yeast, the F-box protein (which controls substrate specifity) is Dia2 (*4*). Intriguingly, SCF^{Dia2} was previously identified as a replisome component (*8*).

Maric *et al.* and Priego Moreno *et al.* observed that polyubiquitylation of Mcm7 is required for the disassembly and release of the CMG complex from DNA upon termination of synthesis. Maric *et al.* show that elimination of SCF^{Dia2} results in the retention of DNA-associated CMG even after cells enter the next G_1 phase. Similarly, Priego Moreno *et al.* report that inhibition of polyubiquitin chain formation prevents release of CMG complexes from chromatin after replication is completed. Because the CMG complex is the foundation of the replisome, release of the CMG from chromatin results in replisome disassembly.

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