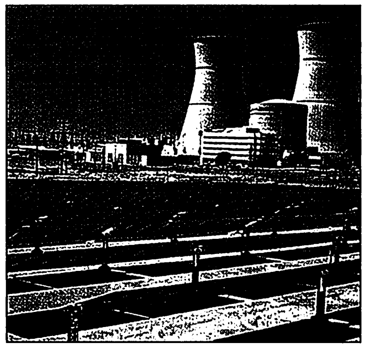
Science's
COMPASS
LETTERS SCIENCE & SOCIETY POLICY FORUM BOOKS *ET AL.* PERSPECTIVES REVIEWS

Choosing the Sources of Sustainable Energy

RENEWABLE ENERGY "WILL BE THE CENTRAL pillar of a sustainable high-technology civilization," says Terry Collins in his Essay "Toward sustainable chemistry" (*Science*'s Compass, 5 Jan., p. 48). This view, however, dismisses the potential long-term contributions of nuclear energy technologies. "Toxic elements are the prototypical persistent pollutants," says Collins; "long-lived radioactive elements are especially dangerous examples." But "danger" does not depend solely on toxicity—sources, pathways, and doses must also be factored into the equation.

When extrapolated to global scales, renewable energy technologies inherently involve large material flows that make it difficult to avoid discharging waste streams into the accessible environment. The fireplace is an example of a widely used, highly distributed renewable energy technology that has proven difficult to regulate effectively and is problematic for public health in urban areas and developing countries. In contrast, the nuclear energy technologies now in use involve much smaller mass flows and thus present realistic possibilities to permanently isolate high-level waste streams from the accessible environment. The upcoming U.S. Department of Energy's Generation IV Nuclear Energy Systems Initiative (*1*) is expected to identify fission technologies that combine substantially improved economics, safety, proliferation resistance, and waste minimization. When designed to use uranium resources with sufficient efficiency, such nuclear systems would qualify as sustainable.



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If we strive to continuously improve nuclear energy technologies at the same time that we are working toward equivalent improvements in renewable technologies, we can provide future generations with a mix of energy sources that can be more readily optimized to meet the important goal of sustainability.

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References and Notes

1. A description of the Initiative is available at http://www.inel.gov/resources/newsletters/inews-2000/12-05-00/1205gen42.htm

Response

WE FACE AN IMPORTANT CHOICE FOR ENERGY research: either we attempt to improve energy sources that are inherently flawed with respect to sustainability, such as fission or fossilized carbon, or we work toward new approaches for the sake of sustainability.

In my Essay, I argued for an emphasis on the latter course. In contrast, Per Peterson suggests that nuclear fission is sustainable; however, the persistence and toxicity of the radioisotopes involved amply justify the aversion of many nations to fission. If nuclear fusion can be developed free of long-lived radioisotopes, then it could contribute to sustainability.

Every 20 days Earth receives from sunlight the energy equivalent of the entire planetary reserves of coal, oil, and natural gas (*1*). Research on photochemical, photovoltaic, and passive and active solar technologies could speed our civilization toward sustainable energy. Last summer, engineers from Tokyo Denki University completed an 18,000-kilometer multicontinent journey in a solar cell–mounted electric car; 10% of the energy came from the sun, about the conversion efficiency of the silicon cells used. With expanded research support, more efficient photovoltaic materials could be discovered to allow cars to be completely solar powered. A catalyst/material ensemble capable of efficiently converting solar-irradiated water to hydrogen and oxygen could be found. Either development would revolutionize energy technology in favor of sustainability.

> **"We face an important choice for energy research..."**

For many decades, the large established energy research communities have used most of the energy research funding to study nuclear and fossilized carbon approaches. If solar research had received anything like this colossal support, solar-rich California would almost certainly not now be experiencing energy shortages. However, even a leading fossil fuel provider like Royal Dutch/Shell has seen the light and is now making a 5-year, $0.5 billion commitment to solar research. Perhaps our future will be endowed with sustainable solar technologies and will not remain shackled to energy technologies that are devastating to the environment.

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1. Royal Dutch/Shell Web site, at http://www.shell.com/royal-en/content/0,5028,25644-51311,00.html

Longisquama Fossil and Feather Morphology

THE TRIASSIC REPTILE *LONGISQUAMA* HAS blade-like integumental appendages that Terry D. Jones and colleagues propose in their report "Nonavian feathers in a Late Triassic archosaur" (*1*) are homologous with avian feathers. However, examination of their evidence suggests that this conclusion is flawed.

The authors refer to these appendages as "pinnate" but provide little support for this conjecture [see reference 5 in (*1*)]. I examined the *Longisquama* fossil with the authors in April 1999 and observed no evidence of branched structure. Rather, the appendages consist of a membraneous blade with a continuous, unfrayed "ribbon-like margin" and periodic (but not omnipresent) ripples radiating from a central shaft. Jones *et al.* propose that these ripples are separate branches that are distally fused in a manner similar to certain feathers (*2*). They do not mention that in such feathers, fused barbs occur with the overdeposition of melanin or carotenoid pigments (*2, 3*). Further, these feathers are known from only a few dozen species, and they function in communication, not flight (*2, 3*). The illusory nature of this branched structure proposed by Jones *et al.* has also been discussed by others (*4*). In addition, unlike pennaceous feathers, these membraneous appendages are so thin that these fossil structures are transparent. The underlying appendages can be seen through the superficial ones [Fig. 5 in (*1*)]. Fossil pennaceous feathers are not transparent because a coherent vane of keratin filaments will obscure the keratin filaments below them [for example, *Archaeopteryx* remiges (*5*)].

"[F]eatures such as the 'hollow remnant of spongy air-filled pith' and 'pulp cavities'...are artifacts [of preservation]..."

Additional features documented by Jones *et al.* demonstrate how dissimilar *Longisquama*'s appendages are from feathers. The vane of a feather is composed entirely of barbs, but many portions of the membraneous "vanes" of the *Longisquama* appendages lack any such structures. A pennaceous feather vane is created by interlocking barbules, yet the *Longisquama* "pinnae" lack them (*1*). Feather barbs fuse to the rachis at their bases, but as reconstructed by Jones *et al.*, the pinnae in the proximal portions of the *Longisquama* appendages meet the shaft at their distal tips (that is, the ends furthest from the base of the feather). Thus, these "pinnae" point inward toward the rachis as they extend toward the distal tip of the structure, not outward as in a feather [Fig. 3 in (*1*)]. In a pennaceous feather, the rachis ridge is created by the fusion of the dorsalmost barbs early in feather growth (*6*). So, with few exceptions, the rachis intergrades in size with the barb rami toward the dorsal tip of the feather. In contrast, the shaft in *Longisquama* continues all the way to the distal tip, without changing in size, and the distal tip of the shaft is not formed by the fusion of "pinnae" [Fig. 4 in (*1*)].

Jones *et al.* also say that these appendages are proximately ensheathed. However, the rachis and barbs of an ensheathed feather form a tubular epidermal tissue surrounding the central dermal pulp (*7*). The rachis should be peripherally located in a cylindrical ensheathed feather, but in *Longisquama* the shaft is central to the appendage within its proposed "sheath" [Fig. 3 in (*1*)]. In the *Longisquama* appendages, there is no space for the dermal pulp, which is a defining feature of a feather follicle and a component of every growing feather.

The authors also propose that the cylindrical base of the *Longisquama* appendages indicates that they grew from a follicle as feathers do. However, the absence of a dermal pulp, the morphology of the distal tip of the shaft, and the union of "pinnae" to the shaft at their distal tips all demonstrate that these appendages could not have grown at their bases from cylindrical follicles as feathers do. Further, the cylindrical base of these appendages has an obvious, convergent, functional explanation as a design for the insertion of muscles to move these appendages.

"Claims that [the features of the appendages] are merely artifacts of preservation strain credulity..."

Although the integumental appendages of *Longisquama* have a superficial similarity with avian feathers, examination of the evidence of their structure indicates that these structures are not homologous with avian feathers.

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7. A. M. Lucas and P. R. Stettenheim, *Avian Anatomy: Integument* (U.S. Department of Agriculture Handbook, Washington, DC, 1972).

THE ELONGATE INTEGUMENTARY STRUCTURES borne along the dorsal axis of the fossil vertebrate *Longisquama* are interpreted by Jones *et al.* (*1*) as being homologous with feathers, and in the News Focus article "Feathers, or flight of fancy?" by E. Stokstad (23 June, p. 2124), they say that *Longisquama* is "an ideal bird ancestor." On the basis of our study (*2*) of the type material and analysis of the morphology and evolutionary relationships of *Longisquama*, we reject these proposals for the following two reasons.

First, the supposed row of paired, pinnate "nonavian feathers" that Jones *et al.* describe consists of a single row of elongate scales that are inserted on the dorsal midline. The scales are not branched, as the authors say, but are solid, sheetlike structures with a continuous margin, and the so-called "pinnae" are pleats that helped to stiffen the thin, sail-like distal expansion. Each scale was supported by a solid central spar, and features such as the "hollow remnant of spongy air-filled pith" and "pulp cavities" reported by Jones *et al.* are artifacts resulting from the manner in which the main slab and counter slab split through the sediment that replicated the external surfaces of each scale. Structures identified as "sheath" and "pinnae" are all parts of the same impression of the external surface of the scale. Because of the three-dimensional nature of the animal's body, during the process of its collapse or compaction the proximal regions of integumentary structures experienced much greater disruption than distal regions and became distorted and displaced. Consequently, it is uncertain whether the base of each scale tapers as Jones *et al.* suggest, or whether this is due to distortion or displacement. Even if the scales were tapered proximally, the inference that they developed in follicles is highly speculative.

Second, Sharov's identification of *Longisquama* as a "pseudosuchian" (in other words, a derived archosaur) (*3*) has been followed by other researchers including Jones *et al.* (*1*), but Sharov relied on just two features: an antorbital fenestra and a mandibular fenestra. However, neither of these openings is at all clear in the *Longisquama* skull and could simply represent damage. Moreover, the location of the mandibular fenestra, lying high in the lower jaw, immediately below and behind the

Letters to the Editor

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tooth row, is unusual and unlike the situation in any other archosaur. The known skeletal remains of *Longisquama* lack any other diagnostic archosaurian characters [the furcula mentioned by Jones *et al.* consists of paired clavicles, as Sharov originally noted], but they exhibit two features, acrodont teeth and an interclavicle (*3*), that are typical of lepidosaurs. Consequently, we suspect that *Longisquama* is not an archosaur.

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3. A. G. Sharov, *Palaeontol. J.* **1970** (no. 1), 127 (1970).

Response

RICHARD PRUM SAYS THAT HE "EXAMINED *Longisquama* with the authors in April 1999." Although each coauthor of our report spent many hours over 3 to 4 days studying all the available material [reference 4 in (*1*)], Prum's "examination" (witnessed by all coauthors) consisted of 5 to 10 minutes of cursory perusal of only the main slab. Many of his other statements are equally misleading, or incorrect.

Prum asserts that, rather than being branched as are feathers (*2*), *Longisquama*'s appendages "consist of a membranous blade with a continuous, unfrayed 'ribbon-like margin' and periodic…ripples radiating from a central shaft." This inaccurate view, echoed in statements by Reisz and Dieter-Sues (*3*) and by D. M. Unwin and M. J. Benton in their letter, denies observable facts. In a *Longisquama* feather, the distal vane includes individual, subdivided barbs, some of which were preserved in an overlapped position (Fig. 1). Additionally, the proximal portion is obviously hollow where the retained sheath surrounds the rachis and barbs [see Fig. 3 in (*1*)].

We agree that *Longisquama*-like, fused barbs are known from only a few dozen species of birds; however, Prum implies a causal relation between "overdeposition of melanin or carotenoid pigments" and barb fusion and says "[such specialized feathers] function in communication, not flight." The references he provides do not support that implication, in our opinion, and we have been unable to trace appropriate documentation elsewhere. Whether the fused distal ends of modern feathers function for flight or display is irrelevant. We sought only to document existing knowledge of mechanisms underlying barb fusion. If distal barb fusion can occur in experimentally perturbed avian feathers [see reference 7 in (*1*)], the cellular mechanisms involved can be inferred to be relevant to the morphogenesis of nonavian feathers (*2*).

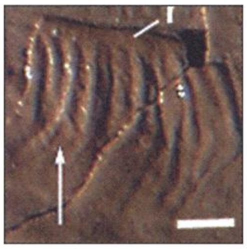

Fig. 1. Detail of the distinct barbs in the distal vane of a feather from *Longisquama* (PIN #2584/5). The arrow indicates where one barb crosses another (r, rachis; scale bar = 1 mm).

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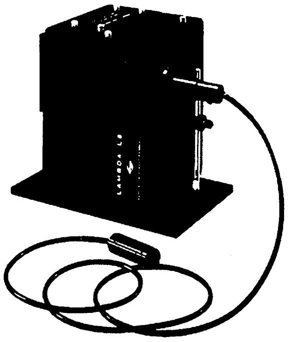
Longisquama's appendages are depositionally transparent because they are so thin, says Prum, unlike fossil avian feathers that "are not transparent because a coherent vane of [more superficial] keratin filaments will obscure the keratin filaments below them (for example, *Archaeopteryx*



remiges)." This is incorrect. The right wing of the Berlin *Archaeopteryx* shows impressions of feathers overlaid by other impressions. As in *Longisquama*, the underlying impressions are visible [see Plate 2, inserts, in (*4*)]. The term "keratin filaments" refers to intracellular organelles resolvable only by transmission electron microscopy; therefore, they play no role in the issues raised here. Prum implies that, whatever their morphology, *Longisquama*'s appendages were not keratinous, whereas in fact, all amniote epidermal appendages consist of keratin (*2*).

Prum contrasts an avian pennaceous feather with a *Longisquama* appendage, saying that in the former, the rachis is created by the fusion of barbs, whereas in the latter, the shaft continues all the way to the distal tip and is not formed by fusion of "pinnae." These statements are not consistent with current understanding of feather development (*2*, *5*). The avian rachis is not formed by fusion of barbs. It derives from the anterior rachidial ridge of the distal epidermal collar to which the proximal ends of developing barb ridges become joined as the feather grows distally. The rachis core may extend to the feather's distal tip, as it does in *Longisquama*. In fact, this explains the distal spangles (that is, expanded rachi) in birds such as cedar waxwings. Prum's questions regarding which end of the ensheathed barbs contacts the rachis arise from his defining "proximal" and "distal" relative to the base of the feather instead of to the rachis.

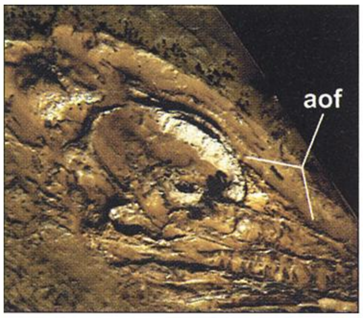


Fig. 2 (left). The skull of *Longisquama* (PIN #2584/4) in right lateral view (aof, antorbital fenestra; overall skull length = 2 cm). **Fig. 3** (right). The furculae of *Longisquama* [above (PIN #2584/4)] and *Archaeopteryx* [below (London specimen)] (scale bar = 1 mm, 1 cm, respectively).

"[T]here is no space for the dermal pulp [in *Longisquama*]," according to Prum, and in questioning our identification of a persistent, proximal sheath (*1*), he describes "the rachis and barbs of an ensheathed [avian] feather [as forming] a tubular epidermal tissue surrounding the central dermal pulp." These statements do not reflect the spatiotemporal complexity of feather development: only immature epidermal cells and tissues ever "surround" dermal tissues (*2*, *5*). In *Longisquama* appendages and avian feathers, the differentiated rachis and vane—sheathed or unsheathed—are solid, and traces of "surrounded" dermal tissues are to be found only in the so-called "pulp cavities" of the tubular calamus (*1*, *2*, *5*).

Prum's statement that "the cylindrical base [of a *Longisquama* appendage] has an obvious, convergent, functional [design for muscle insertion]" supports our interpretation that the structure must have developed in a follicle. Judging from his other comments, perhaps he would agree with us that these muscles would have inserted on the follicle itself and not on the structure that grows therefrom. The formation of avian feathers and mammalian hairs within follicles accommodates a developmental constraint on the cytodifferentiation of complex, keratinous appendages (*2*).

Regarding the letter of Unwin and Benton, they disagree with our conclusion that *Longisquama*'s appendages were paired, featherlike structures. However, beyond repeating assertions (dealt with above) that they are merely elaborate scales, Unwin and Benton offer little specific evidence contradicting our interpretation. Claims that they are merely artifacts of preservation strain credulity, especially given *Longisquama*'s series of detailed, featherlike features (for example, follicularly shaped feather base, calamus, sheath, rachis, and barbs). With respect to questions regarding the midline versus paired distribution of these structures, we note that, as in our report (*1*), Haubold and Buffetaut (*6*) also recognized the paired, bilaterally symmetrical nature of *Longisquama*'s appendages.

Although Unwin and Benton suggest that *Longisquama* was not an archosaur, an antorbital fenestra, the hallmark of the Archosauria, is clearly visible in the counterslab (Fig. 2). Additionally, statements by Unwin and Benton notwithstanding, the interclavicle is retained in a number of archosaurs (for example, *Euparkeria*) and birds, and the furcula of *Longisquama* is virtually identical to that of *Archaeopteryx* (Fig. 3). Because of poor preservation, the exact nature of tooth attachment cannot presently be determined from known specimens. We agree with Sharov, and all previous authors, on the likely archosaurian status of *Longisquama*.

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Bird Song in His Heart

LOVELY PERSPECTIVES ON MUSIC IN ANIMALS, those by P. M. Gray *et al.* and M. J. Tramo (5 Jan., p. 52 and p. 54), but neither mentioned the composer Olivier Messiaen, who recorded bird songs all over the world and transformed them into heavenly music. The "Sermon to the birds" in his opera *St. Francois d'Assise* is perhaps the most wonderful, but you can hear all kinds of birds, transformed into human music, in "Des canyons aux etoiles," or "Le reveil des oiseaux." And, of course, Mozart bought a goldfinch because of its lovely song, listened often to its song, and immortalized it in the last movement of his Piano Concerto in G, No. 17, K. 453. Even allowing for some improvements by Mozart, the song is one of the most charming themes of all his piano concertos. Obviously, the songs of birds and of humans can be transposed from one to the other.

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CORRECTIONS AND CLARIFICATIONS

REPORTS: "NMDA receptor–dependent synaptic reinforcement as a crucial process for memory consolidation" by E. Shimizu *et al.* (10 Nov., p. 1170). In Figs. 2 and 3, the values plotted in the graphs and bar charts were means ± SD (standard deviation), not means ± SEM (standard error of the mean) as stated in the legends.

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