

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 cre-

tiotemporal 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 pre-

vious 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 \pm SD (standard deviation), not means \pm SEM (standard error of the mean) as stated in the legends.

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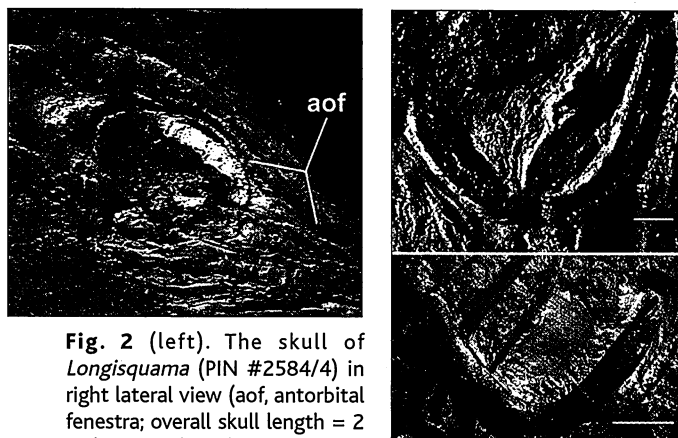


Fig. 2 (left). The skull of *Longisquama* (PIN #2584/4) in right lateral view (aof, antorbital fenestra; overall skull length = 2 cm). **Fig. 3** (right). The furculae of *Longisquama* [above (PIN #2584/4)] and *Archaeopteryx* [below (London specimen)] (scale bar = 1 mm, 1 cm, respectively).

ated 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.

"[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 spa-