Flight capabilities of *Archaeopteryx*

SIR — *Archaeopteryx lithographica* has a mixture of avian and reptilian features and so is not only an important link between two major vertebrate lineages but also offers a key to understanding the evolution of avian flight[1]. Evaluations of muscle power[2] and osteology of the wrist[3] both concluded that *Archaeopteryx* could not sustain powered (flapping) flight, but this is at odds with the asymmetry of its flight feathers, which is indicative of aerodynamic function[4,5]. Here we compare feather vane asymmetry in *Archaeopteryx* with extant birds that fly, glide and are flightless.

Vane asymmetry varies with the position on the feather, the location of the feather in the wing, and the flight capability of the species. Before inferences of flight capability can be made, the other two sources of variation must be controlled. We examined the effects of feather position in wing, and position on the feather, on vane asymmetry in 17 species of flying birds (17 families). The first primary feathers were the most asymmetric (Fig. 1). At the point a quarter of the way up from the feather tip, the high ratio was maintained across the first four primaries; thereafter asymmetry was reduced. In 78 species (78 families) of flying birds (71 species using flapping flight, and 7 that predominantly glide) and 18 species (10 families) of flightless birds, we measured vane asymmetry 25% from the feather tip on the first or second (outermost) primaries (Fig. 2*a–c*). There was extensive asymmetry in the first primaries of both flapping and gliding birds, which was significantly greater than in the flightless birds (either including or excluding aquatic species).

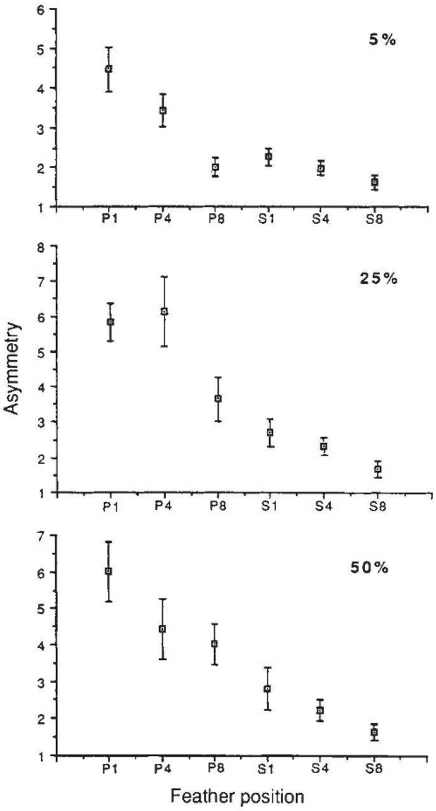

FIG. 1 Vane asymmetry (trailing-vane width divided by leading-vane width) in the wings of 17 species of flying birds drawn from 17 families, as a function of position on the feather (5, 25 and 50 per cent from tip) and feather position in the wing (P1, P4 and P8 represent the first, fourth and eighth primaries, counting the outermost feather as 1, and S1, S4 and S8 represent the first, fourth and eighth secondaries, respectively). Data shown are means plus and minus standard errors. Both feather position in the wing and position on the feather have significant effects on the extent of vane asymmetry. There is no signicant interaction of these effects.

Only three specimens of *A. lithographica* have the feathers sufficiently preserved to measure vane asymmetry: the Berlin and London specimens and the single feather. The single feather has an asymmetry of 2.2 at the 25% point, but where this feather comes from in the wing, and indeed whether it is from the same species, is unknown[6]. In the Berlin and London specimens the feathers are embedded in wings and therefore overlap each other. The distal ends of some of the feathers are sufficiently exposed to make measurements of vane asymmetry at the 25% position from the feather tips. We measured primary feathers 4,5 and 6 of the left wing of the Berlin specimen and primary feathers 3 and 4 from the left wing of the London specimen. Vane asymmetry averaged 1.44 for the London specimen and 1.46 for the Berlin specimen (Fig. 2*d*). The asymmetry in the primary four feathers of *Archaeopteryx* is not significantly different to that of modern flightless birds (t-test, t=0.94, P=0.36) and substantially and significantly lower than that of modern flying birds (whether flapping (t=12.52, P<0.0001) or gliding (t= 5.26, P<0.001). The asymmetry is considerably lower than the lowest value (2.22) at equivalent positions for any flying bird across the 78 different families considered.

The extent of asymmetry in the feathers of *Archaeopteryx* is only slight, significantly lower than in modern flying birds and comparable to that of extant non-flying birds. Our feather asymmetry results are thus consistent with data suggesting that its muscles were insufficient to power sustained flapping flight[2] and that the structure of its wrist could not execute a flapping motion in the wings[3].

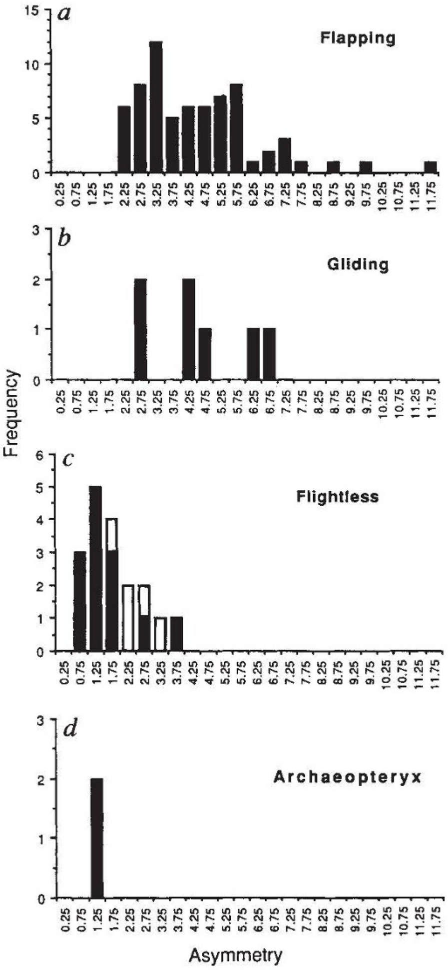

FIG. 2 Frequency distributions of vane asymmetry (trailing-vane width divided by leading-vane width) 25 per cent from the tip of the feather for the first or second primary of *a*, 71 bird species that use predominantly flapping flight *b*, 7 using predominantly gliding flight; and *c*, for 18 species of flightless birds. Data for flightless aquatic birds are shaded; non-aquatic flightless species are unshaded. *d*, Vane asymmetry 25 per cent from the feather tip for the fourth primary of the Berlin and London specimens of *Archaeopteryx*.

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