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8. Hpa II was obtained from Bethesda Research Laboratories. Msp I, purified from Moraxella, sp., was obtained from New England Biolabs. Double-stranded ϕX174, pBR345, and pBR333 were gifts from Drs. A. Razin, J. Kan, and H. W. Boyer, respectively. Reactions with Hpa II took place in 20 m*M* tris-HCl, *p*H 7.4, 7 m*M* $MgCl_2$, 1 m*M* dithiothreitol, and autoclaved gelatin (100 μg/ml); reactions with Msp I took place in 10 m*M* tris-HCl (*p*H 7.1), 10 m*M* $MgCl_2$, 6 m*M* KCl, 1 m*M* dithiothreitol, and autoclaved gelatin (100 μg/ml). Reaction mixtures were incubated for 1 hour at 37°C, and stopped by the addition of one-third volume of 14 percent Ficoll 40 (Sigma), 1 percent sodium dodecyl sulfate, 0.4 percent bromphenol blue, and 0.05*M* EDTA.
9. Mice were supplied by F. Luthardt. DNA was purified [J. Marmur, in *Methods in Enzymology*, S. P. Colowick and N. O. Kaplan, Eds. (Academic Press, New York, 1963), vol. 5, p. 726] with modifications [N. Blin and W. Stafford, *Nucleic Acid Res.* **3**, 2303 (1976)].
10. Five percent acrylamide gels (4.87 percent acrylamide and 0.13 percent bis) were cast and electrophoresis was performed at room temperature in tris-borate buffer (0.05*M*; *p*H 8.3), and 0.001*M* EDTA. Agarose gels (1.1 to 3 percent, depending on the size of DNA to be fractionated) were cast and run in buffer E [tris-acetate (*p*H 7.8), 0.04*M*; sodium acetate, 0.005*M*; and Na_2EDTA, 0.001*M*] [G. S. Hayward and M. G. Smith, *J. Mol. Biol.* **63**, 383 (1972)]. After electrophoresis, gels were stained in ethidium bromide (0.75 μg/ml), for at least 30 minutes, and were then destained in water. They were photographed in long-wave ultraviolet light with a Polaroid MP3 Land camera equipped with a Tiffen 29A red filter. The light source was a Chromato-Vue Transilluminator Model C-62 (Ultraviolet Products, Inc.). Negatives were scanned with a Joce-Loebl microdensitometer.
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Feathers of *Archaeopteryx*: Asymmetric Vanes Indicate Aerodynamic Function

Abstract. *Vanes in the primary flight feathers of* Archaeopteryx *conform to the asymmetric pattern in modern flying birds. The asymmetry has aerodynamic functions and can be assumed to have evolved in the selective context of flight.*

Was *Archaeopteryx* terrestrial or arboreal? Was it able to fly by flapping its wings or by gliding? Description of new specimens of *Archaeopteryx* (*1*) has led to a reevaluation of the ancestry of birds (*2*) and to reassessment of the general behavior of *Archaeopteryx* (*2*). It has been suggested that *Archaeopteryx* was strictly terrestrial and could not fly and that its wing feathers were therefore used, perhaps, as insect traps (*2*). We now present evidence that the primary feathers on the manus of *Archaeopteryx*, like those of modern flying birds, show an asymmetry that can be associated with an aerodynamic function. *Archaeopteryx* was therefore at least able to glide.

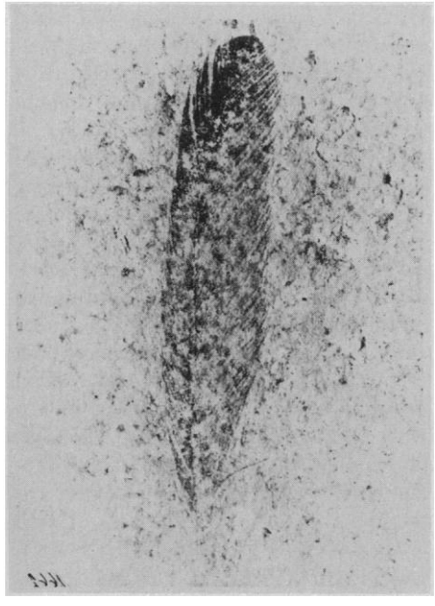

Fig. 1. The counterslab of the isolated feather attributed to *Archaeopteryx* by Hermann von Meyer in 1861. The asymmetric vanes are clearly seen and prove an aerodynamic function; thus, evidence for flight in *Archaeopteryx* has been available for more than 100 years. [Courtesy of Dr. Hermann Jaeger, Humboldt Museum für Naturkunde, East Berlin]

Arguments have been proposed to explain the early evolution of feathers from scales in the context of flight (*3*), heat shields (*4*), and as heat-retaining insulation for endothermic dinosaurs (*2*, *5*). However, the function of feathers on the wings and tail of *Archaeopteryx* can be discussed independently of the origin of feathers (*2*, *4*).

The long, tapered central support of a typical feather is termed the rachis; it separates interlocking barbs on each side which constitute a sheet known as a vane. Typical body contour feathers have symmetrical vanes (or nearly so). Asymmetry in modern birds is strong in the primary wing feathers and is somewhat less pronounced on the secondary wing feathers and usually all but the central pair of tail feathers. The rachis in asymmetric feathers lies toward the leading edge, which is thicker, stiffer, and narrower, rather than at the middle of the feather. Asymmetry is thus found in feathers that have their leading edges in close contact with the flow of air in flight. In some strong flyers, the outer vane is reduced almost to absence. The asymmetry gives each feather an airfoil cross section. In most birds the outer primary feathers function as individual airfoils, each of which produces lift in flapping flight. The asymmetry in the inner primaries, secondaries, and tail feathers stiffens the leading edge of each feather and thus improves the aerodynamic functioning of the wings and tail. Asymmetry also provides differential pressure on the two vanes, acting as "valves" to allow a surface formed by adjacent overlapping feathers to open or close as required by flapping flight.

In the Berlin specimen of *Archaeopteryx* the wings are preserved in a spread posture, and the primaries are clearly asymmetric with the outer vanes reduced as in modern flying birds; the secondary wing feathers and the tail feathers are not so easily seen. However, the first specimen of *Archaeopteryx*, a single feather discovered in 1861, clearly exhibits asymmetric vanes (Fig. 1).

As a test of the hypothesis that asymmetry in primary feathers evolved on the context of an aerodynamic function we have examined the feathers of a variety of birds. In strong fliers such as swifts,

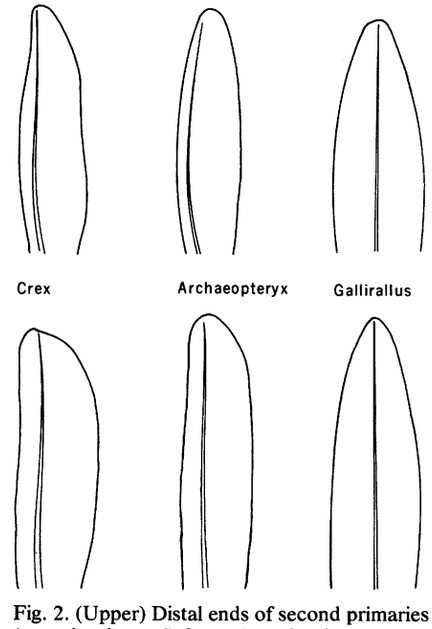

Fig. 2. (Upper) Distal ends of second primaries (counting inward) from the left wings of (left to right) *Crex crex* (a flying rail), *Archaeopteryx*, and *Gallirallus australis* (a flightless rail). (Lower) Similar views of the sixth primaries of the above forms. All drawn to scale.

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falcons, shorebirds, and hummingbirds, the primaries are extremely asymmetric. In poor fliers, such as galliform birds, the asymmetry is less pronounced. Ostriches (*Struthio*) and rheas (*Rhea* and *Pterocnemia*) are flightless and are thought to have evolved from flying birds (*6*). They apparently have retained the wing and flight feathers for display and perhaps for thermoregulation and balance in running. In these birds the vanes of the primaries have reverted to symmetry. In other island birds that have presumably become secondarily flightless more recently (*7*), such as the Kagu (*Rhinochetos jubatus*) and the Brown Mesites (*Mesoenas unicolor*), the rectrices are perfectly symmetric; the primaries show only a slight asymmetry. The flightless Galapagos Cormorant (*Phalacrocorax harrisi*) has nearly symmetric vanes on the primary feathers but has retained asymmetric vanes in the retrices, presumably for a hydrodynamic function, as it swims through the water. Flying species of modern cormorants have asymmetric primary and tail feathers. The flightless grebes *Centropelma micropterum* and *Podilymbus gigas* of Lake Titicaca and Lake Atitlán, respectively, have asymmetric primary vanes but use their wings to some degree. The rails (Rallidae) show the greatest proclivity among modern birds to become flightless, and in this family one sees all degrees of flightlessness and a corresponding diminution in the degree of asymmetry of the vanes of the primaries (*3*) (Fig. 2). Such absolutely flightless rails as *Atlantisia rogersi* and *Gallirallus australis* have perfectly symmetric vanes on the primaries.

The shape and general proportions of the wing and wing feathers in *Archaeopteryx* are essentially like those of modern birds. The fact that the basic pattern and proportions of the modern avian wing were present in *Archaeopteryx* and have remained essentially unchanged for approximately 150 million years (since late Jurassic time), and that the individual flight feathers showed the asymmetry characteristic of airfoils seems to show that *Archaeopteryx* had an aerodynamically designed wing and was capable of at least gliding. Any argument that *Archaeopteryx* was flightless must explain selection for asymmetry in the wing feathers in some context other than flight.

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Capture Enhancement in a Carnivorous Aquatic Plant: Function of Antennae and Bristles in *Utricularia vulgaris*

Abstract. *Traps of the carnivorous hydrophyte* Utricularia vulgaris *Linnaeus (Lentibulariaceae) have structures termed antennae and bristles around their trapdoors that increase their rate of entrapment of the substrate-dwelling prey* Chydorus sphaericus *(Chydoridae, Crustacea). The kind and number of these structures are important in determining capture rate. Experimental data and corresponding behavioral observations support Darwin's hypothesis that antennae and bristles function as a "funnel" leading potential prey toward the trapdoor and their capture by offering the prey a favorable substrate that exploits their natural locomotor and feeding behavior.*

Utricularia, commonly known as bladderwort, encompasses over 250 species, more than any other genus of carnivorous plant, and is distributed throughout the tropical and temperate climates of the world (*1–4*). A member of the family Lentibulariaceae, *Utricularia* is unique among carnivorous plants because of (i) the structural complexity of its traps, thought to be the most intricate in the plant kingdom (*2*), and (ii) the rapid movement of the opening and closing of its trapdoors, by far the fastest-acting botanical trapping mechanism known (15 to 25 msec) (*2, 5*). *Utricularia vulgaris* Linnaeus, the most widely distributed species of bladderwort, is a free-floating hydrophyte common in shallow, still, circumboreal waters, although its range extends into the tropics (*1, 3, 6*). Morphologically, this plant is composed of a central stem from which radiate at various intervals finely dissected leaves (*7*) (Fig. 1A). To each leaf are attached 20 or more traps (Fig. 1B).

A trap or "bladder" is a hollow, egg-shaped structure 0.3 to 5.0 mm long and having a trapdoor at its tapered end (*4*) (Fig. 1C). Darwin, in his classic treatise *Insectivorous Plants*, termed the multicellular, branched extensions arising from the top corners of the trapdoor arch "antennae," and the unbranched, filamentous projections occurring in sets on either side of the door frame "bristles" (*8*). He used these terms, still in use today (*4, 7, 9*), because a trap and its associated structures reminded him of an aquatic microcrustacean. The functional significance of these structures, he proposed, is to guide potential prey to their doom by creating a "funnel" that directs animals toward the trapdoor. This speculation that antennae and bristles provide an adaptive advantage in prey capture has been generally accepted for more than a century (*2, 4, 9*), but to the best of our knowledge has never been experimentally tested.

We now report results from a series of experiments that support Darwin's "funnel" hypothesis. Selective removal of antennae, bristle-sets, or both significantly reduces the rate of capture by *U. vulgaris* traps on microcrustacean prey (Chydoridae, Cladocera). Prey traveling over antennae and bristles are more likely to be captured than those meandering on the surface of the bladder. Because antennae and bristles structurally resemble filamentous algae, a frequent substrate for Chydoridae, they furnish a pathway similar to an algal strand down which these animals graze off epiphytes while being led toward the trapdoor; consequently, these structures substantially increase the probability of prey entrapment.

The action of the trapping mechanism of *U. vulgaris* has been well studied (*2, 5*). A negative hydrostatic pressure maintained within the trap is released when an animal touches one of the trigger hairs at the base of the trapdoor, causing a rapid opening of the door, expansion of the bladder, and inflow of water and prey (Fig. 1D). The door then shuts, and specialized cells within the

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