FUNCTIONAL MORPHOLOGY OF THE VANES OF THE FLIGHT FEATHERS OF THE PIGEON *COLUMBA LIVIA*

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Summary

The functional morphology of feather vanes was examined by combining morphological examination with mechanical tests. A geometrical model was derived which related the in-plane behaviour of the vane to the orientation of the barbs and barbules. This predicted that the small branching angles of both barbs and proximal barbules should result in a vane which is easier to move distally than proximally. These predictions were verified by mechanical tests on primary and secondary feathers of the pigeon *Columba livia*. A further prediction, that the inclination of the barbs' cross section should make the vanes more resistant to forces from below than those from above, was also confirmed by mechanical tests.

Differences in the mechanical behaviour of feathers are related to differences in their morphology and function. The vanes of outer primaries are more resistant to out-of-plane forces than those of the inner primaries and secondaries, particularly towards their tip, a property which will help them withstand the larger aerodynamic forces to which they may be subjected in flight. The outermost primary vane also showed the least asymmetry to out-of-plane forces as a result of the more vertical orientation of its barbs. This may help it to act as a reversible aerofoil during take-off.

Key words: feather, vane, strength, attachment, pigeon, *Columba livia*.

Introduction

The microscopic structure of the vanes of feathers was first observed by Robert Hooke (1665), who found that adjacent barbs of goose quills are linked by two series of barbules which diverge from the proximal and distal margins of the barbs. The barbules on the distal surface of each barb are provided with hooks on their ventral surface which interlock with grooves on the proximal barbules of the next distal barb (Fig. 1). Hooke commented that this arrangement produces a light structure which, because of the large number of points of attachment, is relatively strong and, if broken, may be easily mended by the bird drawing the vane through its bill. Later scientists (Sick, 1937; Nachtigall, 1974) have corroborated this story. The reason for the asymmetry in the flight feathers is also well known (Gordon, 1978); in many flight feathers, the shaft is situated approximately at the quarter chord position, close to the front of the blade, where the aerodynamic forces would be centred if the feather was acting as an independent aerofoil. The shaft will therefore be subjected to bending forces alone and will not be twisted.

However, despite the important aerodynamic function of the vane, the mechanical significance of its geometry seems to have escaped serious study. To minimise weight, simple mechanical models would suggest that the barbs should branch off the shaft at right angles; since their length would be minimised, they would be subjected to lower bending moments and could be made lighter. Real feathers, however, are very different: both the barbs and barbules branch off at acute angles from the shaft and barbs respectively. In the present paper, we develop a model to examine the behaviour of the attachment mechanism of the feather blade when subjected to in-plane movements. This model is then tested by combining mechanical investigations with morphological measurements. The morphological studies further suggest that the mechanics of attachment should affect the out-of-plane rigidity of the vane. This possibility is tested by a second series of mechanical tests.

The geometrical model of vane behaviour

Consider two adjacent barbs branching a distance D apart along the shaft at an angle θ (Figs 2, 3) and which are free to rotate in the plane of the vane about a flexible 'hinge' at their base that prevents them from moving out of the plane. Altering the orientation of both barbs by the same angle will have two effects on their relative positions. (i) As θ increases, the two barbs will slide relative to each other along their length, so that the longitudinal displacement x of the base of the distal barb relative to that of the proximal one is given by the expression:

$$x = D\cos\theta. \tag{1}$$

(ii) As θ rises to 90°, the barbs will get further apart, so that the lateral displacement y of the base of the distal barb relative to that of the proximal one is given by the expression:

$$y = D\sin\theta. \tag{2}$$

These movements will cause a hook on the distal barbule of the proximal barb to move relative to a groove on the proximal barbule of the distal barb in a way that depends on the branching angle ϕ of the proximal barbule (Fig. 3). The displacement L_{pe} of the base of the distal barbule (point A, Fig. 3) perpendicular to the proximal barbule which emerges from the next barb (point B, Fig. 3) is given by the geometrical formula:

$$L_{pe} = D\sin(180 - \theta - \phi)$$
$$= D\sin(\theta + \phi). \tag{3}$$

The perpendicular displacement of the hook of the distal barbule relative to the grooved barbule on the next barb, L_{PE}, is therefore given by the more general formula:

$$L_{PE} = K_1 - D\sin(\theta + \phi), \tag{4}$$

or, expanding the trigonometric expression:

$$L_{PE} = K_1 - D\cos\theta\sin\phi - D\sin\theta\cos\phi, \tag{5}$$

where the first term, K_1, is a constant that depends on the exact position, length and orientation of the barbule, the second term
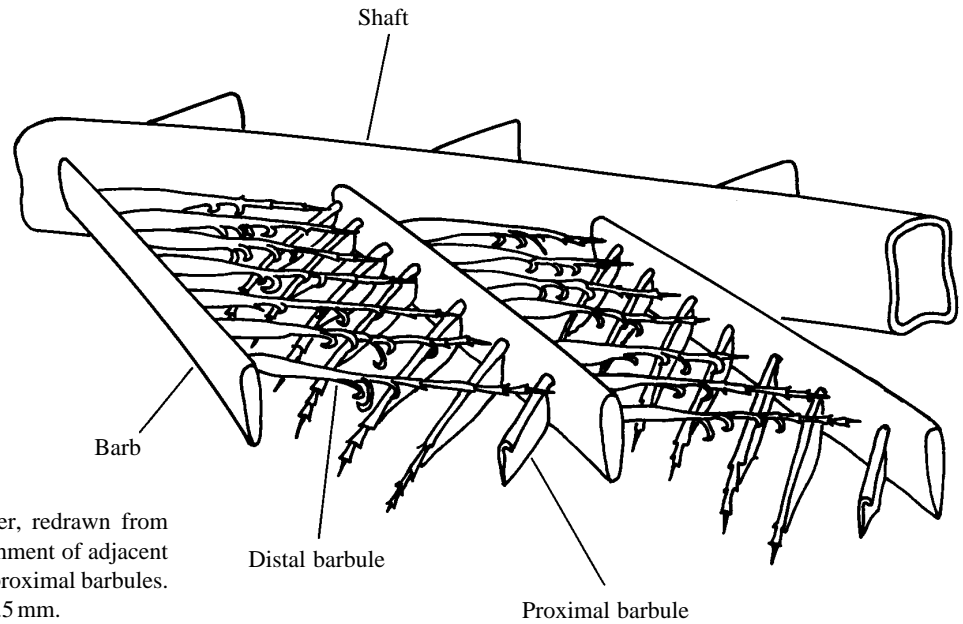

Fig. 1. Structure of a primary flight feather, redrawn from Storer (1943). Note the mechanism of attachment of adjacent barbs; hooked distal barbules grip grooved proximal barbules. Distance between barbs is approximately 0.5 mm.
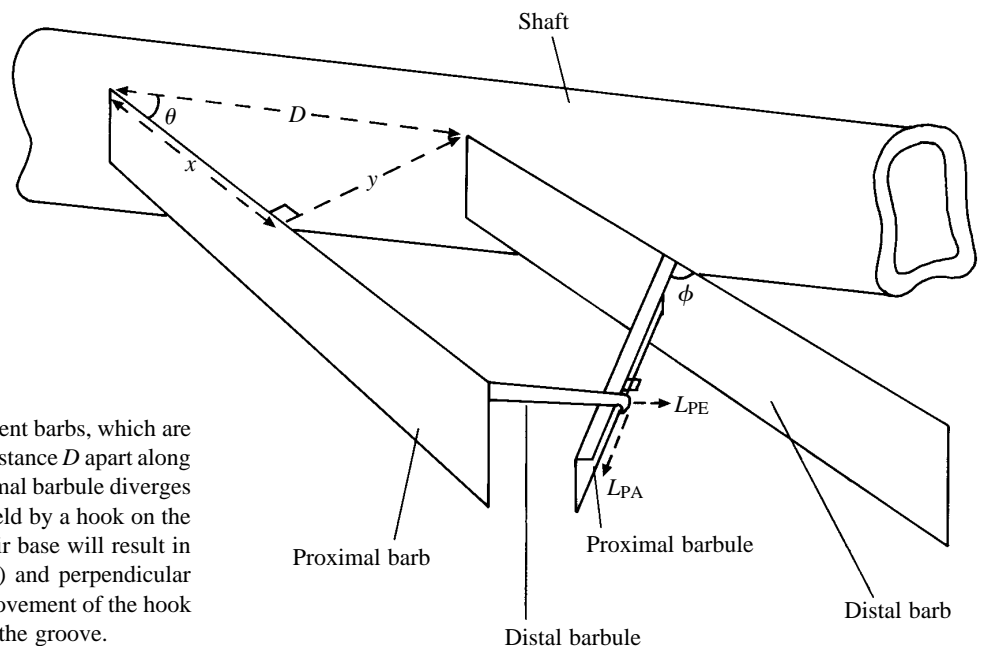

Fig. 2. The geometrical model. Two adjacent barbs, which are free to flex about their base, are placed a distance D apart along the shaft at an angle θ. The grooved proximal barbule diverges fom the distal barb at an angle ϕ and is held by a hook on the distal barbule. Flexure of the barbs at their base will result in changes in their displacement parallel (x) and perpendicular (y) to each other; this will in turn cause movement of the hook parallel (L_{PA}) and perpendicular (L_{PE}) to the groove.
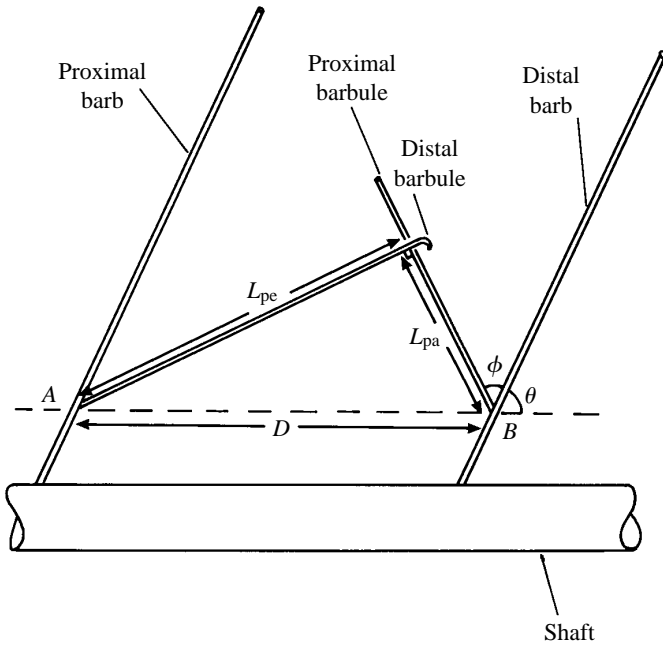
Fig. 3. Details of the model (Fig. 2) showing how the parallel (L_{pa}) and perpendicular (L_{pe}) displacements of the base of a distal barbule relative to the base of the proximal barbule on the next barb can be calculated. A, the base of the distal barbule; B, the base of the proximal barbule.
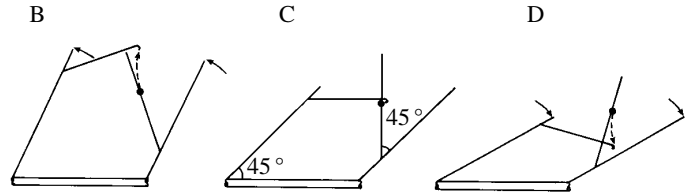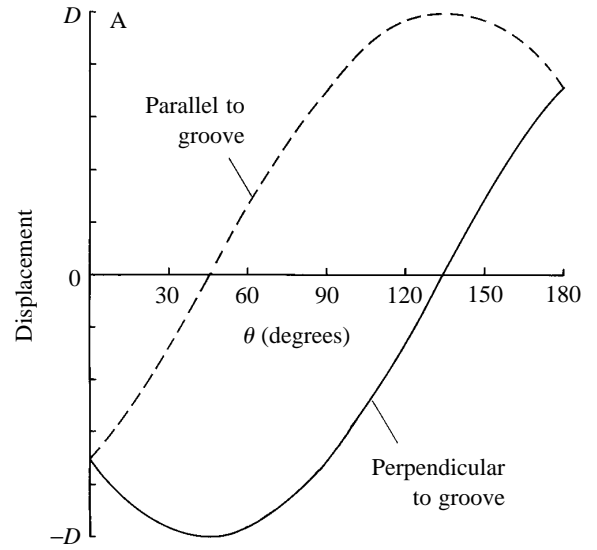

Fig. 4. (A) Displacement of the hook on the distal barbule parallel and perpendicular to a grooved proximal barbule which is oriented at 45° to the barb (ϕ=45°), as the branching angle θ of the barbs is changed. At only one angle, θ=45° (C), does the hook travel parallel to the groove. Rotating the barbs away from this angle (as shown in B and D) will cause the hook to loosen as well as to travel along the groove.

is the displacement due to the sliding of the two barbs, and the third term is due to the separation of the two barbs.

In the same way, the displacement L_{pa} of the base of the distal barbule (point A, in Fig. 3) parallel to the barbule emerging from the next barb (point B, in Fig. 3) is given by the expression:

$$L_{pa} = D\cos(180 - \theta - \phi)$$
$$= -D\cos(\theta + \phi). \qquad (6)$$

The parallel displacement of a hook of a distal barbule relative to the grooved barbule on the next barb, L_{PA}, is therefore given by the more general formula:

$$L_{PA} = K_2 - D\cos(\theta + \phi), \qquad (7)$$

or, expanding the trigonometric expression:

$$L_{PA} = K_2 + D\sin\theta\sin\phi - D\cos\theta\cos\phi, \qquad (8)$$

where K_2 is again a constant that depends on the exact position, length and orientation of the barbule, the second term is the displacement due to the sliding of the two barbs, and the third term is due to the separation of the two barbs.

The relative displacements of the hook and groove are shown in Fig. 4A for the case in which barbules are orientated at 45° to the barb (ϕ=45°). It can be seen that there is only one point, θ=45° (Fig. 4C), at which movement of the barbs causes no perpendicular displacement of the hook relative to the groove. In this case, the hooks will slide parallel to the restraining grooves, so that as θ is increased, the hooks will move towards the tip of the grooved barbules (Fig. 4B), and as

θ is decreased the hooks will move towards their base (Fig. 4D). At 45°, the overlap of hooks and grooves is maximal so that rotation of the barbs away from 45° will eventually also cause the hooks to loosen on the barbules (Fig. 4B,D).

Such an arrangement, with both barbs and barbules branching at 45°, will therefore allow the barbs to rotate freely both distally and proximally without risk of becoming detached from each other. The feather vane which resulted from this design would be flexible to in-plane movements in both directions.

This two-way flexibility can also be achieved even when the barbules diverge at angles of ϕ other than 45°. In this case, however, the barbs must also be arranged at a different angle so that rotation of the barbs results in motion of the attaching hooks parallel to the barbule grooves over which they hook. This will occur only when perpendicular movement is zero, that is when $dL_{PE}/d\theta$=0. Differentiating equation 5, therefore, gives:

$$dL_{PE}/d\theta = D\sin\theta\sin\phi - D\cos\theta\cos\phi = 0, \qquad (9)$$

$$\sin\theta\sin\phi = \cos\theta\cos\phi, \qquad (10)$$

$$\sin\theta/\cos\theta = \cos\phi/\sin\phi, \qquad (11)$$

$$\tan\theta = \cotan\phi. \qquad (12)$$

Therefore, for angles of θ less than 90°, θ and ϕ are related by the expression:

$$\phi = 90 - \theta,$$

$$\theta + \phi = 90°. \tag{13}$$

So, if the barbules diverge at a high angle from the barbs, the barbs must diverge at a low angle from the shaft and *vice versa*. The proximal barbules will then be oriented perpendicular to the feather shaft.

What happens if the sum of the two angles is not 90°? If both barbs and barbules diverge at a large angle, so that $\theta+\phi>90°$, the barbs will be free to rotate proximally towards the base of the feather, so that θ increases; however, movement in the other direction will be prevented since the hooks will tighten on the grooves. Similarly, if both barbs and barbules diverge at a small angle, so that $\theta+\phi<90°$, the barbs will be free to rotate distally towards the tip of the feather so that θ decreases; however, movement in the other direction will be prevented by tightening of the hooks.

The in-plane behaviour of a feather vane will therefore depend crucially on the orientation of its barbs and barbules. For these reasons, it was decided to concentrate morphological investigations on the geometry of the vane and mechanical investigations on the resistance of the vane to inward and outward motion.

If the barbs are mounted on the shaft with the long axis of their cross section sloping, rather than vertical as shown in Fig. 1, the in-plane behaviour of the vane may also affect its out-of-plane behaviour; proximal and distal movements of the barbs would also result in dorsal and ventral movement of the vane. For this reason, it was also decided to investigate the attachment angle of the barbs and the resistance of the vane to upward and downward movement.

Materials and methods

The practical work was carried out on feathers from both wings of three pigeons *Columba livia*. The ten primary feathers (nine in one animal, which was moulting) were studied, together with the four outermost secondaries. Primaries are here numbered from 1 (the innermost) to 10 (the outermost), while it is the *outermost* secondary which is number 1 (Spearman and Hardy, 1985).

Geometry of the vane

The feathers of the left wing of one bird were removed from the wing. Any tears in the vanes were mended and the vane was smoothed out between the fingers to produce an aerodynamically 'perfect' feather. The length of the vane was measured and each was marked at one-quarter, half and three-quarters of the distance from the base to the tip. These points will be called the 'base', 'middle' and 'tip' respectively. Individual feathers were then examined under a binocular dissecting microscope fitted with a protractor graticule supplied by Graticule Ltd. This graticule was used to determine the following measurements. (i) The branching angles θ, at the
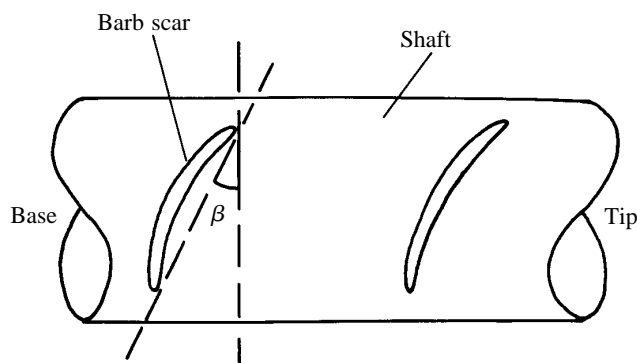

Fig. 5. Diagram showing how the angle of inclination β of a barb was measured, after removal, from the scar at its join with the shaft.

point of their attachment to the shaft, of barbs from both the leading and trailing edge, branching from the base, middle and tip of the feather. (ii) The branching angles ϕ of the proximal grooved barbules at their point of attachment to their barbs at the base, middle and tip of the feather. It was found that ϕ was constant all the way along any one barb. (iii) The inclination β of the barbs at their attachment to the shaft. All the barbs were shaved off the shaft using a single-edged razor blade and the angle of inclination of the scar left by the barb (Fig. 5) was measured at the base, middle and tip of the vane. For four feathers, primaries 2, 6 and 10 and secondary 3, the angle was also measured at 10 mm intervals from the base of the blade.

The shapes of the barbs and barbules of each vane were also examined qualitatively, both under the dissecting microscope and using a scanning electron microscope.

Mechanical tests

In-plane movements

It was impractical to measure the resistance of the entire leading edge and trailing edge vanes to proximal or distal motion. Instead, it was decided to examine the resistance of 20 mm long sections of the broader trailing edge vane at the base, middle and tip of primaries 5 and 9 and secondary 2. It proved impractical to perform similar tests on the narrower leading edge vanes.

Each feather was cut into basal, middle and tip segments and all but a 20 mm length of the trailing edge vane around the one-quarter, half and three-quarter points along the shaft was removed with a single-edged razor blade. These vanes were then subjected to two mechanical tests using an Instron universal testing machine. In the first test, the vane was pulled *distally*. The feather was mounted with the shaft pointing obliquely upwards and the barbs pointing at an angle of 20–30° below the horizontal (Fig. 6A). The distal trailing edge of the vane was then attached to the crosshead of the Instron *via* the head of a rubber-jawed clamp which gripped the vane gently. The vane was then pulled upwards by the clamp at a rate of 20 mm min^{-1}, so bending the barbs distally. The force generated was measured by a 100 N load cell and a force/displacement graph was calculated by an interfacing

A
Leading edge vane

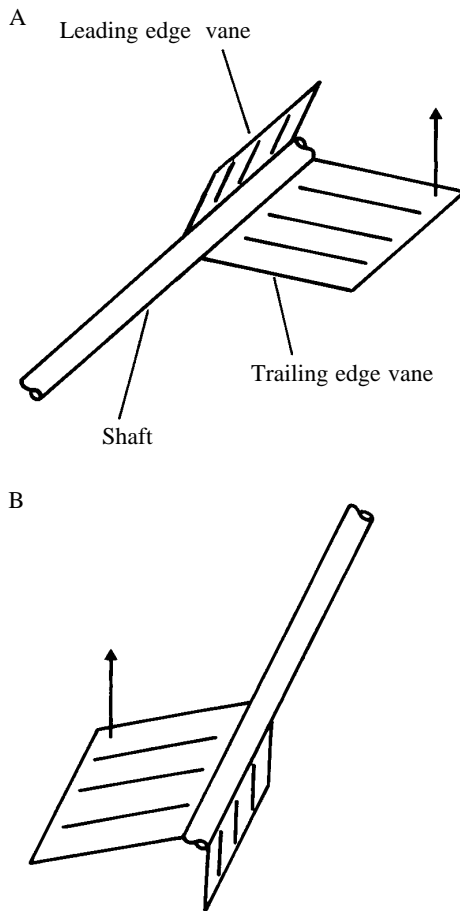Trailing edge vane

Shaft

B

Fig. 6. The orientation of the feather vanes for the in-plane mechanical tests. (A) Orientation for the tests in which the vane was pulled distally. (B) Orientation for tests in which the vane was pulled proximally. The arrows show the direction in which the vane was pulled. The clamps in which the shaft is held are omitted for clarity.

computer. When the distal barbs had been rotated by approximately 30°, the test was stopped and the feather removed. The second test, in which the vane was pulled *proximally*, was carried out in the same way, but the feather was inverted (Fig. 6B) and the clamp was attached to the proximal trailing edge of the vane. The test was continued until failure of the vane occurred.

Out-of-plane movements

The resistance of different regions of feather vanes to both upward and downward forces was also measured using the Instron machine. The complete feather was clamped with the trailing edge vane horizontal. An aluminium probe of length 30 mm and end diameter 3 mm was then attached to the load cell of the Instron and lowered until it just touched the feather vane, with its long axis exactly half way between the shaft and the trailing edge (Fig. 7). The probe was then lowered at a rate of 20 mm min^{-1}, while the force generated was measured by the 100 N load cell and a force/displacement graph was calculated by the interfacing computer. The test was continued until the vane failed and the force required fell, the applied load
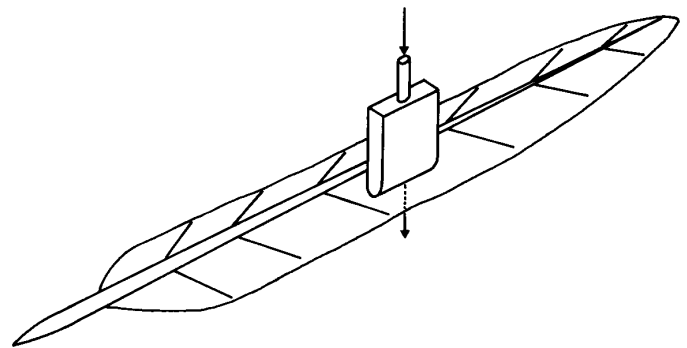

Fig. 7. The apparatus used for the mechanical tests on the out-of-plane behaviour of the feather vanes. The clamps in which the shaft is held, positioned on either side of the probe, are omitted for clarity. The arrows show the direction in which the vane was pushed.

having very crudely mimicked aerodynamic forces. The probe was then raised clear of the vane, which was mended by smoothing between the fingers before the test was repeated. Each feather from the moulting pigeon was tested, the resistance being measured at three positions on each feather, at the base, middle and tip, and against forces acting on both the dorsal and ventral surfaces. Three tests were performed at each position in each direction. Tests were limited to the trailing edge vane alone because camber of the leading edge vane caused the probe to slip off the blade when forces were applied from above, without causing it to fail. It would not, therefore, have been possible to compare the resistance of the leading edge vane to forces from below and above.

Results

Morphology and geometry of the vane

Basic morphology

In most respects, the morphology of the feather vanes was identical to that shown in Fig. 1. However, there were some important differences in the morphology of both barbs and barbules from the 'text-book' diagram.

The barbs differed in two respects (Fig. 8). First, they were not all attached with the long axes of their cross sections vertical. Particularly, near the base of the feather, the dorsal edges of the attachments were further from the base of the shaft than the ventral edges so that the barbs 'leaned outwards'. Second, the barbs did not have a symmetrical cross section. Instead, they were cambered, particularly on the leading edge vanes of the primaries, their distal surface being concave and their proximal surface convex.

The proximal grooved barbules (Fig. 8) also differed from the structure shown in Fig. 1. Rather than being straight, the tips of these barbules curved towards the barb to which they were attached until they ran nearly parallel to it.

Geometry

The mean branching angles of the barbs, θ, and proximal grooved barbules, ϕ, are shown in Table 1 for both leading and

Fig. 8. The structure of the trailing edge vane of a pigeon primary feather. The structure differs in three ways from that shown in Fig. 1. The barbs are inclined from the vertical and cambered in cross section and the proximal barbules curve near their tip. This structure facilitates distal and ventral movement of the blade (arrows) and helps prevent proximal movement and detachment of the barbules. Distance between barbs is approximately 0.5 mm.

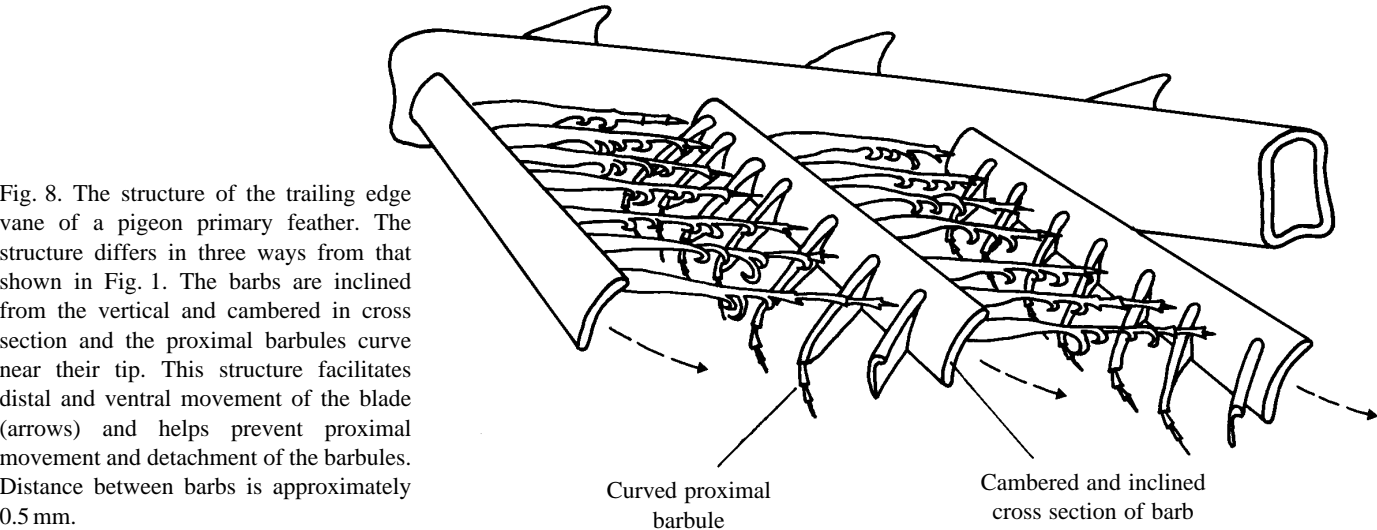Curved proximal barbule

Cambered and inclined cross section of barb

Table 1. *Mean branching angles of barbs θ and proximal barbules, ϕ, from three points on the leading and trailing edges of 14 flight feathers*

	θ (degrees)	ϕ (degrees)
Leading edge	29.6±10.2	28.0±2.9
Trailing edge	41.4±6.1	30.1±2.2

Values are mean ± S.D. for all three points ($N=42$).

Fig. 9. Branching angles θ of leading edge barbs (θ_L, squares) and trailing edge barbs (θ_T, circles) at three different positions along the feather. Mean ± S.D. for ten primary and four secondary feathers. Leading edge barbs, on average, diverge at a lower angle than trailing edge barbs, and barbs also branch off at lower angles nearer the tips of each feather.

trailing edge vanes. There was very little variation in ϕ of the barbules; values were similar for leading edge and trailing edge vanes and there were no significant differences between feathers. In contrast, there were marked differences both within and between feathers in θ. (i) θ decreased towards the tip of each vane (Fig. 9), except in the leading edge of the outermost primary where it remained constant. (ii) The leading edge barbs had lower values of θ than the trailing edge barbs (Figs 9, 10). This was a major reason why the leading edge vane was narrower than that of the trailing edge. This was particularly marked on the outer primary feathers (Fig. 10), which showed the greatest degree of vane asymmetry.

However, despite these trends, the angles θ and ϕ were always low so that in all cases $\theta+\phi<90°$, the lowest values
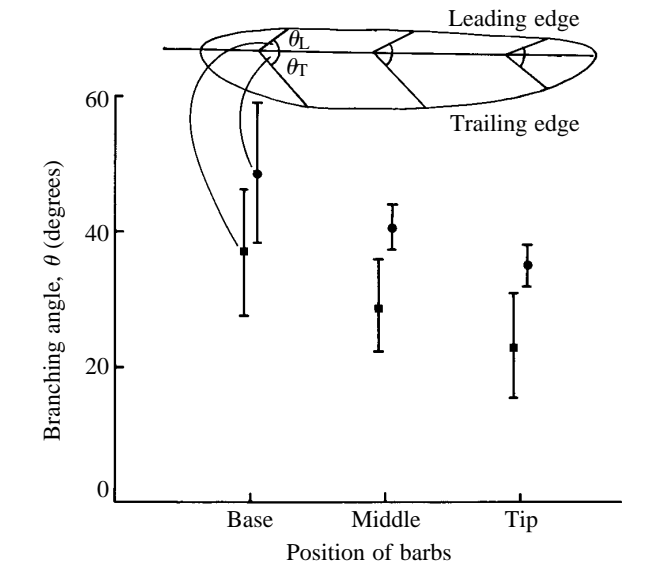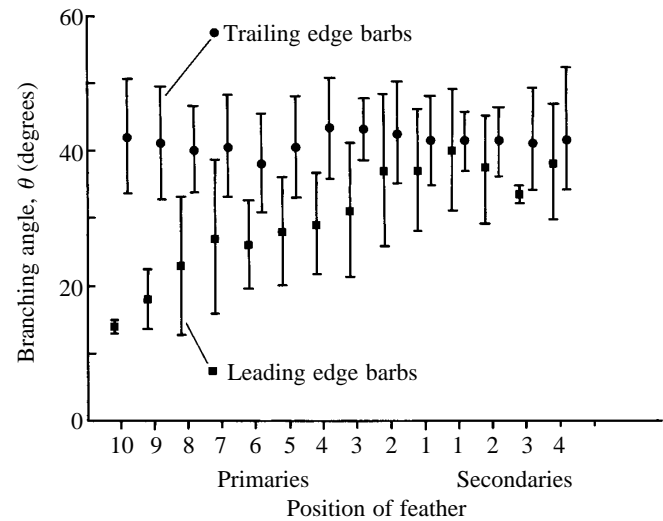

Fig. 10. Branching angles θ of leading edge barbs (squares) and trailing edge barbs (circles) of each feather. Mean ± S.D. for three different points on each feather ($N=3$). Branching angles of trailing edge barbs are similar for all feathers, but the leading edge barbs of outer primaries diverge at lower angles than those of the inner ones.
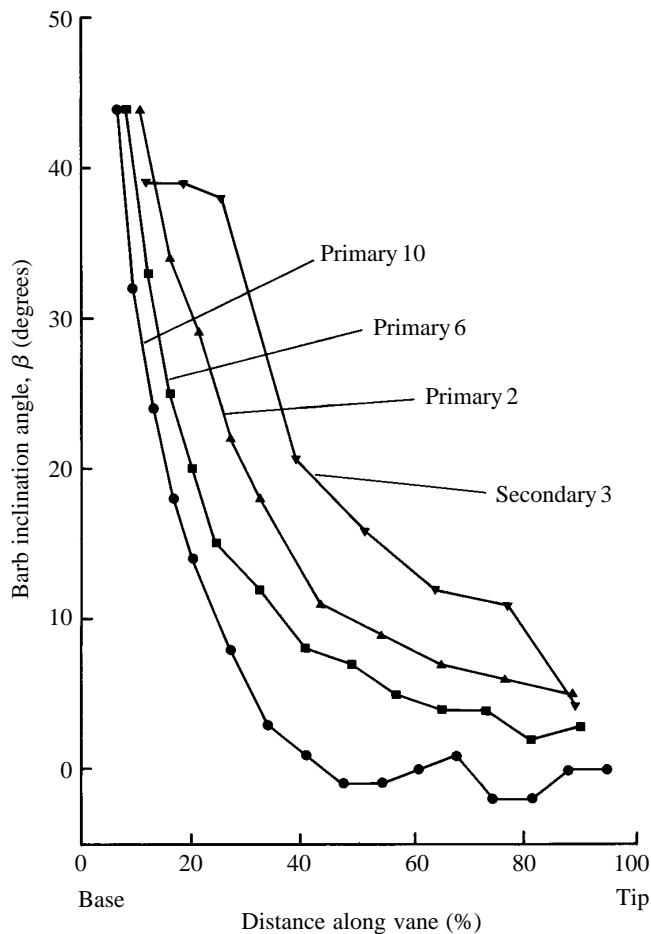
Fig. 11. The angles of inclination β of barbs along four feathers: primaries 10, 6 and 2 and secondary 3. It can be seen that β rises towards the base of each feather and is higher in inner primary and secondary feathers than in outer primary feathers.
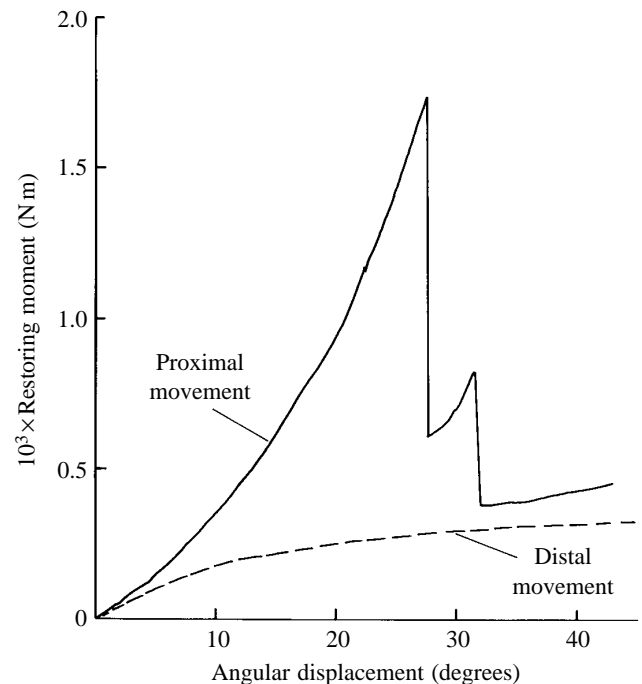

Fig. 12. Graph showing the moment resisting angular in-plane displacement of the tip section of the trailing edge vane of primary 5. Broken line shows distal movement; solid line shows proximal movement. Proximal movement of the vane is much more strongly resisted than distal movement and the vane eventually fails as adjacent barbs split apart. As this happens, the force drops suddenly (solid line).

occurring in the leading edge vane and towards the tip of each feather. The model of vane behaviour would therefore predict that distal movement of the vane should be easier than proximal movement, particularly towards the tip of each feather and in the leading edge vane.

The angle of inclination β of the trailing edge barbs at their attachment with the shaft varied both with their position and with the feather to which they were attached (Fig. 11). β was highest towards the base of each feather ($F_{12,38}=4.37$, $P<0.01$) and on the inner primaries and secondaries ($F_{2,38}=55.1$, $P<0.001$). These differences should affect the behaviour of the vanes in response to out-of-plane movements.

Mechanical tests

In-plane movements

All the feathers tested showed similar mechanical behaviour in response to in-plane movements of the vane. When each vane was pulled distally, proximal regions of the vane showed less movement than at the clamp. No failure of the vane was seen, and the force generated rose only slowly before levelling off at a low value (Fig. 12). In contrast, when the vane was

pulled proximally, distal regions showed just as much movement as at the clamp and the force rose sharply. Eventually, failure of the vane occurred, two barbs splitting apart near the clamp; the distal part of the vane returned to its resting orientation and the force generated fell sharply (Fig. 12). Proximal movement was resisted by a moment (force multiplied by the distance of the clamp from the base of the barb to which it was attached) which was maximally 3.77 ± 2.49 (mean $\pm$ s.d., $N=3$) times larger than that resisting distal movement. There were also marked differences in resistance between and within the feather vanes (Fig. 13). The basal region of each vane had less resistance to in-plane movements than the middle and the tip, while the vanes of the primary feathers had greater resistance to in-plane movements than those of the secondaries.

Out-of-plane movements

The force/deflection curves obtained from the out-of-plane tests were similar in all cases: the force rose linearly at first, before levelling off after the vane had been moved around 30° and falling as the probe subsequently slipped past the vane. However, there were significant differences in resistance to out-of-plane movement between the vanes of different feathers and between different regions of each vane (Fig. 14). The vanes of outer primaries resisted the greatest moments (force multiplied by distance of the probe from the shaft), followed
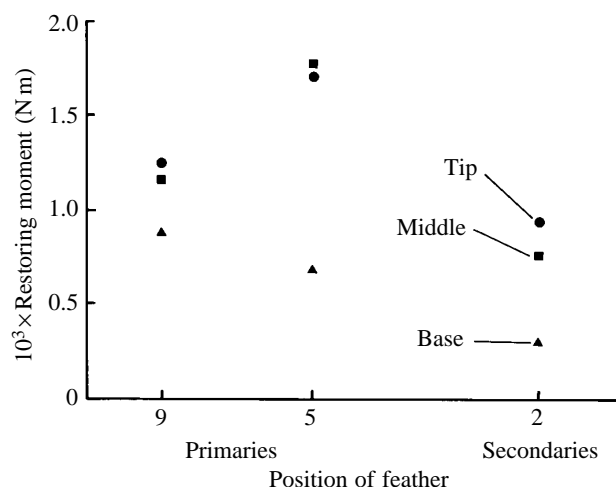
Fig. 13. Maximum resistance of regions of three feather vanes to proximal movement. Circles, tip of feather; squares, middle; triangles, base. Basal regions and the secondary feather show least resistance.

by the inner primaries and the secondaries. The middle and tip regions of each vane also resisted greater moments than the base. There were also differences between and within vanes in their relative resistance to forces on the dorsal and ventral surfaces (Fig. 15); vanes generally resisted greater forces on the ventral surface than on the dorsal surface, particularly at the base of inner primary and secondary feathers. These differences appeared to correlate with differences in the movements of the vanes; in response to forces on the dorsal surface, the vane moved as a unit, each barb moving not only ventrally but also distally. In response to forces on the ventral surface, in contrast, individual barbs tended to twist and buckle, causing some separation of the barbs during their dorsal movement.

Discussion

The results given above show that the mechanical behaviour of feather vanes corresponds well with the predictions of the geometrical model. Since the branching angles of the barbs θ and proximal barbules ϕ are both relatively small, theory predicts that the vane should be more readily moved distally than proximally, as proximal rotation will loosen the hooks in their grooves. This is just what happened; distal movement hardly disturbs barbs which are proximal to the clamp and requires a lower moment than equivalent proximal movement, which results in eventual failure of the vane. Resistance to proximal movement is probably further enhanced by two factors: the curvature of the proximal barbules, which will help prevent the barbule hooks on the distal barbules from slipping off their ends, and the cambered cross section of the barbs, which will make them more resistant to bending proximally than distally. This effect has been previously noted for the shafts of feathers (Purslow and Vincent, 1978), the channel veins of some insects (Wootton, 1981) and the petioles of herbaceous plants (Wainwright *et al.* 1976).
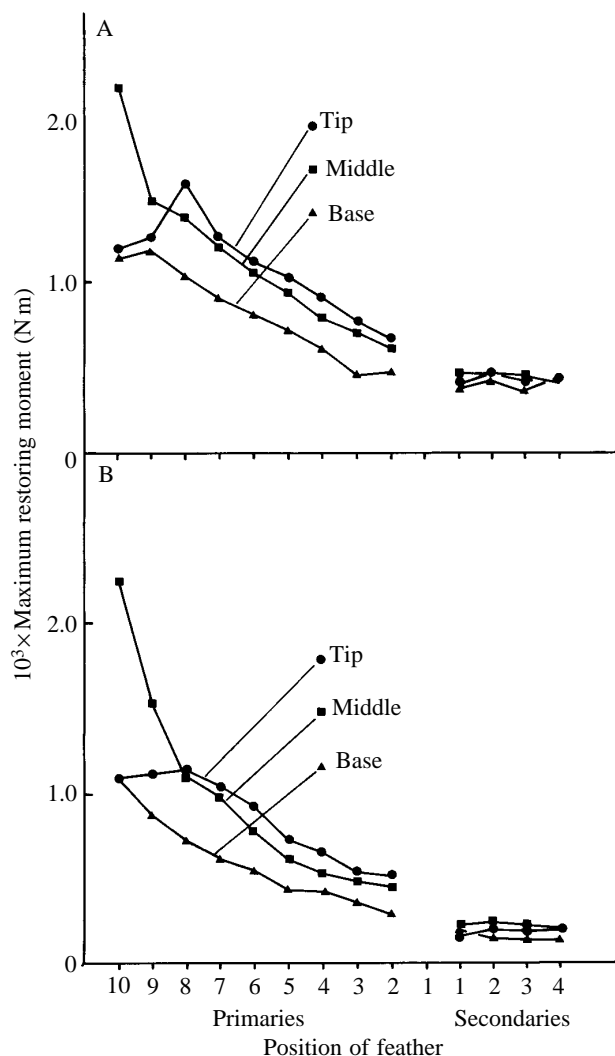

Fig. 14. Resistance of basal, middle and tip regions of trailing edge vanes to out-of plane motion. (A) Resistance to forces on the ventral surface and (B) to forces on the dorsal surface. Outer primaries are stronger than inner primaries and secondaries; and the middle and tip of each feather tends to be stronger than its base.

This asymmetry to in-plane behaviour should also influence the relative resistance of the vanes to forces on the dorsal and ventral surface because, in most feathers, the barbules are attached obliquely to the shaft. Distal movement of the vane will therefore result in its automatic lowering and *vice versa*, while proximal movement will result in automatic raising of the vane. In response to forces on the dorsal surface, therefore, a vane should move downwards easily, the barbs rotating distally from their base (Fig. 8). This is precisely what was found in the mechanical tests. In contrast, a force on the ventral surface should be strongly resisted since this would involve proximal rotation of the barbs. In practice, barbs tended to become separated and to twist near their base before upward movement occurred. The result was marked asymmetry to forces from above and below, as predicted. This asymmetry tended to be greater towards the base of inner primary and secondary feathers, regions where the barbs were attached
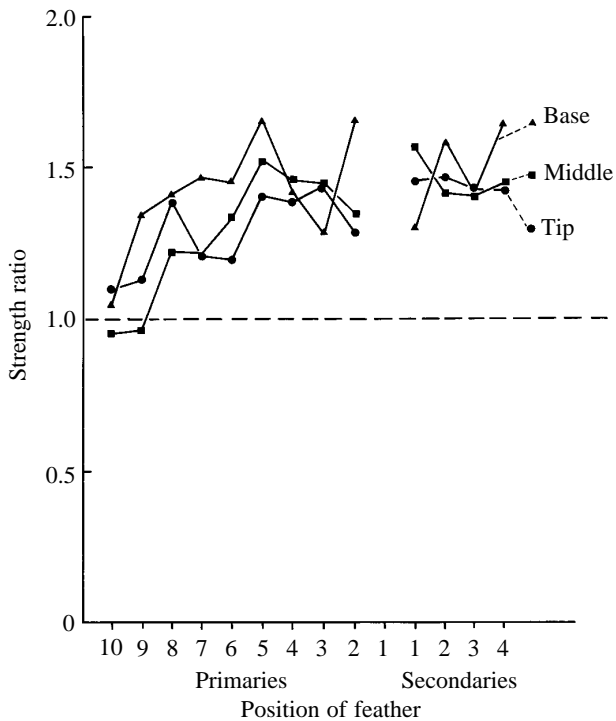
Fig. 15. Graph showing strength ratios of the basal, middle and tip regions of trailing edge vanes. This is the ratio of the resistance to forces from below to those from above. Most feathers resist forces from below more strongly, particularly near their base. The exception is the outermost primary, which resists both forces approximately equally.

most obliquely. A good correlation was found between the ratio of resistances to forces from below and from above and the angle of inclination β of the barbs (r_{39}=0.497, P<0.01), as the model would predict.

So what is the functional significance of these asymmetries in responses of the feathers? One benefit of the asymmetry of in-plane behaviour may be that it allows a bird to smooth its feathers by simply drawing them through its bill from their base to their tip. Adjacent barbs will thereby be drawn together without any chance of breaking up the vane. A further benefit of the in-plane asymmetry is that it allows the out-of-plane asymmetry in bending resistance; the feather vanes are therefore made more resistant to upward aerodynamic forces, to which they are likely to be subjected, than to downward forces.

However, we also found marked differences both between and within feathers in their morphology and mechanical behaviour, differences that it is possible to relate to the different loading conditions they are likely to encounter. The vanes of outer primary feathers, which will be subjected to higher aerodynamic loads during the downstroke in flapping flight, can resist larger out-of-plane forces than the inner primaries and secondaries. The middle and tip of each feather vane can also resist larger out-of-plane forces than the base, which will be protected by covert feathers in life. Undoubtedly, much of the difference between feather vanes resulted from the different amounts of structural material they contained; the

vanes of the outer primary feathers had larger, stronger barbs than those of the inner primaries and the secondaries. However, the vanes of the outermost primary feathers also exhibited qualitatively different behaviour from those of the other feathers because of differences in the orientation and morphology of the barbs. The low branching angles of the leading edge barbs helped to produce the great degree of planform asymmetry in these feathers, which correlates well with their function as independent aerofoils during take-off and landing. The leading edge barbs are furthermore very stiff and highly cambered, which will help prevent them detaching when the feather is pulled through the air. Most intriguingly, however, the trailing edge vanes of the outermost primaries have more symmetrical responses to out-of-plane forces than the other feathers, a fact which results from the near vertical orientation of the cross sections of their barbs. This symmetry may have arisen because the tips of the wings of pigeons can be twisted so that these feathers are reversed and may be used to produce lift on the upstroke during take-off (Dathe and Oehme, 1978; Simpson, 1983), though this has not been verified by investigations of the wake of slow-flying pigeons (Spedding *et al.* 1984). Consequently, they may receive aerodynamic forces on their morphological dorsal surface as well as on the ventral surface and may have evolved to withstand equally large forces from above as from below.

Several conclusions can therefore be drawn from this work but, as a preliminary investigation, it also points the way for further work. It is clear that the vanes of the flight feathers of the pigeon are mechanically competent lattice frameworks whose behaviour is controlled by their geometry, giving a structure which combines lightness, flexibility and mechanical competence. This gives a sound basic mechanical design which allows them to resist the aerodynamic loads they encounter, while facilitating maintenance. Furthermore, the vanes of no two feathers are the same: the geometry of each appears to be adapted to its own particular aerodynamic function. However, to test some of the suggestions we have put forward in this discussion, it would clearly be desirable to investigate a wider range of feathers, including covert, contour and tail feathers. It would also be important to study a wider range of birds, ranging from gliding specialists, such as gulls and swallows whose wings are subjected to aerodynamic forces only from below, to hovering specialists, such as hummingbirds whose wings must withstand forces from both below and above. It might then be possible to obtain a fuller understanding of the functional morphology of feather vanes.

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