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2 *The flight apparatus*

2.1 *Introduction*

Birds are unique because they use feathered front legs as wings. The basic quadruped organization is modified to accommodate the needs required by the special function. Natural selection sacrificed other functions of the arms and hands during the evolutionary process. The whole body plan was reshaped resulting in a bipedal organism with completely decoupled anterior extremities.

Ornithological textbooks usually provide overviews of the anatomy of birds in general and of the flight apparatus in particular. An elaboration of the same here would be superfluous. Instead, brief summaries of flight-related anatomical aspects will be given together with some insight into the relations between form and function and in the variation among groups. The aim is to find out what the apparatus tells us about how birds fly.

Wings will receive most of the attention. There are as many different wings as there are bird species and any classification into a limited number of functional groups only reduces the interesting complexity. Understanding the relation between form and function demands detailed attention for the specific wing structure of each species. On the other hand, wings of all flying birds have important common features: they all consist of an arm and a hand part. The basic construction of the internal and external wing will be described first. Insight into the internal and external anatomy of wings is needed to understand the principle movements allowed by the structural constraints. Wings must be folded and stretched as well as be moved up and down and rotated fore and aft. Bird wings have been the subject of many scaling exercises and it is good to know the main conclusions from these studies without attempting to go into the details of the numerical analyses. Aristotle had already found out that a bird without wings cannot fly, but which parts of the wings are absolutely necessary to allow take-off and flight? Experiments with mutilated wings of live birds have a long history and we will see if the results obtained increase our insight in the function of bird wings.

Hummingbirds and swifts deviate so much from that basic pattern that their wing design receives a separate paragraph. For the same reason the long slender wings of albatrosses and giant petrels require special treatment.

Tails are the next dominant intrinsic parts of the flight apparatus. The internal anatomy and the outer shape have flight-related features and we must try to find out how much of it is understood.

Not only the wings and the tail but also the head, the neck, the body, and the hind limbs have features directly related to flight in many species. Some obvious ones will be discussed.

Feathers are crucial in relation to flight since they determine to a large extent the shape of the bird including the main parts of its flight apparatus. Detailed

treatment of the knowledge about the structure, function, and mechanical properties of the main flight feathers requires a separate chapter that will follow this one.

2.2 *Wing morphology*

The basic structure of wings in general must be treated first before deviating patterns can be distinguished. Internally bird wings have a modified quadruped arm skeleton; on the outside the shape is uniquely determined by feathers, the hallmark structure of birds. Variation on the general pattern can be large and is illustrated by groups containing the smallest and the largest extant birds.

2.2.1 Internal wing design

Wings have to be both strong and light. Strong because they have to exchange forces with the air. During flapping flight the oncoming air flow is deflected and air is accelerated by the wing action. Wings must also be able to receive the reactive forces from the air and transmit these to the body. They must be light to reduce inertial forces during various phases of the wing beat cycle, but in particular during the acceleration phase of the downstroke when the wings are fully stretched. Therefore, the amount of heavy tissue such as muscles and bones decreases towards the tip.

The schematic drawing of Fig. 2.1 shows the approximate position and the names of the main internal parts of a wing. (Appendix 3 explains the meaning of the scientific names and jargon.) The design enables the wings to flap up and down and to fold and extend. Wings are connected to the body at the shoulder joint where the proximal condyle of the humerus, the *caput humeri*, articulates in the glenoid cavity formed by the scapula and the coracoid. The coracoid is firmly connected to the sternum, and its length determines the distance between the shoulder joint and the sternum. Paired clavicles are fused to form the wish-bone (the *furcula*), which is attached to the dorsal parts of the left and right coracoids. The sternum of flying birds has a central bony keel, the *carina*. Ribs, vertebral column, and the sternum form a closed cage. The main flight muscles, the *pectoralis* and the *supracoracoideus*, have their origin on the sternum, on the *carina* and on the coracoid. The *pectoralis* inserts from below on the anterior crest of the humerus. It pulls the wing down and causes forward rotation (pronation) of the wing during the downstroke. The *supracoracoideus* is situated underneath the *pectoralis*. It forms a tendon which passes through the *triosseal canal* in the shoulder joint to insert on the dorsal tubercle on the upper part of the humerus, approaching the insertion from above. The *triosseal canal* is formed either by the scapula, the coracoid and the *furcula*, by the scapula and the coracoid, or even by the coracoid alone. The canal forms an important anatomical feature because it acts as a pulley to make it possible that the *supracoracoideus* contributes to lifting the wing. Together with a few other small muscles the *supracoracoideus* is responsible for the upstroke and for the rearward rotation (supination) of the wing during the upstroke or prior to landing.

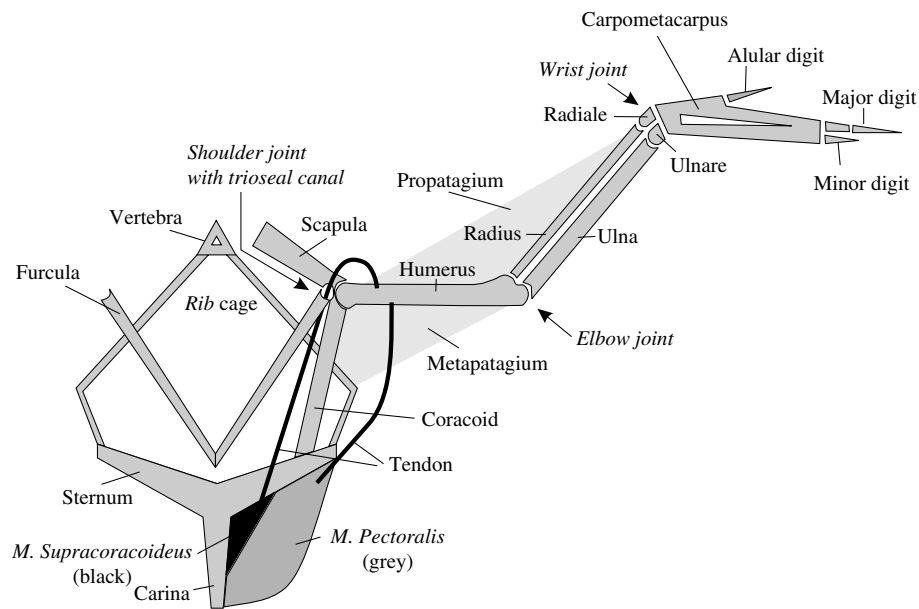


Fig. 2.1 Schematic overview of the flight-related internal anatomy of the left wing and rib cage of a generalized bird (see text for further explanation).

The shoulder joint faces laterally and allows the humerus a great deal of freedom. It can move up and down and fore and backward over large angles in most birds. The wings are supported by the humerus, the radius and ulna, and by the hand skeleton. The propatagium is a fold of skin inside the front part of the arm wing. The metapatagium connects the elbow with the trunk. The radius and ulna articulate with the humerus at the elbow and with two carpal bones (the radiale and the ulnare) in the wrist joint. The wrist is a double joint because the carpal bones articulate also with the carpometacarpus of the hand skeleton. The elbow and wrist joints in avian wings extend and flex in synchrony due to a special configuration of skeletal and muscular elements. A separate paragraph is devoted below to the detailed anatomy and freedom of movement of wings. The hand skeleton consists of the carpometacarpus (fused carpals and metacarpals) and some digits. There are usually only three digits with one or two phalanges each. The first digit is the skeleton of the alula or bastard wing; the others support primary feathers.

The actual and relative dimensions of the 10 skeletal elements of the wing differ among birds. The differences provide insight into specific functions of the arm and hand parts of the wing. Figure 2.2 shows the skeletons of the forelimb of five species scaled in such a way that the skeletons of the hand wing are of the same length. The relative importance of the role of the hand wing is given away by the bowing of radius and ulna. The wider the gap between these bones the more room there is for forelimb musculature inserting on the hand wing. The Laysan albatross has obviously less dynamic control over its hand wing than the others and is less coordinated in unsteady flight situations during flapping, starting, and

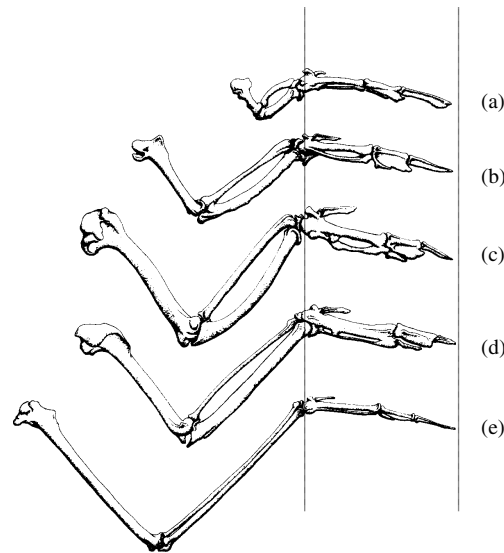


Fig. 2.2 Relative dimensions of the skeleton of the forelimb of five species: (a) Calliope hummingbird; (b) Rock dove; (c) Blue grouse; (d) European starling; (e) Laysan albatross. The skeletons of the hand are drawn at the same length (from Dial (1992)).

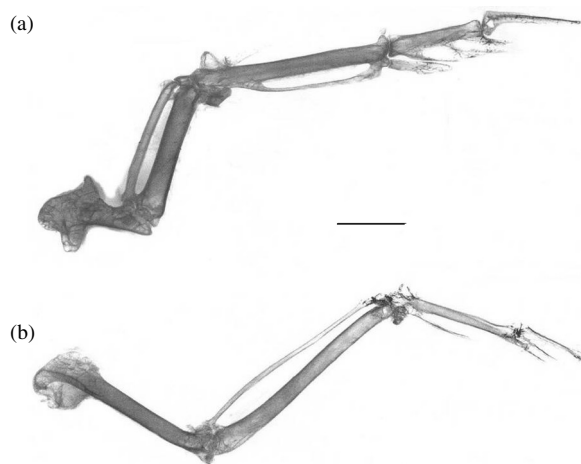


Fig. 2.3 Actual dimensions shown by X-ray pictures of the skeletons of the common swift (a) and a songbird, the European goldfinch (b). The scale bar is 1 cm.

landing. The blue grouse shows the opposite features. Hummingbirds and their close relatives the swifts have extremely long hand skeletons. In flight the arm part of the wing appears shorter than it actually is because the wrist is kept close to the body. X-ray pictures in Fig. 2.3 compare the skeleton of the common swift with that of a song bird (the European goldfinch) to show the substantial difference

between the extremely aerial swift and a generalist. The angle at the elbow of the swift is virtually fixed. Blood vessels and nerves run straight across from the humerus to the radius and ulna. The song bird can stretch and fold the arm almost completely.

Bird wings contain 45 muscles, 11 of these are subdivided into two or three parts. Eight muscles have more than one insertion point (Vanden Berge 1979). General descriptions of their origin and insertions can be found in handbooks on bird anatomy usually together with a description of the specific action (i.e. Proctor and Lynch 1993). Muscle activity during flight of only 18 of these muscles has been seriously studied using electromyogram (EMG) techniques. Results based on these studies regarding the timing of muscle activity during wing beat cycles are summarized in Chapter 7.

The shape of a wing is only marginally determined by the internal anatomy; it is the feathers that make a wing fly.

2.2.2 The external shape of bird wings

Very different kinds and sizes of feathers are implanted in the skin of the wings where rows of follicles follow well-defined tracts (Lucas and Stettenheim 1972). The large flight feathers in the wing are the remiges, wing coverts are termed tectrices. The primary remiges (in short primaries) are 9–11 strong feathers found in the hand part of the wing (grebes are exceptional with 12). These usually have asymmetric vanes with a narrow leading edge (outer) vane and a wider (inner) vane forming the rear part or trailing edge. The asymmetry is stronger towards the outer feathers. The secondary remiges (secondaries) form the larger part of the surface of the arm wing. Their number varies greatly between 6 (usually overlapping) in hummingbirds, 9–11 in songbirds, and 11–15 in pigeons, 25 in large vultures, and up to 40 in the albatrosses. Primaries are stiffer and more pointed than the secondaries. The remiges forming the bastard wing or alula are small versions of the primaries. Tertiary remiges (tertials) cover the space between secondaries and the body. The shape of the arm part of the wing is formed by rows of lesser and greater coverts, covering the propatagium (forming the leading edge) and the follicles of the remiges.

The variation among birds makes it a practical approach to concentrate on the design of one particular wing first and use its features in comparison with other wings. The wing of the northern goshawk serves as an example in Fig. 2.4. Contour feathers cover the front part of the arm wing and the proximal part of the hand wing. These provide the rounded leading edge shown in cross sections (a), (b), and (c). A row of greater coverts covers the implants of the primaries; a row of secondary coverts does that with the implants of the secondaries. Towards the leading edge of the wing, on both the dorsal and ventral side, rows of increasingly smaller so-called marginal coverts overlap each other like the tiles on a roof.

Symmetrical tips of 11 secondary remiges form the sharp trailing edge of the arm wing. The profile of the cross sections (a), (b), and (c), through the arm has a rounded leading edge and is highly cambered. The leading edge resembles that of classical aerodynamic profiles used in aircraft design, but the extreme camber

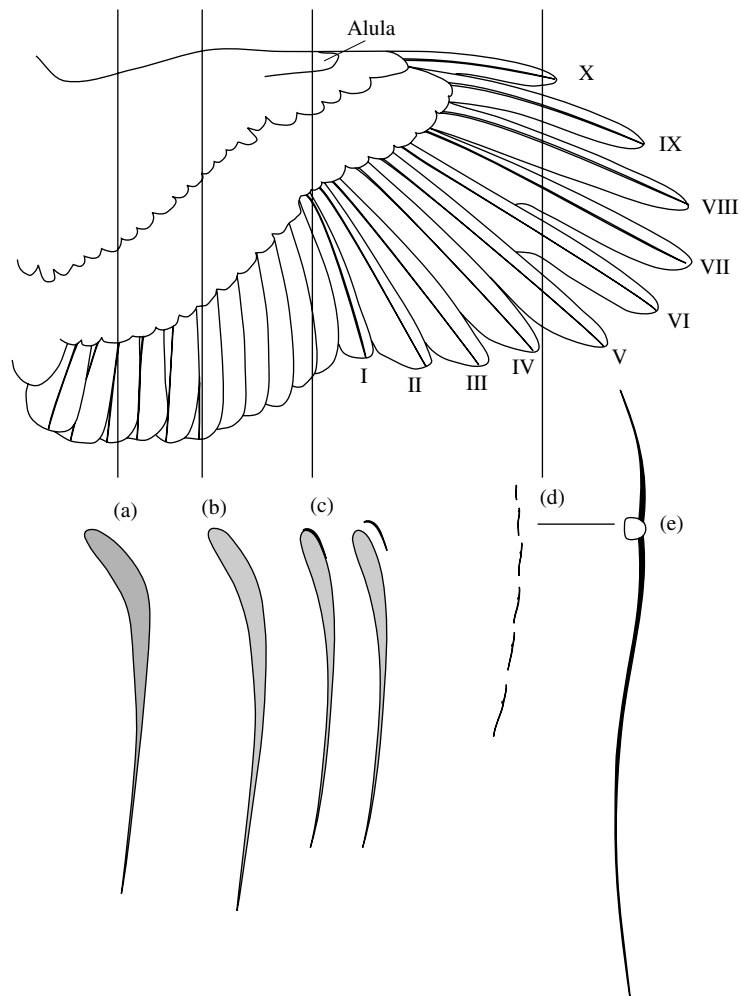


Fig. 2.4 Drawing of the dorsal side of the wing of a goshawk (modified from Herzog (1968)) with cross sectional profiles at four positions ((a)–(d)). The cross section through primary IX in (d) is enlarged to show its actual shape (e) (see text for more details).

makes the cross sectional profiles substantially different from most man made wings. Profile (c) is situated at the transition from arm to hand wing. It also has a rounded leading edge and a sharp trailing edge. The picture shows a cross section through the remiges of the alula on top of the leading edge in two positions. In the section on the left the alula is kept close to the wing; the right-hand drawing shows the situation with the alula extended.

Cross sections through the hand wing differ fundamentally from classical aircraft profiles because they have a sharp leading edge formed by the narrow outer vanes of either primaries X, IX, or VIII. In Fig. 2.4(d), primary X forms the leading edge. There is some distance between the sections through the primaries here

caused by a combination of spreading of the hand feathers and by the emargination of these feathers. Emargination is the term used to indicate that the distal part of the primary vanes decreases rather abruptly in width. This may occur at the narrow leading edge vane, at the wide trailing edge vane, or at both vanes simultaneously. Spreading of the hand wing and emargination forms the slots near the wing tip seen in many groups of birds.

Each of the feathers in cross section (d) is a more or less an independent wing section illustrated by the magnification of the cross section through primary IX in Fig. 2.4(e).

The hand wings of albatrosses and of the southern and northern giant petrel deviate fundamentally from the goshawk wing example and therefore receive special attention in a later paragraph.

There are surprisingly few accurate measurements of sizes of arm and hand wings in the literature. In most birds, the hand wing is longer than the arm part but there are many exceptions especially among large soaring birds. The longest relative hand wing lengths are found in swifts and hummingbirds where the extended length of the arm skeleton is extremely short compared to the hand wing skeleton.

2.2.3 Hummingbird and swift wings

Hummingbirds and swifts deviate so substantially from the general description that they require a separate paragraph. The internal wing design of hummingbird wings will be described first followed by brief comments on that of the swift. The hummingbird configuration is described accurately by Stolpe and Zimmer (1939) and a more recent analysis does not seem to exist. The relative dimensions of the bones of the wing skeleton resemble those of swifts but are very different from other birds (Fig. 2.2). During hovering flight the main axis of the bird is obliquely downward and the wings beat in an approximately horizontal plane. The arm is extremely short because the humerus and radius and ulna are short and kept in a fixed sharp-angled V-shaped position during flight (Fig. 2.5). This angle cannot be enlarged in a stretch because nerves and blood vessels run straight from the shoulder to the hand. The hand wing is relatively the longest found in birds. Hertel (1966) indicated that the hand wing of a hummingbird occupies 81% of the wing length against 41% in the case of a buzzard. There are only 6 partly overlapping secondaries in the arm; 10 long primaries form the main surface of the wings.

The sternum bears a substantial carina. The main flight muscles, the pectoralis and the supracoracoides, occupy about 27% of the body mass, the pectoralis being only 2 times as big as the supracoracoides (these figures are 18% and 12 times in passerines respectively, according to Greenewalt (1975)). An extremely long scapula supports the shoulder joint; it runs down the body to almost reach the pelvic girdle. The humerus is very short and has a bizarre shape; it is kept in an almost vertical position during hovering flight. The articulating surface with the shoulder joint is not at the terminal position of the humerus but there is a condyle at the inner side of the proximal end. The condyle in this position is

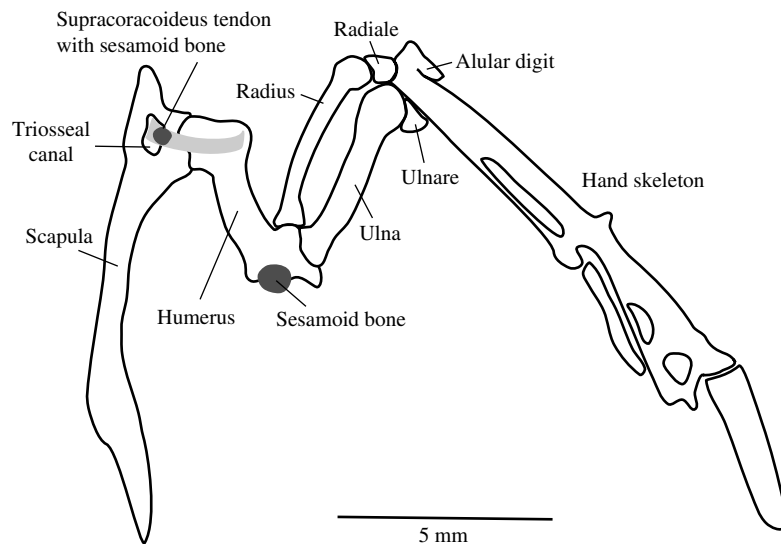


Fig. 2.5 The special skeletal structures of an Amazonia hummingbird wing. The drawing is based on photographs taken from an alizarine stained skeleton of a cleared specimen using the procedure of Taylor and Dyke (1985).

a unique character of hummingbirds. The tendon of the supracoracoid muscle contains a sesamoid bone (Fig. 2.5). It is attached to the outer part of the humerus head, runs through the triosseal canal, and from there down to the muscle on the sternum. Contraction of the supracoracoideus will cause adduction and rearward rotation around the length axis (supination) of the humerus. This rotation causes in fact the back (up) stroke of the wing. Pronation of the humerus by the pectoral muscle inserting on the front part of the humerus head will result in the forward (down) stroke.

The elbow joint is peculiar too because it is obviously not designed to stretch. The muscles of the arm wing are extremely well developed and encapsulate the joint, keeping it in folded position. The extensor muscle (the scapulotriceps) has changed its function. The tendon contains a large sesamoid bone on the rear (upper) side of the elbow (Fig. 2.5) which determines its working direction. The sesamoid bone sits in a dent in the distal end of the humerus. Its presence causes the extensor muscle to rotate the ulna and radius backwards (upwards) instead of stretching the arm.

The capacity to rotate is even bigger in the complex wrist joint between the hand skeleton and the radius and ulna. The alula digit is reduced and immobile. (Hummingbirds have no alula.) The primaries are firmly attached to the bony elements, supported by cartilage and connective tissue. The pectoralis powers the hovering wing beat during the forward stroke and the supracoracoideus during the backstroke. These muscles rotate the vertical triangle formed by the V-shaped humerus and radius and ulna. The hand wing is attached to this triangle at the wrist and follows the movement. Combined rotations of radius and ulna and of

the wrist joint enable the extreme rotation of the wing plane during the backstroke where the wing is used in upside down position.

The wing of the common swift deviates less from the basic bird wing design than the hummingbird wing does. The hand wing is still extremely long covering 75% of the total wing length. The elbow is less confined in its movements than that of the hummingbirds and the humeral joint has the familiar egg shape and allows normal vertical flapping motion. The swift has 11 primaries. Number XI at the leading edge is only 2 cm small, stiff, and almost without vanes. It supports the base of the longest primary number X. There are seven secondaries in the short arm part of the wing. The alula consists of two or three feathers with a total length of about one-eighth of the wing length. All these features witness the fact that the swift is an extremely agile flyer flapping its wings mainly vertically and not horizontally. The description of the swift in the *Birds of the Western Palaearctic* (Snow and Perrins 1998) emphasizes its extreme flight capacities: 'Flight dramatic, showing complete mastery of open air space and marked ability in gliding, wheeling, diving, accelerating or stalling, and climbing; wing-beats rapid and made usually with wings in distinct backward curve...'

2.2.4 The wings of albatrosses and giant petrels

Large oceanic birds that spend nearly as much time on the wing as the swift rely heavily on the extremely long arm wings for the generation of lift. Fast gliding in high winds is their speciality. The most extreme dynamic gliders among birds, the albatrosses and giant petrels, are known to be capable to lock the wings in stretched position and in doing so avoid spending muscular energy to fulfil that task. Both the source of this knowledge and the mechanism behind it are difficult to track down. Hector (1894) gives, after 're-examining the wing of a large albatross in the flesh', the following record of his findings:

The extensor muscular tendon, instead of being attached as in other birds only to a fixed process at the distal extremity of the humerus, is also attached by a subsidiary offset to a projecting patelloid bone which is articulated with the process, and thence proceeds to the radial carpal bone, and thence onward along the radial aspect of the manus, where it expands into fibrillae that embrace the quills. When the wing is fully extended the thrust of this projecting process on the elbow joint causes a slight rotation of the ulna on the humerus, so that the joint becomes locked, which renders the wing a rigid rod as far as the wrist joint. At the same time the slight play permitted by the articulation of the patelloid bone on the process allows of the transmission of the muscular pull from the shoulder to the manus without unlocking the joint.

This description does not explain clearly what is actually happening. Yudin disagrees with the idea that sesamoid bones are involved and offers an alternative explanation. He presented the theory in 1954 at the international ornithological congress in Basel under the name K. Joudine. It was published in the proceedings in French (Joudine 1955). It appeared in Russian in the *Zoologiceskij Zurnal* in 1957 under the name K. A. Yudin (Yudin 1957). The locking mechanism he describes is shown in Fig. 2.6. Tube-nosed birds have a bump in the saddle on the

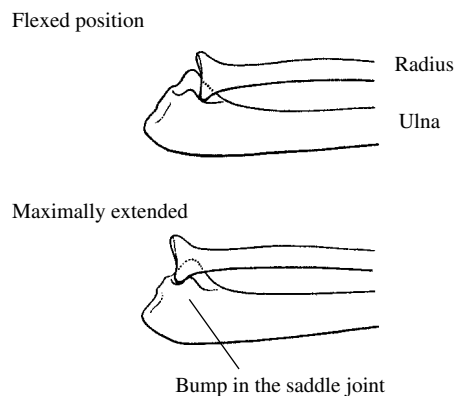


Fig. 2.6 A locking mechanism in the wings of albatrosses and giant petrels (Joudine 1955, with kind permission).

proximal end of the ulna. The sliding radius finds a stable position on each side of the bump. In fully flexed position the radius has moved to the distal-most point pushing via the radiale the carpometacarpus in the folded position. During extension the radius slides along the ulna towards the humerus and needs to be pulled over the bump to reach the stable locked position of the fully stretched wing. Both Yudin and Hector give a description of a locking mechanism of the elbow joint. Pennycuik (1982) found a lock at the shoulder joint of albatross and the southern giant petrel. It consists of a fan-shaped tendon running from the carina to the deltoid crest on the humerus. This tendon is superficial in the wandering albatross, the black-browed albatross, and the light-mantled albatross and deeper inside in the southern giant petrel. By manipulating dead animals Pennycuik found that the shoulder joint came up against a lock when raised to the horizontal position after the stretched wing had been moved forward to the fully protracted position. The lock no longer operated when the humerus was retracted a few degrees from the fully forward position or when the tendon was cut.

The hand wing of albatrosses and giant petrels deviates from that of all other birds because the structure of the primary feathers is different (Boel 1929). This will be further discussed in Chapter 3.

2.3 *Dynamic wing properties*

Wing shapes may differ among species but the change in form during a wing beat cycle is more dramatic. Before take-off, the wings are neatly folded against the body. They unfold and stretch at the onset of flight, flex partly during each upstroke, and extend fully before the beginning of the downstroke. The principle movements of a wing as a whole allowed by the structure of the shoulder joint are up and down, for and aft, backward rotation (supination) and forward rotation (pronation). The head of the humerus in most birds has not a ball but an egg-shape, which reduces the freedom of movement. The range of possible movements is also

limited by ligaments around the joint. Usually, forward and backward rotation of the humerus in a horizontal plane around a vertical axis through the joint is allowed. When the wing is extended the humerus can move up and down and rotate around its lengthwise axis. The angle of the upward movement can be more than 90° , whereas the downward movement is usually restricted to less than 35° . Pronation is commonly much more restricted than supination.

The dimensions may be different but the mechanism moving the wing is surprisingly uniform among flying birds. Here we are first concentrating on the mechanics of the principle movements of the upper arm, the forearm, and the hand. These movements are flexion and extension of the wing and circumduction of the hand. A feeling for the basic mechanisms will enable us to appreciate what is known about the wing beat dynamics in greater detail later.

2.3.1 The drawing parallel action of the radius and ulna

The distal head of the humerus forms the elbow joint with the proximal endings of the ulna and the radius. When the wing is stretched the shape of this joint severely limits dorsoventral rotation of the forearm with respect to the upper arm. Freedom of movement in the horizontal plane allows stretching and flexing of the forearm. During these movements the radius shifts parallel to the ulna inducing flexion and extension of the hand. The parallel shift has long been attributed to the shape of the distal head of the humerus. A knob on the head was thought to push the radius in outward direction. A close examination by Vazquez (1994) however, showed that the shape of the humerus condyls in the plane of interaction with the radius and ulna were circular in flying birds. Rotation around a circular knob will not result in relative shift of the bones involved.

During wing flexion the drawing parallel action of the radius and ulna is caused by collision of bulging muscles of the forearm and the upper arm when the elbow is flexed to angles smaller than 60° (Fig. 2.7(a)). The pressure of the abutting muscles dislocates the radius from the end condyle of the humerus and pushes it against the ulna. The shape of the facets at the position where radius and ulna meet moves the radius distally towards the wrist.

During wing extension elbow and wrist movements are also coupled. When the elbow angle widens the radius will slide along the ulna because collateral ligaments attach it to the humerus. The distal end of the radius pulls via the radiale on the frontal edge of the carpometacarpus, extending it. The automatic action due to the drawing parallel system is enhanced via tendons by muscle activity. The extension of the hand, for example, is enlarged by a pulling action of the propatagial tendon. The wrist moves away from the shoulder by the widening of the elbow and one slip of the propatagial tendon pulls at the extensor process on the carpometacarpus and another slip at the radiale and at the end of the radius (Fig. 2.7(a)). A tendon slip of the biceps muscle also pulls at the extension process of the carpometacarpus. More muscles and tendon complexes play a role in these complicated movements. The relative contributions are difficult to assess by dissecting and manipulating dead wings. Understanding muscle function in flight requires EMG techniques

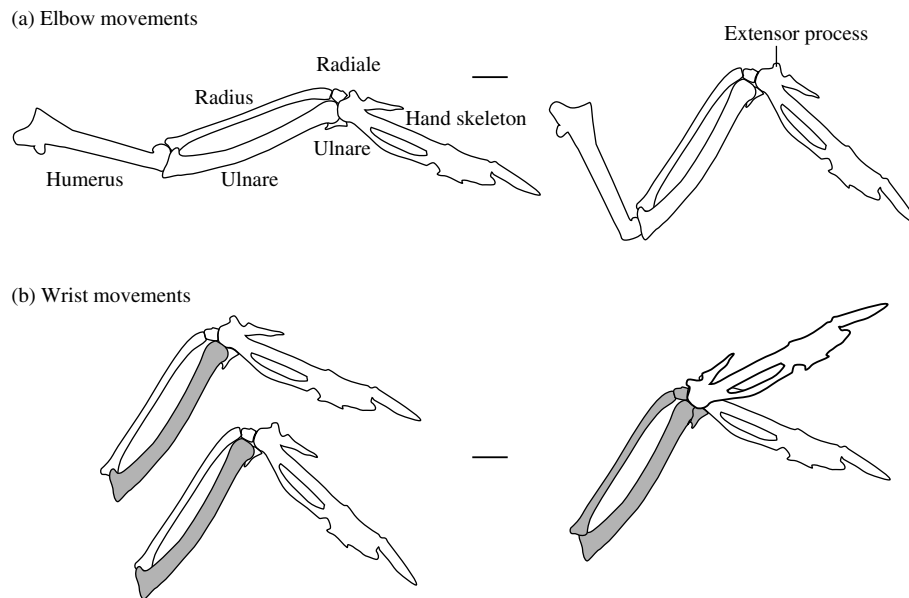


Fig. 2.7 Movements of the skeleton of a pigeon wing. (a) Automatic flexion of the hand via the radius. During flexion of the elbow the angle between humerus and ulna decreases. When the angle reaches about 60° , muscles of the forearm collide against muscles of the upper arm. The abutting muscles dislocate the radius and push it against and along the ulna in the direction of the wrist. The action results in flexion of the hand shown on the right. (b) Hand flexion occurs via two joints in the wrist. (Not moving parts are grey.) The first joint on the left involves rotation of the radius, the radiale, the ulnare, and the hand skeleton around the ulna head. The other wrist joint allows rotation of the hand skeleton around a joint with the radius, the ulna, the radiale, and the ulnare as is illustrated on the right. The scale bars are 1 cm (based on Vazquez (1994)).

combined with high-speed (preferably X-ray) cinematography. An overview of what is known about the role of wing muscles in flight will be given in Chapter 7.

The effect of the drawing parallel system on the movements of the hand becomes clear when we study the multiple joints of the wrist (Fig. 2.7(b)). Five bony elements are connected in the wrist: the radius and ulna, two carpal bones (the radiale and the ulnare) and the hand skeleton. The shape of the connections provides and restricts the freedom of movement between the hand and the forearm. Vazquez (1994) distinguishes two distinct joints. The movement of the radius, both carpal bones and the hand around the ulna head defines the first joint. In the second one the hand flexes and extends with respect to the other bones (Fig. 2.7(b)).

During the downstroke, the plane of the hand is parallel with the plane of the wing. The wing is stretched and the hand cannot flex dorsally or ventrally about the wrist. The only movement possible is flexion in the plane of the wing. During the downstroke, the primaries of the hand wing attain the greatest vertical velocity and inflict large rotational forces on the wrist. The position of the

supporting skeleton in the hand wing is close to the leading edge. The primaries form a large surface behind the skeletal support causing a strong pronation tendency during the downstroke resulting in forward rotational forces on the wrist joint. These forces are counteracted by an interlocking mechanism formed by ridges on the carpometacarpus, the ulnare, and the ulna in the joint. Supination of the hand wing around the skeleton in the leading edge is prevented by the radiale in articulation with the radius and the carpometacarpus where a ridge stops the movement.

In most birds the wrist joint can change from a stiff construction into a flexible one during the early stages of the upstroke. This is caused by the ulnare gliding along the winding articular ridge of the ulna to its other extreme position. Due to this action the hand can rotate over 90° with respect to the plane of the arm wing. Some birds show a backward and upward hand flick also during vertical take-off and landing. A similar movement is also made when the bird folds its wings into the rest position. This aspect of the wrist function was investigated by Vazquez (1992) using the mallard as example of a configuration, which occurs in most orders of flying birds.

2.3.2 The hand wing

The hand skeleton consists of the carpometacarpus, the alular digit and two to three other (major and minor) digits at the tip (Fig. 2.1). The alular digit is supported by 1 or 2 phalanges. The terminal one bears a claw in some orders. The phalangeal joints are saddle joints allowing 2 degrees of freedom. The joint between the alular digit and the carpometacarpus is more complex. It allows the alula to be abducted and adducted from and to the leading edge of the wing as well as be moved up and down. The joint also allows supination in the up and pronation in the down position. The major digit at the distal end of the hand skeleton has 2 or 3 phalanges and a claw in some groups. It attaches with a rather complex joint to the carpometacarpus. The finger can be slightly curved and stretched in the plane of the hand. Movements perpendicular to that plane are limited. The minor digit is a somewhat triangular platelet. Its joint with the carpometacarpus is cylindrical only allowing abduction and adduction. A ligament connects this bone with the first phalange of the major digit. This connection limits the curvature of the major digit and hence the risk of overstretching during the downstroke (Sy 1936).

2.4 *Scaling wings*

The following summary of scaling of dimensions important for flight in birds is based on surveys of Greenewalt (1975); Rayner (1988); and Norberg (1990). The results of scaling exercises are never precise but provide some feeling for the order of magnitude of the relevant dimensions.

Wingspan ranges between about 8 cm in 2 g hummingbirds to values of more than 3 m for 10 kg albatrosses. The relationship with body mass is allometric; the span increases approximately with mass to the power of 0.4. The isometric

exponent of one-third (based on mass being proportional to length cubed) would predict a wingspan of 1.7 m for a 10 kg albatross if compared with a hummingbird. The exponents within various functional or taxonomic groups of birds vary around the value of 0.4. That among hummingbirds is exceptionally high with a value slightly above 0.5. The scatter in general is large. The span of 1 kg birds, for example, varies between 0.5 and 1.7 m.

The special geometric position of the hummingbirds becomes even more apparent when we consider wing areas. An isometric relationship would relate wing areas with a two-third power of mass. Most birds have an exponent in the order of three-quarter but that of hummingbirds is about 1. The wing area of a 3 g hummingbird is about 10 cm² and that of an individual belonging to a species which grows to up to 12 g, reaches 40 cm². Again, the variation found among birds in general is large. The areas of 1 kg birds show an 8-fold variation.

Wing loading (body weight divided by wing area) is low and practically constant at 20 N m⁻² for hummingbirds but varies greatly among other groups. Isometrically, values would have to increase with body mass to the power of one-third. In reality the exponents are lower varying between 0 for hummingbirds, 0.22 for passerines, and 0.29 for ducks and other shore birds. Large auks have the highest wing loadings. Murres of about 1 kg reach, for example, values of more than 230 N m⁻². This is more than twice as much as values found for other birds, ducks, for example, of the same size. The high value must be a reflection of the capacity to use the wings for underwater flight. Auks do not stretch the wings fully during underwater flight but nevertheless the structures have to move a medium of a factor 1000 denser than air. Flight in air of these birds demands high wing beat frequencies to compensate for the relatively small wing dimensions. The wing loading of birds of prey is usually low around 30 N m⁻², indicating their capacity to carry large prey.

Aspect ratio (AR = span squared divided by the area of the wings) is large for birds with large spans and narrow wings such as albatrosses (AR: 14) and swift (AR: 10) and low for, for example, pheasants (AR: 5) with short broad wings. It is a shape factor which is more or less independent of body mass. What it tells us about flight performance depends on which parts of the wing contribute to the span and area of the wing. In general, birds with high aspect ratios are fast, low drag gliders. Their manoeuvring capacity may differ considerably depending on how much of the span is taken by the hand wings. It is less than 50% in albatross and about 75% in the swift. This partly explains why albatrosses are not good at low-speed manoeuvring, especially not under difficult wind conditions. Birds with a low AR are capable to glide slowly and take-off steeply or are good at complex manoeuvring at short range. A broad hand wing usually forms the larger part of the wing area in this category.

Preliminary measurements of the proportion of the wing length occupied by the sharp leading edge of the hand wing show large differences with rather good correlation with the predominant flight behaviour. The hand wings of notoriously soaring birds (i.e. buzzards and storks) occupy between 40% and 45% of the total length. That proportion is slightly less than half the total wing length in extreme

gliders (albatrosses). Song bird hand wing lengths cluster around 70% whereas more agile faster flyers, including the swift and the peregrine falcon, reach usually 75%. We saw that the hummingbird wings are most extreme with a hand wing length of more than 80% of the total wing length.

2.5 *Attempts to a functional interpretation of bird wings*

Aerodynamic interpretation of bird wings is extremely difficult not only because of their complexity including the differentiation in an arm and hand part and the presence of the bastard wing, but also because of the highly dynamic shape which changes drastically during the stroke cycle.

A simple approach to study wing function is to remove various parts of the wing and observe the flight performance of the victims in some way or another. Pettigrew (1873) removed half the secondaries and one-fourth of the primaries of the house sparrow to reach the conclusion that the maiming did not impair flight. His paper does not indicate how the removal took place and which feathers were removed. Lilienthal (1889) did experiments with pigeons. He did not remove the feathers but tightened some groups together as shown in Fig. 2.8. The drawing shows the most extreme case where the bird could still repeatedly fly high and fast. Boel (1929) refers to experiments by C. Richet whose pigeons were capable of apparently normal flight with all secondary, tertiary, and 3–4 proximal primaries removed. Much more recently Brown and Cogley (1996) reached the same conclusion as Pettigrew using the same species. They removed all secondary and tertiary feathers with their coverts and most proximal primaries, leaving only the six distal-most primaries on the wing. This treatment did not have a noticeable affect on the distance flown in a windless corridor. Even after additional removal of 8 and 16 mm of the tip of the remaining primaries the distance flown hardly decreased during repeated tests. Cutting 24 mm of the remaining primaries obviously was a dramatic change because the birds would only fly less than 10% of the distance they flew under the other conditions. The same feather treatment was applied to birds of which the propatagium was severed by an incision perpendicular to the leading edge. About 50% of the surface of

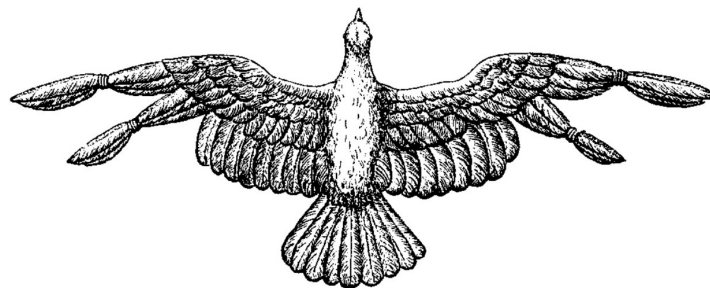


Fig. 2.8 Lilienthal's (1889) Fig. 23 showing his most extreme experiment where the pigeon was still capable to fly fast and high.

the arm wing remained after this mutilation. The performance of the birds was not affected in the cases where the 6 primaries had their full length or where 8 mm was removed from the top. The average distance flown dropped dramatically when 16 and 24 mm were removed from the tip of the primaries. I must admit that I do not like this type of experiment, but since the birds have been sacrificed we better use the results to improve our understanding of avian flight. Strangely enough, Brown and Cogley used an extremely simple two-dimensional steady state aerodynamic computer model to reach the unjustified conclusion that the cambered propatagium is the major lift generating component of the wing proximal to the wrist. They ignored their own important finding that the 6 remaining distal-most primaries were sufficient to let the birds fly repeatedly over the distance they would normally fly even after additional removal of 8 mm of the feather tips and decreasing the surface of the propatagium by 50%. These experiments tell us that the distal-most primaries play a dominant role in generating lift and thrust during flapping flight in birds, not more and not less.

2.6 *Tail structure and function*

The tail is supported by a few caudal vertebrae and the pygostyle, a fusion of the last vertebrae of the vertebral column (Baumel 1979). There is considerable variety in tail shapes and sizes. Hypotheses on the relationships between form and function of flight-related aspects are discussed in the last paragraph.

The anatomy of the tail of birds is complex and derived. Tail feathers, termed rectrices, are implanted on a broad stubby tail supported by highly modified vertebrae. The tail of the pigeon is studied in great detail by Baumel (1988) and by Gatesy and Dial (1993). The functional morphology of tails of flying birds is rather uniform; the pigeon tail in Fig. 2.9 can therefore be used as a model for most species. The moveable part of the tail skeleton is composed of five, six, or even seven caudal vertebrae ending in a pygostyle. More cranially some caudal vertebrae are fused with the synsacrum. The concave anterior and convex posterior globular surfaces forming the articulations between the free vertebrae allow movements in all directions. The pygostyle consists of a vertebra type body extending caudally into a vertical plate. Its connection with the last free vertebra is a horizontal hinge joint with a transverse hemi cylindrical notch in the anterior part of the body of the pygostyle. On each side of the pygostyle the recticial bulbs form the seat of the 12 rectrices. The bulbs are fibro adipose structures, partly encapsulated by a striated muscle, the bulbi rectricium. Sockets on each side of the caudal vertebral column form joints in which the bulbs can move. Six pairs of muscles connect the vertebrae, the pygostyle, and the bulbs to the pelvis, synsacrum, femur, and vent. The bulbi rectricium are responsible for spreading the tail fan by pulling the calami of the rectrices together. The other caudal muscles function to hold and move the adjustable tail fan. EMG recordings of these muscles during take-off, level flight, and landing are discussed in Chapter 7.

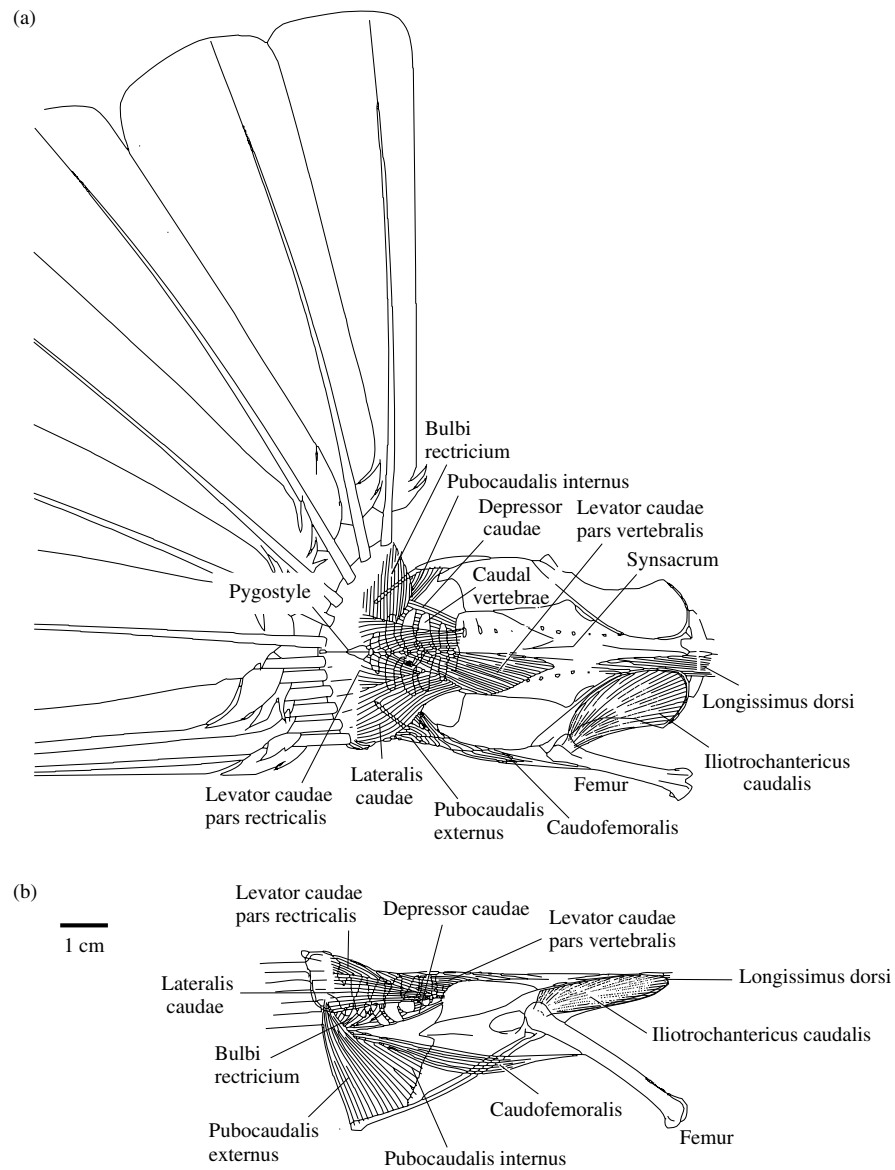


Fig. 2.9 Morphology of the pigeon tail as a model for bird tails in general: (a) dorsal view; (b) lateral view (Baumel 1988; Gatesy and Dial 1993, with kind permission of The Company of Biologists).

Up to 24 rectrices in the tails of birds differ in length and shape to form an almost infinite number of tail designs. Not all the diversity is flight-related. Ornamental tails play an important role in reproductive behaviour.

The shape and size of the tail vary considerably among birds. The variety might be even greater than that of wings. However, not all of the variation is related

Table 2.1 Numbers of rectrices in the tails of some major groups of flying birds (based on Lucas and Stettenheim 1972; Van Tyne and Berger 1976).

Vestigial	Grebes
8–10	Cuckoos
8–12	Hérons
8–14	Rails, gallinules
10	Swifts, hummingbirds, nighthawks (but the common swift has 12: polyrectricity)
12	Woodpeckers, trogons, kingfishers, parrots, macaws, typical owls, pigeons, doves, cranes, sandpipers, plovers, gulls, terns, alcids, songbirds
12–14	Hawks, eagles, osprey, falcons, caracaras, cormorants, new world vultures
12–18	Quails, pheasants
12–24	Ducks, geese, swans
16–20	Loons
22–24	Pelicans

to flight. Many extreme tails belong to males only and are obviously intended to impress females in some way or another (i.e. to show that he is even strong enough to fly with a handicap). If we concentrate on the tails of females and on those of species without sexually dimorphic tails, the variety is still large but reducible to a few general patterns. However, little of it has been functionally explained. Tail shapes not only vary among species, but may also change quickly in time due to spreading and closing of the tail fan. The left and right halves are usually symmetrical but differences in the amount of spreading and tilting can create high degrees of asymmetry. The outer tail feathers can have a narrower outer and a wider inner vane but most other feathers are left and right symmetrical. Table 2.1 shows that most major groups of birds have 12 rectrices, some have twice as many, whereas 8 seem to be a minimum. Ducks, geese, swans, and pelicans may have up to 24, whereas grebes have no functional rectrices. In most flying birds, the vanes of the outermost rectrices are usually asymmetrical with the outer ones much narrower than the inner vanes. In many birds the feathers are equally long. The folded tail in that case has a narrow rectangular shape, when spread it forms the segment of a circle. In forked tails the rectrices become increasingly shorter towards the centre. Deeply forked tails have an inverse circular shape when spread. Shallow fork tails may show a straight trailing edge in the spread out position. Birds like the common magpie, mousebirds, pheasants, gannets, some doves, and cuckoos have a wedge-shaped tail with slightly longer central feathers and shorter outer ones. Such a tail is slender spade shaped when spread out. Extremely elongated central feathers occur in both sexes in very distant groups as tropic birds, skuas, bee-eaters, and some species of sandgrouse and in a few single species, for example, the South American long-tailed tyrant and the secretary bird.

Variation within one functional group can be large as well. Among aerial feeders as swallows, martins, and swifts the tail shapes range from short square or pointed stubby ones to extremely long-forked tails such as those of the barn swallow. Some swifts have hair like shafts sticking out (i.e. the brown-backed needletail). Stiff shaft elongations are found in various tree creeping birds. Tail feathers of the southern emu wren seem to consist of a shaft with loose barbs.

Flight-related functional explanations of tail configurations are usually fairly general, and rarely if ever backed by experimental proof. They require insight into the aerodynamics of tails. Chapter 4 shows how far that insight goes.

2.7 *The rest of the body in relation to flight*

We have not yet paid attention to the role of the body, the head, and the hind legs in flight. In flying birds we expect the body and head to form a well-streamlined body of rotation with a rounded leading surface and a pointed trailing end. The largest diameter should be situated at approximately one-third of the length and the ratio of diameter over length ought to be between one-quarter and one-fifth. Such a body, the fuselage in aircraft terms, is optimal in the sense that it offers the smallest drag for the largest volume. Cayley first described it in 1809 (see Gibbs-Smith 1962). The shape of the head and body of a starling, for example, is close to this ideal if we exclude the sharp beak at the point.

Birds with long necks either stretch these during flight, as storks and swans do, for example, or keep the necks folded as pelicans and herons do. The neck length determines the position of the heavy head with respect to the centre of gravity. Birds can be expected to use the stretch ability to adjust the position of the centre of gravity. Windhovering birds may use the possibility to stretch or contract the neck to keep the head in a fixed position with respect to the ground (see Chapter 6). In Chapter 1 we saw how Borrelli worried about the effect of sideways movements of a long neck and head during flight (Fig. 1.2, picture 6). Beaks form the leading structures in the flight direction of the flying birds. The existing variety of bizarre bill shapes among flying birds leaves the suggestion that there is no heavy aerodynamic penalty connected to the possession of extravagant frontal parts. Aerial feeders such as the swift have a small beak but open it wide to catch insects. Other birds carry substantial objects, large prey items or nesting material in their bills. Serious investigations into the effects of structures up front are however lacking and we have no idea how large a handicap these represent and how birds adapt their flight to cope.

Take-off and landing require an undercarriage. Birds use legs and feet to push off or even run some distance prior to take-off and to absorb excess forces during landing. Legs can also be used to dynamically control the position of the centre of gravity. Some birds tuck them away under the feathers; others stretch them rearward underneath the tail. Birds of prey carry their victims underneath close to the body or in the claws at the end of stretched legs. The osprey is well known for carrying big fish in the head first streamlined position. I saw how a tawny eagle did that with giant mole rats in the Bale Mountains of Ethiopia. Legs and feet are of course important devices during take-off and landing in many species. They are used as airbrakes by many birds, especially those with webbed feet, sea gulls and cormorants, for example, can be seen using this trick. Note that if the drawing on the cover is a landing cormorant, the artist forgot to indicate the webs between the toes. It is an understandable omission because while watching a cormorant's landing action the extreme spreading of the toes is more impressive

than the presence of the webs in between. Wilson's storm petrel sticks its webbed feet in the water to use them as a sea anchor during soaring close to the water surface. Gliding against the wind, the bird is blown backward with respect to the water. This produces a hydrodynamic drag force on the feet, which can balance the drag force on the body and makes the backward speed of the bird smaller than the wind speed creating a horizontal wind component relative to the bird, which generates lift on the wings. The bird operates as a kite, where the tension in the string counterbalances the aerodynamic drag on the kite (Withers 1979).

2.8 *Summary and conclusions*

The highly derived internal anatomy of avian wings shows a common pattern which is interesting from a comparative anatomical point of view. However, specific features deserve more attention in future research on bird flight.

The outside of the wings of all flying birds consist of two distinct parts: the arm wing and the hand wing. Cross sections through the arm wings have classical aerodynamic profiles with a round leading edge, a cambered shape, and a sharp trailing edge. The hand wing consists mainly of the primary feathers. The leading edge of that part is sharp because it is formed by the narrow vane of the outermost primary. Cross sections through the hand wing are usually flat or slightly curved, the leading edge and the trailing edge are both sharp. Feather emargination and spreading of the primaries create slots near the wing tip of many species of larger birds.

The hand wing in most birds takes up more than half the total wing length. Extremely specialized flyers (i.e. hummingbirds and swifts) have the longest hand wings and almost exclusively use these to fly. Albatrosses and giant petrels on the other side of the scale have long arm wings and are able to lock the wings in extreme stretched position during gliding.

Both the possible movements of the wing as a whole with respect to the body and the freedom of movement inside the wing is restricted but not to the same extent in all species. The shoulder joint allows the largest freedom of movement in most groups. The folding and stretching is reasonably well understood although this knowledge is based on a few species only. The wrist joint is complicated by the possibility to change its dynamic characteristics depending on the configuration of the bony elements.

Scaling of the dimensions of the flight apparatus of birds provides insight into differences among functional groups. Hummingbirds and auks do not obey the rules that seem to emerge for other groups. We have to be aware that in some cases similar dimensions are based on different morphologies and may require different functional explanations.

Experimental testing of the influence on flight performance by removing various parts of the wings provide a remarkably consistent conclusion: the distal-most five–six primaries are crucial for the ability to fly. Other parts of the wing hardly affect that ability.

Bird tails are unique, extremely derived structures among vertebrates mainly consisting of a few caudal vertebrae, a pygostyle, rectricial bulbs encapsulated in

muscles and up to 24 rectrices. The tails are left right symmetrical and can be spread and folded and tilted sideways. The shape varies greatly and depends on the amount of spreading and on the distribution of the feathers of various lengths. There are functional explanations for some tail shapes but evidence that these reflect the truth is usually circumstantial.

The shape of bird bodies, including the head, is usually fairly accurately streamlined offering the largest volume for the lowest drag. Some birds with bizarre beaks probably evolved under selection pressures where aerodynamic design did not play an important role. Legs and feet are important during take-off and landing, they can operate as air brakes, carry load, regulate the position of the centre of gravity and serve (in Wilson's storm petrel) even as sea anchors.

Our insight in the functional morphology requires a closer look at the unique structures which made flight possible in this group of animals in the first place: the feathers.