In an earlier classification, now no longer formally recognized, birds were grouped together according to how extensively the keel of the sternum was developed. One group included the large flightless birds (i.e. the Ostrich, rheas, Emu, cassowaries and kiwis) and was given the name Ratitae (from Latin ratis, a raft) since its members possessed a sternum without a keel. All other birds with a keeled sternum were called Carinatae (from Latin carina, a keel). Although much controversy has surrounded the precise relationship of the large flightless birds, the available evidence now indicates that the ratites do in fact have a monophyletic origin and with the tinamous can be placed within the same group.

A list of the English common names of the birds referred to in the text together with their Latin scientific names is provided in the Appendix on page 315. The names of the domestic birds in the text refer to the following species: domestic duck, domestic form of Mallard; domestic goose, domestic form of Graylag Goose; domestic pigeon, domestic form of Rock Dove; domestic turkey, domestic form of Turkey; domestic fowl, domestic form of Red Jungle Fowl; domestic quail, domestic form of the genus Coturnix.

Further reading
end of the tomia and ending caudally at the angle of the mouth. Alternatively, it means the entire oral opening (or gape). It can also refer to the area of skin immediately surrounding the angle of the mouth (as on p. 27). The maxillary rhamphotheca carries the paired nostrils (Fig 2-1). In most small passerine birds and some other species each nostril opens into a slight depression, the nasal fossa (Fig 2-1).

The remainder of the head can be divided into the regions shown in Fig 2-2, although the boundaries between them are not sharply defined. The top of the head is divided into the forehead, crown and the back of the head, the three regions together being sometimes known as the pileum. As Fig 2–3 shows, these three regions may carry a crown stripe (or median line), a lateral crown stripe (or head stripe) and a superciliary stripe (also known as the supercilium or superciliary line). The orbital region (Fig 2–2) is a narrow zone round the eye which includes the dorsal and ventral eyelids (palpebrae). The ear region (Fig 2–2) surrounds the external acoustic meatus (p. 302), and is recognizable by the particular texture of the ear coverts which overlie the meatus (Fig 14–2). In most birds the meatus is caudal and slightly ventral to the eye (Fig 2–2), but in woodcock and snipe it lies ventral to the eye. The opening is generally quite small, but in owls it is enormous (Fig 16–12) and in many strigiform species has a movable flap along its rostral edge, the operculum (p. 302). The lore (Latin lorum, a strap) is the narrow elongated area between the eye and the maxillary rhamphotheca. Much of it lies directly rostral to (in front of) the eye.
Adaptations of the bill for feeding are illustrated in Fig 2-4. Seed-cracking birds such as finches (Fig 2-4b) have a stout conical bill, and in crossbills (Fig 2-4c) the sharply-pointed upper and lower components of the bill cross over to hold the scales of fir cones (Red Crossbill); d, bill for cracking fruit stones (parrot); e, chisel-like bill for penetrating wood (Green Woodpecker); f, bill for thrusting into flowers for pollen and nectar (Sword-billed Hummingbird); g, bill for probing mud (Eurasian Woodcock); h, short wide bill with rictal bristles for netting insects on the wing (European Nightjar); i, raptorial bill for tearing flesh (Steller’s Sea Eagle); j, long sturdy bill for forcing open molluscs (Oystercatcher); k, filtering bill (Common Pochard); l, filtering bill (flamingo); m, saw-edged bill for catching fish (Red-breasted Merganser); n, daggerlike bill for spearling fish (Anhinga); o, pouchlike interramal region for catching fish by dip-net action (European White Pelican); p, knife-like projecting mandibular rostrum for ploughing water (Black Skimmer).

The water with a long knife-like mandibular rostrum. In nocturnal and diurnal birds of prey the hooked bill is powerful and sharp-pointed (Fig 2-4i).

**Neck**

The length of the neck varies with the number of (cervical) vertebrae, which ranges from 11 to 25 (p. 52). Its minimum length is long enough to enable the beak to reach the uropygial gland (oil gland) on the rump, and is usually proportional to the length of the legs. Thus long legs are generally matched by a long neck, to enable the bill to reach the ground. On the other hand, a long neck is not necessarily accompanied by long legs (consider their relative proportions in geese). Long necks occur in many waders, although some (e.g., plovers) have short necks. The length tends to be intermediate in swimming
birds, but some (e.g. swans) have exceptionally long necks. The shortest necks occur in the great majority of the small passeriform species. Characteristically, the neck is carried in a double curve, in the form of an 'S'. Because the forelimb has been totally committed to flight in birds as a group, the bill assumes responsibility for grooming, nest building, and many other manipulative procedures which are generally the province of the mammalian forelimb. Consequently, the avian neck is extremely flexible and mobile, as well as being long enough to carry out these tasks. For descriptive purposes the neck can be divided into several regions. One of these, the *nape* (Fig 2–2), is applicable to birds in general and seems to be widely used by ornithologists. In birds with relatively long necks, such as waders, it is sometimes convenient to recognize the 'foreneck' (pars cranialis of the neck), 'side of the neck' (pars intermedia) and 'hindneck' (pars caudalis).

**Trunk**

The trunk is the whole of the body between the neck and the tail. It can be divided into thorax, abdomen and pelvis. The *thorax* is bounded externally by the rib cage, sternum and vertebral column. The *abdomen* and *pelvis* are not separated by any well-defined boundary, since in nearly all birds the bony pelvis (os coxae) is open ventrally. The dorsal part of the trunk is divided into the *back* and the *rump* (Fig 2–2). The region between the left and right scapulae is known as the *interscapular region*, and often carries distinctive streaks or colours. The whole back, together with the dorsal surface of the wings, may have a characteristic colour and is then known as the *mantle*. The lateral part of the trunk is called the *side* or *flank* (Fig 2–2). The ventral part consists of the *breast*, *belly*, and *undertail* (Fig 2–2). The term *crissum* refers to the general area round the vent, together with the undertail coverts; the term *vent* is often applied to this area, but should be restricted to the actual orifice (p. 192).

**Tail**

The flight feathers of the tail, or *rectrices* (Latin *rectrix*, *rectrices*, rudders), are always paired. They overlie each other as in Fig 2–5, the most dorsal one (the central tail feather, 1a in Fig 2–5; Fig 2–2) lying in the midline. In the great majority of birds, including the songbirds, there are twelve rectrices (six pairs), but in other species the number ranges from 6 to 32. Numerous *tail-coverts* overlie and underlie the rectrices. These are nearly always small feathers, but in the peacock they become greatly enlarged to form the eyed feathers of the train.

**Wing**

The feathers of the wing can be divided into *flight feathers* or *remiges* (Latin *remex*, *remiges*, rowers) and *coverts* or *tectrices* (Latin *tectrix*, *tectrices*, coverers).
the humerus become enlarged and function as flight feathers, but these are modified coverts and should not be called 'tertiaries' or 'tertials'. All flight feathers overlap each other in the same manner (Figs 2–6, 2–7 and 2–8). Thus, when the dorsal surface of the wing is examined, as in Fig 2–7, the trailing edge of primary 10 is seen to be covered by the leading edge of primary 9, and so on.

The **primaries** should always be numbered in a proximal (medial) to distal (lateral) direction as in Fig 2–6. When primaries have disappeared, as has occurred in some groups of birds, they have been lost from the distal end of the series. Therefore homologous primaries have the same number only if their numbering begins at the proximal end of the series. Species that are capable of flight have from 12 to 9 primaries. Of the flightless birds the rheas and Ostrich have more than this number, for decoration, while other flightless birds have less. In many species the outermost (most distal) primary is so reduced in size that it is hard to see, and is then called a **remicle** (Fig 2–6). Passerine birds have 10 primaries, but in some families the tenth is such a short remicle that the wing is said to have 9 'functional' primaries. All members of a family usually have the same number of functional primaries. The number of metacarpal primaries is rather constant, six being the general rule (Fig 2–6), but a few species have seven.

The **secondaries** are much more variable in number than the primaries, ranging from 6 to 32 depending on the length of the forearm. They attach to the ulna at quill knobs (p. 59). In many species there is a relatively wide space between the fourth and fifth secondaries, with an extra major covert above; this was originally believed to be due to the loss of a secondary and gave rise to the concept of **diastataxy**, meaning arranged with a gap. This feature is not shown in Figs 2–6, 2–7 and 2–8.

Between the primaries and secondaries there is an extra **carpal flight feather** (carpal remex) in many species, complete with a major upper covert. This is not present in the wing shown in Fig 2–6.

The alular digit bears from two to seven quills forming the **alula** or **bastard wing**. Like the primaries these feathers should be numbered proximally to distally.

The shaft of each flight feather is covered, on both the dorsal and the ventral surface, by a series of **wing coverts**. The coverts covering the primaries are known as **primary coverts**, and those covering the secondaries are called **secondary coverts**. On the dorsal surface (Fig 2–7) there is a single row of **major coverts**, a single row of **median coverts**, several rows of **minor coverts** and an indeterminate number of **marginal coverts** on the leading edge of the propatagium. All the major coverts overlap each other in the same manner as the flight feathers (Figs 2–7 and 2–8), and are therefore said to have a **conforming overlap**. Several of the rows, or parts of the rows, of the smaller coverts overlap in the reverse manner to the flight feathers, i.e. the trailing edge overlaps the leading edge of the adjacent, more proximal, feather (as in the first row of median coverts covering the secondaries in Fig 2–7); this arrangement is designated as a **contrary overlap**.

On the ventral surface (the underneath) of the wing the coverts are arranged essentially like those of the dorsal surface (Fig 2–8), but the rows are less regular.

The triangular fold of (feathered) skin on the leading edge of the wing between the shoulder and carpal joints is known as the **propatagium** (Figs 2–6 and 2–7). In its cranial free edge is the elastic propatagial ligament. The **metapatagium** is the fold of skin on the trailing edge of the wing between the trunk and the brachium. The **postpatagium** is the fold of skin on the caudal margin of the forearm and manus. The **alular patagium** is the fold of skin which unites the alular and major digits. In the ringing or banding of birds, especially young Anatidae, wing clips are sometimes passed through the propatagium.

**Fig 2–7** Drawing of the dorsal surface of the left wing of a Common Murre. In the region of the secondaries some of the median coverts overlap each other in the opposite manner to the flight feathers (contrary overlap). This wing has a fairly high aspect ratio. The inset shows a galliform wing (Willow Ptarmigan), with a low aspect ratio.

**Fig 2–8** Drawing of the ventral surface of the left wing in Fig 2–7.
There are four general types of wing, with numerous intermediate forms. Many passeriform species and some galliforms and pigeons manoeuvre with extreme precision through narrow spaces in vegetation, and these birds have an **elliptical wing**. The shape is short and broad with a low aspect ratio as in the inset in Fig 2-7 (aspect ratio = wing span divided by average width). The outline of the elliptical wing tends to resemble that of the mark II Spitfire of the Second World War. Wing loading is moderate or low (wing loading = body weight divided by the surface area of the wing). There is a large alula, and additional wing slots are formed by separation of the primaries to prevent stalling at low speeds. The wing beat is fairly fast and the amplitude of each beat is moderately great. Manoeuvrability is good. The **broad soaring wing** occurs in eagles, pelicans and New World vultures. enabling these birds to soar at low speeds. This type of wing is fairly long and broad with a medium aspect ratio and moderate wing loading. The alula and wing slots are conspicuous. The **long soaring wing** is restricted to oceanic species such as albatrosses, the Gannets and gulls. The shape is long, slender and pointed (Fig 2-7), with a high aspect ratio and high wing loading. The alula is sometimes large but there are no wing slots. Such wings allow gliding at high speed, but also satisfy the competing needs of flapping flight. However, their relative fragility and clumsiness demand a habitat that is free from obstacles. The **high speed wing** of swifts, falcons and hummingbirds, and to a lesser extent ducks and terns, is relatively small with a moderately high aspect ratio and high wing loading. The wing tip is tapered and may be swept back. There are no wing slots, except in falcons, and these birds can close them in fast flight. The wing beat is rapid and the amplitude of each stroke is small.

**Pelvic limb**

The pelvic limb articulates with the trunk at the hip joint. The first segment of the limb is the **thigh**, and contains the femur. The first (most proximal) joint within the limb itself is the **knee joint**, between the femur and tibia (Fig. 4–11). The next segment is the **leg** proper, or anatomically the **crus**, and this is based on the tibiotarsus and fibula (Fig 4–11). In scientific ornithology this segment is sometimes designated as the 'lower leg', a term which is not entirely accurate anatomically but is reasonably precise. Unfortunately, in bird identification manuals the part of this region that shows below the feathers of the belly is sometimes called the 'thigh', but this term is so inaccurate that it really ought to be avoided. The **intertarsal joint** (ankle joint or hock joint) comes next (Fig 4–11). Identification manuals sometimes call this the 'knee', but again it would be better not to use such an anatomically inaccurate term. The intertarsal joint is succeeded, in strict anatomical terms, by the foot or pes. The first part of the pes is formed by the **tarsometatarsus** (Fig 4–11), which corresponds to the instep of the human foot. In birds, this region is commonly called either the 'tarsus' or the 'metatarsus'. Neither of these terms is entirely correct anatomically, since the skeletal basis of this region is constituted by the fusion of the distal row of tarsal bones with the metatarsal bones thus forming the composite tarsometatarsal bone; however, the term **metatarsus** is reasonable, since the metatarsal component forms the great majority of the tarsometatarsus (Fig 4–11). The same region is sometimes popularly known as the 'shank', but this term is not clearly defined and is occasionally applied either to the whole limb or to all of the visible part of the limb. The next joint is between the distal end of the metatarsal bone and the toes (Fig 4–11). Unfortunately, some identification manuals call this the 'ankle', which is another very inaccurate term since it is the **intertarsal joint** that corresponds to the human ankle. The **toes** or **digits** (Fig 4–11), form the final component of the anatomical pes, but through long-established usage in scientific ornithology the term 'foot' is generally restricted to the toes. In birds in general the (true) **thigh**, the (true) **knee joint** and the proximal (upper) part of the (true) **leg** are entirely concealed by the feathers of the belly and flank as in Fig 2–2. Thus, only the distal (lower) part of the (true) leg, the intertarsal (hock or ankle) joint, the tarsometatarsus and the toes are visible. In descriptive ornithology these visible components together are commonly referred to as the 'leg', but this term is not satisfactory since it is also used for the whole limb and is anatomically inaccurate anyway.

**Foot**

The 'foot' of a typical bird has four toes (e.g. Fig 2–9e), and no bird has more than this number. Species from several orders, including rheas, cassowaries and the Emu, many waders, diving-petrels, auks, some woodpeckers and one passerine species, have only three functional toes; in most of these it is the first digit (hallux, homologous to the big toe of man) which is either vestigial (Fig 2–9a) or absent (Fig 2–9b), but in some kingfishers it is the second toe that is lost. Thus true or functional **tridactylism** occurs in running birds, wading birds (some of which, like certain plovers, are fast running), birds that mainly use their wings to swim under water and climbing birds. One species alone, the Ostrich, has only two toes, digits I and II being lost (Fig 2–9d).

The arrangement of the toes when all four are present depends on function. Most birds have three toes pointing forwards and one (digit I) backwards (the **anisodactyl foot**), as in songbirds (Fig 2–9e) and in Archaeopteryx (Fig 1–2C). Among the species with four toes the main variation is to have two (digits II and III) directed forwards and the other two (I and IV) backwards (Fig 2–9f) as in woodpeckers, toucans, cuckoos and parrots (the **zygodactyl or yoke-toed foot**). Owls, tucanacos and the Osprey have a basically zygodactyl foot, but nevertheless can move the outer toe (digit IV) readily from the backwards to the forwards position. In one group of birds, the trogons (which adopt an arboreal habitat), it is digits I and II that are turned backwards (sometimes known as the **heterodactyl foot**). Essentially, the zygodactyl foot is adapted for climbing and grasping. In most swifts (Fig 2–9g) all four toes point forwards as an adaptation for climbing vertically, and in mousebirds the first digit can be turned forwards to join the other three forward-pointing toes (both of these forms constituting the **pamprodactyl foot**). Lastly, digits III and IV may be partly united as in some kingfishers (Fig 2–9c), forming the **syndactyl foot**.
Functionally, there are three main types of foot, although there are also many intermediate forms.

1. The grasping foot. This is adapted for holding either perch or prey. In the anisodactyl perching foot of passerines (Fig 2-9e) all the toes are freely mobile, and the well-developed backward toe is fully apposable giving a firm grip. An even better hold is obtained by the zygodactyl foot with its two pairs of apposable toes (Fig 2-9f), a device which parrots use like a hand when feeding. The raptorial foot (anisodactyl) has widely spread toes and needle-sharp curved claws with formidable holding powers (Fig 2-9h).

2. The walking and wading foot. The capacity to grip is largely sacrificed in such feet, the backward pointing first digit losing contact with the ground and being reduced in size or lost altogether. The toes are partly or completely webbed in some wading birds (flamingos, storks and avocets), so enabling the bird to walk over soft surfaces and also to swim well (Fig 2-9a, -9b and -9i). The toes are greatly elongated in some rails and especially in the 'lily-trotter' jacanas (Fig 2-9i), thus spreading the weight over a wide surface and enabling the bird to walk on floating vegetation. The ptarmigans that walk on snow have raised the first digit off the ground, but have greatly increased the surface area of the foot by forming 'snowshoes' in winter consisting of a dense mat of stiff feathers on their toes (Fig 2-9k) even on the under surface.

3. The swimming foot. In the fully adapted swimming foot all four toes are webbed as in cormorants (Fig 2-9l), this being known as the totipalmate foot. In gulls and ducks, flamingos, storks, and avocets (Fig 2-9a, -9b and -9i) the three toes are webbed to varying extents, but the first digit is free and usually underdeveloped; this variation is designated as the palmate.

Fig 2-9 Examples of the avian foot. a, vestigial first digit (the short projection visible on the upper left side of the foot), but the other three toes are webbed forming the palmate foot for swimming (left foot of Little Gull); b, another palmate foot for swimming, but the first digit is lost altogether (left foot of Razorbill); c, digits III and IV are partly united forming the syndactyl foot (left foot of a kingfisher); d, digits I and II are lost, leaving only two toes (right foot of Ostrich); e, a typical avian foot for perching, with three toes pointing forwards and one (digit I) backwards, the anisodactyl foot (Greek anisos, unequal; dactyl, toes), left foot of Blackbird; f, the main variant from the typical four-toed foot, digits II and III pointing forwards and I and IV backwards, the zygodactyl foot (Greek, yoke-toed) for grasping (left foot of Blue-and-yellow Macaw); g, all four toes point forwards for vertical climbing, the pempomadactyl foot (Greek, pom, pro, front; dactyl, toes) (right foot of a swift); h, another anisodactyl foot, but with widely-spread needle-sharp curved raptorial claws for grasping (right foot of Common Kestrel); i, another palmate foot for walking over soft surfaces (right foot of Avocet); j, an anisodactyl foot with very long toes for walking on floating vegetation (right foot of a jacana); k, an anisodactyl foot with a vestigial first digit, but with surface area greatly increased by feathered toes for walking on snow (right foot of Rock Ptarmigan); l, all four toes pointing forwards and webbed together, forming a totipalmate foot that is totally adapted for swimming (right foot of Great Cormorant); m, an anisodactyl foot, but all four digits possess broad lobes forming a lobate foot for swimming (left foot of Little Grebe).
foot. Grebes, coots and phalaropes have broad lobes along the sides of all four toes (Fig 2-9m), and this type is called the lobate foot.

Further reading
Wray, R.S. (1887) On some points in the morphology of the wings of birds. Proc. zool. Soc. Lond., 343-357.

Chapter 3
INTEGUMENT

SKIN

The skin is generally much thinner and more delicate than in mammals. It is attached to the muscles in relatively few places, but has extensive attachments to the skeleton, for example to the bones of the manus (hand) and pes (foot). It consists of the epithelium of the epidermis, and the connective tissue of the dermis and subcutaneous layer.

The epidermis consists of a deep layer of living cells and a superficial layer of cornified dead cells. The living layer or germinal layer comprises three strata: the basal, intermediate and transitional layers. The basal layer is adjacent to the dermis and constantly produces cells to replace those which are lost at the surface. Next comes the intermediate layer, consisting of enlarged polygonal cells which are characterized by desmosomes and are homologous to the prickle cell layer of mammalian skin. This layer merges with the transitional cell layer in which keratinization is almost complete. Superficial to these living layers lies the cornified layer (stratum corneum) consisting of horny dead cells which contain mainly keratin and keratin-bound substances. In feathered areas the whole epidermis is only about ten cells thick, these being more or less equally divided between the living layer and the dead horny layer. In the beak and foot pads the epidermis is greatly thickened to resist mechanical stresses.

Compared to that of mammals the dermis is thin. It is made up of superficial and deep layers. The superficial layer varies in thickness according to age and the part of the body. Within the deep layer an outer compact component and an inner loose compartment can be distinguished. The loose component contains the smooth muscles of the feathers and of the non-feathered regions of skin (apteria), these muscles being interconnected by elastic tendons. Within the dermis lie the feather follicles. Movement of the feathers (apart from the filoplumes) is brought about by the feather muscles, which attach to the walls of the follicles (Fig 3-2). The apertial muscles exert tension on the skin lying between the tracts of feathers. The dermis contains many blood vessels and in some sites, such as the wattles, these are especially numerous.

The subcutaneous layer is formed mainly by loose connective tissue. It contains fat, both as a layer and as discrete fat bodies, the latter being attached.