CHAPTER 1

INTRODUCTION

The Palaeognathae

The evolution of birds has fascinated biologist for many years. Many aspects of the evolution of birds are still uncertain, and only recently biologists seem to have reached a consensus that dinosaurs and birds are closely related (Padian & Chiappe, 1998). However, the phylogenetic relationship within birds, and the monophyly of the taxon Aves are still under dispute.

The evolution of the avian taxon Palaeognathae, especially, has puzzled biologist for more than a century. It is still unclear whether this taxon is monophyletic and what the phylogenetic relation is between this taxon and all other birds.

In this thesis functional and evolutionary morphology is used to investigate the evolution of the Palaeognathous birds with special focus on cranial characters and their interrelation with feeding behaviour.

The species

Following the systematics of Sibley and Monroe (1990), the taxon Palaeognathae consists of a very limited number of extant species. The taxon Palaeognathae is divided into two subtaxa, the Ratites and the Tinamous. The Ratite taxon consists of only 10 species: the greater and smaller Rhea (*Rhea americana, Pterocnemia pennata*) from South-America, the Ostrich (*Struthio camelus*) from Africa, three species of cassowaries from New-Guinea and northern Australia (*Casuarius casuarius, C. bennetti, C. unappendiculatus*), the Emu (*Dromaius novaehollandiae*) from Australia and three species of Kiwis (*Apteryx australis, A. owenii, A.haastii*) from New-Zealand. The second sub-taxon is represented by approximately 50 species of Tinamous in 9 genera (*Tinamus, Nothocercus, Crypturellus, Rhynchotus, Nothoprocta, Nothura, Taoniscus, Eudromia, Tinamotis*) all from South-America. All the Ratites are flightless, while the Tinamous are all poor flyers.

In addition to the extant species a number of fossil groups is also considered to belong to the Palaeognathae. The two best-known fossil palaeognathous groups are the Aepyornithidae or Elephant-birds of Madagascar (Rich, 1979, 1980) and the Dinornithidae or Moas from New-Zealand (Owen, 1840; Archey, 1941; Oliver, 1949; Cracraft, 1976; Millener, 1982; Worthy, 1988a,b; 1989). Another group of Palaeognathae, found in Europe and North America, are the Lithornithidae (Houde, 1988). Finally, some incidental findings have been considered to be Palaeognathae also, but their taxonomical position is still uncertain. (Ambiortidae: Kurochkin, 1982; Eleutherornithidae: Harrison & Walker, 1979; Houde & Haubold, 1987; Gansuidea: Hou & Lui, 1984; Opisthodactylidae: Alvarenga, 1983; Palaeocursornithidae: Kessler & Jurcsak, 1984; Bock & Bühler, 1996; Remiornithidae: Lemoine, 1881; Lydekker, 1891; Martin, 1992 Patagopterygidae: Alvarenga & Bonaparte, 1992, but see also Chiappe & Calvo, 1989; Chiappe 1990, 1991). For the phylogeny of these fossil bird groups I refer to the work of Kurochkin (1995).

Morphological characters

The first who made a distinction between the Palaeognathae and all other birds was Merrem (1813). His distinction was mainly based on the keelless sternum of the Ratites. Since then various morphological characters have been used to describe the differences between the Palaeognathae and all other birds. Many of the characters proved not to be completely distinctive and only a few characters remain.

The first character that is considered to be specific for the Palaeognathae is the unfused condition of the pelvis. This character was first noted by Pycraft (1900) and is described as the open ilioischiatic fenestra. The fenestra is called open because the *ilium* and the *ischium* are not fused as in neognathous birds. The second character is the apparent segmentation of the rhamphotheca as described by Parkes and Clark (1966). They describe very distinct grooves in the rhamphotheca that separate the medial nail-like section from the lateral parts. The third character is the morphology of the ear, described by several derived characters (Starck, 1995).



Figure 1.1. Ventral view of the palaeognathous Pterygoid-Palatinum Complex (PPC) in the Greater Rhea (Rhea americana).

The fourth character is the presence of the *Musculus geniohyoideus* (Müller and Weber, 1998), which is present in reptiles and the Palaeognathae only. Finally, the most important character is probably the palaeognathous palate, first recognised by Huxley (1867). Although always referred to as the palaeognathous or dromaeognathous palate, the character is a combination of characters found in the bony elements of the ventral aspect of the facial part of the skull. These elements include the quadrates, (*Os quadratum*), the pterygoids (*Os pterygoideum*), the palates (*Os palatinum*), and the vomer (*Vomer*). This combination of the pterygoids, palates and vomer ('the palate') will be referred to as the Pterygoid-Palatinum Complex (PPC).

The existence of the palaeognathous PPC has often been discussed. The first complete description of the PPC's of all the Palaeognathae was given by McDowell (1948). Based on the



Figure 1.2. Types of cranial kinesis in birds (Adapted from Zusi, 1984). P=protraction, R=retraction; solid pointers indicate the nasal-frontal hinge; open pointers indicate additional bending zones in the dorsal bar.

large variation in the morphology of these PPC's he concluded that a uniform palaeognathous PPC does not exist and that the palaeognathous PPC was therefore not a true character. This was later opposed by Bock (1963), who stated that a uniform palaeognathous PPC could be described and that it was a character found in the Palaeognathae only. He described the palaeognathous PPC with the following characters (Fig. 1.1; Bock 1963, p. 50): a) the vomer is relatively large and articulates with the premaxillae and the maxillo-palatines anteriorly and (except for the Ostrich) with the pterygoids posteriorly; b) the pterygoid prevents the palatine from articulating with the *Rostrum parasphenoidale*; c) the palatine connects to the pterygoid along a suture; d) the basitemporal articulation is large, and is found near the posterior end of the pterygoid; e) the articulation between the pterygoid and the quadrate is complex, and includes part of the orbital process of the quadrate. He concluded that the palaeognathous palate as a whole presents a general configuration similar in all birds possessing it, and sharply distinct from the condition found in all other birds.



Figure 1.3. Different types of nostrils. Grey areas indicate inter-orbital and inter-nasal septa.

- A. Neognathous holorhinal
- B. Neognathous schizorhinal
- C. Palaeognathous holorhinal

The function of the PPC has been described for neognathous birds only (Bock, 1964). The PPC plays an important role in the movement of the upper bill. The movement of the upper bill is induced by a rotation of the quadrate. The rotation is transferred into a rostral/caudal movement of the pterygoid and palate. The rostral/caudal movement of the palate results in a rostral/caudal movement of the lower part of the upper bill, which results in a rotation around a hinge or flexible zone in the upper bill. Based on the position of the flexible zones three main types of kinesis are distinguished (Fig. 1.2; Zusi, 1984). The first and the most common type is prokinesis. In this type the upper bill consists of three rigid bones, which do not move relative to each other. The upper bill moves as a whole around the nasal-frontal hinge. In the second type, rhynchokinesis, bending occurs within the upper bill through bending zones in both the dorsal and ventral part. The third type, amphikinesis can be considered a combination of prokinesis and rhynchokinesis. Rhynchokinesis itself can be divided into five subtypes based on the number and position of the bending zones in the upper bill. Three types have a clear narrow bending zone and are named after the position of the bending zone in the upper bill: proximal rhynchokinesis, distal

rhynchokinesis, and central kinesis. In double rhynchokinetic bills two bending zones are present: one at the proximal and one at the distal end. Finally, extensive rhynchokinesis is characterised by an elongated bending area along the central area of the upper bill.

To make rhynchokinesis possible, not only flexible zones must be present in the upper bill, but the movement inducing the rotation must also be transferred by the non-rotating proximal part of the upper bill, to the rotating distal part. This can be achieved by a uncoupling of the movement of the dorsal and ventral bony bars of the upper bill. Uncoupling allows the ventral bar to slide forward while the dorsal bar remains stationary. This is achieved in two different ways in avian evolution. The first and most common solution is the development of a special type of nostril, the schizorhinal nostril (Fig. 1.3). In prokinetic birds the dorsal and ventral bars are connected at the caudal side through a rigid lateral bar that has its dorsal end rostral to the nasal-frontal hinge. To uncouple the movement of the dorsal and ventral bar, this lateral bar becomes flexible and its dorsal connection shifts caudally to the area behind the nasal-frontal hinge. This change improves bending in the lateral bar and therefore the uncoupling of the dorsal and ventral bar. In the second more rigorous solution the lateral bar is broken, or more accurately, reduced to a small highly flexible ligament. The position of the dorsal end of the lateral bar, however, is still positioned in front of the nasal-frontal area, and the nostril is therefore holorhinal (Fig. 1.3).

All prokinetic Neognathae have a holorhinal nostril. All rhynchokinetic Neognathae possess a schizorhinal nostril. The Palaeognathae are the only living birds that possess central rhynchokinesis according to the definition of Zusi (1984) and achieved uncoupling of the dorsal and ventral bar with a holorhinal nostril and a ligamentous lateral bar. As mentioned earlier the Palaeognathae also have a special configuration of the PPC. Since this combination is only found in the Palaeognathae several authors have tried to connect these three characters (Hofer 1954, Simonetta, 1960, Bock 1963) by a functional explanation. The validity of the proposed functions will be discussed later in this thesis.

Phylogeny and evolution of the Palaeognathae

An important question has always been whether the Palaeognathae are a monophyletic taxon or not. Based on the morphology of the PPC Huxley (1867) considered the Palaeognathae monophyletic. This was later confirmed by characters of the axial skeleton (Mivart, 1877). Fürbringer (1888) proposed that the large diversity in the morphology of the palaeognathous palate indicated independent origins of the different Palaeognathae and that they were therefore polyphyletic. The discussion about the monophyly of the Palaeognathae lasted until methods came available that were not directly dependent on morphological differences. From 1960 onward (Sibley, 1960) several molecular techniques were used to test the monophyly of the Palaeognathae. These studies seem to have solved the dispute since they all indicate that the Palaeognathae are monophyletic (e.g. Sibley & Ahlquist, 1990; Cooper *et al.*, 1992; Cooper, 1994; Caspers *et al.*, 1994; Lee *et al.*, 1997; Cooper & Penny, 1997; Cooper, 1997).

The origin of the Palaeognathae, however, has never been solved and several hypotheses about the evolution of this taxon have been postulated. The first and most generally accepted one states that the Palaeognathae are the most basal group within modern birds (Fig. 1.4a; Feduccia, 1995). This is confirmed by a large number of molecular analyses (e.g. Sibley & Ahlquist, 1990; Cooper et al., 1992; Cooper, 1994; Caspers et al., 1994; Lee et al., 1997; Cooper & Penny, 1997; Cooper, 1997; van Tuinen et al., 1998; Groth & Barrowclough, 1999) and morphological analyses including extinct taxa (Elzanowski, 1995; Kurochkin, 1995). The alternative theory states that the Palaeognathae are a non-basal group and that the characters that are presumed to be primitive have evolved through neoteny (Fig. 1.4b; de Beer, 1956; Jollie, 1976). This hypothesis is supported by some recent molecular phylogenetic analyses (Mindell et al., 1997; Mindell et al., 1999; Härlid & Arnason, 1999) and experiments in which palaeognathous characters were found in neognathous songbirds after neonatal thyroidectomy (Dawson et al., 1994). Based on the present knowledge it is very difficult to decide which of the two hypotheses is correct. At present only the argument that a majority of studies indicate a basal position of the Palaeognathae within birds can be used to prefer that hypothesis to the hypothesis that the Palaeognathae have a neotenous origin.



Figure 1.4. Alternative avian phylogenies. A. Palaeognathae at a basal position (DNA-DNA hybridization; Sibley & Ahlquist, 1990). B. Palaeognathae at a derived position (DNA-sequencing; Härlid et al., 1998).

Avian evolution

Although several hypotheses exist about the origin of birds, the most generally accepted hypothesis states that the birds have evolved from a Theropod dinosaur (Padian & Chiappe, 1998; Sereno, 1999). The origin of birds is more precisely situated within the Maniraptora, a taxon within the Coelurosauria. Within the Maniraptora birds are probably closely related to the Dromaeosauridae. Other taxa within the Maniraptora are the Troodontidae and the Oviraptorosauridae (Sereno, 1999). The origin of the earliest birds is estimated to have been in the Late Jurassic (150 MYA), while orders of modern birds are thought to have originated in the Mid-Cretaceous (100 MYA). At the transition of the Cretaceous to the Tertiary (65 MYA) a mass-extinction took place in which the majority of the dinosaurs became extinct. The only groups from the taxon Dinosauria that were able to pass the Cretaceous-Tertiary (K-T) boundary were representatives of the extant avian orders, which showed a large radiation during the Tertiary.

Two different hypotheses have been postulated about the survival of the extant bird orders across the K-T boundary. The first and most generally accepted hypothesis, states that about 20 modern avian orders were present in the Cretaceous and that all passed the K-T boundary without severe extinction (Chiappe 1995; Cracraft, 1986; Sibley and Ahlquist, 1990). In contrast to this hypothesis Feduccia (1995) states that a large number of bird-orders was present in the Cretaceous, which almost all became extinct during the Cretaceous-Tertiary transition. Of all modern orders only one type was assumed already present in the Late Cretaceous. Feduccia describes this bird as a 'Transitional shorebird'. Feduccia states that from all bird orders present in the Late Cretaceous only this 'Transitional shorebird' survived the mass-extinction during the Cretaceous-Tertiary boundary. Subsequently this 'Transitional-shorebird' gave rise to all modern avian taxa.

Functional (evolutionary) morphology offers a good framework to solve the conflict between the 'single bird survivor' and the 'multiple bird survivor' theory. Because wide-scale extinction took place both within and between taxa, it is clear that the change in environment in the period of the K-T transition resulted in high selection pressures. Organisms that were sufficiently adapted to the new environment were able to pass the K-T boundary, while others were not. In other words, the environment put high functional demands on the morphology of all organisms.

It is possible to determine the specific functional demands that were acting on the avian morphology during the K-T transition. These functional demands can be combined with the known morphology of the fossil bird groups from the Cretaceous, and for each group it can be tested whether it fits the functional demands. Only when the morphology is adapted to the functional demands the bird group is expected to survive. This method makes it possible to determine whether only the 'Transitional Shorebird' of Feduccia was able to survive the K-T transition or that other groups of birds were able to pass the transition as well.

This method was developed and used by Zweers *et al.* (1997; see also Zweers & Vanden Berge, 1997b) to describe a possible avian evolutionary pathway. Their analysis focused only on cranial morphology in relation to the trophic system of birds and cannot be unconditionally

extrapolated to the entire organism. According to Zweers *et al.* (1997) the available food during the K-T transition can be divided into five different groups: 1) aquatic invertebrates and fish, 2) burrowed invertebrates, such as crabs, worms and molluscs in coastal mudflats 3) aquatic plants, including seaweeds 4) tough foliages, such as grasses, supplemented by seeds, insects and possibly small vertebrates and 5) predators on the first four groups. Based on these food-types the authors hypothesise that dinosaurs needed large biting forces, a highly modifiable feeding apparatus and a wear-resistant keratin-layer on the jaws. The extra biting force is needed to process the often tough food-items; the wear-resistant keratin-layer is needed since these food-items may damage the beaks, and keratin is easy to replace. The keratin-layer is also highly adaptable and special features such as holding ridges can easily evolve in keratin.

According to Zweers *et al.* (1997) these functional demands are fulfilled by two adaptations of the skull. The first is the evolution of a keratin-layer along the beak, known as the rhamphotheca. The second is a detached palate in combination with upper bill kinesis. In their hypothesis this uncoupling of the palate results in an extra contribution of the pterygoid muscles to the biting forces through the moveable upper bill. This detachment of the palate resulted in three different types of moveable upper bills: 1) a meso-/pre-kinetic lineage including *Archaeopteryx*, 2) a central rhynchokinetic lineage including the Palaeognathae and 3) a prokinetic lineage including the Neognathae. Since only birds had a moveable upper bill in combination with a rhamphotheca they were able to survive the K-T boundary. It was suggested that not just a single "Transitional shorebird' survived the K-T Transition (Feduccia, 1995) but four different trophic types of birds. These bird-types are a browser type (Palaeognathae lineage) and three other trophic types from the neognathous lineage (grebe-like catcher, plover-like prober and rail-like slicers).

In this hypothesis especially the position of the Palaeognathae is remarkable since they are conventionally considered the most basal group within modern birds and the sister group of the Neognathae. In this thesis an analysis is made of the feeding apparatus of the Palaeognathae in order to test the hypotheses of Zweers *et al.* (1997) that a) the morphology of the palaeognathous skull results in additional biting forces and b) the Palaeognathae and Neognathae are phylogenetically not closely related. The Palaeognathae are especially of interest since their morphology of the PPC, the element that plays the key-role in the hypothesis of Zweers *et al.* (1997), is so remarkably different.

To study the evolutionary significance of the palaeognathous PPC a number of questions must be answered. First the question will be addressed whether the palaeognathous PPC can be defined and whether it is found within the Palaeognathae only. Using an outgroup comparison method it will be investigated whether the palaeognathous PPC represents a primitive or derived condition within birds. After the presence of the character has been established it is necessary to determine its role and function, and the effect of this function on the morphology. In neognathous birds the PPC is important in the movement of the upper bill. Because the Palaeognathae possess both a unique PPC morphology and a unique type of kinesis (central rhynchokinesis) it must be tested whether the type of kinesis has an effect on

the PPC morphology. The PPC morphology of a neognathous rhynchokinetic species will be analysed and characters specific to either rhynchokinesis or to the feeding behaviour will be described. In addition the feeding behaviour of the neognathous rhynchokinetic bird will be described in order to determine the advantage of rhynchokinesis and to determine when maximal rhynchokinesis occurs. These characteristics of rhynchokinetic feeding behaviour can then be used to test whether the morphology of the palaeognathous skull is adapted to rhynchokinesis and whether it serves the same function in Palaeognathae as in Neognathae. This is tested by determining the displacement patterns of the bony elements in the skull during upper bill elevation. To measure these displacements a new roentgen-stereophotogrammetry method is developed, which makes it possible to determine the displacement in three dimensions with an accuracy of 0.12mm. The displacement of bony elements in the skull during upper bill elevation was determined in three palaeognathous species, and for comparison in a rhynchokinetic and a prokinetic neognathous bird. The palaeognathous skull was further investigated for the presence of characters specific for rhynchokinesis and a configuration of the skull that is optimal for rhynchokinetic feeding behaviour. The feeding behaviour of the Palaeognathae is analysed to investigate the role of rhynchokinesis and to determine which functional demands have resulted in the specific palaeognathous PPC morphology. Finally, it is tested whether the palaeognathous PPC might have evolved through neoteny. This is done by a comparison of adult palaeognathous skulls, with the skulls of a neognathous bird in several stages of development. The results of these studies will be used to determine which selective forces have resulted in the specific morphology of the palaeognathous skull.