CHAPTER 9

SUMMARY & GENERAL DISCUSSION

General Summary

The evolutionary history of the Palaeognathae has puzzled biologists for more than a century. The main questions have always been the monophyly of the taxon, and the question whether the Palaeognathae are primitive or derived within modern birds. The first problem seemed to have been solved since the development of molecular phylogenetic techniques. Almost all molecular phylogenetic studies point in the direction of a monophyletic origin of the Palaeognathae. The second dispute in the evolutionary theory about the Palaeognathae is the point of origin of the taxon. The most generally accepted hypothesis claims that the Palaeognathae are the most basal group within modern birds. An opposing hypothesis claims that the Palaeognathae are derived within modern birds and that their characters have evolved through neoteny.

In this thesis an attempt is made to solve the question where in the avian phylogeny and how in avian evolution the bifurcation between the Neognathae and Palaeognathae took place. This is done by analysing one of the most characteristic features of the Palaeognathae: the palaeognathous Pterygoid-Palatinum Complex (PPC). The PPC in neognathous birds is part of the mechanism that elevates the upper bill. This function has, however, never been confirmed for the Palaeognathae, nor is it clear what selective forces have resulted in the special morphology of the palaeognathous PPC.

Although the Palaeognathous PPC was already recognised at the end of the 19th century (Huxley, 1867), some authors disputed the existence of the character (McDowell, 1948). In chapter two it was shown that the palaeognathous PPC is indeed a character complex that is clearly different from the neognathous condition and can be quantitatively described. An outgroup analysis showed that the palaeognathous condition is more primitive than the neognathous condition. The main characters of the PPC that differ between the palaeognathous and neognathous PPC are: a large *Processus basipterygoideus*, a short *Processus orbitalis quadrati*, a broad and rostrally situated pterygoid-palate articulation, a broad vomer and broad pterygoids. In general the five qualitative characters given by Bock (1963) describe the palaeognathous palate accurately. We can therefore conclude that the palaeognathous PPC is a true character that distinguishes the Palaeognathae from the Neognathae. Our study of the PPC showed that the palaeognathous condition is only found in the Palaeognathae, also indicating a monophyletic origin of this condition.

This allows us to consider the Palaeognathae to be monophyletic and their characters specific for this group. This allows us to compare our findings about the palaeognathous PPC with the evolutionary pathway as proposed by Zweers *et al.* (1997; see also Zweers & Vanden Berge, 1997). To do this a functional analysis is made of the PPC with special attention to the proposed linkage between the morphology of the palaeognathous PPC and central rhynchokinesis.

To determine the relation between PPC morphology and the type of kinesis, the morphology of a neognathous rhynchokinetic bird was investigated. To distinguish between neognathous characters and rhynchokinetic characters, this neognathous rhynchokinetic bird was first compared with the general prokinetic morphology. In chapter three an analysis is made of the morphological characters and feeding patterns of the Red Knot (*Calidris canutus*), a specialised rhynchokinetic prober. This analysis showed that features that can be related to rhynchokinetic feeding behaviour are mostly found in the bill itself. The main characters are the clearly recognisable flexible zones in the dorsal and ventral bars and the uncoupling of the dorsal and ventral bar through a schizorhinal nostril. Morphological differences in the PPC of the rhynchokinetic Red Knot compared to that of prokinetic birds were not found, indicating that the type of kinesis does not have a large effect on the configuration of the PPC. This might indicate that there is no relation between the palaeognathous PPC and central rhynchokinesis.

Although no large differences could be found between the PPC morphology of neognathous prokinetic and neognathous rhynchokinetic birds, it is possible that the special PPC of the Palaeognathae is the result of a difference in function between the Palaeognathae and the Neognathae. To test this we determined the movement pattern of the PPC during elevation of the upper bill. To give an accurate and complete description of the relatively small movements, the displacement of the PPC had to be determined in three-dimensions. For this three-dimensional analysis a new roentgen-stereophotogrammetry technique was developed.

Chapter four describes the method that was used to determine the displacement of bony elements in skulls with different types of cranial kinesis. The method is a combination of roentgen-photography and stereophotogrammetry. Stereophotogrammetry is used to determine three-dimensional co-ordinates of object markers from at least two photographs of the object from different angles. Normally these two photographs are obtained by moving the camera around the object or by using two cameras. Neither of these methods could be used in combination with roentgen-photography since only one roentgen-source was available and movement of a roentgen-camera leads to a change in the interior orientation of the camera. In roentgen-photogrammetry the roentgen-source and the film are not connected and movement of the camera (source and receiver) results in a change of the configuration of the camera. Any change in configuration decreases the accuracy of the calculations. In collaboration with the Delft University of Technology a new method was developed to overcome these problems. A single roentgen-source was used, and instead of moving the camera, the object was moved within the roentgen-bundle, and photographed from six different angles. From these radiograms the co-ordinates of markers are calculated with an accuracy of 0.12 mm.

In chapter five the stereo roentgen-photogrammetry method was used to determine the displacement of several bony elements of the jaw apparatus, including the PPC, after elevation of the upper bill in skulls of five different species with prokinetic (*Corvus corone*), and rhynchokinetic skulls (*Calidris canutus*, *Struthio camelus*, *Dromaius novaehollandiae*, *Rhea americana*). It was shown that Bock's qualitative description (1964) of the movement of the PPC during bill opening was accurate, and that no large differences are present in the movement patterns of birds with different types of kinesis. This indicates that the functional demands for movement acting on the PPC for elevating the upper bill are similar for all types of kinesis.

In the three-dimensional kinematic analysis elevation was imposed by applying external forces. Since any structure will bend if sufficient force is applied, it was investigated whether the bill morphology of the Palaeognathae was adapted to rhynchokinesis. In this analysis we used the bill characters found in the distal rhynchokinetic Red Knot (*Calidris canutus*) to define a rhynchokinetic bill. The morphological adaptations that have to be present for rhynchokinesis are: clear bending zones in the dorsal and ventral bars, uncoupling of the dorsal and ventral bar, and sufficient muscle force to elevate the upper bill. In addition we investigated whether the force of the pterygoid muscles contribute to biting force as suggested by Zweers *et al.* (1997) for the palaeognathous ancestral trophic system. We found that uncoupling of the dorsal and ventral bar of the upper bill is present. However, no clear bending zones could be detected in the bars of the upper bill. Some thinner zones are present in the bars of the upper bill, but the position of these zones differs from the position where bending is observed. The analysis of muscle force showed that the force of the *Musculus protractor pterygoideus et quadrati* is sufficient to elevate the upper bill. The analysis also showed that the configuration of the muscles and the skull of the Palaeognathae results in very low biting force. A remarkable feature of the Palaeognathous skull is the presence of the large *Processus basipterygoideus*. It was found that this element, in combination with the large *Musculus pterygoideus* can act as a stabilising mechanism, which prevents the upper bill from being depressed or elevated by external forces. Large elevation forces may occur when the birds pull leaves from plants. These findings indicate that the upper bill of the Palaeognathae is not ‘adapted’ to active rhynchokinesis, but that movement in the upper bill occurs as a result of intrinsic flexibility in the bone itself.

In chapter seven the feeding behaviour of the Palaeognathae was studied. The transport phase of the feeding pattern is a very simple inertial ‘Catch & Throw’ type. Drinking behaviour is basal and consists of a scooping movement followed by a low-amplitude tip-up phase only. Cranial kinesis is limited and occurs only during gaping and is always orientated dorsally (elevation). It was also found that bending occurs over the full length of the upper bill, but is most prominent at the bill tip. The grasping and transport phases in palaeognathous feeding behaviour strongly resembles that of neognathous birds and there is no indication that Palaeognathae experience other selective forces on the PPC than Neognathae as a result of the feeding behaviour investigated. Furthermore, the Palaeognathae are not able to generate large biting forces in their feeding behaviour.

In chapter eight the hypothesis about the neotenous origin of the Palaeognathae was tested. A numerical method was used to compare the PPC of adult palaeognathous species with the PPC of stages in the development of a neognathous bird. This showed that there are large differences between the morphology of the Palaeognathae and the embryonic stages of the neognathous bird, indicating a non-neotenous origin of the Palaeognathae.

Avian Evolution during the Cretaceous

Our findings will be used to test the evolutionary pathway proposed by Zweers *et al.* (1997; see also Zweers & Vanden Berge, 1997). I consider the origin of all birds to be within the Coelosauria and probably closely related to the Dromaeosauria (Padian & Chiappe, 1998). The first step in the direction of the avian feeding mechanism is the fenestration of the skull and reduction of the bars in the lateral aspect of the skull as described by Zweers *et al*. (1997). This reduction resulted in a flexible skull without a mechanism for cranial kinesis. The next step in the evolution of birds is assumed to be the detachment of the palate, which was achieved in three different ways resulting in a trifurcation of evolutionary pathways. The three lineages are described as a non-kinetic Dromaeosauro-/Archeopterygo-/Enantiornithomorf lineage, a pre-rhynchokinetic Ornithomimo-/Hesperornitho-/Ratitomorph (now called Palaeognathous) lineage and a (pre-)prokinetic Troodonto-/Neognathomorph (now called Neognathous) lineage. Because modern birds are only found in the latter two, we will focus on these two lineages. This trifold radiation was assumed on the basis of the reduction of the pterygoid and the capacity to transfer force between upper bill and quadrate. The main difference between the proposed Palaeognathous lineage and the Neognathous lineage described by Zweers *et al.* (1997) is the presence of a vomeral-maxillary bar. Other characters discriminating between the two lineages are found in the pterygoids, but these do not differentiate the Palaeognathous and Neognathous lineages completely. In both lineages two pterygoids are present during development, of which the rostral part becomes either incorporated in the palato-vomeral-maxillary apparatus or disappears completely. Remarkable is also that the primary division described by Zweers *et al.* (1997) results in akinetic species in all three lineages, and that in each lineage an independent development of kinesis occurs. Our study (Chapter 5) showed that in each of the proposed kinetic lineages both the role and position of bony elements (except for the vomer) and the movement pattern of the PPC are very similar. This indicates that the detachment of the palate has occurred earlier in evolution resulting in a bifurcation in a non-kinetic and a kinetic lineage. With this modification, the transformation pattern of Zweers *et al.* (1997) represents the classical situation in which the Palaeognathae are basal within modern birds, and the sister group of the Neognathae (Cracraft, 1986; Sibley & Ahlquist, 1990). Based on the findings of Cooper & Penny (1997) the kinetic-lineage must have originated during the Cretaceous, followed by a very early bifurcation between the Palaeognathae and Neognathae.

The K-T transition

The next step in the evolutionary pathway is the transition at the K-T boundary. A large ecological effect during the K-T transition was a change in climate what resulted in a decline in food resources. For the palaeognathous lineage Zweers *et al.* (1997) described the available food resources as tough foliage that requires large biting forces, a highly modifiable rhamphotheca and hetereocoelic vertebrae. In our analysis we mainly focused on biting force since this is the functional demand that directly acts on the jaw-apparatus. A large biting force is thought to arise from a kinetic skull, a detached palate (PPC), and an extra force-component from the *Musculus pterygoideus*. After the detachment of the palate, the *Musculus pterygoideus* is assumed to add an additional component to the closing forces on both the upper and lower bill.

This seems incorrect for the palaeognathous lineage. However, the feeding behaviour as described for the extant palaeognathous birds seems fit for eating tough foliage also indicating an alternative solution. For this feeding behaviour the birds do not use large biting force for their food-uptake (Chapter 7) but have developed a mechanism that resists upper beak elevation due to external forces. The overall morphology also indicates that the Palaeognathae are not adapted to rhynchokinesis. Most important it was shown that the well-developed pterygoid muscles in the Palaeognathae do not contribute significantly to total biting force (Chapter 6). I therefore conclude that the hypothesis of Zweers *et al.* (1997) that the *Musculus pterygoideus* in combination with a moveable increases biting force is incorrect for the Palaeognathae. As observed correctly by Zweers *et al.* (1997) the additional force from the pterygoid muscles acts on both the upper and lower bill. However, due to the very ineffective position of the pterygoid muscles on the lower bill, the contribution to upper jaw depression is much higher than the contribution to lower jaw elevation. The depression of the lower bill must therefore be counteracted by an activation of the lower jaw adductor muscles. If therefore the pterygoid muscles become larger, the adductor muscles have to become larger as well, to counteract the forces of the pterygoid muscles.

Although biting force does not increase it is not impossible that the palaeognathous PPC configuration made the transition of the K-T boundary possible but for a reason different from biting force. If the ancestral Palaeognathae fed on tough foliage during the K-T transition it is likely that they used the same mechanism as the extant Palaeognathae. These birds remove leaves from plants, or from the ground, by a caudal pull of the vertically orientated head (Chapter 7). These movements result in large external forces on the upper bill, which might result in opening of the upper bill. The large *Musculus pterygoideus* can be used to counteract these external forces. To prevent the risk of overcompensation, resulting in depression of the upper jaw, the *Processus basipterygoideus* is present, which is used to ‘block’ the depression of the upper bill (Chapter 6).

The fact that the upper bill has to be stabilised by a muscle indicates that the ancestor of the Palaeognathae must have had a kinetic skull, and that the upper bill was stabilised later in evolution. The main question that results from this conclusion is whether the ancestor of the Palaeognathae was prokinetic or rhynchokinetic. As mentioned before, the morphology does not confirm a rhynchokinetic condition, since flexible zones are absent. However, the dorsal and ventral bar of the upper bill are uncoupled, but by a mechanism that is not found in other rhynchokinetic birds. The presence of the holorhinal nostril indicates that the palaeognathous mechanism has either evolved from an akinetic, or a prokinetic ancestor.

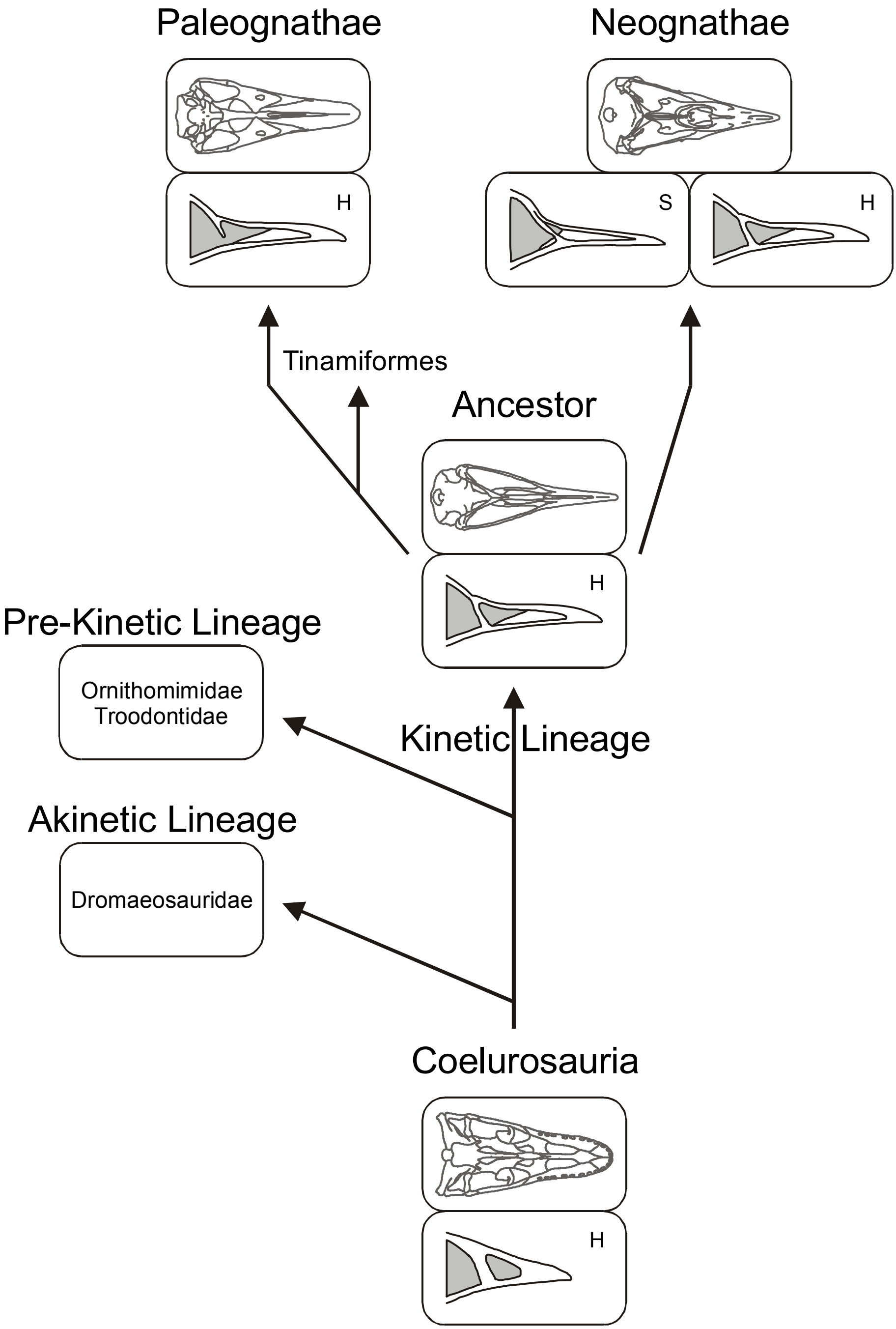

Figure 9.1. Caption on facing page.

An alternative hypothesis is that the holorhinal nostril is one of the characters that might have evolved through neoteny. In that case it is still possible that the ancestor of the Palaeognathae had a schizorhinal nostril and was rhynchokinetic. Our analysis of the PPC indicated that the PPC does not possess characters that are also found in embryological stages of neognathous development. I therefore reject the hypothesis about neotenous-origin of the palaeognathous PPC. It is still possible that characters such as flightlessness and downy feathers might be the effect of neoteny (de Beer, 1956).

The evolution of the Palaeognathous birds

In accordance with the findings described above a new evolutionary pathway for the Palaeognathae is postulated (Fig. 9.1). The different morphology of the Palaeognathae made it possible to resists external forces opening the upper bill during grazing on tough foliage. This adaptation made it possible for the Palaeognathous lineage to pass the K-T boundary confirming the hypothesis that the bifurcation between the Palaeognathae and Neognathae must have occurred in the Cretaceous period (Cooper & Penny, 1997; Zweers *et al.*, 1997). The similar movement patterns of the PPC suggest that the skull of the ancestral bird must have been kinetic with a detached palate. From this ancestral design two lineages evolved, the Palaeognathae and Neognathae. The main question is to determine the ancestral design. Since both the palaeognathous and neognathous lineage evolved directly from the ancestral design (neoteny did not play a role) all elements present in both lineages must have been present in the ancestral design. Therefore the ancestor of the modern birds must have possessed both a vomer and a *Processus basipterygoideus*. Since a holorhinal nostril is present both in the Palaeognathae and Neognathae it is expected that the ancestral bird also had a holorhinal nostril and was probably (pre-)prokinetic. The overall skull configuration of the ancestral type might resemble the morphology of the modern Tinamiformes. The skull morphology of the Tinamiformes possesses all elements of the Palaeognathous PPC, possesses a holorhinal nostril and a complete lateral bar. A diversification in feeding behaviour probably resulted in the bifurcation of the Neognathae and Palaeognathae. The palaeognathous lineage started feeding

Figure 9.1. (on facing page) Adapted evolutionary pathway of the Paleognathae based on the hypothesis of Zweers et al. (1997). Within the Coelurosauria first an akinetic lineage splits of, including the Dromaeosauridea. The other lineage has reduced cranial bars and is considered pre-kinetic. This latter lineage divides in a kinetic (Avialae) and a pre-kinetic lineage based on the detachment of the palate. The pre-kinetic lineage includes the Ornithomimidae and the Troodontidae. The ancestral design within the kinetic lineage has a moveable palate, a holorhinal nostril and is (pre-) prokinetic. Based on differences in food acquisition a bifurcation in the Paleognathae and Neognathae occurred. This last bifurcation most probably occurred before the Cretaceous-Tertiary boundary. Within the paleognathous lineage the Tinamiformes are probably the most basal group. H=holorhinal nostril, S=schizorhinal nostril.

on food-types that required large forces to acquire and process. Although I doubt that the Palaeognathae were the only group that fed on this food-type, I assume a different solution to the specific problems of feeding on these food-types between the two lineages. While in neognathous birds the tough food-items were probably sliced with the sharp edges of the rhamphotheca, these sharp ridges did not evolve in the Palaeognathae. To acquire food, the Palaeognathae used forces generated by the neck to pull off leaves and without the ability to reduce the food-items in size developed a feeding mechanism optimised for the intra-oral transport of large objects. The use of neck muscle force resulted in a secondary demand to strengthen the bill configuration, which was achieved by a strongly developed PPC. It can be hypothesised that the method of feeding, in which the neck produces the main forces to acquire food, has resulted in the increase in size of the Palaeognathae so that forces can become larger.

I therefore concur with the hypothesis of Zweers *et al.* (1997) that the Palaeognathae had a sufficient design to pass the K-T boundary. I also conclude that the Palaeognathae must have evolved before the K-T boundary from an already (pre-) prokinetic ancestor. Based on the presence of the large *Processus basipterygoideus* and the large *Vomer* the PPC must resemble a very basal condition. I conclude that the Palaeognathae are the most basal group in modern birds and the sister-groups of all other living birds.