

CHAPTER 2

THE PALAEOGNATHOUS PTERYGOID-PALATINUM COMPLEX. A TRUE CHARACTER?

Summary

Molecular analyses show that modern birds can be divided into two major taxa, the Palaeognathae and the Neognathae. This division was already proposed by Merrem in 1813, based on morphological characters. One of the most prominent discriminating characters is the morphology of the Pterygoid-Palatinum Complex (PPC), which is different in palaeognathous and neognathous birds. There are very few other morphological characters that support this division and even the differences in PPC have been under dispute. A discriminant analysis based on quantitative measurements of the PPC shows that a large difference between the two morphologies exists, and that the Tinamidae possess an intermediate form. An evolutionary maximum-likelihood analysis suggests that the PPC of the Palaeognathae is more primitive than that of the Neognathae. A functional interpretation of the differences in the PPC between the Palaeognathae and the Neognathae indicates that the palaeognathous PPC is not, as generally accepted, an adaptation related to rhynchokinesis, but probably contributes to reinforcement of the skull after the loss of both the postorbital and nasal bar.

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Introduction

Ever since Merrem (1813) divided birds into two groups, the Carinatae and the Ratitae, the latter group has been the source of many disputes. The Ratitae, later grouped with the Tinamous in the superorder Palaeognathae by Pycraft (1900), consists of ten living species (Ostrich, *Struthio camelus*; Rheas, *Rhea americana*, *Pterocnemia pennata*; Cassowaries, *Casuarus casuarus*, *C. bennetti*, *C. unappendiculatus*; Emu, *Dromaius novaehollandiae*; Kiwis, *Apteryx australis*, *Apteryx owenii*, *Apteryx haastii*) and a number of extinct taxa, such as Moas (Oliver, 1949, Cracraft 1976) and Elephantbirds (Cracraft, 1974). The Tinamous comprise approximately 50 living species from Latin America. The systematic position of the Tinamous is uncertain. Several authors place the Tinamous with the Ratites (Cracraft 1974, Sibley & Ahlquist 1990), while others consider them to be neognathous (Gingerich, 1976). The dispute around the division between neognathous and palaeognathous birds includes the existence of the group as a systematic or phylogenetic entity, the monophyly of the group, and the question whether this group is primitive or derived within birds. The first issue is of course essential and the specific characters that discriminate the Palaeognathae from all other birds are of great importance. Although a large number of recent molecular studies has indicated that the Palaeognathae are a single monophyletic taxon (Sibley & Ahlquist, 1990; Cooper *et al.*, 1992; Cooper, 1994; Caspers *et al.*, 1994; Lee *et al.*, 1997; Cooper, 1997) only a few morphological characters have been described that are typical for the Palaeognathae. These specific morphological characters are the palaeognathous palate (=dromaeognathous palate), first described by Huxley (1867), the unfused condition of the pelvis, first described by Pycraft (1900), the apparent segmentation of the rhamphotheca described by Parkes & Clark (1966), and the presence of the *Musculus geniohyoideus* in the palaeognathous lingual apparatus (Müller & Weber, 1998). The most prominent character in the discussion about the Palaeognathae has always been the palaeognathous palate. Since this term does not fully describe the morphology, it will be further referred to as the palaeognathous Pterygoid-Palatinum Complex (palaeognathous PPC).

Huxley (1867) found that in the palaeognathous PPC the caudal ends of the palatines and the rostral ends of the pterygoids do not articulate with the *Rostrum parasphenoidale* and that there is a strong *Processus basipterygoideus*. McDowell (1948) was the first to make a thorough osteological analysis of the palaeognathous palate. He concluded that a palaeognathous PPC cannot be defined, because of the large variation in morphology within the Palaeognathae, and the presence of some of the 'palaeognathous' characters in neognathous birds. This was later disputed by Bock (1963), who claimed that the palaeognathous PPC as a whole can be distinguished from the neognathous PPC. As he puts it: 'The palaeognathous palate as a whole presents a general configuration similar in all birds possessing it, and sharply distinct from the condition in all other birds'. The characters used by Bock to describe this condition include the shape of the vomer, the pterygoid-palate articulation and in its relation to the *Rostrum parasphenoidale*, the articulation with the *Processus basipterygoideus* and the pterygoid-quadrangle articulation. Bock was also one of the few authors who gave a functional interpretation of the palaeognathous PPC. All functional interpretations relate the morphology of the complex

to rhynchokinesis (Hofer, 1954; Simonetta 1960; Bock, 1963). In this type of cranial kinesis only a small rostral part of the upper bill can be elevated (Bock, 1964; Zusi, 1984). Hofer (1954) considers the palaeognathous PPC similar to the desmognathous condition as found in Anseriformes (Huxley, 1867; de Beer, 1937). The desmognathous condition is never found in combination with rhynchokinesis outside the Palaeognathae. Hofer considers the special morphology of the palaeognathous PPC as a condition for the combination of a holorhinal nostril and rhynchokinesis. Holorhinal nostrils are characterised by bony external nares whose concave caudal borders lie rostral to the caudal end of the nasal process of the premaxillae. In neognathous birds that show rhynchokinesis a schizorhinal nostril is present, which is characterised by a slit-like caudal border, situated caudal to the end of the nasal process of the premaxilla. Since in all rhynchokinetic birds the ventral part of the upper bill must move forward relative to the dorsal part, an uncoupling of dorsal and ventral bars is necessary. While schizorhinal nostrils uncouple the dorsal and ventral bars, a bony bridge connects these bars when holorhinal nostrils are present. Bock (1963) follows Hofer in saying that rhynchokinesis is always observed in combination with a schizorhinal nostril, but that in the rhynchokinetic Palaeognathae the nostril can be described as holorhinal. When the nostril is holorhinal uncoupling can be accomplished by a gap in the nasal bone, as found in Palaeognathae. The more rigid structure of the palaeognathous PPC is explained by Bock as an adaptation to the rigid dorsal bar of the upper bill. This bar is relatively thick and large forces are necessary to bend it. To ensure efficient transfer of force the elements of the PPC are strong and rigid, and placed in a straight line as observed in the Palaeognathae (Bock, 1963, p. 48).

To test the hypothesis that the morphology of the PPC within the Palaeognathae is different from that of all other birds, several quantitative characters of skulls of 26 extant bird species were taken. A discriminant analysis is used to test whether these characters allow a complete separation between Palaeognathae and Neognathae. The PPC characters are also used for a comparative analysis. An outgroup is used to determine possible evolutionary patterns, which might indicate whether the Palaeognathae are primitive or derived within modern birds. Functional implications of the differences in characters will be formulated, and their consequences for a connection between a palaeognathous PPC and rhynchokinesis are discussed.

Materials and Methods

Taxonomical names of all bird species and families are according to the classification of Sibley and Monroe (1990, 1993). For the analysis 26 species of the Class Aves and one species of the Class Reptilia were used. The avian species were taken from 9 orders, 18 families, and 26 genera. The species of the Class Reptilia (order Crocodylia) was used as outgroup for the phylogenetic analysis. This taxon was chosen as a near living relative of all birds (Hedges & Poling, 1999). No fossil birds or dinosauria were used for this analysis due to the lack of good fossil material of the PPC. All 26 avian species and the outgroup are summarised in table 2.1.

For the similarity analysis of the PPC 17 descriptive characters and one standard measure were taken of all 27 specimens. The characters were distributed over the whole PPC and are summarised in table 2.2 and figure 2.1. Anatomical nomenclature is according to Baumel *et al.* (1993).

Not all characters are present in all specimens; especially the vomer is highly variable and is reduced in many species. When a character is totally absent the measure of the character was determined to be zero. Characters were measured using an electronic calliper rule (Sylvac, accuracy 0.01 mm). Each measurement was taken twice and the average was used for further calculations. Differences between repeated measurements did not exceed 0.1 mm. To eliminate size effects, all measurements were standardised by dividing them by the value of a standard character A (skull width, see table 2.2).

A stepwise discriminant analysis was performed to determine the discriminating characters between the palaeognathous PPC configuration, the neognathous PPC configuration and the configuration in the outgroup. In a discriminant analysis each individual is appointed to a group *a priori*, in this case either to the Palaeognathae or the Neognathae. Based on that division two

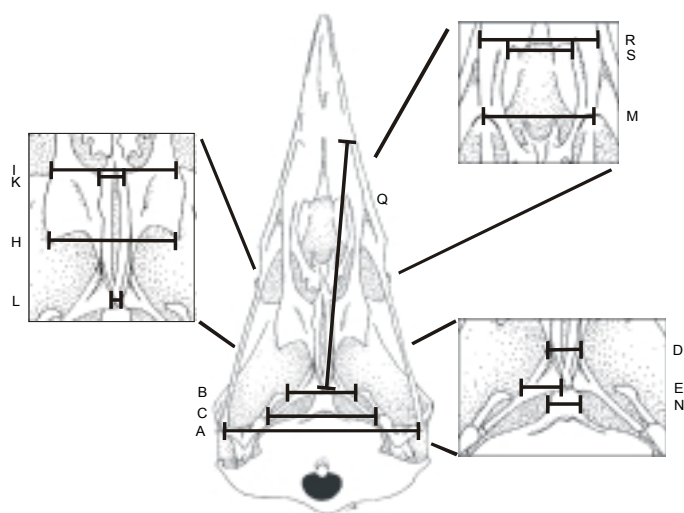


Figure 2.1. Skull of the crow (*Corvus corone*) in ventral view. Inserts are enlargements of areas indicated by the lines. Letters refer to characters in table 2.1. The characters of the vomer cannot be represented since the vomer is reduced in this species. Other characters omitted from this figure for clarity are: O, P, and L. Character O and P are measured in the sagittal plane. Character L is measured at the most caudal point of the pterygoid-palatine articulation.

Table 2.1. Species used in distance analysis. Names according to the classification of Sibley and Monroe (1990, 1993).

No	Order	Family	Species	Common name
0		Alligatoridae	<i>Caiman spec.</i>	Cayman
1	Struthioniformes	Struthionidae	<i>Struthio camelus</i>	Ostrich
2		Rheidae	<i>Rhea americana</i>	Greater Rhea
3		Casuariidae	<i>Casuaris casuaris</i>	Southern Cassowary
4		Casuariidae	<i>Dromaius novaehollandiae</i>	Emu
5		Apterygidae	<i>Apteryx owenii</i>	Little spotted Kiwi
6	Tinamiformes	Tinamidae	<i>Rhynchotus rufescens</i>	Red-winged Tinamou
7	Galliformes	Phasianidae	<i>Gallus gallus domesticus</i>	Chicken
8		Phasianidae	<i>Phasianus colchicus</i>	Common Pheasant
9	Anseriformes	Anhimidae	<i>Anhima cornuta</i>	Horned Screamer
10		Anatidae	<i>Anas platyrhynchos</i>	Mallard
11		Anatidae	<i>Anser domesticus</i>	Goose
12	Psittaciformes	Psittacidae	<i>Ara macao</i>	Scarlet Macaw
13	Columbiformes	Columbidae	<i>Columba palembus</i>	Common Wood-Pigeon
14	Gruiformes	Rallidae	<i>Fulica atra</i>	Common Coot
15	Ciconiiformes	Scolopacidae	<i>Calidris canutus</i>	Red Knot
16		Charadriidae	<i>Recurvirostra avosetta</i>	Pied Avocet
17		Laridae	<i>Alca torda</i>	Razorbill
18		Laridae	<i>Larus spec.</i>	Gull
19		Laridae	<i>Uria aalge</i>	Dovekie
20		Accipitridae	<i>Buteo buteo</i>	Common Buzzard
21		Podicipedidae	<i>Podiceps cristatus</i>	Great Crested Grebe
22		Sulidae	<i>Morus bassanus</i>	Northern Gannet
23		Phalacrocoracidae	<i>Phalacrocorax spec.</i>	Cormorant
24		Threskiornithidae	<i>Platalea leucorodia</i>	Eurasian Spoonbill
25	Passeriformes	Corvidae	<i>Corvus corone</i>	Carion Crow
26		Fringillidae	<i>Passer domesticus</i>	House Sparrow

canonical discriminant functions are calculated, which describe the maximum separation between the two groups. Since the exact position of the Tinamidae is not known, the Tinamid-species was not appointed to any group *a priori*. The discriminant functions are used by the procedure to assign each individual to either the Palaeognathae or Neognathae independent of their *a priori* group membership. When the discriminant functions completely separate the groups, the *a priori* group-membership is the same as the membership determined from the discriminant functions (Manly, 1994).

An evolutionary tree was estimated using a Continuous Characters Maximum Likelihood Method (Felsenstein, 1981, 1993). The tree is rooted by the Cayman and is assumed to represent the pathways in PPC morphology evolution. Within the Maximum Likelihood method the options 'Global rearrangements' was used to optimise the tree. Species were added at random to the tree, and this random procedure was repeated a thousand times to find the

optimum tree from all these runs. The Cayman was appointed outgroup as closest living relative of all birds. As comparison for the Maximum likelihood analyses, a phylogenetic tree based on DNA-DNA hybridisation was used. The data for this tree were obtained from Sibley and Monroe (1990, 1993). Species not in the DNA-DNA hybridisation tree were placed at the position of a closely related species.

Table 2.2. Characters used for distance analysis.

-	Character
A	Skull width at the quadrate-jugal articulation [standard]
B	Distance between most distal points of <i>Processi Orbitalis Quadrati</i>
C	Width at pterygoids at quadrate-ptyergoid articulation
D	Width of pterygoids at pterygoid-palate articulation
E	Maximal width of the right pterygoid in the transversal plane
F	Width of the vomer [caudal]
G	Width of the vomer [rostral]
H	Width of the caudal part of the palatal wings (pars lateralis]
I	Maximal width of the palate at the medial ending of pars lateralis
K	Width between palates at position 'I'
L	Width of palate at pterygoid-palate articulation
M	Internal width at the jugal-premaxilla articulation
N	Width of the <i>R. parasphenoidale</i> incl. <i>P. basipterygoidei</i> if present
O	Distance <i>Foramen magnum</i> to measurement 'N'
P	Distance <i>Foramen magnum</i> to medial fusion of bony elements
Q	Maximal length palate
R	Width at palate-premaxilla articulation
S	Internal width at palate-premaxilla articulation

Results

PPC characters discriminating between Palaeognathae, Neognathae and the outgroup

The results of the discriminant analysis show that the measured characters can define very accurately the difference between Palaeognathae, Neognathae and the outgroup. Two canonical discriminant functions are determined by the analysis, each with its own discriminating meaning. The first function describes the differences between Neognathae and Palaeognathae, while the second function describes mainly the differences between the outgroup and all birds. The discriminating characters and their relative importance in the discriminating functions are given in table 2.3. The first discriminating function describes seven characters important in the discrimination between the Palaeognathae and the Neognathae. These seven characters can be combined to the following description of the palaeognathous PPC: the *Processus basipterygoideus* is relatively large, the *Processi orbitalis quadrati* are

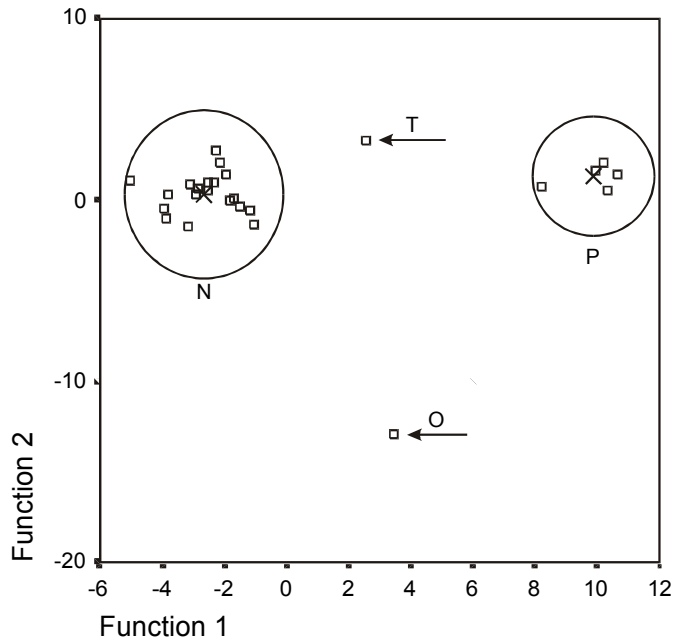


Figure 2.2. Discriminant plot. The X-axis represent the axis of maximal differentiation, the Y-axis of second maximal differentiation. N=Neognathae, P=Palaeognathae, T=Tinamidae, O=Outgroup. Crosses indicate the centre of each group.

relatively small, and the Pterygoid-Palate articulation, the vomer, and the pterygoids are all broader in Palaeognathae (Fig. 1.1). The distance between the *Foramen magnum* and the medial fusion of the Pterygoid/Palate is larger in Palaeognathae. Figure 2.2 shows the distribution of the species when the two discriminant functions are plotted against each other. It is clear that the functions can be used to distinguish between the different groups. When the results of the discriminant analysis are used to determine the position of the specimens without an *a priori* group membership a 100% correct placement is obtained. Since the Tinamou was not appointed an *a priori* group membership, its placement could not be tested. The Tinamou is placed almost exactly in between the Palaeognathae and the Neognathae. Using the discriminant functions the Tinamou is calculated to be neognathous based on the somewhat smaller distance to the Neognathae than to the Palaeognathae.

Evolutionary Morphological Clustering

A total of 22775 different trees were analysed; the tree with the highest likelihood is given in figure 2.3. The logarithmic likelihood of this tree is 836.89. This unrooted tree shows clearly that the Palaeognathae are clustered together and are more closely related to the outgroup than all other birds. When considering these characters for their taxonomical value the tree shows that

Table 2.3. Discriminating characters between palaeognathous and neognathous PPC's.

Variable	Function 1	Function 2
N Width of the <i>R. parasphenoidale</i> incl. <i>P. basipterygoidei</i> if present	1.249	0.463
B Distance between most distal points of <i>Processi orbitalis quadrati</i>	1.025	0.370
L Width of palate at pterygoid-palate articulation	0.851	-0.118
P Distance <i>Foramen magnum</i> to medial fusion of bony elements	-0.770	0.804
F Width of the vomer [caudal]	0.656	0.169
E Maximal width of the right pterygoid in the transversal plane	0.442	-0.822
D Width of pterygoids at pterygoid-palate articulation	-0.094	-0.804

members of the same family (based on molecular data) are always clustered closely together. Only the members of the family Laridae are situated at different branches, but the total distance between the members is small. At a higher taxonomical level the clustering based on PPC-characters does not follow the molecular clustering completely. In almost all cases the members of the ordines with multiple species in the analysis (Struthioniformes, Galliformes, Anseriformes, Passeriformes and Ciconiiformes) are clustered together. The species of the order with the largest number of specimens (Ciconiiformes) are all represented in one large cluster. Only the Coot, Crow and Galliformes can be considered 'misplaced' within this group. The three Anseriformes are also represented by one cluster. The position of the Ara, as a sister group of the Screamer (*Anhima*), is probably due to 'long branch attraction' (Hendy & Penny, 1989). Long branch attraction is an effect of parsimony methods, which tends to cluster specimens with long evolutionary branches. The specimens of the Passeriformes are placed at relatively large distances from each other. However, no intermediates were present in this analysis, which might, in combination with 'long branch attraction', result in the different placement.

Discussion

From the analysis it is clear that the PPC of the Palaeognathae is completely different from that of neognathous birds and that a uniform palaeognathous PPC can be described. Although the morphology of the PPC of the Tinamidae seems to be intermediate between the Ratites and the neognathous birds it is clearly distinct from neognathous birds. In this study the single species representing the Tinamidae was grouped together with the Neognathae but this was based on a very small difference in distance. This makes the exact position of the Tinamidae unclear, but other independent morphological characters (Pycraft, 1900; Parkes & Clark, 1966, Müller & Weber, 1998) and molecular data (Sibley & Ahlquist, 1990; Cooper *et al.*, 1992; Cooper, 1994; Caspers *et al.*, 1994; Lee *et al.*, 1997; Cooper, 1997) show that the Tinamous are palaeognathous.

The characters found in this analysis are all quantitative measurements and can therefore not be used to test all the characters of the palaeognathous PPC as given by Bock (1963), who also included qualitative characters. It is however clear that the discriminating characters found in this analysis are similar to those reported by Bock. The main differences between the

Palaeognathae and Neognathae found in this study are 1) a large *Processus basipterygoideus*, 2) relatively short *Processi orbitalis quadrati*, 3) a broad articulation between the pterygoid and palatine bones, 4) the articulation between pterygoids and palates is relatively rostrally situated, 5) the vomer is broad and 6) the pterygoids are well developed in a medio-lateral plane.

The discriminant analysis and the maximum-likelihood method show similar results for the difference between the Ratites, the neognathous birds and the intermediate position of the Tinamous. Based on other characters the Tinamous are considered to be palaeognathous. In our study the Tinamous are represented by a single species only, which is neither the most primitive nor the most derived species of all Tinamidae (Sibley and Monroe, 1990). When adding more species of the Tinamidae, especially the more primitive ones, the calculated position of the Tinamidae may shift toward a more Ratite position on the first discriminant function confirming a Ratite classification for the Tinamidae.

The demonstration of a typical palaeognathous PPC indicates a monophyly of the Ratites. The position of the Tinamous remains uncertain but it is clear that the Tinamidae are the closest relatives of the Ratites. Although the morphology of the PPC of the Tinamous does not fit closely in the definition, it is still very distinct from the neognathous condition. We therefore consider the PPC of the Tinamous also Palaeognathous.

When we assume that the Cayman outgroup is a good representative for the nearest relatives of birds, the evolutionary analysis including outgroup comparison shows, that the PPC of Ratites and Tinamous is primitive within birds. Other groups of birds that are considered primitive within the Neognathae, the Galliformes and Anseriformes (Sibley & Ahlquist, 1990; Sibley & Monroe 1990), are not found close to the Palaeognathae but close to the Ciconiiformes. This was also found by Mindell (1992) after re-analysing the data of Sibley & Ahlquist (1990). From an analysis of the tree at ordinal level it is clear that most members of an order group together. The few that do not, have relatively long evolutionary branches and may be misplaced due to 'long branch attraction' (Hendy & Penny, 1989). The ordinal clustering might be the reason why other groups are apparently misplaced. Within the Ciconiiformes the branches are separated by relatively small internodes, while the distances to other orders are relatively large. This difference in branch length might have disturbed the analysis. Although the phylogenetic structure is not clear from this analysis it can be concluded from the ordinal clustering that for each order a prototype PPC can be determined which diverged within the order, resulting in a variety of forms.

Modifications of the PPC are probably highly dependent on its function. This raises the question about the special functional demands that might have resulted in the palaeognathous PPC. The function of the PPC has been described by Bock (1964) for a prokinetic neognathous bird. He showed that the PPC plays a role in the movement of the upper bill. The functional explanations given for the palaeognathous PPC so far are always in the context of rynchokinesis, a special form of cranial kinesis. In rynchokinesis only a short, rostral part of the upper bill moves relative to the rest of the upper bill. The rest of the upper bill remains stable relative to the cranium. The discriminating characters found in this analysis confirm the

hypothesis of Bock (1963) that the overall palaeognathous PPC configuration is more rigid and strongly built than in Neognathae. This rigid configuration is apparent from the broad Pterygoid-Palate articulation, a broad vomer and broad pterygoids. A strong PPC would be necessary to carry the forces to bend the rather stiff upper bill. Two characters however oppose the hypothesis that the configuration of the palaeognathous PPC is related to rhynchokinesis: the large *Processus basipterygoideus* and the small orbital processes of the quadrate.

Bock (1964) states that the large *Processus basipterygoideus* is a holdover from reptilian ancestors. He suggests that the *Processus basipterygoideus* played an important role in meta- and mesokinesis without explaining what this role might be. Similarly, Bock does not appoint a specific function to the basipterygoid process in birds. Hofer (1945) and Elzanowski (1977) suggested that this process plays an important role in shock-absorption in pecking birds. The process limits the caudal movement of the quadrate and pterygoids, and redirects forces from the quadrate to the cranium. The rostral movement is limited by the *Processus zygomaticus* of the *Os Squamosum* and the relatively diagonal orientation of the merged *Capitula oticum* on the *Processus oticus* of the quadrate. These limitations are at odds with the hypothesis that Palaeognathae are rhynchokinetic; rhynchokinesis implies a freely movable quadrate. The short orbital process of the quadrate also argues against the existence of rhynchokinesis in palaeognathous birds. The *Musculus protractor pterygoidei et quadrati* inserts on the orbital process. This muscle rotates the quadrate forward, resulting in elevation of the upper bill. As the orbital process is rather small, the working arm of the forces generated is small, resulting in relatively small forces to elevate the upper bill. If the forces necessary to bend the upper bill are indeed large (cf. Bock, 1963) it seems unlikely that the Palaeognathae have a highly kinetic bill. Only a kinematic analysis of feeding behaviour can show whether the Palaeognathae do possess a kinetic skull. Furthermore, an analysis of movements and forces working on the PPC and upper bill is necessary to establish a functional relationship between the palaeognathous PPC and rhynchokinesis.

An alternative interpretation for the rigidity of the PPC is that after the loss of two lateral bony bars (postorbital and nasal bar), the palaeognathous skull was reinforced by a much more rigid Pterygoid-Palatinum Complex. During the evolution of birds several elements have slenderised and fenestration has occurred. This process is described by Zweers *et al.* (1997) and includes, starting from the ancestral diapsid/saurian skull, the following phases: 1. a pre-orbital fenestra evolved rostral to the orbit and caudal to the naris. This fenestra is bordered by the lacrimal and jugal bar. 2. The orbit is enlarged, the lacrimal and postorbital bars are slenderised and the anterior fenestra is enlarged. 3. The third or pre-bird stage is characterised by fused postorbital fenestra, bordered caudally by a slender quadrato-jugalquadrato-squamosal bar and rostrally by a slender jugal postorbital bar, large orbits, and slenderised lacrimal bars. In this pre-bird stage four lateral bars are present: the quadrato-jugalquadrato-squamosal bar, the jugal -postorbital bar, the lacrimal bar and the nasal bar. According to Zweers *et al.* (1997) the slenderising of these bars together with the detachment of the secondary palate resulted in the kinetic skull typical for birds. In Neognathae the quadrato-

jugalquadrato-squamosal bar has vanished completely and the postorbital bar has disappeared or is replaced by a ligament. In Palaeognathous birds the reduction of lateral elements is even more severe. All bars, except the lacrimal, are either absent or replaced by ligaments. Interestingly, the data available suggest that this continued reduction of bony elements in Palaeognathae is not related to cranial kinesis. However, a broad and rigid PPC would make sense if it is assumed that Palaeognathae secondarily lost their need for cranial kinesis. To make the skull akinetic it is necessary to stabilise the upper bill, through a reinforcement of the skull. The PPC offers one of the few possibilities to reinforce the skull in the absence of a postorbital and nasal bar. Therefore the PPC is considered to reinforce the skull so that movement in the upper bill as a result of external forces due to feeding are limited.

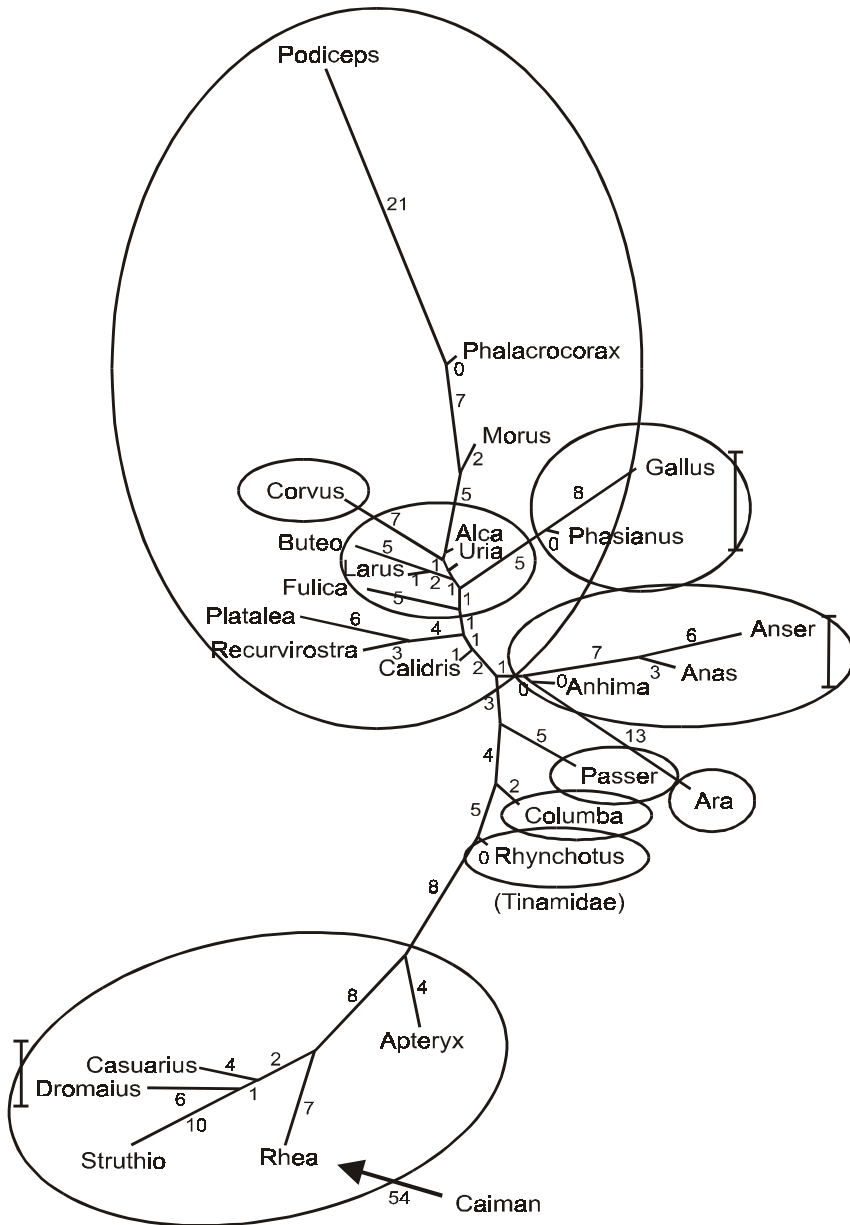


Figure 2.3. Unrooted maximum likelihood tree. The point of attachment of the outgroup is indicated by the arrow and is near Rhea. Numbers indicate the distances between nodes, for clarity nodes with distance nil are indicated with small lines. Systematic units, orders and families, based on molecular data are indicated.

