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Haemothermia or Archosauria? The interrelationships of mammals, birds and crocodiles

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The recently proposed hypothesis that the living birds and the living mammals are sister groups, together forming a natural taxon Haemothermia, is contrasted with the more traditional view, that birds and crocodiles are living sister groups within the taxon Archosauria. Of the 28 or so characters claimed to be unique to the Haemothermia, several are found to be structurally or developmentally different in birds compared to mammals. Others are found to occur also in crocodiles. In either case the status of the characters as homologues categorizing the group becomes doubtful, and only about eight characters remain as potentially acceptable. In contrast, some 24 characters are identified as potential homologues of birds plus crocodiles and therefore categorizing the group Archosauria, and this hypothesis must be judged preferable. The evidence of the characters of fossils can be used legitimately to test cladograms, but only to a limited extent. Nevertheless, the relevant fossils do support the Archosauria rather than the Haemothermia hypothesis. Cladograms logically may, and methodologically should, be taken as theories of phylogenetic relationships, and are potentially subject to independent evolutionary tests. *A priori* character weighting is sound in principle but cannot be applied in practice for want of the necessary, independently acquired knowledge of how characters change in evolution. The relative dates of the fossils is shown to be more compatible with the Archosauria than the Haemothermia classification. Finally, the hypothetical common ancestors that are implied by the two respective cladograms are compared. That shared by mammals and birds, as implied by the Haemothermia theory, would have been functionally incongruent, and therefore less probable than that shared by birds and crocodiles. These several lines of evidence all lead to the conclusion that the traditional theory of a relationship between birds and crocodiles, *vis à vis* mammals is substantially the better supported.

KEY WORDS:— Mammals – birds – crocodiles – Haemothermia – Archosauria – systematics – classification.

CONTENTS

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INTRODUCTION

In the course of his reconsideration of the classification of tetrapods, Gardiner (1982a) presented the heterodox view that amongst living amniotes, the birds and the mammals are primary sister groups, and that together they form the sister group of the crocodiles (Fig. 1A). He reintroduced the taxon Haemothermia for the two endothermic groups, a taxon originally created by Latreille, and subsequently accepted by Owen (1866). This hypothesis contrasts sharply with that held by virtually all biologists for the last century, that birds and crocodiles are sister groups, forming a taxon Archosauria (Fig. 1B).

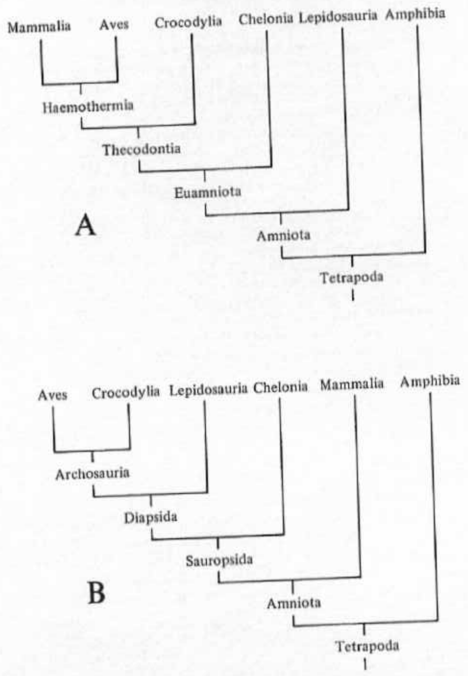

Figure 1. A, Classification of the tetrapods according to Gardiner (1982a). B. Conventional classification of the tetrapods.

Although in pre-cladistic classifications this taxon was not always formally named, it was certainly implied by the variously stated phylogenetic beliefs that linked the birds to the archosaur 'reptiles', the mammals being only distantly related to the archosaurs within the amniotes. Gardiner was able to list no less than 17 characters that he regarded as unique to (i.e. synapomorphies, or homologues of) the Haemothermia, and at the same time he criticized the three main characters allegedly unique to the birds plus crocodiles. This left "only one or two" characters in support of the taxon Archosauria, characters which he therefore took to be homoplastic (non-congruent or convergent). In a brief second paper (Gardiner, 1982b), he extended the list of Haemothermia characters to 22. Subsequently, Janvier (1983, 1984) and Løvtrup (1984) have enthusiastically accepted the reality of the Haemothermia, and Rosen (1984) a little more cautiously embraced the concept. Løvtrup (1985) has recently reiterated his support, with the addition of five further characters.

Although many, probably the great majority of vertebrate biologists have dismissed Gardiner's hypothesis as simply outrageous (e.g. Cox, 1982; Devillers & Ricqles, 1984), it must actually be taken seriously. As presented, the list of characters supporting the taxon Haemothermia is indeed formidable, and on the face of it does appear to outweigh any list of characters assembled in support of the taxon Archosauria. Perhaps because of this initial impression, Gardiner's hypothesis seems to be gaining increasing currency in the zoological literature, if not in the form of support, then at least as a tenable alternative to the traditional view. The purpose of this essay is to attempt an objective comparison of the two alternative ideas of relationships. Rather than undertake the mammoth task of a review of the relationships of all the amniotes, I have reduced the question to a simple choice between two alternative three-taxon statements: are the birds more closely related to the mammals or to the crocodiles?

The taxonomic method used by Gardiner is that of pattern (transformed) cladism, and is recognizably characterized by three principles:

(i) The best hypothesis of relationships is that which corresponds to the distribution of the largest set of congruent characters amongst the hierarchy of groups erected, irrespective of exactly what those characters are.

(ii) Fossils cannot affect a classification that has been established for living organisms.

(iii) No *a priori* evolutionary considerations can be used logically in the creation of a hypothesis of relationships.

Gardiner's hypothesis about the interrelationships of birds, mammals and crocodiles will be inspected on the basis of these three respective methodological assumptions: firstly, whether in strictly pattern cladist terms it is the best hypothesis of relationships of the living forms: secondly, whether the relevant fossils can legitimately test the hypothesis: and thirdly, whether there are any evolutionary considerations that can legitimately test the hypothesis.

An incidental characteristic of pattern cladism is a tendency to appeal to pre-evolutionary authority. This is presumably on the grounds that much of modern taxonomic procedure has been allegedly at fault because of its ill-considered reliance on uncorroborated assumptions about the nature of the evolutionary processes, and how they affect characters. Pre-evolutionary or non-evolutionary taxonomists were not so handicapped. In the present instance, it is interesting to compare Gardiner's approval of Owen's use of the taxon Haemothermia with what Owen actually had to say regarding the birds and mammals:

> Although the last two classes [birds and mammals] agree as hot-blooded vertebrates in their higher cerebral development, and in the more complex heart and lungs, birds, by genetic and developmental characters as well as by the general plan of their organisation, are more intimately and naturally allied to the oviparous saurians than to the viviparous mammals [Owen, 1866: 6].

And again, of haematothermal and haematocryal forms: ". . . each of these divisions are artificial and convenient" (Owen, 1866: 7). Clearly even Owen was less than fully convinced of the naturalness of the Haemothermia.

THE CHARACTERS OF LIVING MAMMALS, BIRDS AND CROCODILES

Homology

In pattern cladist terms, the evidence for the naturalness, or reality of a proposed taxon is that all the members share characters otherwise unique to that group of organisms. Where alternative groupings can be proposed, the preferred taxon is that whose members share the greatest number of such unique characters. In the present instance therefore, the question becomes very simply that of whether birds share more characters uniquely with mammals or with crocodiles, as Janvier (1984) has pointed out.

Patterson (1982) reviewed the various concepts that have been associated with the term 'homology', and concluded that for taxonomic purposes, a homology is simply a character that specifies a group, i.e. a similarity present in all, but only, the members of that group. Any evolutionary connotations associated with the term are vacuous, in that they can serve no additional purpose in classifying organisms. It follows from Patterson's comments that a putative unique character, or homology, is a hypothesis that must fulfil three empirical criteria (see also Neff, 1986). The primary one is that the character is sufficiently similar in structure, position and development to be taken to be an expression of the same thing in different organisms; taxonomy might well be described as the act of recognizing and expressing the distribution of such similarities amongst different organisms. There is an inevitable degree of subjectivity in utilizing this criterion, since it is not entirely clear how detailed the similarity of a character in different organisms must be for a confident hypothesis of homology to be proposed. Nevertheless, some such hypotheses will be perceived to be manifestly more strongly supported than others, and several of the actual characters discussed shortly will appear to be very weak as judged by this criterion.

The second criterion that a hypothesis of homology must fulfil is that it is indeed unique to the members of the proposed taxon. A problem here is that a putative homology defining a particular taxon may occur in another group, not because the hypothesis of homology is incorrect, but because the other group is itself related to the proposed taxon. If, for example, a character otherwise unique to mammals and birds turns up in turtles, this could be because the turtles are themselves related to the mammal-bird group; the character in question would still be evidence of a mammal-bird relationship with respect to crocodiles. However, the problem can be avoided by looking for characters that really are unique only to two of the three taxa under consideration, and discarding characters found in any other organisms amongst the remaining amniotes, or amphibians. The cost of this approach is possibly to ignore certain characters that are actually relevant. The benefit is twofold: first it avoids the growing complexity of the exercise as more and more taxa are considered: second it leaves open a possible test of the resulting cladogram. The best cladogram of the birds, mammals and crocodiles alone should withstand the future addition to it of further taxa.

The third criterion of a hypothesis of homology is the congruence test. Any putative homology must have a distribution compatible with the majority of other putative homologies. This will be the concluding test after discussion of the individual characters.

Characters unique to mammals and birds (Haemothermia)

The characters claimed to be unique to mammals and birds, and therefore the evidence for the reality of a group Haemothermia are listed in Table 1. It includes the characters given by Gardiner (1982a), those additional ones in Gardiner (1982b), and the five added subsequently by Løvtrup (1985).

TABLE 1. Published characters claimed to be unique to mammals and birds. From Gardiner (1982a, b) and Løvtrup (1985)

1. Separation of oxygenated and deoxygenated blood
2. Single aortic trunk with three semilunar valves
3. Pulmonary artery with three semilunar valves
4. Endothermy
5. Similar thermoregulatory mechanisms
6. Three meninges
7. Folded cerebellum, pons varolii, inferior olive and pontine nuclei
8. Scroll-like turbinals
9. Maxillary process
10. Adventitious cartilage
11. Atlas, axis single ossifications
12. Vascularised islets of pancreas
13. Pinealocytes, oxytocin, prolactin
14. Macula densa
15. Loop of Henle
16. LDXH
17. Epidermal–melanin unit
18. Similar embryology including primitive streak
19. Similar behaviour patterns including incubation (monotremes and birds)
20. Diving birds and mammals show anaerobis and bradycardia
21. Similar dumbbell shaped otoconia in the foetus
22. β-Crystallin (lens protein)
23. Histology of the neurohypophysis
24. Pars tuberis (only monotremes among mammals)
25. Postganglionic nerves through plexuses and ganglia
26. Sino-auricular and auriculo-ventricular nodes
27. Dermal bones below skin
28. Similar myoglobin and α-crystallin sequences

1. Separation of oxygenated and deoxygenated blood: As so expressed, this character is fairly meaningless and must be re-stated as the actual structures which are responsible for it. These are the septa of the heart, along with the structure of the aortic arches dealt with under character 2. As Gardiner (1982a) states, it is now clear that the complete interventricular septum of mammals and birds is structurally and developmentally very similar (Shaner, 1962; Holmes, 1975), and is formed from the homologue of the reptilian muscular septum, completed by secondary membranous growth from the endocardium. However these same authors show that the interventricular septum of the crocodiles is also complete, and formed in an identical manner, and therefore this structure is not unique to mammals and birds.

The inter-atrial septum appears to be identical in all amniotes. Gardiner (1982a: 212) mentions the foramen ovale between the embryonic right and left atria. Such secondary perforations of the septum are standard throughout the amniotes (e.g. Goodrich, 1930: 557).

He also claims that the left atrio-ventricular valve of birds and monotremes consists of three membranous folds, in contrast to one fold in other non-mammalian amniotes, and the two folds of the mammalian mitral valve. In fact, there is no such clearly defined left atrio-ventricular valve condition in birds. Goodrich (1930: 563) describes it as developing from two valves, an inner one from the septum and an outer one from the ventricular wall. Romanoff (1960: 706) states that this valve usually consists of two cusps, but is occasionally tricuspid. Finally West, Lowell & Jones (1981: 239) state: "The valve [left A-V] forms a continuous sheet around the orifice and exhibits only poorly defined cusps, a feature which has led to some confusion over whether it should be described as mitral or tricuspid." The monotreme valve also differs from the bird valve in being controlled by papillary muscles (Griffiths, 1978: 103, quoting Dowd). Incidentally, the right atrio-ventricular valve of birds has a unique, muscular structure, quite unlike that of any mammal (Goodrich, 1930: 563; West *et al.*, 1981).

Although not included in his list of unique characters of birds and mammals, Gardiner (1982a: 212) mentions that: "the venous drainage of the heart walls is by the great cardiac vein which opens directly into the right atrium in monotremes, marsupials, and birds (Griffiths, 1978)." This is not quite the case in birds. In *Gallus domesticus*, Lindsay (1967) describes several veins, including great cardiac, middle cardiac, left circumflex and several smaller ones. These tend to open separately from one another, although Lindsay noted considerable variation in the details.

2. Single aortic trunk with three semilunar valves: Gardiner (1982a: 211) quotes Holmes (1975) to challenge the belief that the aortic trunk of mammals is the left trunk, and of the birds the right trunk. As Holmes demonstrates, the single trunk in both cases can best be interpreted as identical in these two groups, differing from the crocodilian condition in its failure to divide by an internal septum. This would seem to be a good homologue of mammals and birds compared to crocodiles. However, the whole aortic arch should be compared, not one selected part, whereupon the alleged homology becomes gravely doubtful. The arch of mammals is composed of the undivided trunk plus the left fourth systemic arch and that part of the left dorsal aorta lying anterior to the common dorsal aorta. The right fourth systemic arch is retained as part of the right subclavian artery, but the right dorsal aorta is lost during development. In contrast, the aortic arch of the birds incorporates the right fourth systemic arch, and part of the right dorsal aorta.

There are only two semilunar valves in each aortic arch of reptiles, including crocodiles, compared to the three in both mammals and birds. Shaner (1962) has described the development of the semilunar valves in detail for these three groups, showing that they form from endocardial cushions in the embryonic bulbus. In mammals, there are four such cushions, and in crocodiles there are also four but differently arranged. In birds there are intially only three, with a further two appearing later, after the formation of the septum dividing the bulbus into pulmonary and aortic channels. This embryological difference throws doubt on the homology of the valves in mammals and birds respectively. Indeed, Shaner regards the bird condition as more comparable to the crocodilian than to the mammalian, although admittedly this is not very convincing.

3. Pulmonary artery with three semilunar valves: As with the valves of the aortic arch, the differences in the developmental pattern of the pulmonary valves, indicate that they too are not homologous in birds and mammals (Shaner, 1962).

4. Endothermy: As with character 1, this character can only be assessed with reference to the actual structures responsible for it, in this case presumably the presence of a large number of mitochondria indulging in aerobic respiration and thereby creating a high basal metabolic rate. As such, it is indeed a unique character of mammals and birds.

5. Similar thermoregulatory mechanisms: Gardiner (1982a) mentions the following thermoregulatory devices as unique to mammals and birds: a possible additional mechanism for monitoring core temperature in the spinal cord; calorigenic and regulatory effect of thyroid hormones; non-shivering thermogenesis; behavioural responses such as huddling; insulating layer (fur or feathers); piloerection or filoerection; shivering; panting. Several of these are actually found in reptiles as well. Bartholomew (1982) notes the use of gaping and panting, huddling, and the role of thyroid hormones in increasing metabolic rate (see also Firth & Turner, 1982). It should also be noted that the existence of non-shivering thermogenesis is uncertain in birds (e.g. Bartholomew, 1977). Shivering seems to be unique to these two groups, but otherwise only insulation, and the associated piloerection and filoerection, appears to be a clear-cut candidate for uniqueness in mammals and birds. Whether it is homologous obviously depends in the first place on whether hair and feathers can be regarded as homologous structures. Gardiner regards them as such because of their general similarity, but there are strong arguments against this interpretation. Baden & Madderson (1970; Madderson, 1972) showed that mammals have only α-keratin, in both hair and, where present, scales. In contrast, birds and crocodiles have scales with β-keratin on the outer surface and α-keratin restricted to the hinge regions between scales. The avian feather is composed of β-keratin. Furthermore, Oster & Alberch (1982), following Wake (1979), describe a very early divergence in the developmental pathways of feathers compared to hairs. A similar epidermal placode forms, but then it either invaginates, in which case a hair (or skin gland) forms, or else evaginates to develop into a feather (or scale). Such a fundamental morphogenetic difference would not be expected of homologous structures. The contribution of neural crest cells to both hairs and feathers (Gardiner, 1982a: 213) is not significant, because these cells are involved in the formation of all vertebrate dermal–epidermal structures (e.g. Northcutt & Gans, 1983).

6. Three meninges: Three cellular layers are distinguished surrounding the central nervous system of mammals and birds, the dura mater externally, the arachnoid layer in the middle, and the pia mater internally. Kuhlenbeck (1973: 677–679) reports three layers in anurans and reptiles, and there is some disagreement about whether these are equivalent to the mammalian and bird layers. One view is that the arachnoid layer is not represented and the dura mater is double. However Kuhlenbeck states (1973: 682):

> I believe that, in accordance with Gegenbaur's concept [of the avian condition], arachnoid membrane, trabeculae, and pia of Hansen-Pruss represent a differentiated endomeninx, comparable to the leptomeninx of mammals, and, moreover, that the arachnoid membrane of Palay in Anurans, and the reptilian 'dura' of Kappers are homologous with the above-mentioned avian arachnoid membrane. The dura, on the other hand, may be conceived as a fairly well differentiated ectomeninx.

Given also the variation in the details of the relationships between the membranes in different regions of the mammalian central nervous system, this character does not clearly categorize only mammals and birds.

7. Folded cerebellum, pons varolii, inferior olive and pontine nuclei: The division of the cerebellum into a series of folia by transverse fissures is perhaps the most striking similarity between mammals and birds. Despite his firm belief in the phylogenetic independence of the two groups, Kuhlenbeck (1975: 751) regards Larsell's homologies of individual mammalian and avian folia as basically valid, despite minor disagreements about the precise details. Pearson & Pearson (1976: 197) take the same view, although they do warn that: "Although we may hazard the suggestion that the same type of functional organization characterizes both birds and mammals this remains unproven at the present time." Such 'proof' would be necessary for the hypothesis of homology to be fully established.

The pontine nuclei and inferior olive in the brain stem do appear to be unique to mammals and birds, and as far as is known their fibres project onto comparable regions of the cerebellum. However Kuhlenbeck (1975: 744) states that the macroscopically well defined pons of mammals is not present as such in any other vertebrates.

8. Scroll-like turbinals: Gardiner (1982a: 214) refers to the presence of "prominent, scroll-like turbinals, often supported by bone, and a maxilloturbinal devoid of olfactory epithelium". However, there is very great difficulty in recognizing homologies between particular turbinals or conchae amongst the various amniote groups. Parsons (1970: 103) remarked quite simply: "The presently available evidence is insufficient to permit more than guess-work." Even De Beer (1937: 277–279), who was fully prepared to indulge in informed guesses, remained doubtful and suggested only that the maxilloturbinals and atrioturbinals respectively may be homologous in crocodiles, birds and mammals. The more posterior and dorsal structures in the three groups defied close comparison.

9. Maxillary process: This refers to a postero-medial process of the maxilla developed in the embryo during early ossification. It is very variable in development within the groups, its homology in mammals and birds is to say the least doubtful, and crocodiles have a comparable structure. In birds, Romanoff (1960: 987) refers to it as the palatine process of the maxilla, and describes it as projecting medially and posteriorly to form an angle of 30° with the jugal process. Later it extends medially into the pars palatini. In *Ornithorhynchus*, De Beer (1937: 299) states: "The maxilla consists of an alveolar portion, an ascending portion which covers the lower part of the paries nasi, a palatine process which extends inwards beneath the ventral edge of the paries nasi and a zygomatic process which extends back as far as the similarly named process of the squamosal." In *Crocodylus* (De Beer, 1937: 266–267): "The maxilla has large alveolar and ascending portions, and a well developed palatine process which eventually meets its fellow of the opposite side in the midline ventrally to the prevomers and nasopharyngeal passage, thus forming part of the false palate." It is not even clear which particular processes Gardiner (1982a) is comparing; the ambiguity is in any event obvious.

10. Adventitious cartilage: The tendency to form cartilage directly along the margins of the developing dermal bones does seem to be unique to mammals and birds, as far as currently known (Patterson, 1977), although Hall (1984) does not regard the question of whether reptiles have this ability as closed yet.

11. Atlas, axis single ossifications: De Beer (1937: 386) shows differences in the development of the cranio-verebral joint. In birds and crocodiles (and also chelonians), the pleurocentrum of the embryonic proatlas vertebra fuses to the skull to form the occipital condyle. In mammals (and also *Sphenodon* and lizards), the proatlas pleurocentrum fuses to the atlas pleurocentrum. Therefore the homology of the single bone forming the atlas of birds with that of mammals is very doubtful. (A more impressive argument against this alleged homology of mammals and birds is that the atlas of the early Jurassic undisputed mammalian fossil *Morganucodon* has its atlas unfused (Jenkins & Parrington, 1976) a point discussed in a later section.) The formation of the axis as a single ossification is common to most living amniotes.

12. Vascularized islets of pancreas: This character appears to be correct, for there is less vascularization and the islet tissues depend more on exocrine ducts in reptiles (Miller & Lagios, 1970). Some fish have a mammal-like arrangement.

13. Pinealocytes, oxytocin, prolactin: None of these three characters is unique to mammals and birds. Collin & Oksche (1981: 40) say of pinealocytes: "This cell type is predominant in the solid pineal parenchyma of ophidians and mammals: it may also be found in other Sauropsida, in certain regions of the pineal, e.g., in its solid proximal portion." Quay (1979) specifically mentions pinealocytes in lizards. Gardiner (1982a: 214) also mentions the autonomic sympathetic innervation of the pineal gland as a unique feature of mammals and birds. According to Collin & Oksche (1981: 46), "The sympathetic innervation becomes distinct in lacertilians and is very abundant in the ophidian and avian pineal organs." Crocodiles lack a pineal organ (Quay, 1979: 248), and therefore no comparison between them and mammals and birds is possible.

Both oxytocin and prolactin are more or less universal in vertebrates (e.g. Hoar, 1975).

14. Macula densa: This is part of the juxtaglomerular complex, and consists of specialized kidney tubule cells where the ascending limb of the tubule meets its renal corpuscle. Sokabe & Ogawa (1974) note the presence of juxtaglomerular (renin) granules in the reptilian arterioles close to the glomerulus, indicating that a simple juxtaglomerular apparatus is present, even though there is no differentiated macula densa as such. In birds, the epithelial cells of the distal tubule in contact with the renal corpuscle differ from those of the rest of the distal tubule, but these authors claim that cytologically they are intermediate between normal distal tubule cells and the macula densa cells of mammals. Thus they argue that the birds do not possess a true macula. Johnson (1979) disagrees, arguing that the structure is the same in birds and mammals. It certainly seems that birds and mammals together show a more complex version of the basic reptilian juxtaglomerular apparatus, and that this is a true unique character of the two groups.

15. Loop of Henle: Only a proportion of the avian nephrons possess a loop of Henle, and these have the appearance of the 'short' mammalian type. Most of the other nephrons have no loop, but some are intermediate in structure. Sperber (1960) and Johnson (1979) both note certain histological differences between avian and mammalian loops of Henle. In birds, the thin segment of the loop has much taller cells than the endothelial-like cells of the corresponding region in mammals. Also the loop of Henle of birds shows a gradual transition from the proximal convoluted tubule, compared to the abrupt transition in mammals.

There are also unexpected physiological differences between them. According to Sturkie (1976), urea plays no part in the formation of a medullary osmotic gradient in the avain kidney, in contrast to the situation in mammals. Also he states (p. 274): "Differences in concentrating abilities of different mammalian species has been correlated with the lengths of the individual medullary loops of Henle involved, but this is not true in birds. However, it is positively correlated in birds with the number of Henle's loops and the amount of medullary tissue generally."

Given these structural and functional differences, the homology of the loops of Henle in birds and mammals respectively must be considered very doubtful.

16. LDHX: Baldwin & Temple-Smith (1973) certainly report the presence of this electrophoretically distinguishable version of lactate dehydrogenase in many species of marsupial and placental mammals and birds. However they showed that it is absent from both of the monotremes groups, and it has not apparently been looked for in any reptiles, including crocodiles. Therefore it is impossible to say whether its presence categorizes the mammals plus the birds alone.

17. Epidermal melanin unit: Quevedo (1972) describes how melanocyte cells below the epidermis of mammals synthesize melanin, package it into melanosomes, and pass the melanosomes into fine dendritic extensions. Epidermal cells then pick up the melanosomes by phagocytosis (e.g. Spearman & Hardy, 1985), after which the melanosomes break up into granules within the epidermal cells. Spearman & Hardy (1985) describe similar dendritic melanocytes in birds and suggest that they functioned in a similar way to mammals. However, Spearman & Riley (1969) showed that crocodiles also possess melanin containing melanocytes, which also have dendritic processes in intimate association with epidermal cells. Furthermore, the spatial distribution of the melanocytes below the epidermis coincides with the distribution of melanin granules in the overlying epidermal cells. Therefore the evidence that crocodiles possess the mammalian type of epidermal melanin unit is the same as that which suggests that birds do, and this unit cannot therefore be taken as a character unique to birds and mammals.

18. Similar embryology including primitive streak: The primitive streak is a general amniote character (e.g. Nelson, 1953). No other specific embryonic characters are mentioned by Gardiner (1982a).

19. Similar behaviour patterns in birds and monotremes, which both incubate their eggs: As a necessary functional correlate of oviparous endothermy, this character must be accepted as unique to these two groups.

20. Diving birds and mammals both show anaerobis and bradycardia (drowning syndrome): Seymour (1982) reviews physiological adaptations to diving in reptiles, and shows that severe bradycardia is normal. Because of their lower basal metabolic rates, demonstration of adaptive anaerobis is less clear cut, since longer aerobic dives can be maintained. Nevertheless, it has been shown in sea snakes, and probably *Amblyrhynchus cristatus* and *Iguana iguana*.

21. Similar dumb-bell-shaped otoconia in the foetus: I have been unable to trace appropriate references to the embryonic form of the otoconia (statoconia, or otoliths) in the relevant groups.

22. β-crystallin (lens protein): This version of crystallin is also present in fishes, amphibians and reptiles (De Jong, 1982).

23. Histology of the neurohypophysis: Løvtrup (1985) quotes Wingstrand (1951) in support of this character. Reading Wingstrand is instructive. He found enormous variation even within groups. For example the histology is described as simple in *Sphenodon* and most lizards, with thin walls and a hollow neural lobe, while in snakes and certain lizards the neural lobe is compact and the eminentia media thick and mammal-like. Much the same degree of variation occurs in birds, such that he can write (p. 242): "We are thus able to state that the neurohypophysis in reptiles shows variations of similar kinds as those stated for birds. The primitive type of neurohypophysis found in *Phasianus*, *Gallus*, *Diomedea* and owls may be directly compared with the type found in *Sphenodon* and many lizards, whereas the advanced type found in *Anser*, *Larus*, etc. is similar to that in snakes" and (p. 242): "The mammalian neurohypophysis is invariably of a more complicated kind".

24. Pars tuberis (only monotremes): Wingstrand (1951: 126–127), again quoted by Løvtrup (1985), does not actually support this character, because he describes a pars tuberis in the neurohypophysis of Chelonia and crocodiles, and, variably developed, in lizards.

25. Post-ganglionic nerves from segmental ganglia through plexuses and ganglia: Pick (1970), in reviewing the thoracic and abdominal regions of the sympathetic system states (p. 244): "Visceral nerve plexuses occur along the abdominal aorta and at the end of the intestine in turtles, are suggested in the mesogastrium and mesentery in saurians, but are most conspicuous in crocodiles." There is also difficulty in homologizing the exact arrangement of the plexuses in birds and mammals respectively. In birds, Pick follows Hirt (1934) in recognizing a ganglionated coeliac plexus around the coeliac artery, which serves the stomach, intestine, liver, spleen and pancreas. There is a second, less complex renal plexus. In any case, the arrangement in birds is highly variable (Akester, 1979). In mammals, as represented by the cat, there are coeliac, superior mesenteric, inferior mesenteric and pelvic plexuses, which have no clear correspondence with those of birds.

26. Sino-auricular and auriculo-ventricular nodes: An atrio-ventricular connecting system of specialized cells is present in reptiles, for example in lizards where sino-atrial and atrio-ventricular 'plugs' have been described (Robb, 1965: 383). However the cells are not so histologically distinct as in birds and mammals. Robb (1965: 387) refers to Mori in concluding that "the crocodilian connecting system was intermediate between that of reptiles and birds." The further specialization of the system in mammals and birds is therefore an apparent homologue between these two groups.

27. Dermal bones below the skin: The thick dermal layer covering the cranial bones of mammals and birds correlates functionally with the presence of hair and feathers, respectively. The latter could not occur without the former, and it is therefore uncertain whether this should be considered an independent character, particularly as hair and feathers are of doubtful homology (p. 73). Nevertheless, at face value it is certainly unique to these two groups.

28. Similar myoglobin and α-crystallin (lens) sequences: Amino acid sequences have failed to establish clear-cut relationships amongst the amniotes. The most parsimonious cladograms constructed from different protein sequences usually show different relationships for the same taxa. Furthermore, different relationships can be generated with quite insignificant differences in the numbers of implied nucleotide replacements (NRs) for the same protein (Maeda & Fitch, 1981: Goodman, Weiss & Czelusniak, 1982).

Dene, Sazy, Goodman & Romero-Herrera (1982) found that the maximum parsimony cladogram for myoglobin had mammals and birds as sister groups, and the two together as the sister group of crocodiles, as in Gardiner's (1982a) classification. This required 630 NRs. However only 638 NRs were required in order to have the birds and crocodiles as sister groups, a difference of only 1.27%. Given the possibility of silent nucleotide differences (i.e. differences not translated into amino acid differences), it is difficult to accept this percentage as significant. Maeda & Fitch (1981) added a lizard myoglobin sequence and found again that the most parsimonious scheme had mammals and birds as sister groups. In their cladogram, 801 NRs were implied, while the conventional classification needed only a further 12 NRs.

In contrast to Gardiner's (1982b) claim, De Jong, Zweers, Versteeg, Dessauer & Goodman (1985) have recently found that α-crystallin A most parsimoniously gives crocodiles and birds as sister groups, their cladogram requiring 267 NRs. In fact, this also had the marsupial mammals as the sister group of birds plus reptiles, rather than the sister group of eutherians. To 'correct' this anomaly requires a further six NRs.

Cytochrome c, which is not yet available for crocodiles, supports a relationship between birds and squamates (lizards and snakes) rather than between birds and mammals (Goodman, Weiss & Czelusniak, 1982).

The α-haemoglobin molecule most parsimoniously indicates a bird and crocodile sister group pairing (Perutz *et al.*, 1981), while Goodman *et al.* (1982) find general support for this hypothesis from both α- and β-haemoglobin.

Thus the amino acid sequence data certainly do not support a bird-mammal relationship. De Jong *et al.* (1985: 491) state categorically: "Although the phylogenetic inferences derived from comparisons of these homologous amniote proteins have not always been consistent (as has been amply discussed by Maeda & Fitch (1981) and Goodman *et al.* (1982), the cytochrome c and haemoglobin data, like α-crystallin A, generally supports the grouping of birds and crocodiles in the monophyletic subclass Archosauria."

No doubt appropriate homologous DNA sequences will become available shortly, and these may be expected to dispose of at least one problem, that of silent nucleotide differences. Whether they, or DNA–DNA hybridization techniques (e.g. Sibley & Ahlquish, 1984) will give less ambiguous indications of relationships, or merely pose new problems of interpretation (Ruvolo & Smith, 1986; Templeton, 1986) remains to be seen.

For the moment, macromolecular evidence cannot claim to give acceptable support to a relationship between living mammals and birds.

Of these 28 putatively unique characters of birds and mammals (Table 1), relatively few remain as confidently held hypotheses of homologues of a natural group Haemothermia (Table 2). Several of them are also present in crocodiles, or at least in other amniotes (characters 1, 5 (in part), 6, 13, 17, 18, 20, 22, 23, 24). Others of them are sufficiently different on structural or developmental grounds to effectively refute the idea that they are homologues (characters 2, 3, 8, 9, 11, 15, 25).

In two the state of the character is unknown in crocodiles (characters 16 and 21); and in another the difference from crocodiles is of no statistical significance (character 28, myoglobin sequence).

This leaves only nine of the characters as reasonably unambiguous candidates

TABLE 2. The characters of mammals and birds that withstand testing for potential homology

1. Mitochondria generating high metabolic rate (4)
2. Shivering (part of 5)
3. Folded cerebellum, inferior olive and pontine nuclei (most of 7)
4. Adventitious cartilage (10)
5. More extensively vascularized islets of pancreas (12)
6. More differentiated macula densa (14)
7. Incubation of the eggs (monotremes) (19)
8. More differentiated conduction tissues in the heart (26)
9. Dermal bones below the skin (27)

for homologies of a taxon Haemothermia, and of these, three of them (12, 14 and 26) show a state only a little more differentiated compared to the crocodilian character state, rather than a clear cut novelty.

Characters unique to crocodiles and birds (Archosauria)

Gardiner (1982a) concedes that crocodiles and birds "do share one or two unique features", but actually considerably more have been described in the literature (Table 3), notably by De Beer (1937: 463) and Bellairs & Kamal (1981: 245–246) in the embryonic skull. Walker (1972), Whetstone & Martin (1979) and Molnar (1985) have reviewed unique similarities of birds and crocodiles, although in the particular context of discussing which fossil archosaur group is most closely related to the birds. As discussed earlier (p. 71), the problem of what constitutes the outgroup *vis-à-vis* the three taxa mammals, birds and crocodiles is avoided by restricting the following list to characters unique to birds and crocodiles amongst all tetrapods.

Characters of the embryonic skull

1. Median prenasal process, extending anterior to the nasal septum.

2. Infrapolar cartilages that extend back from the basitrabecular processes, underlying the carotid artery. Suprapolar cartilages present (Bellairs & Kamal, 1981).

3. Substantial development of the pleurosphenoid (ossified pila antotica), which cannot be the homologue of the mammalian alisphenoid as claimed by Gardiner (1982a). Apart from the different chondrocranial origin of the two (Starck, 1979), crocodiles possess a vestigial epipterygoid in addition to the pleurosphenoid (Bellairs & Kamal, 1981). Nor is the pleurosphenoid homologous to the superficially similar latero-sphenoid of snakes (Bellairs & Kamal, 1981).

TABLE 3. Characters unique to crocodiles and birds amongst living tetrapods

1. Median nasal process
2. Infrapolar cartilages
3. Ossified pleurosphenoid
4. Parasphenoid in three parts
5. Metotic cartilage
6. Form of planum supraseptale
7. Structure and position of the quadrate
8. Pneumatisation of bones
9. Fenestra pseudorotunda
10. Slightly curved cochlea
11. Eustachian tube opens medially in pharynx
12. Elongated coracoid
13. Nature of forelimb joints
14. Deflection of wrist in embryo
15. Similar embryonic tarsus
16. Reduction of fifth toe
17. Elongation of pubis and ischium
18. Hind limb musculature
19. Absence of septomaxilla
20. Right aortic arch better developed
21. Dorsal ventricular ridge
22. ε-Crystallin present
23. Chemistry of the scales
24. α-Crystallin A and haemoglobin sequences

4. Parasphenoid forms separate median rostrum and paired basitemporals.

5. A presumed cranial rib forms a metotic cartilage (subcapsular process), flooring the recessus scala tympani between the basal plate and the otic capsule. (De Beer (1937) regards this as unique to crocodiles and birds, although according to Bellairs & Kamal (1981) it is also present in chelonians. If they are correct then this character is a doubtful homologue of crocodiles and birds.)

6. Similar shape of the planum supraseptale, before it regresses in birds (Bellairs & Kamal, 1981).

7. The primary articulation of the head of the quadrate is in a relatively anterior position, contacting the squamosal and prootic but not the opisthotic as in other amniotes (Walker, 1972). In mammals, the incus (quadrate) articulates with the crista parotica (opisthotic) and therefore corresponds to non-crocodilian reptiles (De Beer, 1937: 405). Walker (1985: 132) has recently suggested that this character is not homologous in crocodiles and birds, because in crocodiles the stapedial artery passes dorso-medially to the quadrate, while in birds it passes ventrally as in other amniotes. Nevertheless, the general structure of the quadrate is uniquely similar in birds and crocodiles.

Characters of the ear region

8. Pneumatization of the bones surrounding the middle ear cavity, and the presence of a siphonium from the quadrate to the lower jaw (Bellairs & Kamal, 1981). Whetstone & Whybrow (1983) were able to homologize the individual pneumatic spaces in birds and crocodiles respectively.

9. Perilymphatic duct opens as a fenestra pseudorotunda, close to the fenestra ovalis. The fenestra pseudorotunda is formed by the subcapsular process (character 5), in a manner quite unlike the formation of the mammalian foramen rotundum (Whetstone & Martin, 1981).

10. Cochlea elongated and slightly curved, compared to other reptiles. In monotremes, the shape of the cochlea is superficially similar, but it is slightly coiled at its distal end, and the curvature is outwards instead of inwards as in birds and crocodiles (Pritchard, 1881). The structure of the basilar membrane inside the cochlea of crocodiles and birds is entirely different from the organ of Corti of mammals including monotremes (Griffiths, 1978).

11. Form of the eustachian tube, passing through the cranial base to open by a medial foramen in the roof of the pharynx, a unique character of birds and crocodiles that is conceded by Gardiner (1982a: 214).

Postcranial characters

12. Elongated coracoid in shoulder girdle.

13. Arrangement of the elbow and wrist joints, whereby when the elbow flexes a ridge on the humerus pushes on the radius, causing the radiale, ulnare and manus to rotate laterally (Walker, 1972).

14. A similar lateral deflection of the wrist plus manus in the embryo (Walker, 1972).

15. Similar embryonic tarsus. The calcaneal heel of the crocodile has a similar relationship to the gastrocnemius and peroneus longus muscles as does the tibial

cartilage of the bird, and each is functionally part of the pes, suggesting that they are homologous. In both groups, there is a dorso-lateral process of the astragalus that contacts the lower end of the fibula above the calcaneum (Walker, 1972).

16. Fifth toe greatly reduced (crocodiles) or absent (birds).

17. Both the pubis and the ischium elongated.

18. There are a number of unique features of the hind limb musculature noted by Romer (1923). The ilio-tibialis muscle has three heads in crocodiles and four in birds, compared to one or two in other amniotes including mammals. The ambiens tendon crosses over the knee joint in a unique fashion. The femoro-tibialis muscle (vasti) has an additional head. The pubo-ischio-tibialis (mammalian gracilis) muscle is absent. The caudi femoralis has acquired an additional head. Rowe (1986) demonstrated several apparent homologies of the thigh musculature of crocodiles and chick embryo.

Other characters

19. Absence of a septomaxilla.

20. The right aortic arch is better developed than the left, which is incomplete in the adult bird (see pp. 72–73).

21. The organization of the dorsal ventricular ridge of the forebrain differs from that of other reptiles, and cannot be homologized with specific components of the mammalian forebrain (Ulinski, 1983).

22. ε-crystallin is uniquely present in crocodiles and birds (De Jong *et al.*, 1985). (δ-crystallin is also present in crocodiles and birds but not mammals, but it also occurs in the other amniote groups.)

23. The scales of birds and crocodiles have β-keratin over the surface and α-keratin restricted to the hinge regions, unlike other reptiles where α- and β-keratin alternate in the vertical axis of the scale. Mammals have only α-keratin (see p. 73; Baden & Madderson, 1970).

24. The amino acid sequence of α-crystallin A and haemoglobin support the grouping of crocodiles with birds, although not strongly (see pp. 78–79).

The preferred pattern cladogram

Bearing in mind the pattern cladist methodology which insists that the preferred taxonomic grouping is the one supported by the greater number of congruently distributed, uniquely similar characters, there can be no doubt that, at the moment, the taxon Archosauria represents a better supported hypothesis than does the taxon Haemothermia. About nine characters support a relationship between birds and mammals, compared with around 24 characters indicating the alternative, a relationship between birds and crocodiles.

Nevertheless, there remains a not inconsiderable amount of support for the Haemothermia hypothesis. Over one quarter of the characters finally accepted here as potential homologues have turned out to be homoplastic, and no attention has been given to the obvious, if unhelpful fact that some of the characters seem intuitively more important than others. Confidence in the superiority of the Archosauria hypothesis is not overwhelming in pattern cladist terms, and it behoves us to seek further arguments that might tend to corroborate or to refute it, relative to the alternative.

FOSSIL TESTS OF THE CLADOGRAM

Part of Gardiner's (1982a, b; see also Løvtrup, 1985) methodology is the refusal to accept that fossil evidence has a valid role to play in testing hypotheses of relationships of living organisms. As the fossil synapsids (mammal-like reptiles) and archosaurs have traditionally been regarded as important in deciding the relationships of mammals, birds and crocodiles, Gardiner's assertion needs investigating.

Patterson (1981) reviewed the criticisms levelled at the role of palaeontology in taxonomy, recognizing two general kinds. 'Cladistic' objections are that fossils and fossil groups are usually paraphyletic ('ancestral'), lack unique, defining characteristics, and are therefore artefacts of no objective use in testing cladograms. Secondly, what he termed 'philosophical' objections are effectively epistemological, to the effect that the fossil record is too incomplete to overthrow classifications based on the wealth of characters available for living organisms. A third criticism has also appeared, namely that fossils often show transformational homologies (morphoclines, Gaffney, 1979) whose role in specifying groups is claimed to be of doubtful legitimacy (Patterson, 1982; Gardiner, 1982b).

Fossils as paraphyletic

Under the influence of evolutionary theory, many palaeontologists have taken the view that ancestral groups should be recognizable amongst fossils. Such a group will not possess unique characters, but only a combination of characters of the group that it supposedly gave rise to, with general (primitive or plesiomorphic) characters. Cladistic theory demands that to be objective, a natural group of organisms must all posses unique, defining characteristics, and therefore the ancestral groups of the palaeontologist must be rejected (see Kemp (1985) for a review). They are artefact groups, in the sense that different combinations of particular organisms can be made into ancestral groups, simply by different arbitrary choices of general characters to define them. However it is unnecessary to go from this impeccable principle of cladism to the conclusion that fossils in principle cannot affect classifications of living taxa.

In many, probably most cases, the fossils can be re-classified into acceptable cladistic groups, by the use of the unique characters they are already known to possess. A traditional classification of the synapsid reptiles (Fig. 2A) contains several paraphyletic, or arbitrary groups, such as Synapsida itself, Pelycosauria, Therapsida and Cynodontia. However, the cladistic relationships amongst the synapsids can be determined quite satisfactorily (Kemp, 1982, 1988; Hopson & Barghusen, 1986), and the group potentially reclassified along with the mammals in acceptable cladistic fashion (Fig. 2B).

There may well remain certain fossil forms which actually have no known unique characters of their own, and which cannot be fully classified cladistically. Suppose, for example, that a fossil was to be found that possessed several mammalian characters, but no characters otherwise unique to itself (Fig. 3). It would not be possible to classify this fossil as a natural, or cladistic group, and its precise relationship to the mammals would be indeterminate. But it could still be recognized as part of a larger group consisting of the fossil plus the mammals, and would therefore still have a potential bearing upon the relationship of the