The origin and early evolution of birds

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ABSTRACT

Birds evolved from and are phylogenetically recognized as members of the theropod dinosaurs; their first known member is the Late Jurassic *Archaeopteryx*, now represented by seven skeletons and a feather, and their closest known non-avian relatives are the dromaeosaurid theropods such as *Deinonychus*. Bird flight is widely thought to have evolved from the trees down, but *Archaeopteryx* and its outgroups show no obvious arboreal or tree-climbing characters, and its wing planform and wing loading do not resemble those of gliders. The ancestors of birds were bipedal, terrestrial, agile, cursorial and carnivorous or omnivorous. Apart from a perching foot and some skeletal fusions, a great many characters that are usually considered 'avian' (e.g. the furcula, the elongated forearm, the laterally flexing wrist and apparently feathers) evolved in non-avian theropods for reasons unrelated to birds or to flight. Soon after *Archaeopteryx*, avian features such as the pygostyle, fusion of the carpometacarpus, and elongated curved pedal claws with a reversed, fully descended and opposable hallux, indicate improved flying ability and arboreal habits. In the further evolution of birds, characters related to the flight apparatus phylogenetically preceded those related to the rest of the skeleton and skull. Mesozoic birds are more diverse and numerous than thought previously and the most diverse known group of Cretaceous birds, the Enantiornithes, was not even recognized until 1981. The vast majority of Mesozoic bird groups have no Tertiary records: Enantiornithes, Hesperornithiformes, Ichthyornithiformes and several other lineages disappeared by the end of the Cretaceous. By that time, a few Linnean 'Orders' of extant birds had appeared, but none of these taxa belongs to extant 'families', and it is not until the Paleocene or (in most cases) the Eocene that the majority of extant bird 'Orders' are known in the fossil record. There is no evidence for a major or mass extinction of birds at the end of the Cretaceous, nor for a sudden 'bottleneck' in diversity that fostered the early Tertiary origination of living bird 'Orders'.

Key words: Bird origins, bird evolution, bird extinctions, flight evolution, Dinosauria.

CONTENTS

I. INTRODUCTION

The higher taxa of living birds have fossil records extending back to the Early Tertiary (later than 65 million years ago) or, in the cases of several possible records of Charadriiformes, Gaviiformes, Anseriformes and Procellariiformes, the Late Cretaceous (perhaps as early as 75 million years ago). Given that the first known fossil bird, *Archaeopteryx*, is from the Late Jurassic (approximately 150 million years ago), it is evident that nearly half the history of birds transpired before the living groups are recorded. How much of our knowledge of living birds is useful in helping to explain the origin of birds and their early evolution? What other methods and lines of evidence are needed to explain the patterns and elucidate the processes that led to feathers, flight, the early diversification of birds into many different habitats, and the rise of the living groups of birds?

In this paper, we review and comment upon the present state of knowledge of Mesozoic (pre-Tertiary) birds. Beginning approximately two decades ago, the field of paleornithology experienced a renaissance that continues unabated to the present by new discoveries from the fossil record, new methods of comparative analysis, and new phylogenetic and functional studies that have formed exciting new pictures about the early history of birds. We focus on these discoveries, methods and analyses in the context of advancing the understanding of the early evolution of birds. Our purpose is to provide a synopsis and update of the principal issues, discoveries and viewpoints related to Mesozoic birds and early avian evolution. Ours is not the only possible viewpoint, nor the study one within integrative biology, and some workers have presented other conclusions or chosen other approaches. However, we base our approach on currently accepted methods of comparative, integrative biology with a strong foundation in phylogenetic systematics. All views must, of course, be regarded as subjective. Recent reviews of some of the topics addressed here include those of Feduccia (1980, 1996), Martin (1983a, b, 1987, 1991), Hecht *et al.* (1985), Olson (1985), Gauthier (1986), Bock (1986), Witmer (1991), Tarsitano (1991), Wellnhofer (1994), Chiappe (1995a), Elzanowski (1995), and Kurochkin (1995a).
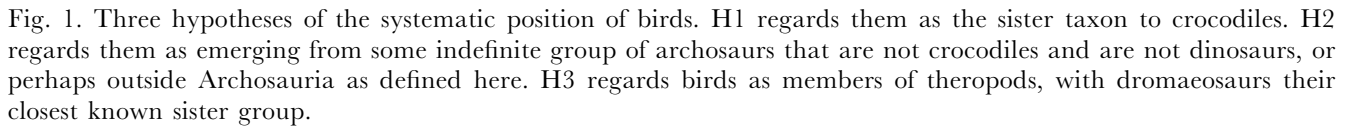
II. THE ORIGIN OF BIRDS

(1) Phylogenetic origins: dinosaurs, 'thecodonts', or crocodylomorphs?

There is no longer reasonable scientific doubt that birds evolved from small theropod (carnivorous) dinosaurs sometime during or shortly before the Middle to Late Jurassic, over 150 million years ago (Witmer, 1991). T. H. Huxley first made this argument in the 1860s (e.g. Huxley 1868, 1870), but it was not sustained because the evidence at the time was not considered sufficiently strong (Desmond, 1975, Gauthier, 1986; Fig. 1). J. H. Ostrom made a detailed case in the 1970s (e.g. Ostrom, 1973, 1974, 1975a, b, 1976a, b), and this was largely accepted by the systematic community. But it was also vigorously contested by several advocates of a 'thecodont' ('primitive' archosaur, a wastebasket group) origin (e.g. Tarsitano & Hecht, 1980; Hecht, 1985; Tarsitano, 1991) or of a crocodilian (or crocodylomorph, a phylogenetically wider group) relationship (e.g. Walker, 1972, 1977; Whetstone & Martin, 1979. 1981; Martin, Stewart & Whetstone, 1980; Martin, 1983a, b). Witmer (1991) has ably reviewed this problem and its history, which obviates much discussion here; readers are strongly referred to his paper for a fair and comprehensive overview.

(a) The 'thecodont' hypothesis

The 'thecodont' hypothesis is actually quite old, although not as old as Huxley's theropod hypothesis; 'thecodonts' were first named and recognized in the 1870s, although with a very different and more sparse constitution than in the mid-1900s (Charig, 1976). 'Thecodonts' (Order Thecodontia) came to comprise archosaurian reptiles that were not dinosaurs, crocodiles or pterosaurs, but that had no diagnostic characters of their own: hence, a 'wastebasket' group of 'Flying Dutchmen' with no real phylogenetic foundation (Gauthier & Padian, 1985; Gauthier, 1986). The 'thecodont' hypothesis for the origin of birds has traditionally been a default option, characterized not by positive association of characters and taxa but by negative statements about such associations with other taxa. Gerhard Heilmann's classic *The Origin of Birds* (1926) is the

Fig. 1. Three hypotheses of the systematic position of birds. H1 regards them as the sister taxon to crocodiles. H2 regards them as emerging from some indefinite group of archosaurs that are not crocodiles and are not dinosaurs, or perhaps outside Archosauria as defined here. H3 regards birds as members of theropods, with dromaeosaurs their closest known sister group.

standard case in point. After examining exhaustively every possible organ system in birds and related animals, and every possible candidate for their close relations and origin, Heilmann (1926) concluded that theropods shared more unusual and telling features with birds than did any other group. But he rejected a theropod ancestry for birds because there was no evidence at the time for clavicles in theropods, and these were assumed to have been lost. By Dollo's Law of irreversibility, or at least his interpretation of it, Heilmann (1926) concluded that such a feature could not re-evolve into the furcula of birds. Hence, birds must have a more ancient origin, so Heilmann (1926) suggested 'thecodonts' (similar to *Euparkeria*, for which clavicles were known), from which all other archosaurs were assumed to have evolved. Ironically, only a decade later clavicles were reported in an Early Jurassic theropod dinosaur, *Segisaurus* (Camp, 1936), and they are also now known in the theropods *Coelophysis*, *Velociraptor*, *Oviraptor*, *Allosaurus*, *Ingenia* and tyrannosaurids, among others. They are known to be fused into a furcula in the last five taxa (see e.g. Chure & Madsen, 1996), and this feature is probably a synapomorphy of tetanuran theropods.

In the 1970s and 1980s, similarly, the advocacy of a 'thecodont' hypothesis was mainly a negative reaction to Ostrom's theropod hypothesis. Tarsitano & Hecht (1980), for example, claimed that Ostrom had used only superficial similarities picked from a range of small theropods that were mostly found in deposits stratigraphically younger than *Archaeopteryx*; hence, one had to search for avian origins in more remote archosaurs that (to these authors) *quid erat demonstratum* could not be theropods. Ostrom had indeed used a range of small theropods for his

comparisons, and had not ordered them phylogenetically or stratigraphically; however, he had not posited that any particular known theropod was the *ancestor* of birds. He established that all these taxa shared derived characters inherited from a common theropod ancestor, without using cladistic methods or terms. But neither did Tarsitano & Hecht (1980) identify a specific 'thecodont' that they hypothesized was the closest known animal to birds (let alone an avian ancestor), nor the derived characters that any 'thecodonts' shared with *Archaeopteryx* and other birds to the exclusion of theropods. They simply stated (p. 177) that 'it is in a group characterized by the lack of dermal armor and the presence of a mesotarsus that the closest relatives of *Archaeopteryx* should be sought'. This hypothesis has been difficult to test (in as much as theropods seem to share unexceptionally the features sought in the closest avian relatives), and has appeared to amount simply to a disagreement with the theropod argument. Most archosaurian systematists appeared to hold the view that you can derive the morphology of *Archaeopteryx* from a 'thecodont', but you have to go through a theropod to do it (Gauthier & Padian, 1985; Gauthier, 1986; Benton & Clark, 1988; Sereno, 1991; Witmer, 1991).

Other authors have pointed to certain fossil forms as 'avimorph' or as 'proto-birds' or 'proavians', or as having striking similarities or 'affinities' (a term last used in a genealogical sense by Victorian biologists) to birds. Sometimes these 'proavians' have turned out to be fishes, but usually they are prolacertiform or related archosauromorphs (e.g. *Cosesaurus*, *Megalancosaurus*), animals outside the common ancestry of crocodiles and birds that flourished in the Triassic, 245–208 million years ago
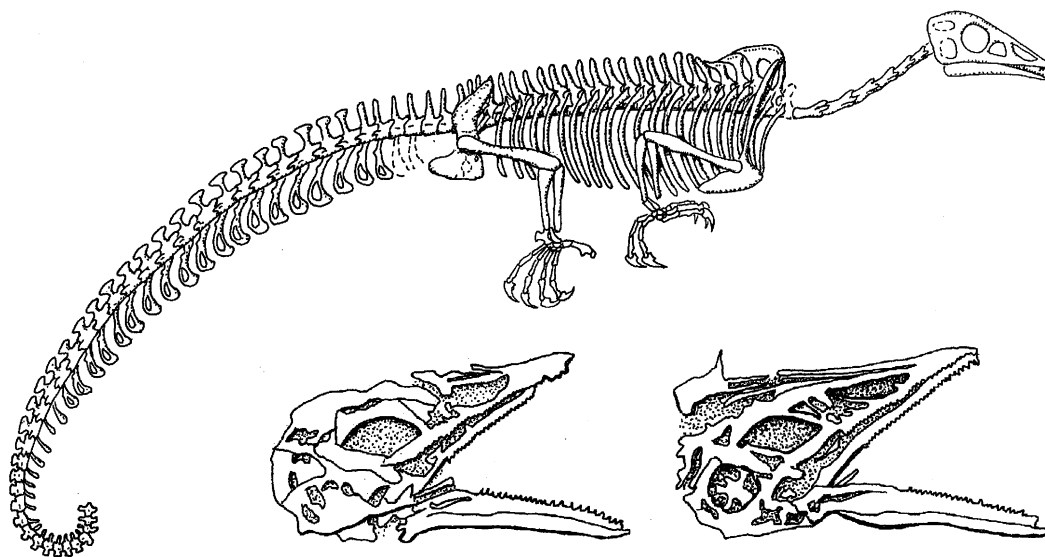
Fig. 2. *Megalancosaurus*, implicated by some authors in the origin of birds, but actually a protorosaurian archosauromorph very distant from birds, and probably aquatic. Skull length approximately 2.5 cm. From Renesto (1994). Inset are drawings based on photographs of the part and counterpart of the best-preserved specimen of the skull; very few bones are identifiable, which makes inferences of avian relationship based on superficial resemblance tenuous.

(Fig. 2). They are usually taken for 'proto-birds' because they have small teeth and triangular skulls, but so do the juveniles of a great number of tetrapods (including non-avian dinosaurs: see Norell *et al.*, 1994), and attempts to recognize early birds and their closest relatives have little value until they bypass these superficial resemblances. Ellenberger (1977), for example, advanced the tiny form called *Cosesaurus*, from the Middle Triassic of Spain, as a proto-bird, on the basis of such features, plus interpretations of birdlike shoulder girdles and furcula, and even putative feather traces. Martin (1983*a*) accepted these interpretations, and used them to advance the idea that avian-like features and taxa were in evidence long before theropods evolved. No subsequent analysis has supported this, and many studies (e.g. Olsen, 1979; Sanz & Lopez-Martinez, 1984; Evans, 1988) have established *Cosesaurus* as a member of the Prolacertiformes, a group of Triassic amphibious reptiles common in Europe and North America. Martin (1983*b*) also suggested that the small, long-limbed *Scleromochlus*, from the Late Triassic of Scotland, was a possible relative of birds; however, a number of synapomorphies indicate that it is instead the closest known animal to pterosaurs, which are in turn the closest major sister group to dinosaurs (von Huene, 1914; Padian, 1984; Gauthier, 1986; Sereno, 1991; Padian, Gauthier & Fraser, 1995; K. Padian, J. A. Gauthier & N. C. Fraser, unpublished data).

Feduccia & Wild (1993) recently revived the issue of *Megalancosaurus* (Calzavara, Muscio & Wild, 1981), a small reptile from the Late Triassic of Italy, as a possible avian ancestor or close relative (see also Martin, 1991; Tarsitano, 1991), contending that 'the theropod origin of birds is widely accepted, but the evidence is not convincing'. The analysis that follows this statement, unfortunately, is difficult to evaluate because it does not appear to use most of the evidence and methods of modern comparative biology. The authors did not cite any opposing views or analyses, did not consider existing cladistic analyses, constructed a 'cladogram' that has no characters and only one monophyletic taxon (Aves), and concluded that because there are two possible views on the subject, neither one can be pre-eminent. Alternative views using the comparative method, with very different conclusions, can be found in Gauthier & Padian (1985), Gauthier (1986), Padian (1987), Evans (1988), Benton & Clark (1988), Sereno (1991), and Holtz (1994). Renesto (1994) restudied *Megalancosaurus* (Fig. 2) and concluded that it is related to the unusual and possibly fossorial *Drepanosaurus*, from the Middle Triassic of Italy, another archosauromorph far outside birds (in fact, even further from birds than are Prolacertiformes: Evans, 1988). The deduction to be drawn from *all* the available evidence is that *Megalancosaurus* has nothing to do with the origin of birds; it was probably aquatic, not arboreal. In order to place

Megalancosaurus as a sister taxon to *Archaeopteryx* and the birds, a reversal of 164 synapomorphies shared by *Archaeopteryx* and dromaeosaurids (to the exclusion of *Megalancosaurus*) is necessary (Gauthier, 1986; Benton & Clark, 1988; Evans, 1988), which would imply the need to discover at least 165 synapomorphies linking *Megalancosaurus* and Aves in order to satisfy even the most minimal demands of numerical parsimony. According to all phylogenetic analyses, *Megalancosaurus* and *Cosesaurus* are not 'thecodonts' and they are not bird ancestors or sister taxa; they are not even archosaurs (i.e. they are outside the group formed by crocodiles, pterosaurs, birds and other dinosaurs, and many other extinct groups; see Fig. 1).

Most of the confusion over these false 'proavian' candidates can be traced to the fact that not all biologists agree on standard methods of comparative biology. As noted above, our preference is to use phylogenetic systematics (the insistence on monophyletic groups diagnosed by shared derived characters) as the method of analysing relationships (including origins). The many possible evolutionary scenarios for morphological, functional and ecological changes should be evaluated against hierarchical character distributions in these phylogenies (Padian, 1982, 1987). The best-supported phylogenies, and the sequences of character change that emerge from them, can be extremely important in pointing out correspondences to one or more evolutionary scenarios, and in failing to support others. Certainly, some workers do not subscribe to these methods, but unless they specify what methods they are using, and how their ideas are to be tested or falsified, there is no basis upon which their conclusions can be evaluated against conclusions based on the accepted methods of comparative biology (e.g. Feduccia, 1980, 1993, 1996; Bock, 1986; Martin, 1991; Tarsitano, 1991; Feduccia & Wild, 1993; Hecht & Hecht, 1994). Specifically, no critic of the theropod ancestry of birds, and no advocate of any other hypothesis, has undertaken a phylogenetic analysis of all the characters and taxa involved, as has been carried out repeatedly by workers who have confirmed that birds evolved from among theropods (e.g. Padian, 1982; Gauthier, 1984, 1986; Gauthier & Padian, 1985; Benton & Clark, 1988; Sereno, 1991; Holtz, 1994; etc.). Some workers reject currently accepted cladistic methods and phylogenies, and that is certainly their privilege: the use of cladistic methods does not by itself assure indisputable results. We make the case only that cladistics provides clearer, more precise, more ex-plicit, and more readily testable hypotheses of relationship than do variably informed arguments based on one or a few features. It has become far less defensible simply to pick and choose features that happen to coincide with *a priori* evolutionary scenarios and hypotheses of adaptation. In the parlance of current comparative biology, phylogenetic tests of evolutionary hypotheses help to move us from the 'how-possibly' to the 'how-actually'.

(b) The crocodylomorph hypothesis

The crocodilian (or crocodylomorph) hypothesis for the origin of birds has fewer problems of analysis than the 'thecodont' hypothesis, because crocodiles are a monophyletic group with a clear diagnosis and definition, and so can be compared explicitly to other taxa. A. D. Walker (1972, 1977) has been the principal advocate of the close crocodilian relationship of birds, based primarily on his intricate studies of the braincase, quadrate and ear region of *Sphenosuchus* (an Early Jurassic crocodylomorph from South Africa), in comparison to homologous regions in extant birds, as well as on other skeletal features. (Crocodylomorphs include crocodiles and some Triassic–Jurassic forms closely related to but outside true crocodiles; *Sphenosuchus* is not a true crocodile.) L. D. Martin and his students (Whetstone & Martin, 1979, 1981; Martin *et al.*, 1980) supported this general view, based on features of the tarsus, skull and teeth, among other features; but they concluded that the *Sphenosuchus* comparison made by Walker (1972, 1977) was outside the crocodile–bird connection. The synapomorphies of birds and crocodylomorphs that they proposed have been tested by other workers in other archosaurs, particularly theropods. Gauthier (1986: pp. 3–4), reviewing much of this work, found that (as its proponents admitted) most hypothesized bird–crocodylomorph synapomorphies were general to archosaurs or other larger taxonomic levels, so they could not be used as evidence; other features applied to certain taxa within birds or within crocodiles, but were not present in the common ancestor of both groups and thereby synapomorphic; other features were difficult to interpret or questionable in distribution (see also Gauthier & Padian, 1985; Gauthier, 1986; Witmer, 1991). Even if one accepted the 15–20 proposed synapomorphies of birds and crocodylomorphs, however, there are over 70 within ornithodiran archosaurs alone (Fig. 1) that place birds within theropods (Gauthier, 1986), and opponents of the theropod view have never systematically falsified this
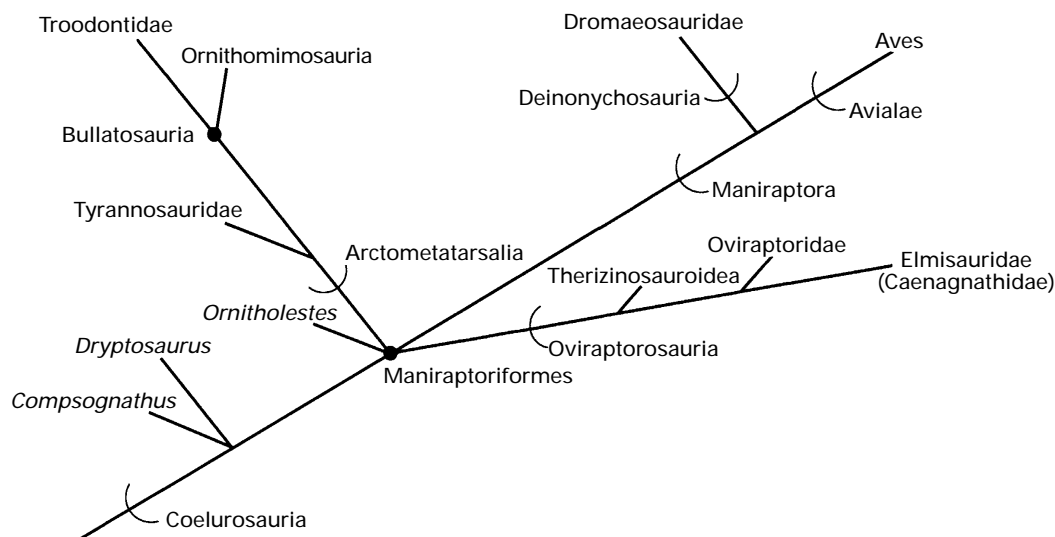
Fig. 3. Phylogeny of the coelurosaurian dinosaurs, after Holtz (1994, 1996) and other sources; details about subordinate groups and synapomorphies are found in Currie & Padian (1997).

analysis or developed a better supported one. A. D. Walker (1985), based on further study of the quadrate and braincase of *Archaeopteryx*, concluded that the crocodile–bird hypothesis could not be sustained, although he did not support the theropod hypothesis as a result.

(c) The theropod hypothesis

In the 1980s, phylogenetic analysis of this problem was pioneered by Gauthier (1984, 1986), who not only supported Ostrom's theropod hypothesis by cladistic analysis, but showed that the closest group of coelurosaurian theropods to birds included the dromaeosaurids such as *Deinonychus*, which Ostrom had described in 1969. Synapomorphies that link dromaeosaurids and *Archaeopteryx* include the presence of dorsal, caudal and rostral tympanic recesses, the semilunate carpal, thin metacarpal III, longer public peduncle, posteroventrally directed pubis with only a posteriorly projecting foot, shortened ischium, and other features of the skull, pectoral girdle and hindlimb. In recent years, there has been no serious challenge to Gauthier's analysis, but it has been refined and strengthened by other characters. Related theropods such as the troodontids and oviraptorids are becoming better known, and although the interrelationships of many theropod groups are shifting (Fig. 3), it is interesting that after ten years of further analysis of theropod relationships, the sister-group relationship of dromaeosaurids and birds has not been affected to date (recent review in Holtz, 1994, and see also Currie &

Padian, 1997; dissenting view in Elzanowski, 1995; see character state changes in Fig. 4).

Authors who have analysed the origin of birds cladistically have found a series of skeletal changes that, in most cases, constitute characters that have traditionally been considered 'avian'. For example (Fig. 4), basal theropod (carnivorous) dinosaurs have lightly built bones and a foot reduced to three main toes, with the first usually held off the ground (judging from footprints) and the fifth lost. Moving through the theropod sequence towards the birds, one sees the reduction and loss of manual digits five and four (considered below), increasing lightness of the skeleton (notably the vertebrae), and the tail vertebrae, which are reduced in number, partly interlock to reinforce the tail's stiffness. In coelurosaurs, which include birds, dromaeosaurids, ornithomimids, oviraptorids and several other groups, the arms become longer, the first toe begins to rotate backwards behind the metatarsals, which themselves become increasingly long, and the scapular blade becomes longer and more straplike. Fused clavicles (furcula) are now apparently basal to Tetanurae (carnosaurs and coelurosaurs; see Chure & Madsen, 1996; Currie & Padian, 1997), and sternal plates are known in a variety of tetanurans. In the pelvis, the pubis and ischium begin to show a greater disparity in length. (This is the transition up to the origin of birds, but the ischium secondarily elongates and thins in later birds, losing its peripheral processes.) Finally, in the dromaeosaurids and *Archaeopteryx*, the pubis begins to point backwards instead of forwards, and is at least 50% longer than the ischium, the
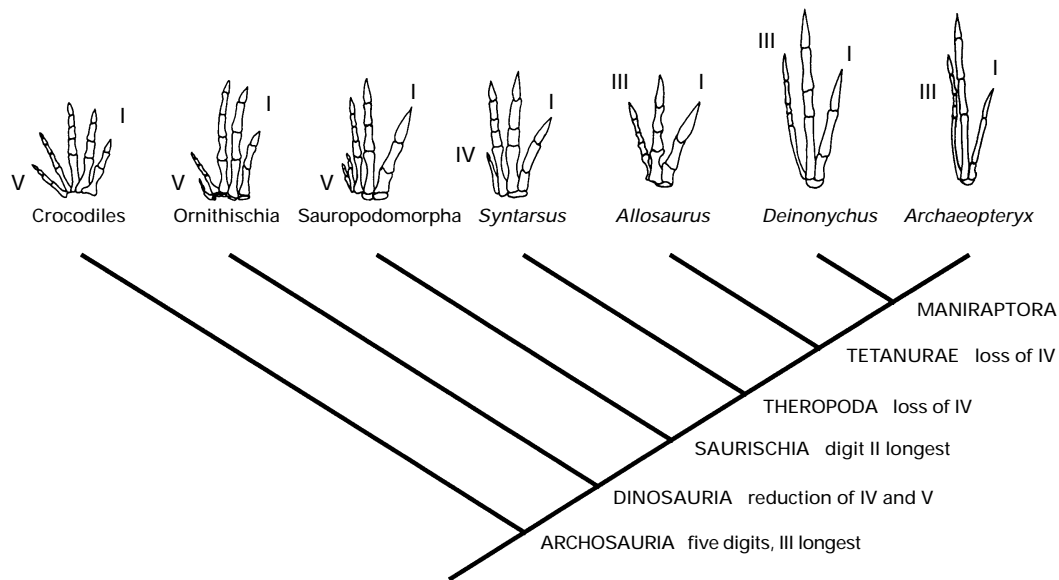
Fig. 4. Major branches of Archosauria leading to birds, showing evolution of the avian hand. The pattern of reduction in the hand, with the successive loss of manual digits V and IV, with retention of the forms, proportions, and numbers of phalanges, appears to pose a problem for the scenario of some developmental biologists that the avian hand comprises digits II, III and IV. For explanation see text. Not all nodes are pictured. THEROPODA: vomers fused anteriorly; pleurocoelous presacrals; five sacrals; transition point in tail distally located; large distal carpal 1 overlaps metacarpals I and II; digits IV and V reduced; large preacetabular portion of ilium; prominent caudofemoralis fossa; bowed femur; tridactyl foot (II–IV, III longest); reduced metatarsal V; furcula. TETANURAE: shorter presacrum; tibial ridge; accessory antorbital fenestra; prominent pubic foot; antorbital tooth row; straplike scapula; manus at least two-thirds forelimb length; loss of manual digits IV and V; expanded pubic foot. MANIRAPTORA: ischium reduced to two-thirds length of pubis; elongated metacarpal III; metacarpal I less than one-third metacarpal II in length; cervical ribs fused to centra; bony sternal plates fused in adults; forelimb at least half the length of the hindlimb and of the presacral vertebral column; elongated hand. DROMAEOSAURIDS AND AVES: pubic foot projects only posteriorly; pubic peduncle extends further ventrally than ischial peduncle; opisthopubic pelvis; loss of fourth trochanter on femur; proximal transition point in tail; semilunate carpal restricts wrist movement to sideways flexion. AVES: forelimb longer than hindlimb, and at least 75% of presacral vertebral column; metacarpal III thin; flight feathers. Characters from Gauthier (1986), Holtz (1994) and Chiappe (1995a).

anterior projection on the foot of the pubis is lost, the tail becomes yet shorter, the fourth trochanter is reduced, and the hyperflexing wrist joint made possible by the pulley-shaped semilunate carpal (Ostrom, 1969, 1974; regarded as the radiale but actually the first distal carpal) allows the action that is crucial to the flight stroke in birds (Padian, 1985; Gauthier & Padian, 1985). The sequence of these changes was laid out by Gauthier (1984, 1986) and updated by Holtz (1994, 1996, and references therein). These features must be seen as passed down to birds from their dinosaurian ancestors, and not as features that evolved specifically for the ways of life of living birds.

(2) Ontogeny and phylogeny of limbs

The identity of digits in the avian hand has long been at issue. Feduccia (1996) reproduces several classic ornithological drawings of the bird hand, which variously configure the digits as I-II-III and II-III-IV (see also Proctor & Lynch, 1993). Following the lead of traditional developmental biology, Hecht (see references in Hecht & Hecht, 1994) has long argued that extant birds have digits II, III and IV, so *Archaeopteryx* must too, because it is a bird (and in his view it cannot have evolved from theropods). However, no embryological evidence of *Archaeopteryx* is available, and because the manus of living birds is not completely pentadactylous (even embryonically), the identification of elements in various stages of ossification, chondrification or condensation has historically been problematic. To argue from developmental evidence [as Hinchliffe & Hecht (1984) and Hinchliffe (1985) do] that the digits are II, III and IV (which seems equivocal, in as much as *Anlage* do not appear in embryology with labels), the first digit, including its carpal and

metacarpal, has to be lost, and digits II, III and IV have to assume *the precise forms*, *articulations and proportions of the aboriginal digits* I, II and III; and digit V is lost as usual (Fig. 4). This may be possible but developmental biology has so far not elucidated mechanisms or examples that support this scenario. For example, Hinchliffe & Hecht (1984) proposed that the avian hand digits are II, III and IV, framing their hypothesis within Morse's law that digit reduction always proceeds from the outside inwards. However, even if we accept this view, it is difficult to place a line of demarcation between 'theropod' and 'bird' because (*a*) the configuration of the theropod digits I, II and III are exactly topologous to the avian digits and (*b*) we have no information about the ontogenetic sequence in *Archaeopteryx* or any other fossil bird.

In contrast, phylogenetic and palaeontological evidence, when used to test the developmental ambiguities, suggests in the strongest possible way that the bird hand is a fusion of digits I, II and III, not II, III and IV (Gauthier, 1986; Padian, 1992; Shubin, 1994). Fig. 4 presents the bones of the hand in a cladogram based on dozens of other synapomorphies (e.g. Gauthier, 1986; Holtz, 1994, 1996; see also Fig. 13). Dinosaurs primitively have five fingers with IV and V reduced, and saurischians further have the derived condition of digit II the longest (e.g. *Plateosaurus*, *Ammosaurus*). The subgroup Theropoda (carnivorous dinosaurs) begins with digit V reduced to a nubbin of the metacarpal, a reduced metacarpal IV, and only a nubbin of the first phalanx of digit IV (e.g. *Coalophysis*). Digit I has a foreshortened, offset metacarpal in all saurischians, and the phalangeal formula of the first three digits continues the 2-3-4 pattern of all other tetrapods. In the theropodan subgroup Tetanurae, which includes Carnosauria such as *Allosaurus* as well as the Coelurosauria that includes Maniraptora, all remnants of digits IV and V are lost; digit I still has the short metacarpal, and digit II is still the longest. Digits I and II are covered by a single distal carpal at their bases, and metacarpal III is thinned. This is the situation in *Archaeopteryx* and the other maniraptorans (e.g. *Deinonychus*), and it is inherited by later birds.
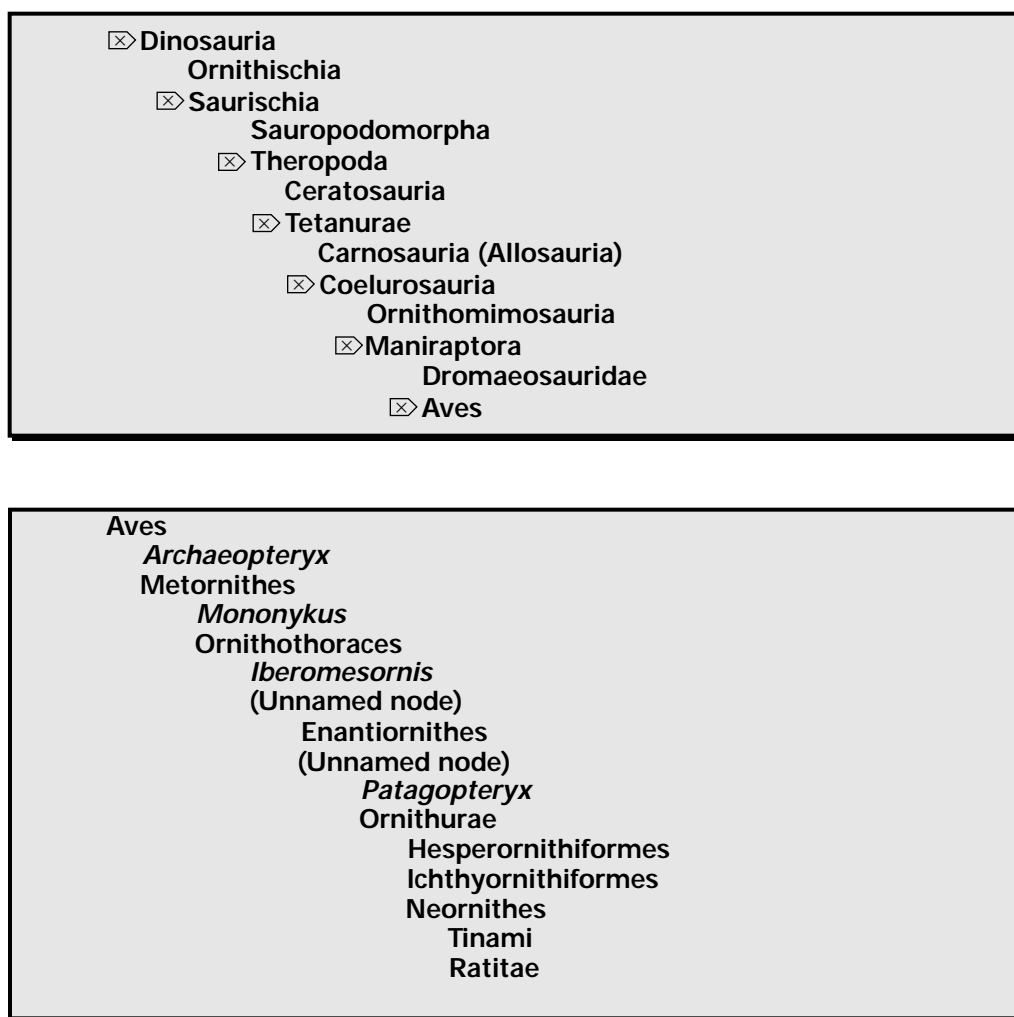
Shubin (1994) noted that the 'digital reduction in the theropod hand follows a consistent pattern: digits from the posterior side of the limb tend to be reduced while other digits remain unchanged'. So, if birds are accepted as theropods, the theropod manual pattern is retained because (*a*) the inner digits remain stable in configuration and (*b*) the theropod pattern of digital and phalangeal reduction remains unchanged through the early evolution of birds, in which a carpometacarpus is not yet completely fused (e.g. Enantiornithes, which like tyrannosaurs retain two phalanges in the first digit and three in the second, but reduced phalanges in the third digit; *Mononykus* has one major digit, the first, with highly reduced second and third digits). Therefore, the generalization that the patterns of phalangeal order of development and reduction in all living tetrapods must be the same is untestable unless phylogenetic patterns of evolution and reduction are taken into consideration (and is probably false). Note (in contrast) that the bird foot is II, III and IV, with digit V lost and digit I offset as in all theropods. The same pattern holds primitively for all the saurischian dinosaurs, which include theropods (and thus birds).

(3) Nomenclature

A more trivial question, but one related to the necessary nomenclatural bookkeeping, has been raised in relation to the taxonomic application of the term Aves (Figs 3–6). *Archaeopteryx* has traditionally been considered a bird and a member of Aves (Fig. 5), but Gauthier (1986) argued to restrict Aves to crown-group birds (extant birds and all the descendants of their most recent common ancestor) so as to maximize the information value of a well-known term. The informal term 'birds' could still include *Archaeopteryx* and other fossil birds, and Gauthier (1986) coined the term Avialae to include *Archaeopteryx* and all taxa closer to (and including) crown-group birds, or Aves (*sensu* Gauthier, 1986).

Gauthier's (1986) proposition was adopted by several authors (e.g. de Queiroz & Gauthier, 1990, 1992; Norell *et al.*, 1994), including at times one of us (e.g. Perle *et al.*, 1993*a*, 1994). Undoubtedly, the growing application of phylogenetic definitions (see de Queiroz & Gauthier, 1990, 1992) is a benchmark in taxonomic practice that is already clarifying and stabilizing many traditional names. However, following Gauthier's (1986) suggestion in the particular case of birds is not an easy choice. For one thing, *Archaeopteryx*, *Hesperornis* and *Ichthyornis* have been considered birds and members of Aves for more than a century, beginning with their first descriptions in the 1860s, 1870s and 1880s, and continuing through standard taxonomic treatments (e.g. Lambrecht, 1933; Romer, 1966; Carroll, 1989; and a host of ornithological texts). Second, in some languages (e.g. Portuguese and Spanish, spoken by over 500

⊠ **Dinosauria**
    Ornithischia
  ⊠ **Saurischia**
      Sauropodomorpha
    ⊠ **Theropoda**
       Ceratosauria
      ⊠ **Tetanurae**
         Carnosauria (Allosauria)
        ⊠ **Coelurosauria**
           Ornithomimosauria
          ⊠ **Maniraptora**
             Dromaeosauridae
           ⊠ **Aves**

Aves
    Archaeopteryx
  Metornithes
      Mononykus
    Ornithothoraces
      Iberomesornis
      (Unnamed node)
        Enantiornithes
        (Unnamed node)
          Patagopteryx
        Ornithurae
          Hesperornithiformes
          Ichthyornithiformes
          Neornithes
            Tinami
            Ratitae

Fig. 5. Indented classifications (unranked) of the Dinosaurian groups that include birds (this classification reflects the phylogeny shown in Figs 3, 4) and the basal groups of birds (as per Fig. 16). Arrows in the first section indicate the hierarchical sequence to which birds belong. A sister-taxon within each hierarchical level (sometimes several exist: see Gauthier, 1986; Holtz, 1994) is included for comparison.

million people), the terms 'aves' and 'birds' are identical. Thus, the application of Gauthier's (1986) suggestion would produce the confusing result that many fossil taxa would be called 'birds' (informally) but not 'Birds' (scientifically) in some languages.

The question to be asked, therefore, is whether the advantages of Gauthier's (1986) proposal are enough to overthrow more than a century of taxonomic stability. A strong argument in his favour is that the use of crown-group taxa (those including the most recent common ancestor of living birds and all its descendants) for well-known terms maximizes information that is often lost in fossils, for which soft tissues and molecules are seldom preserved. In other words, we know far more about living birds than we will ever know about any extinct bird, so we should confine the term Aves to them. However, most of the soft-part characters that unite living birds are unknown in their immediate outgroups, so the value of these characters for diagnosing the crown-groups and anchoring the polarities of characters among these groups (and hence resolving their phylogeny) is at best equivocal. We agree that Aves should be defined phylogenetically, but (with some mixed feelings) we prefer to conserve the traditional understanding (Fig. 6), in which Aves comprises the most recent common ancestor of *Archaeopteryx* and extant (crown-group) birds and all its descendants. Living birds, and all descendants of their most recent common ancestor, comprise Neornithes, a strictly crown-group taxon.

There is also disagreement about the definition and composition of the clade Ornithurae (Fig. 6). Martin (1983*a*) used this name to include Hesperor-
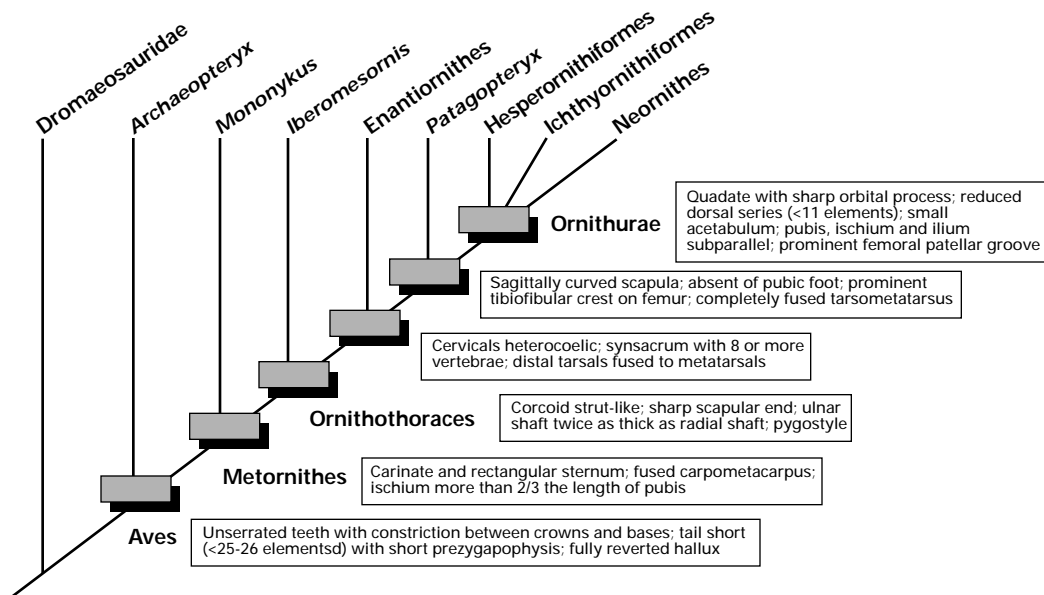
Fig. 6. Phylogeny and classification of basal avian groups. Gauthier (1986) proposed the restriction of the term Aves to what is here called Neornithes (all living birds and the descendants of their most recent common ancestor). What Gauthier (1986) called Avialae we restore as Aves. Gauthier (1986) also proposed the extension of the term Ornithurae for all taxa closer to living birds than to *Archaeopteryx*; here we restore it to Martin's (1983*b*) original sense.

nithiformes, Ichthyornithiformes and Neornithes, a proposition broadly followed by other authors (e.g. Martin, 1984, 1987, 1991; Cracraft, 1986, 1988; Sanz, Bonaparte & Lacasa Ruiz, 1988; Witmer, 1990; Chatterjee, 1991; Chiappe, 1991*a*,*b*, 1995*a*–*c*, 1996; Sanz & Bonaparte, 1992; Sanz & Buscalioni, 1992; Perle *et al.* 1993*a*; Chiappe & Calvo, 1994; Sanz, Chiappe & Buscalioni, 1995). Martin's (1983*a*) use of the term predated the phylogenetic system of de Queiroz & Gauthier (1990, 1992), but because all such taxa are now being scrutinized for their utility in the phylogenetic system, the question of its stability must be asked. Martin's (1983*a*) definition (like a great many proposed in the early days of cladistics, e.g. Gauthier, 1986) is taxon-based (it consists of a list of members), which further philosophical reflection has shown to be much less stable than node-based and stem-based definitions (de Queiroz & Gauthier, 1990, 1992). Gauthier (1986), using a stem-based phylogenetic definition, defined Ornithurae as the clade composed of 'extant birds and all other taxa, such as *Ichthyornis* and Hesperornithes, that are closer to extant birds than is *Archaeopteryx*'. Although Gauthier (1986) included within Ornithurae the same taxa that Martin (1983*a*) and other previous authors did, his definition (because it is stem-based) includes not only the taxa that Martin (1983*a*) named, but also any taxa between them and *Archaeopteryx*, which sub-

stantially altered Martin's (1983*a*) original intent and (by then) traditional usage of the term. Chiappe (1991*a*) redefined Ornithurae as a node-based term, to return it more to Martin's (1983*a*) original intention, namely as the most recent common ancestor of Hesperornithiformes and Neornithes and all its descendants. However, here, as in the case of Aves, until agreement is reached and the names are stabilized, *caveat lector* is urged.

(4) The evolution of feathers

Until very recently, the point at which feathers first developed from scales was not known, nor was there fossil evidence for their precise phylogenetic diversifications into flight, covert and down feathers. This changed with the recent discovery of a small coelurosaurian theropod dinosaur, named *Sinosauropteryx*, which bears a row of small fringed structures along its vertebral column (Ji & Ji, 1996). It is clear that by the time *Archaeopteryx* is known, flight and covert feathers at least were present, although down cannot be recognized from the available specimens (Fig. 7). Many salient differences in early developmental sequences and genic coding sequences and organization remain between scales and feathers, and some biologists are now concluding that feathers and their related avian
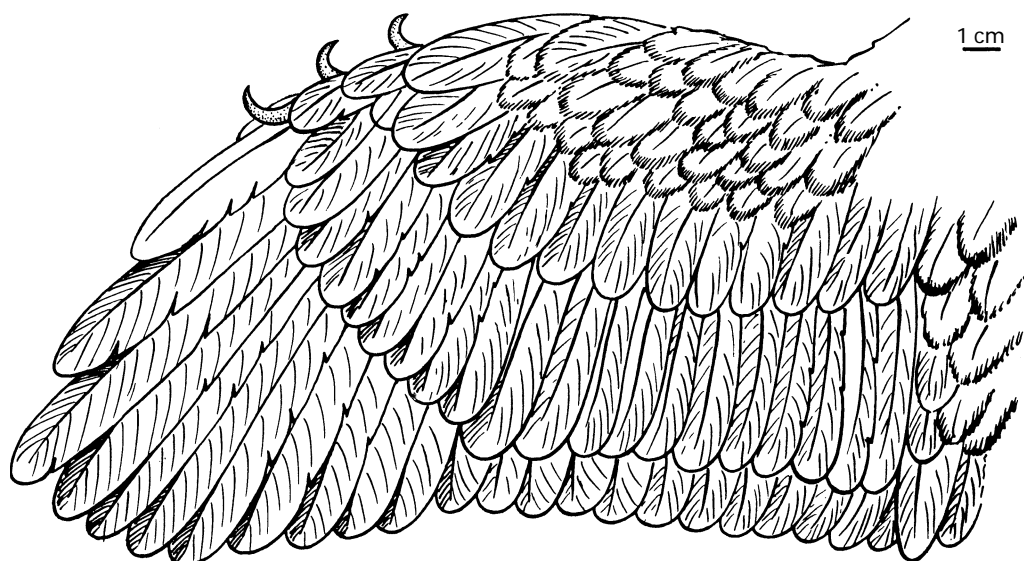
Fig. 7. Restoration of the feather pattern in the wing of *Archaeopteryx*, after Rietschel (1985). Note the extensive layering of the feathers, the orientation of the claws and the apparent absence of an alula.

epidermal structures are evolutionary novelties. Brush (1993, 1996) argues on the basis of molecular and developmental dissimilarities that feathers may not have arisen from reptilian scales, but merely have in common with them general proteinaceous structures and shared epidermal protogenes; instead, gene rearrangement and changes in developmental timing account for many of the salient differences. Historically, the apparent structural gradation between, for example, the scales on a bird's tibiotarsus and the feathers on the thigh has left little doubt to morphologists that feathers are highly modified scales. Fossil evidence, until recently, had little to offer this question beyond the similarities of gross morphology, and the obvious structural advancement of the feathers of *Archaeopteryx* (Rietschel, 1985). However, the recent discovery of *Sinosauropteryx* has changed this. It may be presumed that, however different extant avian feathers are from extant lizard scales, there may well have been more molecular and developmental similarities between feathers and the integumental structures of non-avian theropods – which at present are regrettably unknown. Above all, however, it is clear that feathers are not a synapomorphy of birds; they do not diagnose birds, but are shared by a broader group of animals within the theropod dinosaurs (Ji & Ji, 1997). Hence, feathers did not evolve for flight.

Many hypotheses have been proposed for the original adaptive value of feathers: these include insulation, active thermoregulation, flight, display and camouflage during foraging (contrast, for example, Cowen & Lipps, 1982; Regal, 1975, 1985; Feduccia, 1985; and Thulborn & Hamley, 1985). Proponents of original thermoregulatory functions (active or passive) tend to hypothesize that down and covert feathers evolved first, as a fringing of the basic reptilian scale (although see Brush, 1993, 1996). Proponents of display or flight as original functions tend to hypothesize that covert and flight feathers, respectively, were the first to evolve.

Most of these hypotheses are difficult to test directly, and some are untestable although not necessarily implausible. Proponents have variously invoked for support the patterns of pterylosis in different extant bird groups, the order of development of the different feather types, and the size and presumed functions of the wings and tail feathers in *Archaeopteryx*. These are all interesting lines of evidence. However, (1) the variations in pterylosis patterns have not been phylogenetically polarized in extant birds and we do not know the original avian pattern; (2) patterns of both pterylosis and feather development are as subject to selection and modification as any other features are; and (3) conditions in extant birds do not automatically provide the conditions in the first birds or their ancestors. In complex organisms, adaptive behaviour generally precedes the developmental 'hard-wiring' of morphological features (e.g. Frazzetta, 1975; Waddington, 1975), and a slight advantage in function may over the course of time accrue considerable success. A structure may be used for display without being perfected or even greatly elaborated, and a fringed
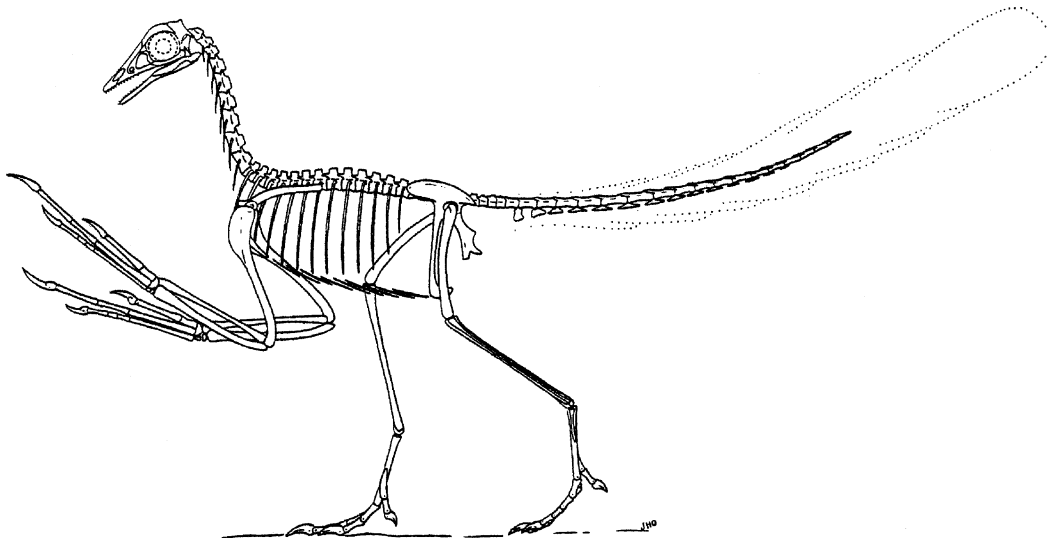
Fig. 8. *Archaeopteryx*, the oldest known bird and the sister group to all other birds, as restored by J. H. Ostrom (1979). Skull length approximately 4 cm.

scale may provide more insulation than an unfringed one, although less than a feather. However, all-out flight cannot occur until the wing is completely airworthy, although power-assisted leaps and glides from modest heights may be enhanced (Rayner, 1985 *a*, *b*). It seems plausible that, from the outset, feathers were used for several purposes, as they are now. But it is unlikely that they originated directly for flight, as their presence in theropod dinosaurs that did not descend from flying animals shows; see also the stunning monograph on the original specimen of *Archaeopteryx*, the isolated feather, by Griffiths (1996).

(5) The first birds

Archaeopteryx, from the Late Jurassic of Bavaria (Fig. 8), is now known from seven skeletons and an isolated feather, the first remnant to be recognized (in 1860). Peter Wellnhofer has masterfully described the seventh (Wellnhofer, 1993), the sixth Wellnhofer, 1988) and the fifth (Wellnhofer, 1974), which was originally identified as a juvenile of the small theropod *Compsognathus*. The fourth specimen had been discovered in 1855 but was originally identified as a pterosaur; Ostrom recognized it as an *Archaeopteryx* in 1970 (see Ostrom, 1972). The previously known specimens are the Maxberg (now lost), the Berlin and the London specimens (review in Ostrom, 1976*b*). The seventh specimen preserves, for the first time, a small sternum. Because the sternum is ossified, and the hind legs appear to be

slightly longer than in other specimens, despite its small size, Wellnhofer (1993) proposed a new species for this specimen, *A. bavarica*, to join *A. lithographica*. In the past, nearly every specimen of *Archaeopteryx* has received a different specific (and often generic) name from at least one worker, based on differences that have appeared worthy of taxonomic separation. As Wellnhofer (1993, 1994) notes, Houck, Gauthier & Strauss (1990) showed that most of these differences are ontogenetic. The known specimens of *Archaeopteryx* range in size by a factor of two (the Eichstätt specimen is approximately half the size of the Solnhofen specimen in most limb bone lengths), which suggests a substantial ontogenetic range. Still, with the small sample available at present, it is difficult to affirm how many taxa (including juveniles and genders) are really represented in the Solnhofen limestones.

Every few years, a new putative 'oldest bird' or 'bird ancestor' comes along to knock *Archaeopteryx* off its perch, and each time to date it has failed, as noted above. *Protoavis* (Chatterjee, 1991, 1995, 1997) is an example of a case still in progress: it was heralded in advance press since 1986 as a Triassic bird from Texas, some 75 million years older than *Archaeopteryx*. Its announcement was controversial for several reasons, the most important of which was that the scientific community did not have the opportunity to evaluate this claim. The reported find, deep in the Late Triassic, was stratigraphically unexpected given the consilience between the order of the bird-theropod cladogram (e.g. Gauthier, 1986) and the sequence of appearance of these taxa,

which suggested that the origin of birds was in the Late (or perhaps Middle) Jurassic (Padian, 1985; Gauthier, 1986).

However, the fundamental issue is centred on the interpretations of the specimens themselves. Contrary to its portrayal in the media and even by some scientists involved (see Zimmer, 1992), the controversy has not been personal, but methodological. To replace the best-supported hypothesis of bird origins requires a complete re-analysis of all available characters and taxa; it is not a matter of simply making a case that a newly discovered form has many apparently birdlike features. It is difficult to settle these questions in the media in advance of publication of peer-reviewed results, and this is one reason why *Protoavis* was not immediately accepted by most workers as a bird. Chatterjee published a description of the skull of *Protoavis* in 1991, along with much interpretation of the meaning of the skull evidence for the origin of birds and their ecological features. In his analysis, *Protoavis* shares 30 cranial synapomorphies of birds, of which 20 place it well within birds. However, this description has apparently not convinced many workers beyond those who already doubted theropod ancestry (commentary in Ostrom, 1991, 1996; Wellnhofer, 1994; Chiappe, 1995*a*; Kurochkin, 1995*a*). In the view of other systematists, even if Chatterjee's (1991) anatomical observations and identifications were to be accepted, his interpretation would not account for the full distribution of synapomorphies among theropods, most of which appear to be absent in the *Protoavis* material [although Chatterjee (1991) regards *Protoavis* as a theropod and does not challenge the theropod ancestry of birds]. This is an intriguing problem, and the acceptance of Chatterjee's (1991) view would appear to require a great number of character reversals and homoplasies. Although this is not *a priori* impossible, it still depends on a complete re-analysis of theropod phylogeny, including the data from previously published cladistic analyses (e.g. Gauthier, 1986; Holtz, 1994), showing that *Protoavis* is within Aves. The trees presented in Chatterjee's publications to date have not fully integrated his data with characters presented in previous cladistic analyses for archosaurs in general, and this is why most workers regard this as an open question, not as a fundamental challenge.

Some features appear to support Chatterjee's argument. The anterior cervical vertebrae appear to have weak or incipient (not fully heterocoelic) saddle-shaped articulations, but there are no avian features in the forearm, the hand has four robust metacarpals, four metatarsals have been reconstructed in some published photographs, and the tail is exceptionally long for birds. With the exception of some of the vertebrae and a theropod-like braincase, most other bones are poorly preserved and different interpretations are feasible. In this context, some workers have concluded that *Protoavis* is more likely a collection of parts of perhaps several small tetrapods that are difficult to identify (e.g. Ostrom, 1996). The material has become a paleontological Rorschach test of one's training, theoretical bias, and predisposition. A description of the postcranial material is now out (Chatterjee, 1997) (although already *Protoavis* has been treated as a bird ancestor in some textbooks). Here, differences between the nature of the material in neontology and paleontology must be appreciated. If there is a report of a new bird species in the Amazon Basin, another scientist could (with permission) go there and try to trap additional specimens. But it will probably be years before the paleontological community has adequate opportunity to evaluate the *Protoavis* material, because it is unique, and reasonable claims to territory are respected. As such, it becomes the intellectual property of the scientist who works on it. After that scientist's work is published and interpretations disseminated, others may have the opportunity to study the material first-hand, if it is made generally available, to test the original observations and conclusions, and to draw their own. We are not yet at that stage with *Protoavis*, so all claims must be treated tentatively, especially in view of the paradoxes it presents.

In 1994 a North Korean bird tentatively identified as from the Jurassic was informally presented to the public in the Japanese magazine *Korean Pictorial* as the 'North Korean *Archaeopteryx*'. It seems to preserve the wing bones, vertebrae and a poorly preserved skull, along with impressions of feathers. Differences from *Archaeopteryx* in the proportions of its wing elements cast doubt on the preliminary taxonomic identification of this specimen (Chiappe, 1995*a*). This specimen is potentially very important because it could test the observation that the diversity of pre-Cretaceous birds known to date is still essentially monotypic. An adequate assessment of its stratigraphic age, however, is still needed, and a formal scientific report is awaited.

Another claim challenging the singular position of *Archaeopteryx* as the only known Late Jurassic bird was presented in the report on *Confuciusornis sanctus*, from the freshwater deposits of the Yixian Formation of Liaoning Province in north-eastern China (Hou *et*

al., 1995, 1996). These authors identified the age of the Yixian Formation as Late Jurassic, and regarded *Confuciusornis sanctus* as an enantiornithine close to the Late Cretaceous *Gobipteryx*. However, neither conclusion may be substantiable. The purported Late Jurassic age of the Yixian Formation does not agree with recent palynological studies assigning these deposits to the Berriasian (Li & Liu, 1994), the oldest stage of the Cretaceous, nor with recent laser-derived Ar^{40}-Ar^{39} studies giving average dates of 121.1 ± 0.2 million years for these beds, which place these deposits well within the Early Cretaceous – possibly even in the Barremian, three stages later (Smith *et al.*, 1995). The assignment of this species to the Enantiornithes is also problematic. In the cladogram published by Hou *et al.* (1995), the allocation of *Confuciusornis sanctus* to the Enantiornithes was based on a single character, the elongated coracoid, regardless of the fact that this element is not preserved in the holotype and that strutlike coracoids are present in all birds except *Archaeopteryx* and *Mononykus*. In Hou *et al.* (1995), this character was changed to 'short tail with development of a pygostyle, and distinct pleurocoels' (one would normally regard these as two unrelated characters). The first feature applies to all birds except *Archaeopteryx* and *Mononykus*; the second was already present in theropod dinosaurs. The 'cladogram' in Hou *et al.* (1995, 1996) lacks outgroups, and so the polarities of their character states cannot be substantiated. This is one reason why other workers get different results from their phylogenetic analyses. The characters that purportedly link *Archaeopteryx* and Enantiornithes in the 'Subclass Sauriurae' (Hou *et al.*, 1995, 1996) – proximal-to-distal metatarsal fusion, posterolateral condylar ridge on the femur, broad, grooved, noncompressible furcula, and anterodorsal ischial process – are all already present in coelurosaurian theropods, which these authors categorically reject as the group from which birds evolved. Other workers regard 'Sauriurae' as a paraphyletic group.

Some other putative Late Jurassic birds have been proposed; these were reviewed by Molnar (1985) and updated by Jensen & Padian (1989). '*Praeornis*', an isolated feather from Karatau (Rautian, 1978), has been reinterpreted as a cycad leaf (Bock, 1986: pp. 59–60), but is still regarded as a bird by others (e.g. Unwin, 1993). *Laopteryx* (Marsh, 1881), from the Morrison Formation of Wyoming, is probably a pterodactyloid braincase (Ostrom, 1986a; Padian, 1997). Bones referred to as *Palaeopteryx* (Jensen, 1981) and associated bones from the Morrison of Colorado are partly pterodactyloid, partly maniraptoran (bird or dromaeosaurid), and partly indeterminate small theropod, but none of these bones is definitely avian (Jensen & Padian, 1989; Padian, 1997). Lockley *et al.* (1992) argue that there are some possible bird tracks in the fossil record as early as the late Early Jurassic (e.g. *Trisauropodiscus* from Arizona and South Africa), but their criteria for recognizing avian footprints are somewhat vague, and have not been demonstrated as unique characters of bird tracks, or of certain taxa within birds (Chiappe, 1995a; Padian, 1997). The degree of divarication of the second and fourth toes figures prominently in their discussions, but other morphological features of the tracks are not clearly diagnostic of Aves; the authors also acknowledge the problematic lack of skeletal evidence of birds until the Late Jurassic. It is not clear that the authors are identifying these tracks as avian; they are noting presumably avian features. Still, 'avian features' can only be either those of true birds or convergent features of other taxa (presumably, in this case, small non-avian theropods), so either way some intriguing questions and doubts are raised.

(6) The false argument of stratigraphic disjunction

A difficulty regarded as insurmountable by opponents of the theropod origin of birds (e.g. Feduccia, 1996) is the presumption that the taxa identified as closest to *Archaeopteryx* among theropods – the dromaeosaurids – do not appear in the fossil record until Albian-Aptian times (perhaps 110 million years ago: *Deinonychus*, Cloverly Formation, Wyoming), whereas *Archaeopteryx* comes from Late Jurassic (Tithonian) times (about 150 million years ago). The apparent absence of earlier records of dromaeosaurids, while puzzling, is not unusual in the Mesozoic fossil record, and the situation is not unique to dinosaurs. Marsupials and placentals are sister-taxa within mammals, and monotremes are their sister-taxon. Hence, the split between therians (marsupials + placentals) and monotremes must have taken place before the first recognizable marsupials and placentals evolved. But the first marsupials and placentals are known from Early Cretaceous times (approximately 100 million years ago), whereas until recently, monotremes were not known until the Oligocene (approximately 20 million years ago), a disjunction of 80 million years, over twice that between *Archaeopteryx* and *Deinonychus*. However, small maniraptorans are not absent from Late

Jurassic sediments: Jensen & Padian (1989) described a collection of bones pertaining to small maniraptorans from the Dry Mesa Quarry (Late Jurassic: possibly Tithonian; Morrison Formation, Colorado). In any event, it would not matter what stratigraphic disjunction existed; arguments about phylogeny are based on characteristics and not on rocks, and the presence of one sister taxon at a point in geologic time implies that its sister taxon was also present then, even if we do not have a good fossil record of it (Norell, 1992).

III. THE ORIGIN OF FLIGHT

(1) Arboreal and cursorial models – and beyond

Since the 1880s, a dichotomy between the 'from the trees down' (arboreal) and the 'from the ground up' (cursorial) theories has polarized this question (Ostrom, 1974; Martin, 1983 *a*, *b*; Hecht *et al.*, 1985; Padian, 1985). The arboreal theory is more popular among some workers, because it is intuitive that flight evolving from an arboreal gliding stage would seem to be relatively easy. But the theory has surprisingly little to support it from rigorous analyses in comparative biology. The arboreal theory, in its extreme form, requires the ability to climb tree trunks and the ability to glide. Neither capacity is well marked in *Archaeopteryx*, nor in its non-avian theropod relatives. *Archaeopteryx* has none of the features of typical vertebrate gliders and is not aerodynamically designed to glide (Yalden, 1971; Padian, 1985; Rayner, 1985 *a*, *b*). Feduccia (1993) argued that the claws of its pes and manus have degrees of curvature typical of perching and trunk-climbing birds, respectively, and concluded that it was a perching bird, not a cursorial predator. He based his work on measurements of the lateral sides of the foot claws of several species of perching, trunk-climbing and ground-living birds. However, Feduccia (1993) did not explicitly consider, although he cited, the work of other authors on this problem. Ostrom (1976 *a*) concluded on the basis of a similar study that *Archaeopteryx* had claws commensurate with those of ground-dwelling birds. Yalden (1985) reached the conclusion that the claws of *Archaeopteryx* suggested arboreality, and supported this further by a conclusion that the proportions of the limbs and backbones were also similar to those of some climbing mammals. However, like Feduccia (1993), Yalden (1985) did not compare the shapes of the claws of *Archaeopteryx* and other theropods [which all have the lateral grooves that Yalden (1985) interpreted as an arboreal specialization], nor the limb proportions, which are similar for reasons of common heritage (coelurosaurs have unusually long arms and short backs); hence, no special evolutionary explanation is required. Peters & Görgner (1992) came to quite different conclusions to Feduccia (1993) by looking at more than one line of evidence. Peters & Görgner (1992) considered both lateral and dorsal views of claws and noted that perching and ground birds have broader claws than tree-climbers. They also noted that the construction of trunk-climbing bird claws occurs in cliff-dwellers and non-climbers too, and to some extent in non-avian theropods (*contra* Feduccia, 1993: p. 792, 1996). The manual claws of *Archaeopteryx* also lack evidence of wear on their distal parts (Wellnhofer, 1985; Peters & Görgner, 1992). Furthermore, the hallux of *Archaeopteryx* is too short and too proximally situated on the metatarsus to be an effective aid in perching (e.g. Wellnhofer, 1993) as compared to the condition in *Sinornis*, *Iberomesornis* and *Neuquenornis* (see below). Feduccia (1993) used the proportion of the hallux to support his view, but this is contradicted by his own Figs 4 and 6. And, using Feduccia's (1993) methodology, the theropod dinosaur *Oviraptor* clusters with tree-climbing birds (Norell *et al.*, 1995). Readers are referred to Peters & Görgner (1992) for a comprehensive conclusion to this issue.

In summary, the most thorough comparative studies fail to support arboreal or scansorial functions in *Archaeopteryx*, although that does not mean that it or other early birds could not get into a tree (Wellnhofer, 1994). It simply means that the evidence for these functions is weak, especially when it is considered that most non-avian theropods, even including large ones such as *Allosaurus* and *Tyrannosaurus*, which were obviously not arboreal, have highly curved manual claws and only slightly less curved pedal claws, with deep lateral grooves for the attachment of horny sheaths. The recent discovery of an excellent skeleton of the theropod *Oviraptor* (Norell *et al.* 1995: fig. 3) shows not only that the manual claws are highly curved, but that traces of the horny sheath made the claws much longer and more curved than the ungual phalanx suggests. Notwithstanding Feduccia's (1993) remark (p. 792) that trees would have provided suitable perches, and Bock's (e.g. 1986) scenario for the pre-adaptive advantages of an arboreal origin of bird flight, paleobotanical evidence fails to support the presence of large trees anywhere near the Solnhofen lagoons in which *Archaeopteryx* is preserved. Pollen tends to
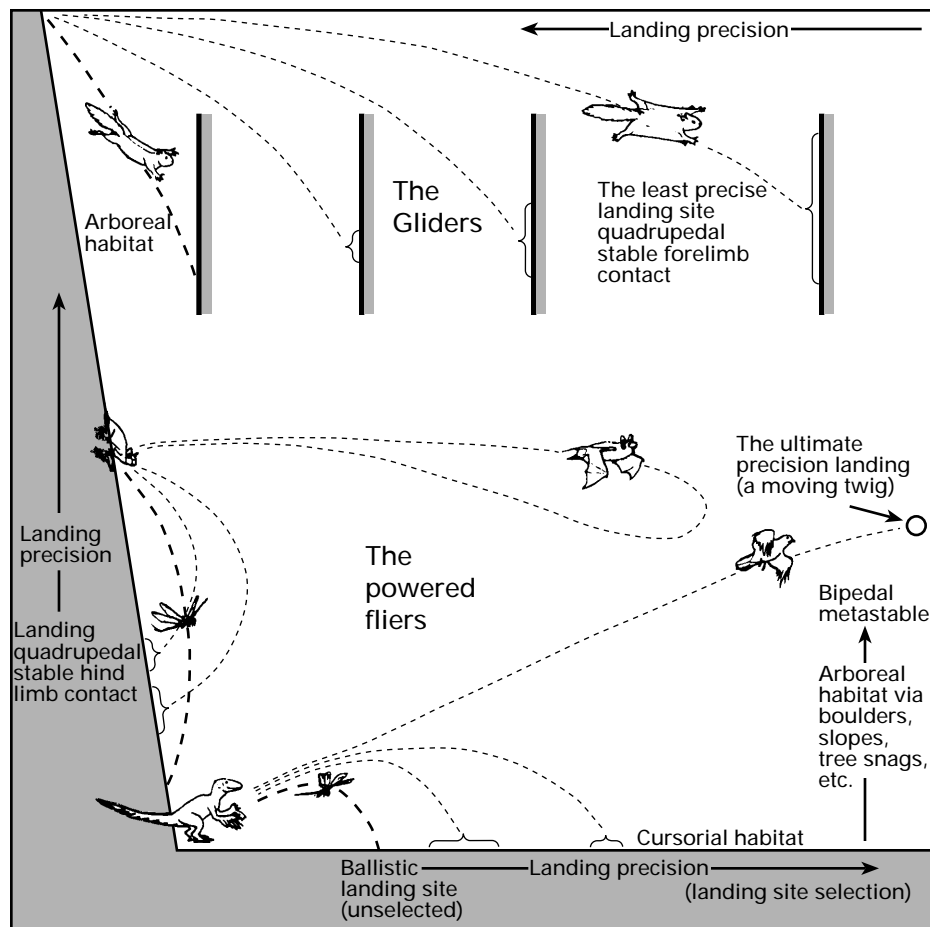
Fig. 9. Contrasting schematic of various models of flight evolution, from Caple *et al*. (1983). Gliders evolve a proximal airfoil, but not a distal one, like those of powered fliers. Bats have gliding features (and gliding relatives), but birds do not. Gliding is a relatively common adaptation, but only in bats can it confidently be said to have led to powered flight in an arboreal setting (Padian, 1985). This figure shows the difficulty of landing on a moving twig in mid-air, compared to landing on the ground from a low height. In a model of flight from the ground up, gliding is still important, but it is propelled mainly by running and jumping, including from low heights.

travel great distances and has broad geographic representation, but tree pollen is unrepresented in the Solnhofen palynoflora (de Buisonjé, 1985; Viohl, 1985). Barthels, Swinburne & Morris (1990) concluded that 'trees were either very rare or absent' and that these 'could never have grown to any substantial height (less than 3 m)'. Hence, the suggested tree-climbing and arboreal habits of *Archaeopteryx* receive only negative evidence from this quarter, as Peters & Görgner (1992) firmly concluded. Regardless of where flight may have evolved, *Archaeopteryx* evidently did not frequent trees.

The cursorial theory is based, first, on the functional-ecological inference that *Archaeopteryx* was a strong, agile biped, given the functional morphology of its skeleton; and secondly, from independent evidence, that birds originated from small, active, running predators. Ostrom, who had

traced the phylogenetic origins of birds to within small theropod dinosaurs, suggested (Ostrom, 1979) that feathers were co-opted for flight by functioning first as enlarged nets to trap insects that attempted to flee from the proto-birds. It has also been suggested that feathers may originally have evolved for thermoregulation (insulation or as heat shields: Regal, 1975, 1985) and (or) sexual display (Cowen & Lipps, 1982). Caple, Balda & Willis (1983; see also Balda, Caple & Willis, 1985) showed that a jumping bird that waved its long, feathered forelimbs after prey would lose its balance by throwing off its angular momentum. They suggested instead transferring the prey-catching function from the forelimbs to the teeth, and holding the arms laterally. Even a slightly increased airfoil surface (1 %) would increase both lift and stability, as long as it was at least three body radii away from the midline. This is especially
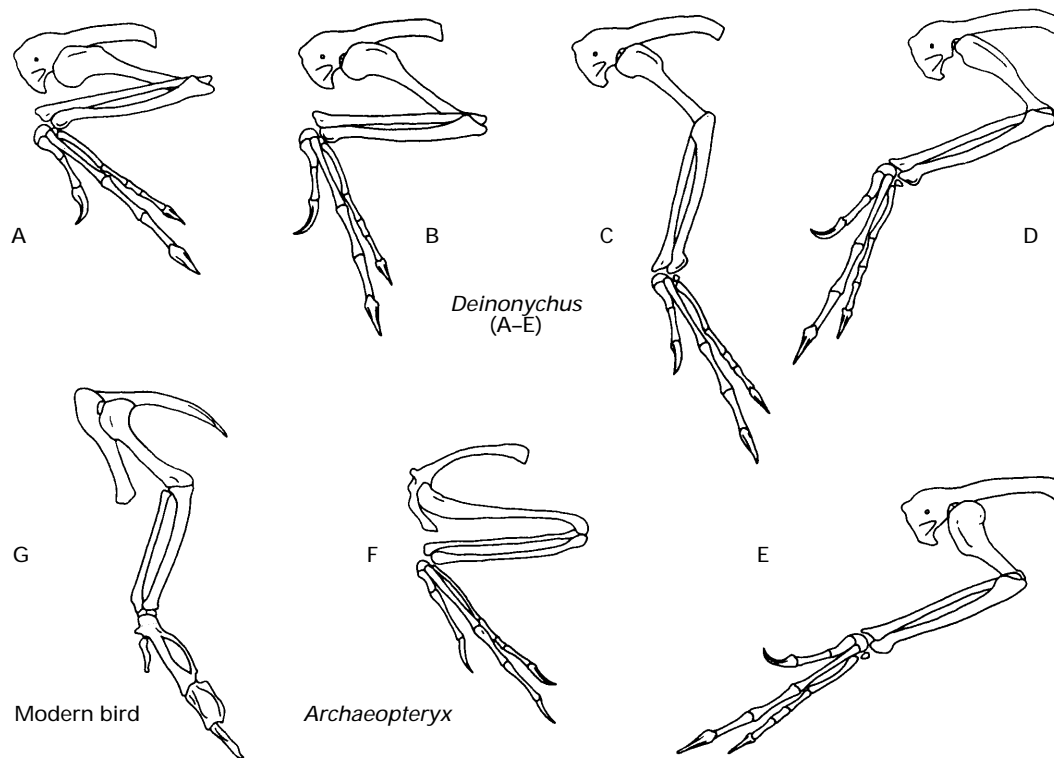
Fig. 10. The sideways-flexing predatory stroke of the dromaeosaurid theropod *Deinonychus* (A–E), showing its mechanical similarity to the flight stroke of birds (F, G). The left scapulocoracoid, humerus, forearm and hand are pictured. From Gauthier & Padian (1985). Lengths of humerus approximately 20 cm (*Deinonychus*), 4 cm (*Archaeopteryx*) and 6 cm (pigeon).

intriguing aerodynamically, because the outer part of the wing is where thrust is generated (Rayner, 1981, 1985a; Padian, 1985: the more proximal part of the wing mostly generates lift). They argued that more airfoil surface would increase lift and stability in a positive feedback situation. Ostrom (1986b) readily agreed. This brought the cursorial theory to the verge of flight: running, leaping and sustaining short, leg-powered glides after aerial prey or away from some predators (Fig. 9).

However, critics charged that this was a dead-end process, or at least very difficult to attain. Ulla Norberg (1985) noted the difficulties of drag and the need to work against gravity, rather than with it as a gliding animal would do. Rayner (1985a, b) showed that *ceteris paribus* it is biomechanically and energetically easier to evolve flight from a gliding stage, although he allowed that this was not evidence against a ground-up origin of flight. An element of concern was the ground speed needed to reach typical flight speeds of 6–7 m s^{-1}: below and above this speed, flight energetics are thought to be more taxing, at least in living birds, and the assumption is that flight would have taken the course of evolving at the least energetically expensive speed. Running

lizards are reported to reach nearly such speeds, but speeds for fossil animals are only guesses. However, both U. Norberg (1985) and Rayner (1985a, b) allowed that their models did not take into account the specific palaeobiology of small coelurosaurian dinosaurs *per se*; and Rayner (1985b) carefully pointed out that the most conspicuous omission of such models was 'the consideration of whether flapping could have accompanied the evolution of the wing – as in the arboreal model – rather than following it'. His preference for the arboreal model was based on doubt that selection could favour improvement of both locomotory systems (forelimb and hindlimb) at the same time. However, this objection may be unwarranted because the coelurosaurs were already rapid runners, and the forelimbs and hindlimbs were unconnected in locomotory function, so selection could have been expected to act completely independently. In fact, Gatesy & Dial (1996) point out that to originate flight, birds not only decoupled fore- and hindlimb locomotory systems (already accomplished in their dinosaurian ancestors), but also eventually decoupled the tail from obligatory co-functioning with the hindlimb as it does in other reptiles.
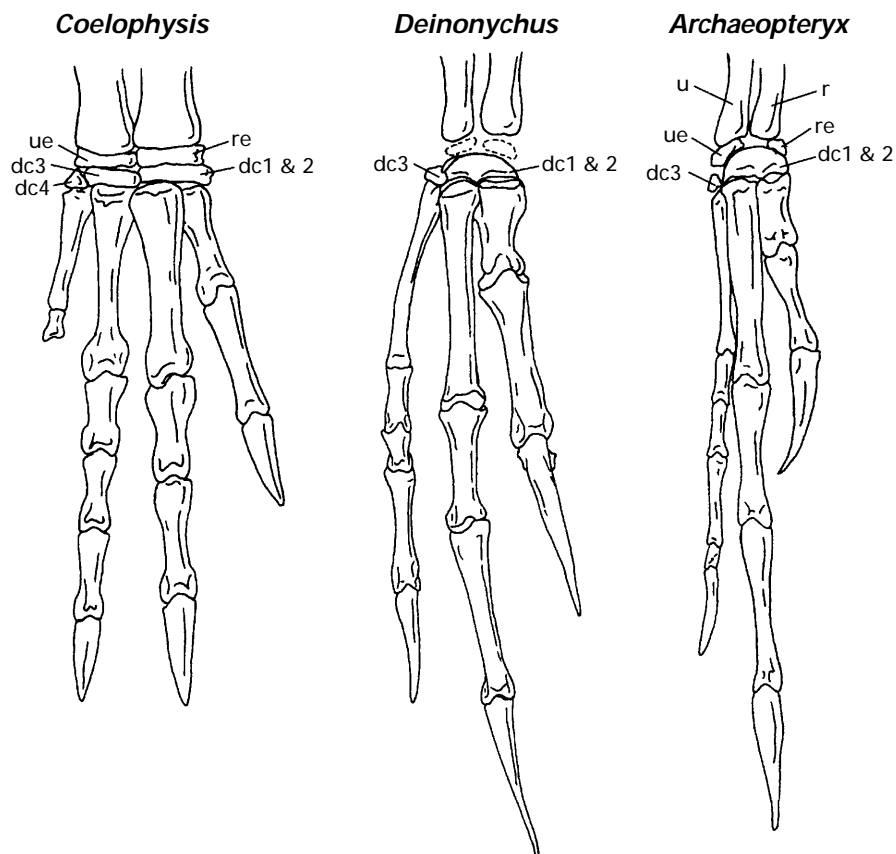
Fig. 11. The wrists of the theropod dinosaurs *Coelophysis*, *Deinonychus* and *Archaeopteryx*, to show the coalescence of distal carpals 1 and 2 into the semilunate carpal. From Currie & Padian (1997). Hand lengths approximately 10 cm (*Coelophysis*), 25 cm (*Deinonychus*), and 5 cm (*Archaeopteryx*). Abbreviations: *cd*, distal carpals (1–4); *re*, radial; *ue*, ulnare.

Running, leaping and gliding bring us only so far; at this point, any model must account for the evolution of the flight stroke, the primary feature of flight. Models for animal flight mechanics were classically based on aeroplanes, which separate the functions of lift (airfoil) and thrust (engines), and have quite different drag profiles from flying animals (e.g. Pennycuick, 1972). Rayner (1979) showed that when vertebrates flap they create a doughnut-shaped vortex wake that propels them forward and this model was confirmed by experimental evidence (Kokshaysky, 1979). This reinforced the central importance of the flight stroke in the evolution of flight. Gauthier & Padian (1985) showed that the immediate sister groups of birds, *Deinonychus* and the other dromaeosaurs, already had the sideways-flexing wrist joint that in birds is essential to the wingbeat and consequently contributes to the production of thrust; in these dinosaurs, however, it was a prey-seizing stroke (Fig. 10). The semilunate carpal covering the base of digits I and II in both groups (Fig. 11) allows this function (Ostrom, 1969),

which is not present in any other animals. This wrist configuration permits hingelike flexion and also a twisting about an axis inclined with respect to the dorsoventral axis (Ostrom, 1969). In tetanurine theropods (carnosaurs plus coelurosaurs, including birds), digits I and II are covered by a single distal carpal at their bases; the form of this carpal is semilunate in Maniraptoriformes, which includes birds, dromaeosaurs, troodontids, oviraptorids, and other forms (Holtz, 1996; see Fig. 3). The tetanurine condition represents a fusion or loss from the condition of two separate distal carpals overlapping metacarpals I and II in basal theropods and other reptiles. The maniraptoran condition is a further transformation of this single-carpal situation.

It would have taken only a slight adjustment of the angle of attack of this predatory stroke (principally an elevation and pronation of the forelimb) to create a suitable vortex wake. Gauthier & Padian (1985) suggested that by running, leaping and a few such strokes, extension of the time in the air, and eventually flight from the ground up, could have

evolved gradually. This scenario requires no features or steps not already known in fossil organisms. Taking advantage of any height or incline could extend this action usefully. Peters (1985) and Peters & Gutmann (1985) suggested a 'ridge-gliding' approach to the origin of flight incorporating some height and mediating between the extreme versions of arboreal and cursorial theories. Hence, it appears that a range of options was functionally and aerodynamically plausible. In these cases, phylogenetic analysis can help to test the plausibility of competing hypotheses (Padian, 1987). The ancestors of birds, according to this evidence, were ground-dwelling cursorial bipeds with no obvious scansorial or arboreal adaptations, and the wings of *Archaeopteryx* do not have the profile or aspect ratios seen in gliding tetrapods (Rayner, 1985*b*). The fully arboreal theory requires a protobird with scansorial adaptations, which the available paleontological and functional evidence has not yet provided.

Several lines of evidence appear to favour a somewhat modified version of the cursorial origin of bird flight (Peters & Gutmann, 1985). In this model, running leaps were aided initially by wings out-stretched for balance; these wings were particularly expanded at the distal ends for increased stability (Caple, Balda & Willis, 1983). The leaps were gradually extended by short flapping sequences that elaborated the down-and-forward motion already present in the sister groups of the first birds (Gauthier & Padian, 1985). This did not have to happen on level ground; running and leaping could have been enhanced by 'ridge-gliding' (Peters, 1985) or jumping from small heights (e.g. slight topographical ridges, fallen trees, etc.). This model, in contrast to the arboreal model, draws on the phylogenetic, functional, ecological and aerodynamic evidence explained above. We will never know all the details of this adaptive breakthrough, of course, and no hypothesis can be summarily excluded. However, if the aim is to work according to accepted scientific methods, then we advance this compromise model as best-supported methodologically. It is clearly time to move past the 'arboreal *versus* cursorial' dichotomy, because the polarized versions of these models have long outlasted their utility.

We recognize that for many colleagues this is not the most intuitive or superficially plausible solution, particularly if one only considers the evidence from living birds. After all, it would appear to be relatively easier to evolve flight through a gliding stage, as U. Norberg (1985) showed theoretically, and bats appear to have done just that (reviews in Padian,

1985, 1987). However, evolution does not always take the easiest path. The fully arboreal, all-out gliding model does not appear to be most consistent with the available evidence in the case of birds, and the orthodox cursorial model, although perhaps truer to the available evidence, still has profited from modification.

(2) Could *Archaeopteryx* flap or only glide?

The flight capabilities of *Archaeopteryx* itself have been considerably argued. Until the seventh specimen was discovered (Wellnhofer, 1993), no trace of a bony sternum was known, but the robust, boomerang-shaped furcula was known in the first-discovered (London) specimen since 1861. Wing aspect ratios and estimated wing loading, as well as the low angle of the shoulder joint and the apparent absence of a 'reverse-pulley' supracoracoideus tendon system in the shoulder, have all contributed to the consensus that *Archaeopteryx* was probably a weakly powered flier (see e.g. Ostrom, 1974, and papers and references in Hecht *et al.*, 1985). Two arguments have been especially influential in this issue. The first is the work of Maurice Sy, who in 1936 reported (in the course of a much larger functional-anatomical study) that a pigeon with a severed supracoracoideus tendon could not take-off from level ground. This fact has impressed proponents of the arboreal theory of avian flight (e.g. Olson & Feduccia, 1979; Tarsitano, 1985; Vazquez, 1994), who have concluded that because *Archaeopteryx* lacks clear evidence of a modern avian supracoracoideus system, it therefore could not have flown from the ground up. Sy (1936) also found that this pigeon could only maintain level flight with difficulty and could not land safely, but this fact is generally overlooked by arboreal proponents. In any case, the relevance of this argument is questionable, because experimental mutilation of living animals does not necessarily simulate an ancestral condition.

Parenthetically it should be noted that virtually all studies of the energetic requirements of flight that have ever been published have either assumed or concluded that high metabolic levels, commensurate with or extremely similar to those of living birds and mammals, were a prerequisite for active, flapping flight. Ruben (1991) challenged this, suggesting that if the earliest birds had reptilian muscle physiologies (which are capable of sustaining twice the power of avian or mammalian muscle for several minutes), this anaerobic muscle power would have been sufficient to sustain flight, and thus endothermy may

not have evolved until much later in the history of birds. Speakman (1993), however, countered that Ruben's (1991) model used unrealistically high levels of muscle output, and that both predicted and experimental evidence indicates that avian and typical reptilian muscles have similar power-generating capacities, so this argument seems to be falsified by the constraints of physiology. Speakman (1993) applied these calculations to *Archaeopteryx*, and concluded that its muscle mass and power were incapable of allowing it to take off from a stationary position on the ground. This affirms the conclusions of both the arboreal model (initial speed would have been generated from a leap) and the cursorial model (a running take-off, used by living ground birds with low pectoral muscle mass, would have provided initial speed), but does not help to decide between them.

However, these inferences are also problematic. Josephson (1993), among others, shows that muscle output depends more on body temperature than any other factor, including endothermy or ectothermy (and this applies equally to vertebrates and invertebrates, regardless, of size), which would appear to beg the question of the metabolic status of *Archaeopteryx*. Marden (1994) found, on the basis of scaling performance with size, that *Archaeopteryx* was probably capable of a ground-up take-off, with at least enough muscle burst power to carry it short distances – as most paleobiologists have traditionally inferred from its skeleton and plumage.

The second argument relevant to this issue is that the feather vanes of *Archaeopteryx* appear to be asymmetrical, which suggested to Feduccia & Tordoff (1979) that it was an active flier in as much as non-flying birds have symmetrical feathers. Speakman & Thomson (1994), however, in a valuable analysis of the feathers of birds from 78 families of flying, gliding and flightless birds, concluded that asymmetry frequently varied along an individual wing and along an individual feather shaft. Their data show that the feathers of *Archaeopteryx* are less asymmetrical than those of living flying and gliding birds, although they are commensurate with those of flightless birds (however, see also Å. Norberg, 1985; Rietschel, 1985; Stephan, 1985). Like the argument about the curvature of the claws, however, this will have little overall relevance to the question of *Archaeopteryx*'s flight ability unless it is assumed that fossil animals must look exactly like living animals if they are to perform the same functions. Clearly, more than one line of evidence is needed, because the fine-tuning of feather asym-

metry could presumably have occurred after the evolution of powered flight; to date, no argument has falsified this hypothesis (see Griffiths, 1996).

In a related argument, Vazquez (1992 *a*, *b*) argued that because the wrist of *Archaeopteryx* does not have all of the oesteological interlockings and fusions of the neornithine carpus, it would not have been able 'to keep the manus from hyperpronating while executing the downstroke with sufficient force to propel itself forward', and hence was not capable of powered flight (Fig. 12). This conclusion, which remains to be supported by energetic and aerodynamic evidence, appears to argue that adaptive structures must be perfected before organisms can use them. If that were true, humans could not swim and goats could not climb trees because they lack fins and prehensile digits, respectively. But organisms do not appear to evolve features suddenly and then decide how to use them.

Vasquez's (1992 *a*, *b*) default conclusion is that *Archaeopteryx* must have been a glider, or at best an extremely feeble flier, but this assumes that gliding is a necessary way-station to powered flight, a disputed assumption (Padian, 1985). Other work (e.g. Yalden, 1971; Rayner, 1985 *b*) has shown that the wing planform and wing loading of *Archaeopteryx* are just as inconsistent with those of living gliders as the feather vane asymmetry appears to be with today's fliers. So there is no positive justification for considering *Archaeopteryx* a glider.

Still, Vazquez (1992 *a*, *b*) and others have found good reason to doubt that *Archaeopteryx* had 'perfected' flight to the degree that extant birds (and even Early Cretaceous birds) have (but see Rietschel, 1985). The glenoid fossa in *Archaeopteryx* seems to be oriented in a somewhat intermediate position between those of non-avian theropod relatives and later birds (Jenkins, 1993), and the girdle lacks a prominent acrocoracoid process and a foramen triosseum, suggesting that the 'reverse pulley' mechanism of the m. supracoracoideus was not effective in contributing to the upstroke (Ostrom, 1976 *a*). This argues both for lower flapping amplitude and poorer flight control. Now that the sternum is known (Wellnhofer, 1993), perhaps arguments about the insufficiency of the m. pectoralis muscle power will be somewhat dampened; on the other hand, the sternum is quite short as Wellnhofer (1993) was able to reconstruct the available material, although it is not clear that this sternum is completely preserved nor ontogenetically fully calcified. Because (1) its wing planform and size are commensurate with those of at least some (weakly
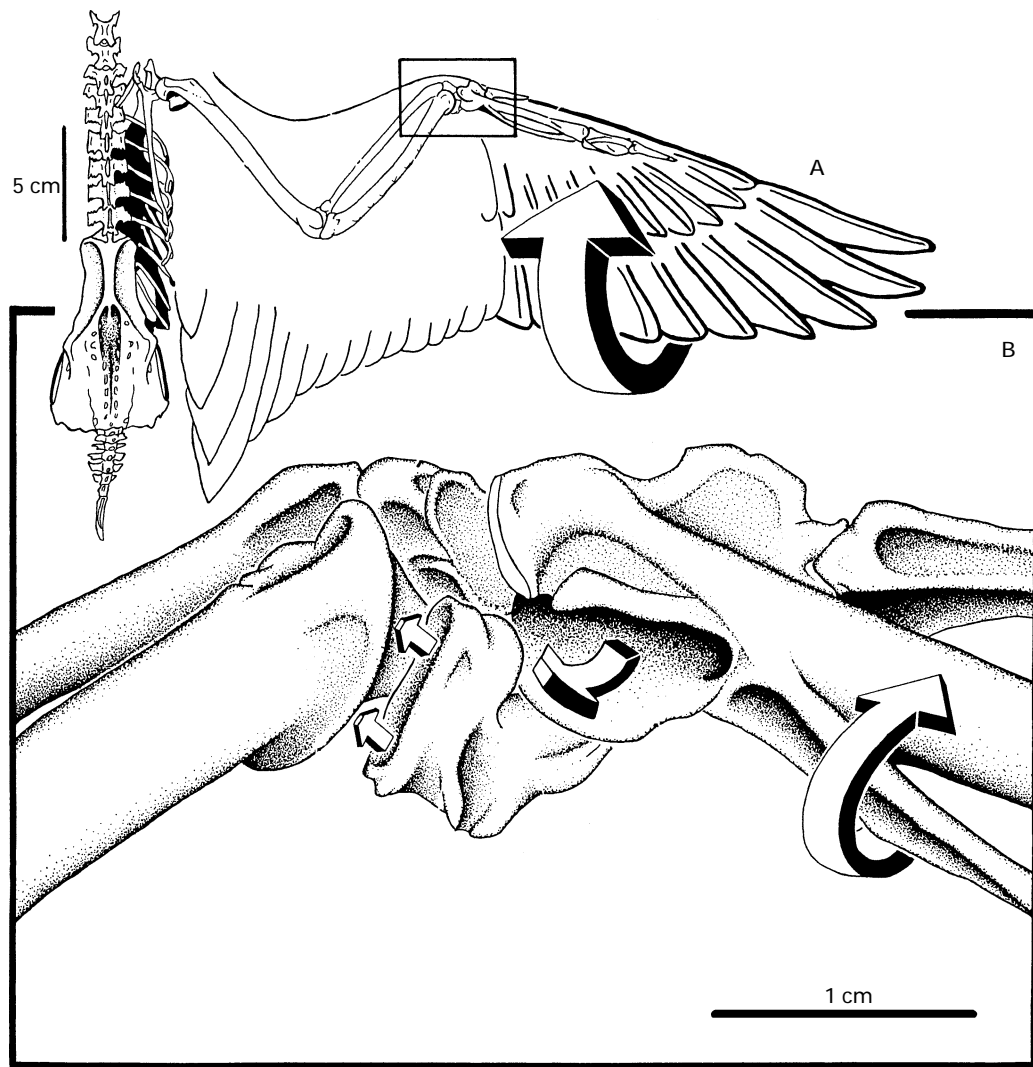
Fig. 12. Flexion of the bird wrist in flight, from Vazquez (1992*a*). For the duck *Anas platyrhynchos* (A), a slightly exploded view of the wrist area (B) shows how the configuration of the wrist bones tends to cause the outer wing (distal to the wrist joint) to hyperpronate during the flight stroke (movements are shown by arrows).

flying) birds, (2) its flight feathers are well developed, (3) the sternum was *prima facie* a strong site of origin for flight muscles, and (4) its aerodynamic planform is dissimilar to those of mere gliders (Padian, 1985), we think it most reasonable to conclude that *Archaeopteryx* was not simply a glider, but could glide as most birds do (although perhaps not as well), and that it was primarily a flapper, although not a strong flapper. It is possible to read too much into this animal in reconstructing the origin of bird flight, as Bock (1986) and Feduccia (1980) have argued.

We stress, however, that the question of the origin of birds, which is strictly a phylogenetic one, must be separated logically from that of the origin of flight, a far more complex problem. Regardless of the ecological milieu in which flight began, or the

functional steps in its evolution, the evidence is clearly that *Archaeopteryx* evolved from (and is a member of) the coelurosaurian theropods. Hence, one cannot strictly link the 'theropod hypothesis' of bird origin to the 'cursorial' origin of flight theory, nor the 'crocodile' or 'thecodont hypothesis' with the 'arboreal' or 'gliding' flight theory, as some arguments have put it. Simply because *Archaeopteryx* was probably not a strong flapper does not mean that it must have been a glider. There are not 'palaeontological' and 'ornithological' views of these questions (*contra* Feduccia, 1996). There is simply the question of whether to use the methods of comparative biology. If one does, then it requires formulating alternate functional-ecological hypotheses on the grounds of the structural evidence, and

then testing these against the most likely phylogenetic patterns in order to arrive at the most robust scenarios (Padian, 1982, 1987; Coddington, 1988).

(3) Flight improvements after *Archaeopteryx*

Phylogenetic analysis has established that many characteristics associated with the origin of flight were already present in theropod dinosaurs before birds (i.e. *Archaeopteryx*) evolved. These include the coalesced scapulocoracoid, the straplike scapula, the coracoid contacting the sternum (which is calcified in various forms), and the furcula; the forelimb that is 75 % of the hindlimb in length, and has a hand at least half as long as the rest of the arm. It now appears clear that feathers evolved in non-avian coelurosaurs, animals whose forelimbs were too short to bear functional wings (Ji & Ji, 1996, 1997).

Archaeopteryx has a forelimb longer than the hindlimb and a full complement of flight feathers on the wings, as well as long tail feathers. As noted above, it is almost universally regarded as an active flier, although perhaps not a very powerful one capable of sustained flights. It is presumed, therefore, to have had a fully evolved flight stroke capable of generating thrust as well as lift.

The discovery of an alula in the small enantiornithine *Eoalulavis*, from the Early Cretaceous Las Hoyas deposits of Spain (Sanz *et al.*, 1996; Padian, 1996), showed that early in bird history the wing mechanism evolved that allowed them to fly at lower speeds and to manoeuvre much as their living relatives do. *Noguernornis*, from the lowest Cretaceous of Spain, has even longer forearms and interlocking hand bones to facilitate flight. *Iberomesornis* (which, like *Eoalulavis*, comes from Las Hoyas, only slightly younger than *Noguernornis*) has a strutlike coracoid clearly braced to the sternum, a tail reduced to a series of free vertebrae and a pygostyle (the fused bony component of the 'Parson's nose'), and a foot with recurved claws and a fully descended hallux (first toe) that clearly show its perching abilities. This is important because before the new fossil bird discoveries of the past fifteen years (beginning with *Sinornis*, from the Early Cretaceous of China), there was very little convincing evidence that birds had arboreal habits much before the early Tertiary (60 million years ago); now they can be established at twice that age (Padian, 1996). The pygostyle is also preserved in the Early Cretaceous Chinese bird *Confuciusornis* (Hou *et al.*, 1996), which is closer to Enantiornithes and later birds than is *Archaeopteryx*.

Such features as the increased calcification and strutlike support of the shoulder girdle, the elongation of the forelimbs, and the fusion of carpometacarpal elements appeared at about the same time as the evolution of hindlimb features related to living in trees, such as enlarged, recurved claws and a fully opposable hallux (Chiappe, 1995a; see *Iberomesornis*).

IV. THE CRETACEOUS AVIAN RADIATION

(1) After *Archaeopteryx*, the deluge?

Mononykus (first called *Mononychus*, a name preoccupied by a beetle; see Perle *et al.*, 1993b) has been an object of controversy since its discovery. It is the most recent dramatic find, and is also the most basal in position on the avian family tree after *Archaeopteryx*, according to its discoverers (Perle *et al.*, 1993a, 1994; Chiappe, 1995a). It is best known from the continental Late Cretaceous of Mongolia (Nemegt, Djadokhta, and Barun Goyot formations), but close relatives have now been reported from the Late Cretaceous of Patagonia (Chiappe, 1995a, c). An unrecognized specimen was collected by a party from the American Museum of Natural History (AMNH) in the 1920s (Norell, Chiappe & Clark, 1993); the holotype was found by a Mongolian expedition in 1987; and the referred Mongolian specimens come from the Mongolian-AMNH expeditions of 1992–1995. Most of the skeletal parts are preserved, including recently found complete skulls; its size range varies up to a femoral length of approximately 14 cm, although Argentine relatives were larger.

Mononykus (Fig. 13) has a skull with very tiny teeth, an elongated neck, long hindlimbs, and very short and unusual forelimbs. Some features suggest that it is closer to neornithine birds than is *Archaeopteryx*: these include a rectangular, keeled sternum, a carpometacarpus, and a pelvis with a prominent antitrochanter and with an ischium close to the length of the pubis (Perle *et al.*, 1993a, 1994). The phylogenetic position of *Mononykus* is also supported by the presence of several characters diagnostic of Aves. These characters are concentrated in the braincase, the teeth and the tail (Chiappe, Norell & Clark, 1996). The orbit and the lower temporal fenestra are connected; the jugal lacks the dorsal bar that articulates with the postorbital. The quadratojugal is not sutured to the quadrate, but is shaped like a tiny fork that was presumably connected to it by ligaments. The
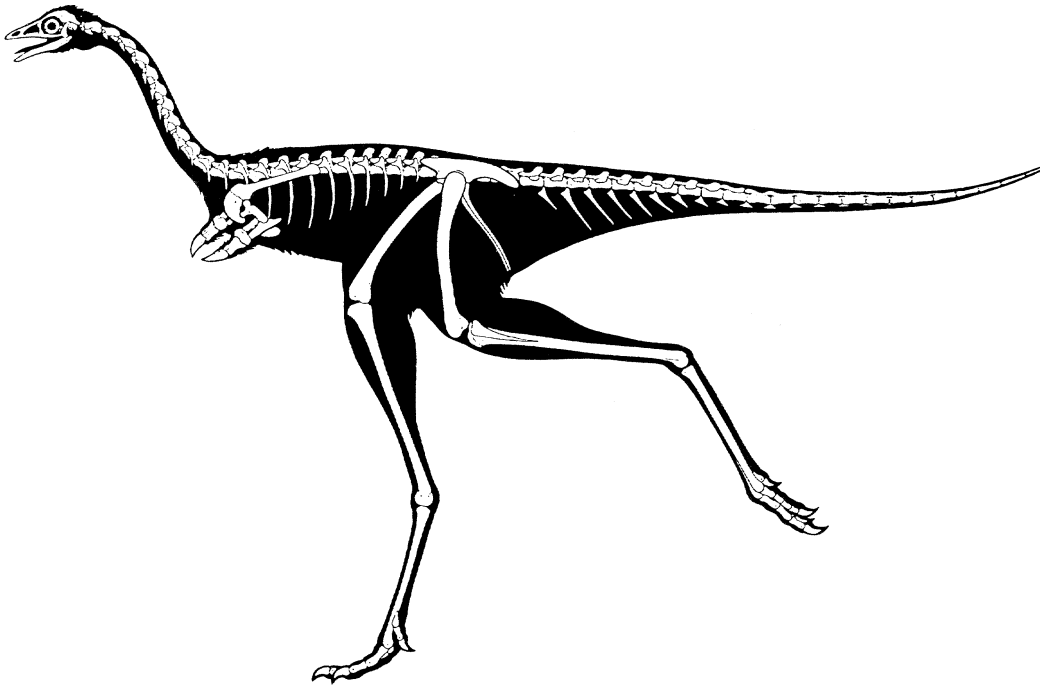
Fig. 13. Restoration of the skeleton of the basal avian *Mononykus*, from Perle *et al*. (1993*a*, 1994). Femoral length approximately 14 cm.

squamosal and quadratojugal do not contact each other. These features are all absent in non-avian theropods. But in the post-cranium, some features are less like those of more derived birds. The sternum in *Mononykus* is unlike those of more advanced birds in that it is triangular in cross-section instead of T-shaped. The forelimb is extremely short but robust and with well-developed processes. The humerus is short, with a bizarre, pillar-like deltopectoral crest and only one distal condyle. The ulna has an olecranon process that is as long as the shaft, and the radius was proximally ankylosed to the ulna to form a single cotyla for the humeral condyle. The carpometacarpus is fused into a block, with metacarpals II and III very reduced; digits II and III must have been very tiny, and the two phalanges of digit I are robust, with a flattened claw. The coracoid is interpreted to be secondarily deep and wide, more like a throwback to the situation in more basal coelurosaurian theropods. There is an unusual biconvex vertebra in the posterior dorsum. The pubis is deflected posteriorly more than in *Archaeopteryx*, but less than in neornithine birds, and it lacks a public foot.

Where does *Mononykus* fit in the avian tree, and what does it tell us? A comprehensive cladistic analysis of dromaeosaurid theropods and birds places *Mononykus* as the sister-taxon of all birds other than *Archaeopteryx* (Chiappe, 1995*a*, Chiappe *et al*., 1996),

the hypothesis originally proposed by Perle *et al*. (1993*a*). This hypothesis has been variously criticized (Feduccia, 1994; Ostrom, 1994; Wellnhofer, 1994; Martin & Rinaldi, 1994; Kurochkin, 1995*a*; Zhou, 1995*a*), but these criticisms are mostly based on assumptions about evolutionary processes regarding the gain and loss of flight and other functions, and not on phylogenetic analyses of the anatomical data, the only direct evidence of evolutionary history (Chiappe, 1995*a*; Chiappe *et al*., 1996; Chiappe, Norell & Clark, 1997). Critics to date have not proposed an alternative specific cladistic hypothesis of relationships, which is necessary to falsify any other phylogenetic hypothesis, and prerequisite to test any hypotheses about evolutionary process. As we emphasized previously, our approach is that of phylogenetic systematics. In this context, the hypothesis of the position of *Mononykus* within Aves might be overthrown with further data (more characters of taxa), but today it is the one that explains *the available evidence* – not speculation about what should or should not have happened in early avian evolution – in the most parsimonious way.

We feel that it is important to examine the discomfort that some scientists have expressed with the placement of *Mononykus* closer to neornithine birds than is *Archaeopteryx*. It is obvious to everyone that, by any superficial examination, *Mononykus* is very unusual, especially in its forelimb; in particular,
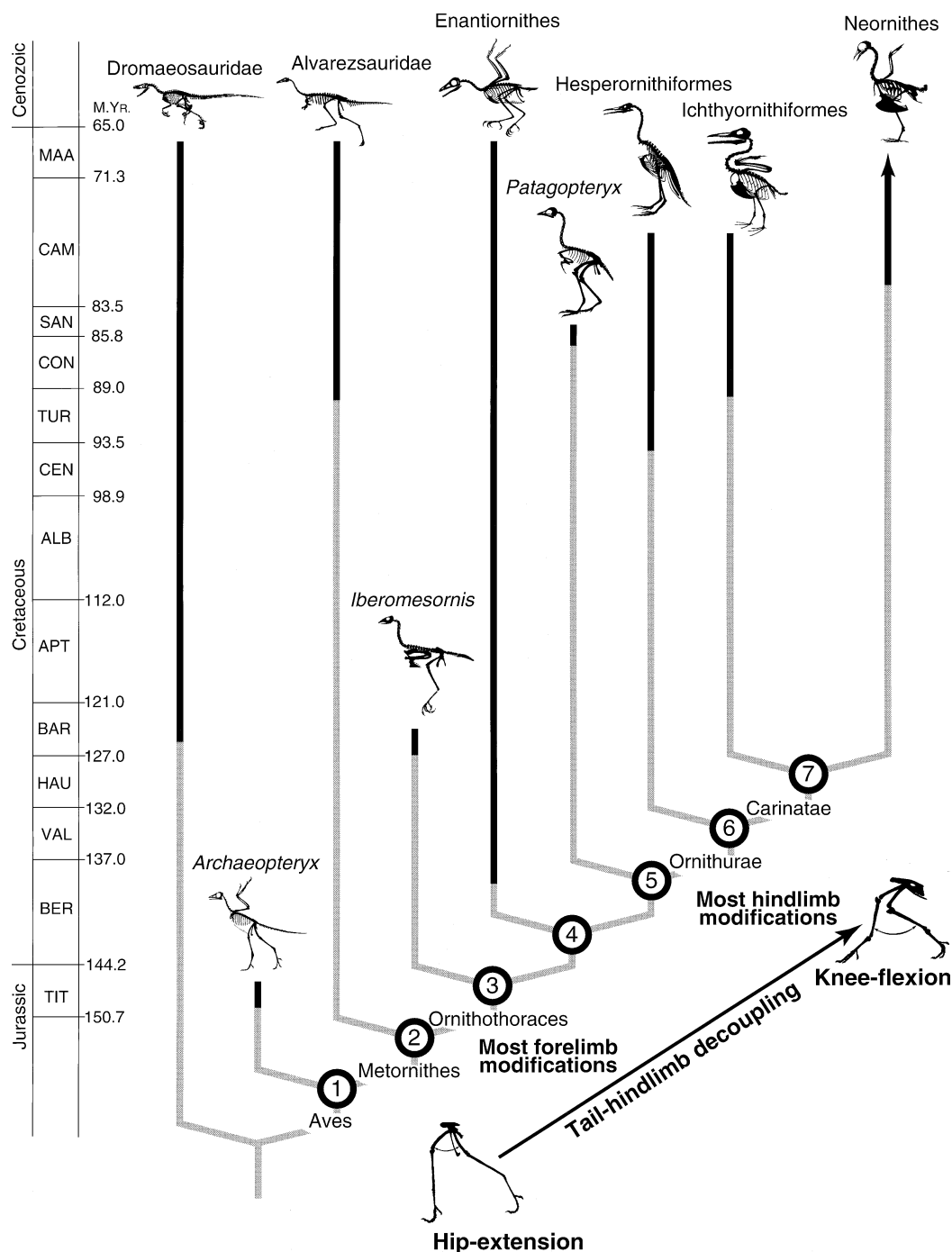
Fig. 14. Detailed cladogram of basal avian taxa described in the text, with stratigraphic ranges. In the evolution of these avian clades, hip-extension gave way to knee-flexion as a principal mechanism of hindlimb locomotion, as the function of the tail in locomotion became dissociated from the hindlimb and associated with the tail. The hindlimb changes mostly followed those of the forelimb related to flight. Modified from Chiappe (1995a) in which nodes 1–7 are explained in detail.

it certainly has nothing like a flying wing. How then can it be a bird? This is the first problem to address. The second follows from the first: why would its ancestors, so early in the history of birds, have left off flying (if they ever did fly) and taken up whatever functions its strange forelimb had?

First, *Mononykus* certainly has a strange forelimb, but the rest of its known skeleton is not so dissimilar to the homologous elements in *Archaeopteryx* and other early birds. However, the autapomorphies (uniquely derived features) of *Mononykus* that make it dissimilar to 'typical' birds (even those of its time)
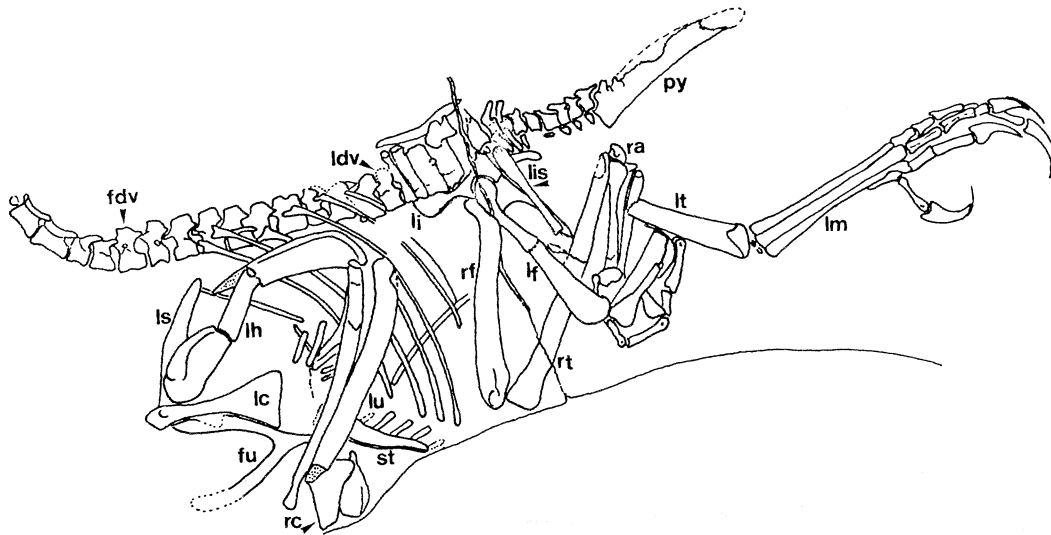
Fig. 15. *Iberomesornis*, from the Early Cretaceous of Spain. Courtesy of J. L. Sanz.

are not the issue here. Bats, whales and humans are hardly 'typical' mammals; the unique features of each allow us to recognize their individuality, while the features they share in common allow us to recognize them as mammals. The issue with *Mononykus* is group membership, which can only be established by phylogenetic analysis of the available characters and taxa. As the anatomy of these animals, and as other new Mesozoic birds, become better known, it may eventuate that the placement of *Mononykus* immediately inside or outside *Archaeopteryx* with respect to other birds will shift slightly. But *Mononykus* will almost certainly not turn out to be an ornithomimid, an oviraptorid, or a tyrannosaurid because, despite its uniquely bizarre features, its less bizarre features show clearly that it belongs at the base of Aves and that it lacks the synapomorphies of the other theropod subgroups. It is also important to remember that, as weird as *Mononykus* seems, it is of Late Cretaceous age, and the split of its lineage from that of *Archaeopteryx* and the other birds must have taken place by the Late Jurassic or earliest Cretaceous. We predict that, as earlier and more basal relatives of *Mononykus* with the Alvarezsauridae become known, less derived characters will be found in this lineage and its basal members will not seem to strange.

A second problem for critics is functional. This animal did not fly and was evidently not arboreal. Did it descend from flying ancestors? The skeleton provides virtually no evidence; it is too transformed to tell. Perle *et al.* (1993*a*) proposed that flight could have arisen twice in birds (once in *Archaeopteryx*, and once in birds after *Mononykus*), or *Mononykus* may simply have lost flight. To assess this question

requires other lines of evidence beyond cladistic analysis for approaching questions of evolutionary process. Looking at *Mononykus* alone tells us nothing about whether its ancestors could fly. Until less derived members of the *Mononykus* clade are known (and/or other taxa, perhaps even more primitive than *Mononykus* and/or *Archaeopteryx*), it will be impossible to assess whether the group ever possessed any characters of the shoulder and forelimb related to flight. Once such animals are known, biomechanical studies may help elucidate questions about flight performance and evolution.

Other early birds are less strange than *Mononykus*; discovered mostly in the last decade, they are providing a much more complete picture of the early evolution of birds and the transformations of characters that lead to fully 'modern' avian features. The next branch of the cladogram (Fig. 14) after *Mononykus* and the Alvarezsauridae is *Iberomesornis* (Sanz *et al.*, 1988; Sanz & Bonaparte, 1992), from the lacustrine Early Cretaceous (Barremian) deposits of Las Hoyas, central Spain (Fig. 15). The sparrow-sized *Iberomesornis* has an ossified sternum, robust coracoids, a pygostyle following eight caudals, and a U-shaped furcula with hypocleideum. The cervical neural spines are low, there are 11 dorsal vertebrae, and the foot claws are large. No evidence of ventral ribs or gastralia has been found. In contrast to the structural advancement of the forelimbs and girdle and the reduced tail, the pelvis and hindlimb do not seem to be much advanced beyond the *Archaeopteryx* stage, perhaps an indication of the selective pressure for powered flight (Chiappe, 1991*a*, 1995*b*). The foot claws in *Iberomesornis* are more curved than in *Archaeopteryx* and non-avian theropods, and the

Fig. 16. Enantiornithine hindlimbs from the Cretaceous: holotype specimens of *Soroavisaurus australis* (A), *Lectavis bretincola* (B), and *Yungavolucris brevipedalis* (C), in anterior (cranial) view. Scale bar = 1 cm.

hallux is proportionally longer and more distally located. They provide at least circumstantial evidence that these birds had arboreal habits. Sereno & Rao (1992) claimed this distinction for *Sinornis*, but (as we note below; see also Kurochkin, 1995*a*) it now turns out that this bird is more likely an enantiornithine; hence, arboreal habits evolved at an even more basal phylogenetic level in birds.

As basal in the phylogenetic diagram as *Ibero-mesornis* is the older, and slightly larger, *Noguerornis* (Lacasa Ruiz, 1989*a*, *b*) from the Late Berriasian or Early Valanginian (the first two stages of the Cretaceous) lake deposits of Montsec, northern Spain. This taxon is known only from a slab containing feathered forelimbs and other remains. Not much can be told about *Noguerornis* because preservation is poor, but it has a robust furcula with a pronounced hypocleideum, and a fused carpometacarpus. Most importantly, *Noguerornis* provides what appears to be the oldest evidence of an avian propatagium (Lacasa Ruiz, 1989*a*). As noted above, an alula has now been reported in the Early Cretaceous bird *Eoalulavis* (Sanz *et al.*, 1996), which suggests that more refined powers of low-speed flight
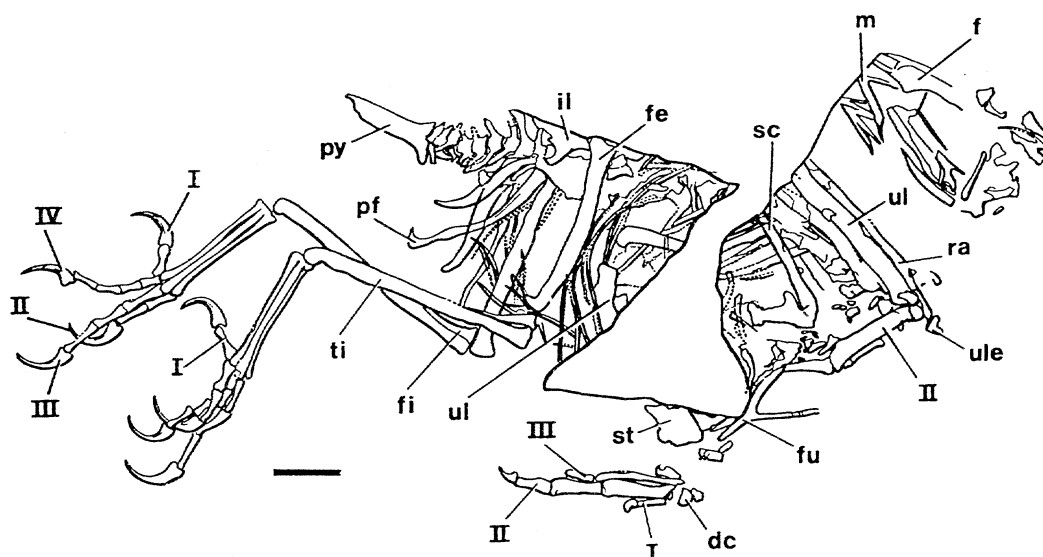
Fig. 17. Reconstruction of *Sinornis*, an enantiornithine bird from the Early Cretaceous of China (from Sereno & Rao, 1992). Scale bar = 1 cm.

and manoeuvrability had clearly evolved by this time.

(2) Enantiornithes – the unsuspected diversity

The most diverse group of early birds, and the most widely distributed (temporally and geographically), is the Enantiornithes (Fig. 16). Given this diversity and distribution, it is particularly surprising that this group was not even recognized until 1981, although a few taxa described earlier were later referred to it. C. A. Walker (1981) first recognized the group, and gave it its name ('opposite birds') based on fragmentary material from Argentina, including strange tarsometatarsi and what appeared to be an 'opposite' articulation between scapula and coracoid (but see Chiappe, 1995c). Today, the Enantiornithes includes approximately 15 taxa from the very Early Cretaceous to the end of this period, known from all continents except Antarctica (see Chiappe, 1992, 1993, 1995a, c, 1996; Kurochkin, 1995a; Elzanowski, 1995). Early Cretaceous members of this group include the superb specimens of the Spanish *Concornis* (Sanz & Buscalioni, 1992; Sanz *et al.*, 1995), the Chinese *Cathayornis* (Zhou, Jin & Zhang, 1992) and *Boluochia* (Zhou, 1995b), and the Australian *Nanantius* (Molnar, 1986), known only from tibiotarsi, as well as the newly discovered *Eoalulavis*, mentioned above. Among the Late Cretaceous enantiornithines are the Argentine *Enantiornis*, *Lectavis*, *Yungavolucris*, *Soroavisaurus* and *Neu-*

quenornis (Walker, 1981; Chiappe, 1993, 1995c; Chiappe & Calvo, 1994), the Mongolian *Gobipteryx* (Elzanowski, 1977; Martin, 1983a), the Mexican *Alexornis* (Brodkorb, 1976; Martin, 1983a), and *Avisaurus* from the United States (Brett-Surman & Paul, 1985; Varricchio & Chiappe, 1995), originally regarded as a nonavian theropod. Other Chinese Early Cretaceous taxa are putative enantiornithines. These include *Otogornis* (Hou, 1994) and *Sinornis* (Sereno & Rao, 1992) (see below; additional review in Kurochkin, 1995a; Elzanowski, 1995).

The anatomy of the Enantiornithes is highly variable (Chiappe, 1996). The skull is best known in *Cathayornis* (Zhou *et al.*, 1992). This taxon has teeth, although in later forms such as *Gobipteryx* the teeth are absent. As in *Archaeopteryx*, *Mononykus* and all other toothed birds, the enantiornithine teeth are unserrated and have constricted bases (Chiappe, 1996). Enantiornithine birds had heterocoelic cervical vertebrae, amphicoelous postcervicals and a pygostyle. The coracoid is a strutlike, elongated bone that articulates with a straight-bladed scapula by means of a dual joint articulation (the original one of birds plus a secondary ligamentous association: *contra* Walker, 1981; see Chiappe, 1995c). The sternum has a large keel and a U-shaped furcula (the interclavicular angle is approximately 60° in *Concornis*; see Sanz *et al.*, 1995). In contrast to many other Mesozoic birds (e.g. *Archaeopteryx*, Hesperornithiformes, Ichthyornithiformes), the Enantiornithes have been mostly recovered from continental, non-marine deposits. Many of these birds (e.g. *Cathayornis*,
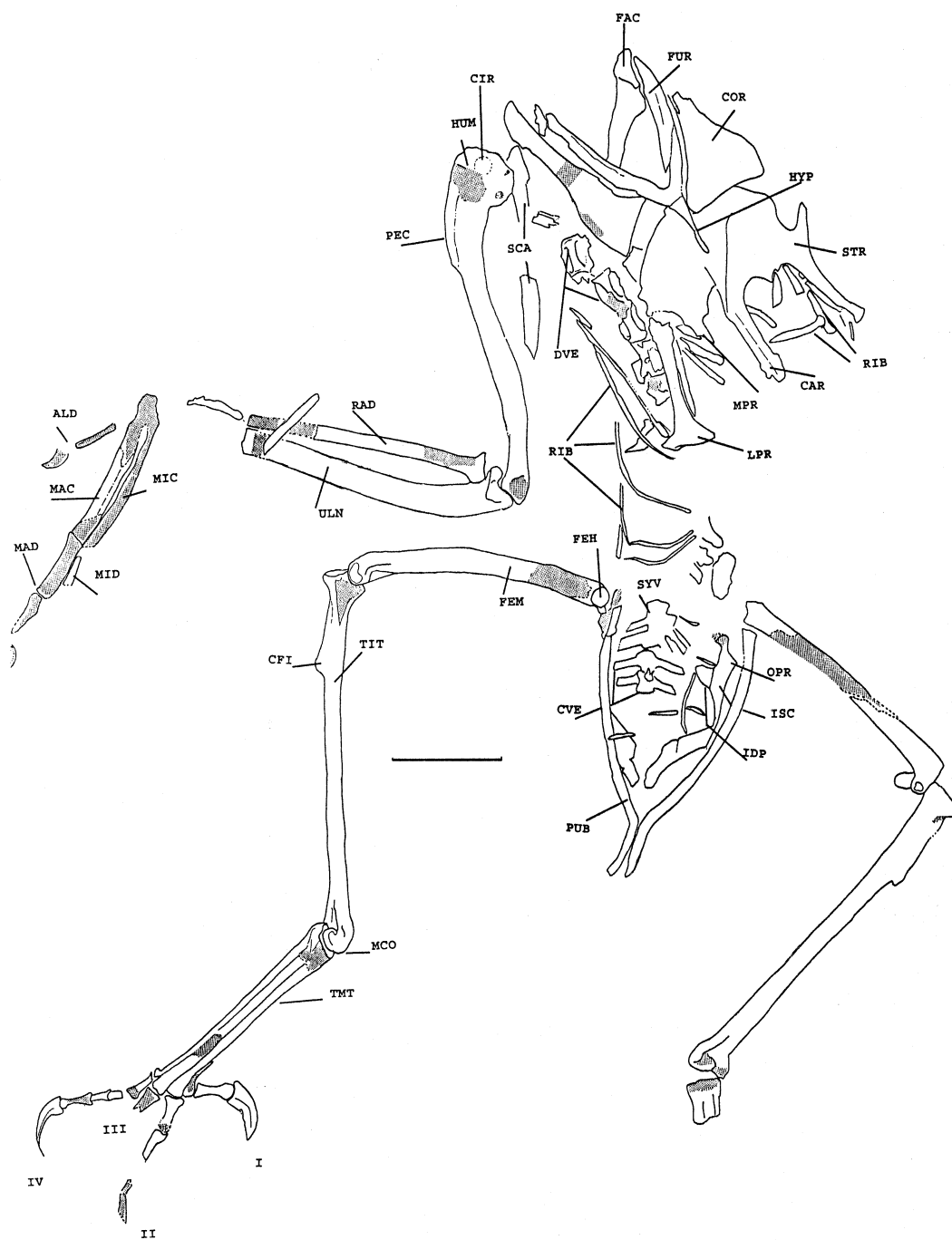
Fig. 18. *Concornis*, an enantiornithine bird from the Early Cretaceous of Argentina. Courtesy of J. L. Sanz.

Concornis, *Neuquenornis*) have a grasping, perching foot, which suggests that they were to some extent arboreal (Chiappe, 1995*a*). Other enantiornithines, however, had different lifestyles. The elongate tibiotarsus and tarsometatarsus of *Lectavis* suggest wading habits, while the asymmetry of the pes of *Yungavolucris* might account for a more aquatic existence (Chiappe, 1995*c*), using some living birds as analogues. Furthermore, the discoveries of em-

bryos referred to *Gobipteryx* (Elzanowski, 1981) and of numerous *in situ* eggs of identical morphology in the Late Cretaceous rocks of Mongolia indicate that at least some enantiornithines laid their eggs in ground nests (Chiappe, 1995*c*). Most enantiornithines were the size of small to medium-sized passerines, but some (e.g. *Enantiornis*) were much larger, reaching at least 1 m in wing span.

Sinornis (Fig. 17; Sereno & Rao, 1992), from the

Jiufotang Formation (Early Cretaceous) of China, was originally regarded as the most basal bird other than *Archaeopteryx*. The stratigraphic age was originally designated as Valangian (the second stage of the Cretaceous), but if the dates relating to *Confuciusornis* (discussed above) are revised, then *Sinornis* may be considerably younger than originally thought. This bird retains many primitive features, although it is not certain whether some are ontogenetic. The lack of fusion of many bones to other bones bespeaks primitive (or ontogenetically early) avian features, but this is not uncommon in basal birds, and some features are more derived than in *Archaeopteryx*. The tail is short, with only eight free vertebrae, and a pygostyle is present. The first toe seems fully reversed and might have been opposable for perching (but see Peters & Görgner, 1992). The foot claws appear to be slender and sharply recurved, commensurate with those of perching birds. Characters justifying the sister-group relationship of *Sinornis* to all birds other than *Archaeopteryx*, proposed by Sereno & Rao (1992), have not yet been published in detail, but would now probably be modified, because since its initial description enantiornithines have become much better known, and *Sinornis* shows some features characteristic of enantiornithine birds (Chiappe 1995*a*; Kurochkin 1995*a*: p. 50).

Some members of the Enantiornithes, including its eponymous genus, were first thought to have had limited flying capabilities (Walker, 1981), but the morphological evidence of the best-known specimens does not support this (Chiappe, 1992). Walker's (1981) inference was based on the fact that the sternum is deeply notched, as in some non-flying or poorly flying birds such as tinamous and galliforms. However, some birds with notched sterna, such as the Galbulidae, are good fliers (see Chiappe & Calvo, 1994, p. 242), and undoubtedly, enantiornithines such as *Concornis* (Fig. 18). *Cathayornis*, *Sinornis* and *Neuquenornis* (Fig. 19) were capable fliers. In fact, the post-*Archaeopteryx* birds discussed so far provide crucial evidence that at least soon after their evolution from non-avian theropods, birds seem to have been able to perch in trees, as their enlarged, more curved foot claws and their longer, more distally placed, and strongly reversed hallux appear to indicate. Before the discoveries of these forms, there was no clear evidence of perching or arboreal habits until the Tertiary, because of the best-known later Cretaceous forms, *Hesperornis* and *Ichthyornis*, clearly show no such adaptations and, as discussed above, the evidence for arboreal habits in *Archaeopteryx* is at best questionable (Padian, 1985, 1987).
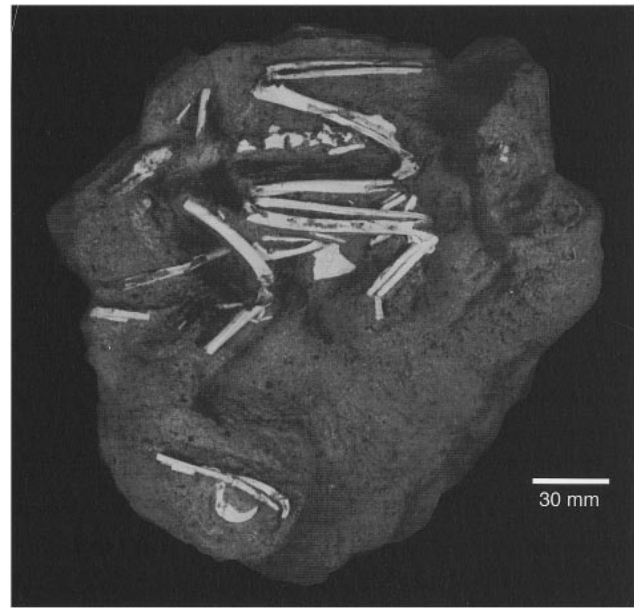

Fig. 19. Holotype of *Neuquenornis*, an enantiornithine bird from the Late Cretaceous of northwestern Patagonia (Chiappe & Calvo, 1994).

The discoveries of the past fifteen years have shown that most of the known Mesozoic avian diversity can be clustered within the Enantiornithes. This clade documents a major radiation of basal birds over the 80 million years of the Cretaceous. Since its recognition in 1981, most authors have acknowledged its primitiveness with respect to other Mesozoic birds such as hesperornithiforms and ichthyornithiforms, although several specific hypotheses of relationships have been proposed (see Chiappe, 1995*b*; Kurochkin, 1995*a*). We regard the Enantiornithes as the sister-group of the clade formed by *Patagopteryx* and Ornithurae (see Chiappe & Calvo, 1994; Chiappe, 1995*a, b*). We are still far, however, from clarifying the phylogenetic relationships among the many enantiornithine species, and only partial results have been published (Chiappe, 1993; Varricchio & Chiappe, 1995).

(3) *Patagopteryx*

Another basal avian is the Late Cretaceous (Coniacian-Santonian) *Patagopteryx* (Fig. 20) from northwestern Patagonia (Alvarenga & Bonaparte, 1992). This bird was chicken-sized, flightless and cursorial, with robust hind limbs and reduced wings (humerus 65 % of femoral length; Chiappe, 1996). *Patagopteryx* was originally referred to the ratites (Alvarenga & Bonaparte, 1992), but as Chiappe
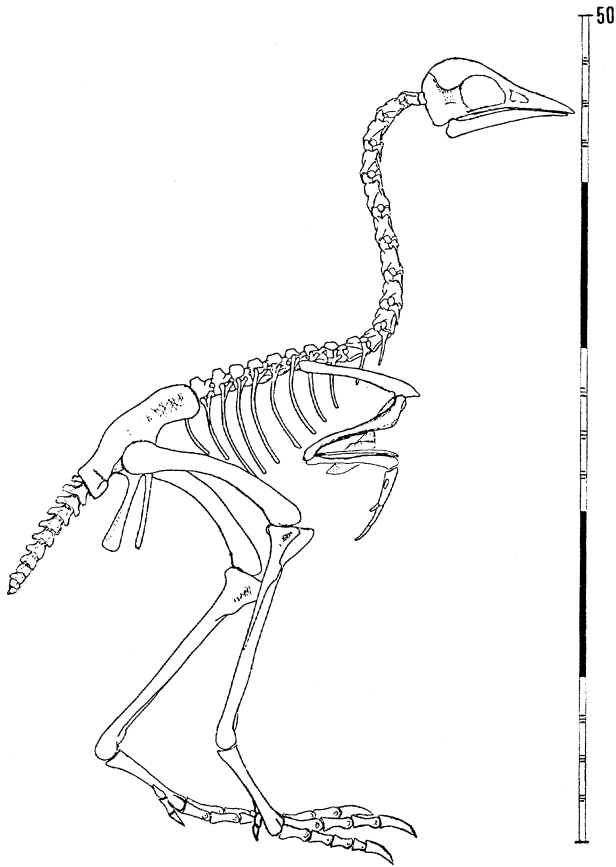
Fig. 20. *Patagopteryx*, the closest known bird to Ornithurae. Reconstruction from Alvarenga & Bonaparte (1992).

(1995 *b*) pointed out, most characters used to support the affinity of *Patagopteryx* to ratites are plesiomorphic or have been misinterpreted. Ratites, like all living birds, are clustered with hesperornithiforms and ichthyornithiforms within the Ornithurae (see below). *Patagopteryx* lacks several ornithurine synapomorphies, such as a pointed orbital process of the quadrate, a procoracoid process on the coracoid, a patellar groove on the femur, two cnemial crests on the tibiotarsus, and so on, but it is still the closest known sister-taxon of Ornithurae (Chiappe & Calvo, 1994; Chiappe, 1995 *b*, 1996). This interpretation suggests that this taxon acquired flightlessness independently from ratites and all other flightless birds.

(4) Ornithurae – Hesperornithiformes, Ichthyornithiformes and Neornithes

The Ornithurae includes Neornithes and all sister-groups descended from its common ancestor with Hesperornithiforms. *Ichthyornis*, a ternlike form, and *Hesperornis*, a flightless loon-like diver, were first described from the Late Cretaceous of the Western Interior by O. C. Marsh in 1880. After *Archaeopteryx* they are probably the most famous fossil birds. However, Elzanowski (1995), who has studied the original specimens and more recently discovered material in detail, concludes that Marsh (1880) made serious errors in his attribution of skeletal elements and in the taxonomic status of these birds, and that these have been perpetuated by generations of paleontologists. Consequently, the situation may be more complex than it appears in classic textbook accounts.

Hesperornis (Fig. 21) is part of a radiation of secondarily flightless divers that include the Late Cretaceous *Baptornis* and *Parahesperornis* from North America, along with several undescribed species (Martin, 1980; Cumbaa & Tokaryk, 1993; although see Elzanowski, 1995). The hesperornithiforms have been well described by L. D. Martin and his associates (e.g. Martin & Tate, 1976; Martin & Bonner, 1977; Martin, 1980, 1984). In recent years, fragmentary remains of this group have also been reported from the Late Cretaceous of Europe and Asia (Nessov, 1992; Kurochkin, 1995 *b*). Most hesperornithiforms come from fully marine environments, although they have been reported from brackish, near-shore deposits (Fox, 1974; Cumbaa & Tokaryk, 1993). Up to now, all reliable occurrences of hesperornithiforms are from the northern continents. Despite earlier claims that the Late Cretaceous Chilean *Neogaeornis* is a hesperornithiform (Lambrecht, 1933; Martin & Tate, 1976; Martin, 1980), Olson (1992) has shown that this taxon, represented only by a tarsometatarsus, is remarkably similar to those of the Gaviiformes, and so may be closer to the true loons of today.

The Lower Cretaceous (Albian) *Enaliornis* was first discovered in the Cambridge Greensand of England in the 1870s; it was therefore one of the first known fossil birds. It was originally regarded as a loon (Seeley, 1876), and was considered a hesperornithiform close to *Baptornis* by Martin & Tate (1976; see also Martin, 1980, 1983 *a*). *Enaliornis* was named on the basis of a series of disarticulated postcranial bones including two braincases (Seeley, 1876). In a recent study of these braincases, Elzanowski & Galton (1991) pointed out that the cranial anatomy 'places a caveat on the hypothesis of closer genealogical relationships between *Enaliornis* and Hesperornithiformes'. If *Enaliornis* is indeed a hesperornithiform, it represents the oldest known record. The next oldest records of hesperornithiforms would be those from the early Late Cretaceous (Cenomanian)

Fig. 21. *Hesperornis*, a flightless ornithurine diver from the Late Cretaceous of the interior seaway of North America. From Marsh (1880). Skull length approximately 25 cm.

of Kansas (Martin, 1983*a*) and Canada (Cumbaa and Tokaryk, 1993). However, the material, despite its historical importance, only provides a faint and unclear signal about early avian evolution.

Ichthyornithiformes (Fig. 22) are known from numerous, although mostly disarticulated, specimens from the marine Late Cretaceous rocks of North America. Since Marsh's (1880) monograph, very few papers have dealt with the anatomy of this group (Gingerich, 1972; Olson, 1975; Martin, 1983*a*; Martin & Stewart, 1977, 1982; Fox, 1984; Witmer, 1990; Parris & Echols, 1992; again, see Elzanowski, 1995) and almost nothing is known about its taxonomic diversity. In recent years, Nessov (1984, 1992) has reported ichthyornithiforms from the Late Cretaceous of Asia, although these are represented by very fragmentary specimens and some of them are likely to be of Enantiornithes (Kurochkin, 1995*b*). Ichthyornithiformes and hesperornithiformes are probably so popularly known
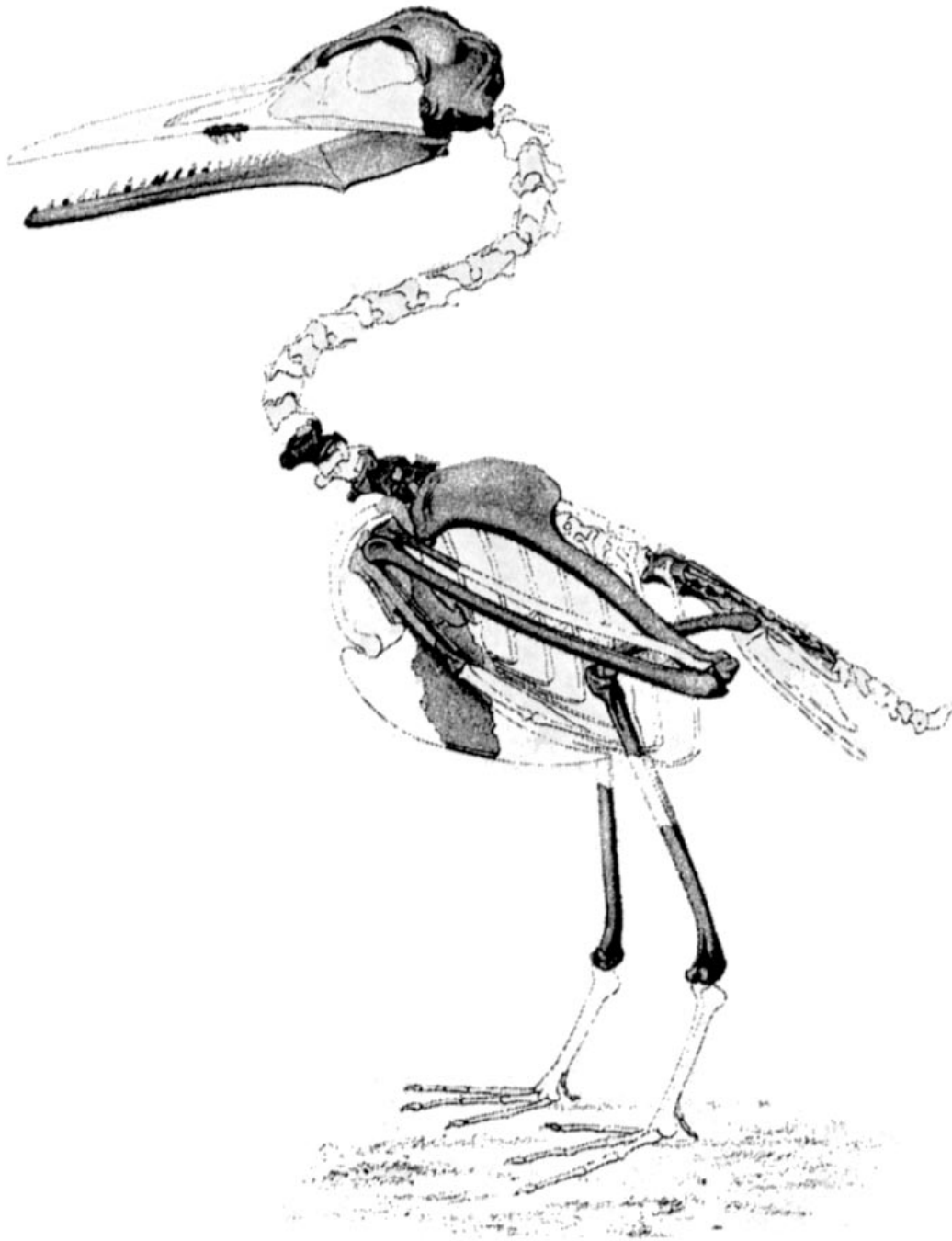
Fig. 22. *Ichthyornis*, a poorly known ornithurine from the Late Cretaceous of the interior seaway of North America. From Marsh (1880). Skull length approximately 7 cm.

because they were discovered so early in the history of avian palaeontology, and were the object of considerable scientific, popular and political attention when they were described. As loonlike and ternlike birds, they had improved chances to fossilize in the shallow marine deposits of the inland sea of the Great Plains during the Cretaceous. However, there is a great deal that we still do not know about their anatomy, especially of the Ichthyornithiformes. General descriptions of both taxa are given by Feduccia (1980), Martin (1983*a*) and Kurochkin (1995*a*).

Other, less well known Cretaceous birds can also be regarded as basal ornithurines. Perhaps the best known are *Ambiortus*, from the Early Cretaceous of Mongolia (Kurochkin, 1985), and *Apatornis*, from

the Late Cretaceous of North America (Marsh, 1880). They were both probably good fliers, but their relationships within Ornithurae are not yet clear.

Earlier workers related or assigned both hesperornithiforms and ichthyornithiforms to extant orders of birds. Nowadays, however, it is generally accepted that these two groups are unrelated to any modern order of birds, and that they are not particularly closely related to each other. Martin (1983*a*, 1987) suggested that ichthyornithiforms were the sister-taxon of Neornithes and that these two formed the sister-group of hesperornithiforms. This hypothesis of relationships was corroborated by Cracraft (1986, 1988) in an extensive cladistic analysis of early birds known at that time. Using the cranial evidence of *Hesperornis*, Elzanowski (1991; see also 1995) suggested that 'hesperornithiforms are the earliest known branch of the neognathous birds', partly because the palatine-pterygoid contact seemed to him to be neognathous, and he provided further evidence and arguments in 1995. This interpretation has not been widely accepted, and the balance of characters shown on our consensus cladogram (Figs 6, 14) suggests that it would require considerable re-evaluation of character polarities. If Elzanowski's (1991, 1995) hypothesis is chosen, an independent tooth reduction has to be accepted for both ratites and tinamous (or palaeognaths if the monophyly of this group is accepted).

(5) Cretaceous extinctions – what is the evidence?

No bird groups that have been discussed so far have been known to survive into the Tertiary. Likewise, very few extant orders of birds (and no extant families) have unquestionable representatives in the Cretaceous. Feduccia (1995) used this pattern to claim that 'birds endured a massive late Mesozoic extinction, underwent a dramatic K–T [Cretaceous–Tertiary] bottleneck, and closely paralleled mammals in their explosive phyletic evolution during the early Tertiary'. Although in general terms the fossil record shows that some groups of birds became extinct sometime during the Late Cretaceous, and new groups of birds radiated in the early Tertiary, Feduccia's (1995) other conclusions are overdrawn, based on the available evidence. The avian fossil record in the latest Cretaceous and early Tertiary, particularly the Paleocene epoch, is simply not sufficient to draw such conclusions. The fossil record of birds in the Maastrichtian, the last stage of the

Cretaceous, is poor, and nowhere near as complete as those of various fish, amphibian, reptile and mammal groups (Archibald & Bryant, 1990). The stratigraphic record of Late Cretaceous birds is so spotty and episodic that we cannot calculate turn-over rates of lower-level avian taxa (e.g. genera) with any confidence; hence, we cannot say that the Late Cretaceous extinction was 'massive' (it could have been gradual, but with characteristically high taxonomic turnover at the generic level), and we cannot discuss these changes in terms of a 'bottle-neck' because we do not know how quickly avian diversity was constricted. In the case of non-avian dinosaurs, for example, diversity decreased over several million years until, during the last years of the Cretaceous, only *Triceratops* and *Tyrannosaurus* are known from Western Interior sediments (Archibald & Bryant, 1990).

Furthermore, the explanatory power of Feduccia's (1995) conclusion is diminished by not integrating phylogeny into the evidence provided by the fossil record. Norell (1992) showed that we can use the order of phylogenetic branching plotted against the stratigraphic order of appearances of taxa to judge how complete the fossil record is, and hence, how reliably the fossil record may be taken at face value as an indicator of macroevolutionary patterns. In the case of mammals [which Feduccia (1995) compared to birds], Norell (1992) demonstrated the probability that '60% of the ordinal diversity of eutherians resulted from phylogenesis occurring before the Tertiary', which is quite at odds with Feduccia's (1995) statement about a Tertiary explosion in ordinal diversity of mammals. The occurrence of several Late Cretaceous taxa allocated within extant orders of birds (see below) suggests that several basal neornithine lineages differentiated well before the Cretaceous–Tertiary boundary. The extent of this pre-Tertiary radiation will only be understood by combining detailed stratigraphic studies of Cretaceous avian fossils with a well-substantiated hypothesis of avian phylogeny. If the fossil record of birds continues to improve at current rates, this goal may be in sight in the near future.

Because their bones are small and fragile, birds are less likely to be preserved and discovered in the fossil record than are, say, large dinosaurs. All organisms are preferentially preserved in environments associated with water, especially in the context of rapid burial and freedom from bioturbation, scavengers and decomposers. So it is no surprise that the terrestrial vertebrate fossil record is biased towards groups that live in or near the water, and towards

individuals who happen to die there (Padian & Clemens, 1985). Seabirds and shorebirds, and birds that frequent lakes, are better represented than plains and forest birds. We are therefore probably only scratching the surface of Mesozoic bird diversity.

(6) Mesozoic records of extant bird groups: do molecules and fossils agree?

In the context of the first records of extant avian taxa, Olson (1985) reviewed the occurrences of Mesozoic and Tertiary birds. Most of the specimens that can be related to extant 'orders' of birds are fragmentary, often represented by a single bone. Olson (1985) noted records of Charadriiformes and possible Procellariiformes from the latest Cretaceous of Wyoming and New Jersey; however, in his view, none of these fossils belongs to extant 'families' of birds. Olson & Parris (1989) later reviewed the material from New Jersey, although recently Olson (1994) has revised his assignment, based on geological evidence that these beds are not Cretaceous but Paleocene; however, the age of the Hornerstown Formation is still in question. Other North American Late Cretaceous neornithine birds have been reported from Canada (Tokaryk & James, 1989), and several other fragmentary remains have been collected from the Lance, Two Medicine, and Hell Creek formations (latest Cretaceous, western North America). Gaviiforms have been reported from the Late Cretaceous of Antarctica (Chatterjee, 1989) and Chile (Olson, 1992). Recently, two fairly complete specimens were found in the Late Cretaceous of the Antarctic Peninsula (Noriega & Tambussi, 1995). These birds were included within the Presbyornithidae, a group of anseriforms well known from early Tertiary deposits of North America and South America (Olson, 1985). In addition to all these finds, some fragmentary Cretaceous material from Europe (e.g. Kessler & Jurcsak, 1986; Nessov & Jarkov, 1989) and Asia (e.g. Hou & Liu, 1984; Kurochkin, 1988; Nessov, 1992) has been assigned to extant groups.

With the material and studies available today, we can only say that a few extant 'orders' of birds (e.g. Charadriiformes, Gaviiformes, Anseriformes, Procellariiformes) were already differentiated by the end of the Mesozoic (Campanian-Maastrichtian, perhaps 75–80 million years ago). Kurochkin (1995 a) feels that neognathous birds were much more diverse in the Cretaceous than we know, and that poor preservation is restricting our knowledge. We tend to agree, although some of the identifications of fragmentary Cretaceous bird remains (especially those of the Early Cretaceous) to living bird 'orders' deserve reconsideration (Olson, 1985), so it may be overly optimistic to expect that an Early Cretaceous diversification of birds into living 'orders' will be vindicated. Hedges et al. (1996) calculate a divergence time in the range of 90–100 million years ago for the neornithine orders, based on molecular data. This is still in the Late Cretaceous, and not so far off from the pattern seen in the fossil record (a gap of perhaps as little as 10 million years). If neornithine fossils are eventually found to close this gap, even partly, it would vindicate the technique of using several comparative lines of molecular evidence, complemented by phylogenetic and stratigraphic approaches. However, there are several problems with the analysis of Hedges et al. (1996) including an incorrect calibration of the diversification of crown-group mammals (against which bird diversification is calculated) in the Late Triassic instead of the Middle to Late Jurassic (a difference of perhaps 60 million years), and a reliance on continental fragmentations as instantaneous 'events' that drive cladogenetic divergences. These authors report that divergence times based on fossil evidence often underestimate actual times by at least 50% because of sampling error. This is sometimes true at a scale of up to 10^6 years, but almost never at scales of 10^7 years and above.

More recently, Cooper & Penny (1997), using both mitochondrial and nuclear DNA, calculated that at least 22 lineages of extant birds diverged well before the Cretaceous–Tertiary boundary, and the extant bird 'orders' began diverging in the Early Cretaceous. Although the sequences they used were relatively short, relative rates of evolution were consistent among taxa, so the remaining question is the accuracy of calibration and the assumption of regular change in molecular structure. Molecular techniques are promising, but analyses to date have not much clarified the Mesozoic avian phylogenetic picture.

(7) Paleognathous birds – the continuing mystery

The origin of living 'paleognathous' birds (ratites and tinamous) is another difficult problem. There are no undoubted Cretaceous fossil records of ratites and tinamous, but if Cretaceous neognath records are valid (and they appear to be), then their ratite outgroups must certainly have evolved by then. The

first question is whether ratites and tinamous form a monophyletic group. This question, and the relationships of ratites and tinamous to other birds, has been reviewed by Olson (1985) and Sibley & Ahlquist (1990), as well as Elzanowski (1995), and the conclusions of all these authors differ from each other in important ways. Several of the characters used to define the 'paleognathous' palate are clearly primitive for birds. McDowell (1948) noted that there were at least seven distinct palaeognathous-type palates in living birds. Furthermore, the large basipterygoid processes and the broad articulation between the pterygoid and the quadrate, for example, are known in *Patagopteryx* (Chiappe, 1996) and Enantiornithes (e.g. *Gobipteryx*; Elzanowski, 1977), as well as *Dromaeosaurus* (Colbert & Russell, 1969), *Allosaurus* (Madsen, 1976), and other non-avian theropods. This evidence suggests that the common ancestor of all Neornithes had at least some features of a 'paleognathous' palate (Cracraft, 1988). Heterochronic arguments (although possible; see Olson, 1985), therefore, may not be necessary to account for the palatal morphology of tinamous and ratites.

Aside from the 'paleognathous' palate, other morphological characters used by Cracraft (1974) to support the monophyly of ratites and tinamous have been shown to be primitive (Olson, 1985), but others have since been proposed (Cracraft, 1986, 1988). Both morphological and non-morphological studies have appeared to support the monophyly of ratites and tinamous (summaries in Sibley & Ahlquist, 1990; Cracraft, 1988). On the contrary, Houde (1986, 1988) proposed that tinamous were closer to neognaths than ratites, based on morphology. The monophyly (or not) of ratites and tinamous is clearly not yet set, although there is a broad consensus that both groups are outgroups of Neognathae. In any case, we expect that further information on primitive bird morphology, available in the many new findings of Mesozoic birds, will shed light on this contentious issue. Kurochkin (1995*a*) ably reviews the Early Tertiary records of paleognathous birds and concludes, as we do, that they must have been present in the Cretaceous.

The presence in the Cretaceous of neognathous birds from extant groups clearly indicates that members of the lineage (or lineages) leading to ratites and tinamous should have differentiated before the end of the Mesozoic. These early birds, however, are still unknown; previous reports of Cretaceous ratites have turned out to be erroneous (e.g. *Patagopteryx*; see above) or based on frag-

mentary, unreliable evidence (e.g. *Paleocursornis*; Kessler & Jurcsak, 1986). The oldest members of ratites and tinamous are from the middle Paleocene (Alvarenga, 1983) and middle Miocene (Chiappe, 1991*b*), respectively. Houde & Olson (1981) reported on early Tertiary flying birds with 'paleognathous' palates. Houde (1986, 1988) described several of these birds and classified them within the paraphyletic 'Lithornithiformes'. We concur with Olson (1985) that there is no paleontological evidence supporting a Gondwanan origin for ratites. This conclusion, in addition to reassessment of the molecular evidence itself (see Sheldon & Bledsoe, 1993), erodes support for inferring absolute dates of differentiation for extant avian lineages based on molecular data alone, or on 'events' such as the separation of continents (Sibley & Ahlquist, 1990), which take many millions of years to complete and so are hardly precise enough to clarify evolutionary events (e.g. Hedges *et al.*, 1996). Fig. 14 provides our own current understanding of the sequence of divergence of basal avian groups. If Ichthyornithiformes are the sister-group to Neornithes, then the divergence of these two groups must be at least as ancient as 89 million years ago.

V. CONCLUSIONS

(1) Since *Archaeopteryx* was first unearthed in the 1860s, many ideas have been advanced about its relationships to birds and to other animals. After 135 years, all the possibilities seem to have been exhausted, and the evidence has come down squarely on the side of an origin of birds from small theropod (carnivorous) dinosaurs, probably in the Middle or early Late Jurassic. *Archaeopteryx* need not be the direct ancestor of later birds; it is structurally close enough that it provides a suitable 'missing link'. *Archaeopteryx* and all the descendants of its closest common ancestor with living birds are defined as Aves.

(2) *Archaeopteryx*, some recent studies notwithstanding, shows no arboreal characters, and many of the structures so interpreted are also common to its theropod relatives. This does not mean that *Archaeopteryx* could not have been arboreal (although no one has yet shown how it could have climbed and flown with the same forelimbs), but there are severe problems with any scenario requiring a fully arboreal, gliding stage in the origin of bird flight (Padian, 1985). Birds probably evolved flight from the ground up, perhaps using gravitational assistance

from a slope or broken topography (Peters, 1985; Peters & Gutmann, 1985). Caple *et al.* (1983) argued that a ground-up source of flight requires far less in the way of precision and stability in landing, whereas an arboreal animal attempting to land on a twig in the breeze would require very high precision and stability in landing (Fig. 9). If *Archaeopteryx* did not have an alula, which seems to be a matter of general agreement, it is difficult to see how it could have performed the low-speed flight and manoeuvrability necessary to land in trees. And if it landed on the ground, Speakman's (1993) results suggest that it could not have become airborne again without a running take-off, which appears possible on physiological grounds (Marden, 1994).

(3) Only superficially do 'clothes make the man', and it is equally misleading to conclude that 'feathers make the bird', Rather, Aves must be *defined phylogenetically* (see above) as *Archaeopteryx* and living birds, and all their common descendants. Feathers could have evolved, and apparently did, in coelurosaurian theropods not closely related to those from which birds evolved – implying that a great many more non-avian theropods probably had feathers, and making it clear that feathers did not evolve directly for the purpose of flight (*contra* Feduccia, 1985, 1996).

(4) Chiappe (1995*a*) notes that immediately after *Archaeopteryx*, bird evolution focused on the improvement of the flight apparatus (except, obviously, in the *Mononykus* lineage). Changes in the pelvis and hindlimb, such as fusion of bones, further development of the opisthopubic condition, and reduction in the number of caudals and dorsals (except the pygostyle, which evolved early on) came later, and steadily (Fig. 14). This correlates well with the hypothesis that the tail was disengaged from an intimate association with hindlimb function early in the evolution of birds (Gatesy & Dial, 1996). Teeth seem to have been retained by birds for some time; they were still present in Late Cretaceous ornithurines such as *Ichthyornis* and Hesperornithiformes, but they were eventually lost at least three times in birds (*Confuciusornis*, Enantiornithes and Neornithes). Fusion of the metacarpus also occurred long after the origin of birds.

(5) The Tertiary bird record is entirely different from the Mesozoic one in relative abundance and faunal composition of taxa; most extant 'Orders' of birds can be traced back to the Eocene or earlier, but only four living 'Orders' have possible relatives in the Cretaceous, although molecular evidence suggests that there may have been more, and these do not belong to extant sub-taxa of these 'Orders'. Flightlessness and large size evolved many times in birds. Arboreal habits do not seem primitive for birds, but may have been taken up very early in their history, certainly by the Early Cretaceous. The most diverse known group of Cretaceous birds (Enantiornithes) was not even recognized until 1981. These and many other features of early avian evolution were not known until the last decade or two of work, and this points to the need for further exploration, new analyses, and rigorous methodology in deciphering the early history of birds.

VI. ACKNOWLEDGEMENTS

VII. REFERENCES

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VIII. NOTE ADDED IN PROOF

The recent discovery of a nestling of another Early Cretaceous bird from the Las Hoyas beds of Spain (Sanz *et al.*, 1997) has provided the opportunity to establish identifications of some bones of the skull that are normally fused in adults. In form and proportions, these bones can be readily identified with those of coelurosaurian dinosaurs; they show, for example, that basal birds had not lost the postorbital, but that it was reduced.

A new Late Cretaceous coelurosaur from Patagonia (Novas & Puerta, 1997) represents a lineage that appears to be the closest yet to birds, based on characters of still fragmentary material. Its pelvis, with shortened ischium and partly retroverted pubis, shares many unique features with *Archaeopteryx*. Moreover, rather than facing downward and backward, as in other reptiles, the shoulder joint of the new animal, named *Unenlagia*, faces laterally. This appears to fill a gap in the sequence of the evolution of the motions of the shoulder joint toward the condition necessary for flight, seen in *Archaeopteryx* and all other birds, that was predicted by Padian & Gauthier (1985; see Section III).

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