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Archaeopteryx and the origin of birds

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The question of the origin of birds can be equated with the origin of *Archaeopteryx*, the oldest known bird. Analysis of the five presently known skeletal specimens of *Archaeopteryx*, and comparison with the skeletal anatomy of the several reptilian groups that have been proposed as possible ancestors of birds (Ornithopoda, Theropoda, Pseudosuchia and Sphenosuchidae), confirm the conclusions (long rejected by most subsequent workers) of Heilmann (1926), Lowe (1935, 1944) and Holmgren (1955), namely, that the skeletal anatomy of *Archaeopteryx* is extraordinarily similar to that of contemporaneous and succeeding coelurosaurian dinosaurs. Rejection of these similarities as adaptive structures only (parallel or convergent similarities), and therefore of no phylogenetic importance, is here considered invalid. Heilmann was the first to identify the only evidence that has been cited so far for dismissing coelurosaurian–avian ancestral–descendant relationships, the supposed absence of clavicles in all theropods, and on that basis suggested a common *Archaeopteryx*–dinosaur ancestry among pseudosuchian reptiles. That evidence is negative and thus inconclusive, and is now known to be false.

With the exception of *fused* clavicles and unique ischial morphology, virtually every skeletal feature of *Archaeopteryx* is known in several contemporaneous or near-contemporary coelurosaurian dinosaurs and many of these conditions are unrelated, specialized features (the detailed morphology of the manus, metacarpus, carpus, humerus, scapulocoracoid, pes, metatarsus, tarsus, femur, pubis, ilium, skull and mandibles). The presence of so many derived characters in common clearly establishes that the closest ancestral affinities of *Archaeopteryx* are with coelurosaurian theropods. There is no contrary evidence and any other explanation is illogical.

Ornithopod-*Archaeopteryx* ancestral-descendant affinities may be dismissed because of the false "avian" organization of the pelvis in the Berlin specimen of *Archaeopteryx* and the merely superficially bird-like construction of the ornithischian pelvis. The suite of specialized characters unique to ornithischians (e.g., predentary, tooth morphology), that occur even in Triassic representatives, is further evidence for dismissing close affinity between ornithopods and *Archaeopteryx*. The supposed close relationship between birds and pseudosuchians is judged to be remote at best, due to the completely primitive nature of the few anatomical features which pseudosuchians have in common with *Archaeopteryx*. *Sphenosuchus*, a primitive and early archosaur, is also a potential avian ancestor, but existing evidence consists of primitive archosaurian features plus a few similarities with certain modern birds. These similarities, which are present in two groups that are separated from each other by more than 200 million years, and which cannot be demonstrated in *Archaeopteryx*, are considered irrelevant to the origins of *Archaeopteryx* and subsequent birds.

All available evidence indicates unequivocally that *Archaeopteryx* evolved from a small coelurosaurian dinosaur and that modern birds are surviving dinosaurian descendants. Stated simply, avian phylogeny was: Pseudosuchia ---→ Coelurosauria ---→ *Archaeopteryx* ---→ higher birds.

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INTRODUCTION

For nearly half a century, a general consensus has placed the origin of birds among pseudosuchian thecodontians, a group of primitive archosaurian reptiles of Triassic age that also are believed to have given rise to the two orders of dinosaurs, flying reptiles (pterosaurs), and crocodiles as well. The pseudosuchian ancestral theory, first explicitly suggested by Broom (1913), achieved general acceptance with the publication of Heilmann's classic monograph on *The origin of birds* in 1926. Since that time, few alternative theories on bird origins have been proposed and today the pseudosuchian origin enjoys almost universal acceptance.

A pseudosuchian ancestry of birds, and of higher archosaurs, quite probably is ultimately correct, considering that pseudosuchians are among the oldest and most primitive archosaurs known. But it is possible now to identify a more immediate ancestry of birds more precisely—one that is post-Triassic and post-pseudosuchian. In the half century since Heilmann assessed the various reptilian groups that might have given rise to birds, critical new evidence has come to light, the most important of which is the discovery or recognition of three more specimens of *Archaeopteryx*. Ornithologists have long recognized that various anatomical features of modern birds suggest that they arose from reptilian stock, but the most persuasive evidence of all rests in the five presently known specimens of that archaic bird.

Possibly no other zoological specimens, fossil or Recent, are considered so important as are those of *Archaeopteryx lithographica* (see Figs 1, 2 and 3). Certainly few other specimens have generated such widespread interest or provoked as much speculation and controversy. The reasons are several: these specimens are the oldest (Tithonian = Late Jurassic) known fossil bird remains; they are extremely rare, only five specimens (excluding the solitary feather) are known at present; several of these preserve remarkably detailed impressions of feathers and an extraordinary mixture of reptilian and avian characters; and most important of all, because of the last fact, out of all presently known fossil and living organisms, these specimens are widely recognized as constituting the best example of an organism perfectly intermediate between two higher taxonomic categories—representing an ideal transitional stage between ancestral and descendant stocks. *Archaeopteryx* may well be the most impressive fossil evidence of the fact of organic evolution.

The objective of this paper is to review and evaluate all available fossil evidence pertaining to the immediate, rather than the remote Triassic, ancestry of *Archaeopteryx* and to offer an up-dated theory of the origin of birds. The data, interpretations and conclusions that follow are founded on the single critical assumption that *Archaeopteryx* holds the key to bird origins, *whether or not it occupied a position directly ancestral to later birds.* After extensive study of all five skeletal specimens, it is my firm conviction that

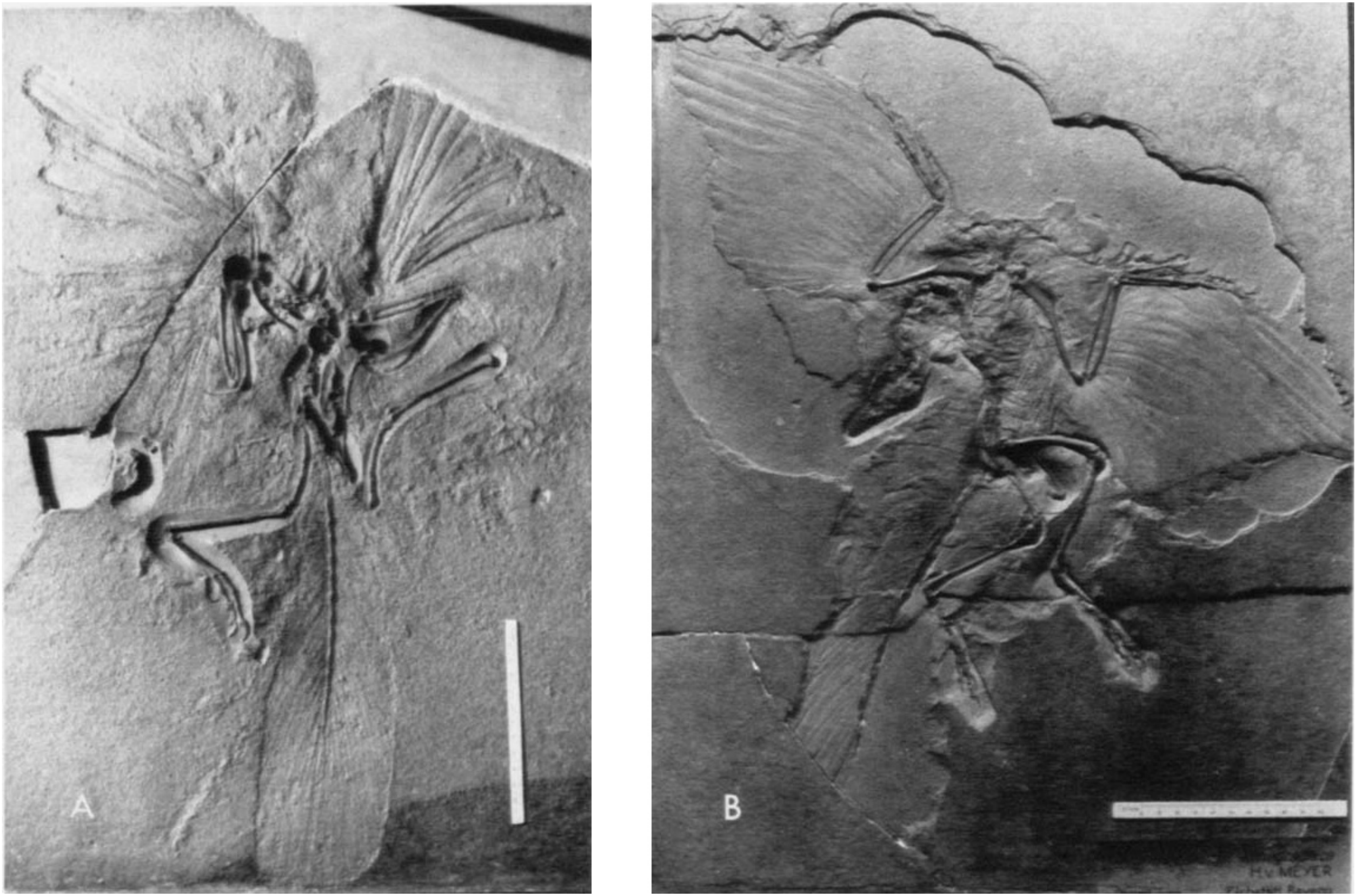

Figure 1. The first two skeletal specimens of *Archaeopteryx lithographica* to be recognized. A, The type specimen, now in the British Museum (Natural History), London; B, the Berlin specimen, once designated *Archaeornis siemensi*, now in the Humboldt Museum für Naturkunde, East Berlin. Scale = 10 cm.

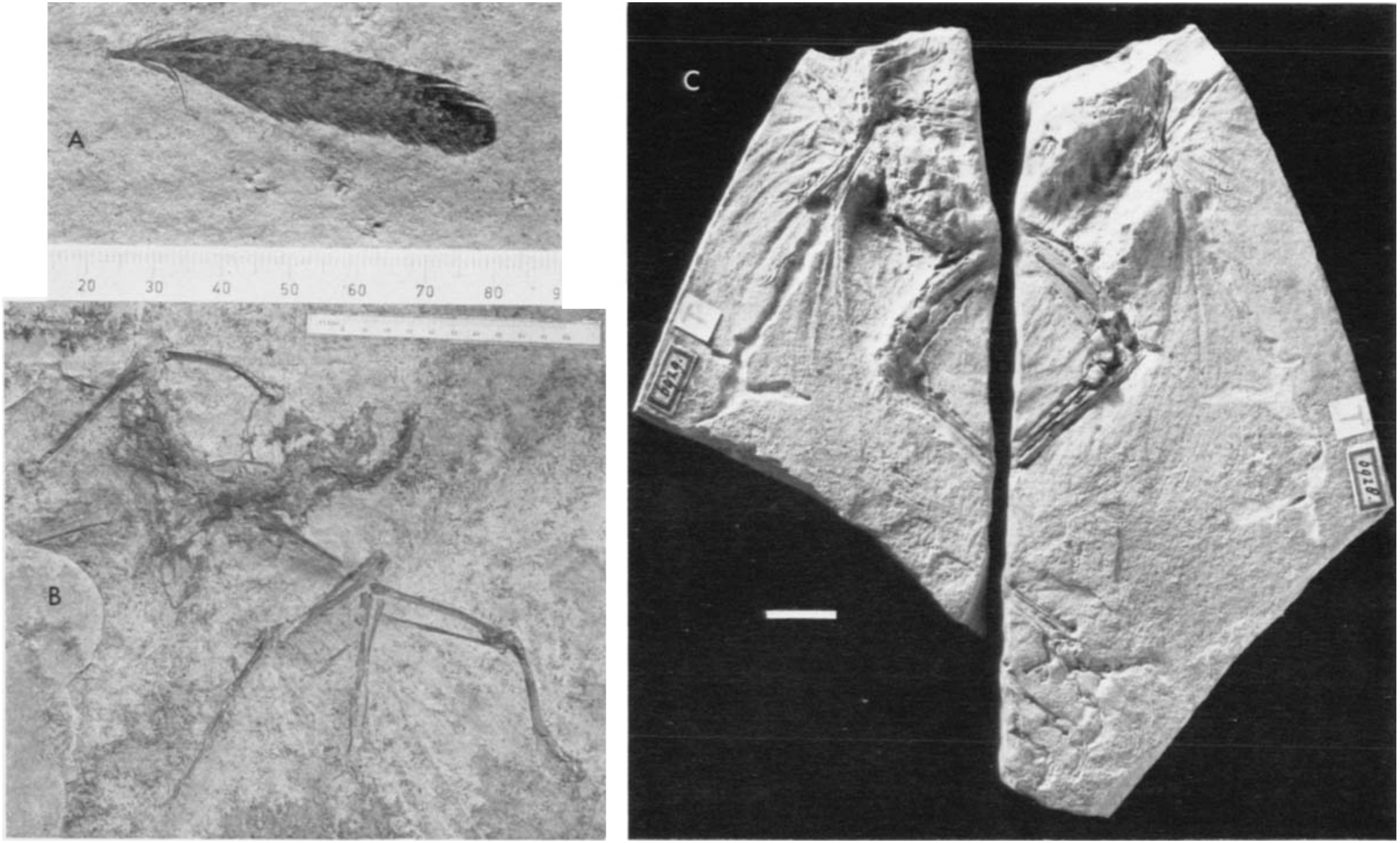

Figure 2. Three of the other four specimens of *Archaeopteryx*. A, The solitary feather reported by von Meyer (1861a); B, the Maxberg specimen found in 1956 (Heller, 1959); C, the Teyler or Haarlem specimen found in 1855 (von Meyer, 1857, 1860), but not recognized as *Archaeopteryx* until 1970 (Ostrom, 1970b, 1972). Scale divisions in A and B = 1.0 mm. Scale in C = 2.0 cm.

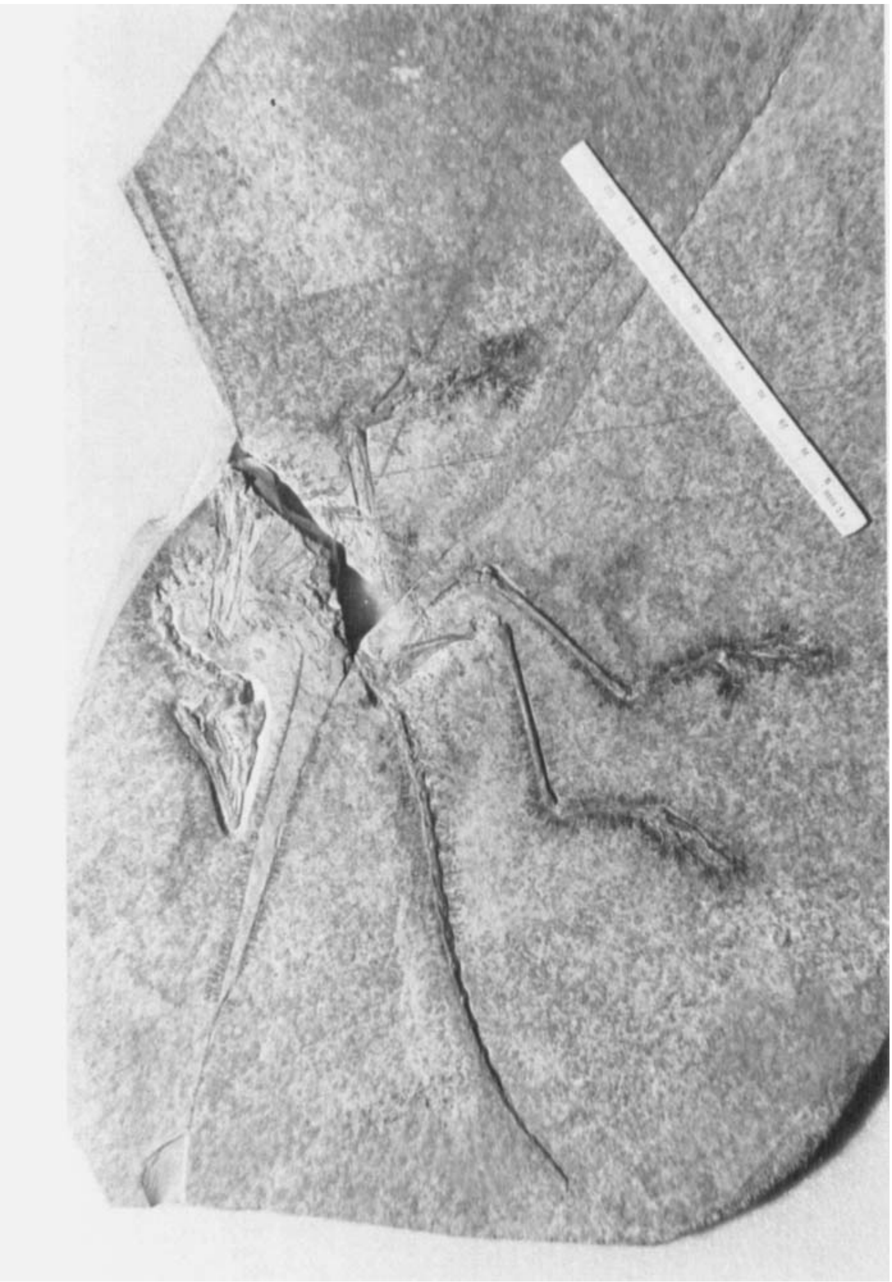

Figure 3. The main slab of the most recently recognized specimen of *Archaeopteryx*, the so-called Eichstätt specimen (Mayr, 1973), just described by Wellnhofer (1974). Found in 1951, it was long thought to be a small specimen of the dinosaur *Compsognathus*. Scale = 10 cm.

pseudosuchians were remote, not only temporally but phylogenetically as well, from the origin of *Archaeopteryx*. The evidence in these five specimens points unequivocally to an immediate ancestor among the small coelurosaurian theropod dinosaurs (Ostrom, 1973, 1975a,b).

HISTORICAL REVIEW

Early in the last century, some scholars believed that birds had existed as far back as Triassic times. That belief stemmed from the abundant occurrence of bird-like footprints in the Late Triassic strata of the Connecticut Valley in North America. These are now believed to be dinosaur footprints, but they were not recognized as such until after the discovery of the first specimen of *Archaeopteryx* in 1861. That discovery apparently led to a revised conclusion that birds had not originated until sometime after the close of the Triassic. Despite the curious plume-like structures in the Early Triassic, presumed thecodontian *Longisquama* (Sharov, 1970), no contrary evidence has turned up as yet. That does not, however, rule out the possibility that Triassic "feathered" vertebrates existed; feathers obviously existed before *Archaeopteryx*.

A brief reference by von Schlotheim (1820) to feathered fossils from the limestone beds near the towns of Pappenheim and Solnhofen in Bavaria is the first published record of the possible existence of birds during Jurassic times, although, in 1820, little of the geologic column had been deciphered and even less was known about geologic time. Unfortunately, the whereabouts of von Schlotheim's feathered fossils are unknown today. The first still-verifiable evidence of Jurassic birds is the imprint of a solitary feather in a small slab of these same Solnhofen limestones (Fig. 2A). This find was reported by von Meyer (1861a) in a letter to Professor H. Bronn, published in Bronn's *Neues Jahrbuch für Mineralogie* (p. 561). Less than two months later, von Meyer (1861b) reported the discovery in the same limestone strata of a partial skeleton associated with distinct impressions of feathers. This find, the now well-known London specimen (Fig. 1A), is currently in the British Museum (Natural History) in London. At first, some scholars questioned the authenticity of both specimens, but von Meyer (1862) established them as genuine.

Early debate centered on the question of the proper systematic assignment of the skeletal remains. Were they the remains of a true Jurassic bird or merely those of a feathered reptile? Wagner (1861), who accepted the specimens as authentic fossils even though he never saw them, finding it impossible to conceive of a "reptilian bird" declared the remains to be those of a "feathered reptile", which he proceeded to name *Griphosaurus problematicus*. Most scholars, however, quickly accepted the opinions of Owen (1862, 1863) and Huxley (1868a) that *Archaeopteryx* was indeed a true bird, albeit very primitive, of great antiquity.

While the avian versus reptilian controversy derived chiefly from the mixture of avian and reptilian characters preserved in the London specimen, another major contributing factor was the particular time of that discovery—1861—

Barely two years after publication of Darwin's *The origin of species* (1859). In that light, some of Wagner's comments are of special interest:

> "In conclusion, I must add a few words to ward off Darwinian misinterpretations of our new Saurian. At first glance at the *Griphosaurus* we might certainly form the notion that we had before us an intermediate creature, engaged in the transition from Saurian to the bird. Darwin and his adherents will probably employ the new discovery as an exceedingly welcome occurrence for the justification of their strange views upon the transformations of animals. But in this they will be wrong." (Translated from Wagner, 1861: 146)

Despite the protests of Wagner and of other anti-evolutionists (even recently; see Armstrong, 1966, and Armstrong & Kroll, 1967 for two recent exorcisms), *Archaeopteryx* has long been recognized (Huxley, 1868a) as the most persuasive—if not compelling—evidence for a reptilian ancestry of birds.

By the time the second skeleton of *Archaeopteryx*, the now famous Berlin specimen (Fig. 1B), was discovered in 1877, the debate had shifted (as Wagner expected it would) from the question of the proper systematic position, to that of the origin of birds and the particular reptilian affinities of *Archaeopteryx*. Over the years, *Archaeopteryx* has been linked with a variety of reptiles including lizards, pterosaurs, ornithopod dinosaurs, theropod dinosaurs and pseudosuchian thecodonts*. Most recently, Walker (1972) has suggested an affinity with primitive, Triassic crocodilomorphs. At first, dinosaurian affinities were favoured, owing largely to the works of Cope (1867), Huxley (1867, 1868b, 1870), Marsh (1877, 1881b), Gegenbaur (1878), Williston (1879), Vogt (1879, 1880), Baur (1883, 1884a,b, 1885a,b) and Abel (1912). Opposition to the dinosaurian theory was expressed by Seeley (1881), Dollo (1882, 1883), Dames (1884, 1885) and Parker (1887). Owen never published his views on this question, but apparently he, too, opposed dinosaurian affinities.

Fürbringer (1888) was the first to suggest what might be called a compromise theory which postulated an unspecified common ancestor for birds and dinosaurs. The common ancestor hypothesis was advocated in later years by Osborn (1900), Broom (1906, 1913), Heilman (1926), Tucker (1938a,b) and, in modified form, by Galton (1970). It is the preferred theory today, although a few contrary schemes have been presented by Boas (1930), Lowe (1935, 1944) and Holmgren (1955). Heilmann's superb study seems to have stilled the debate, for nearly all recent authors have accepted bird origins among Triassic pseudosuchian thecodontians (de Beer, 1954a,b, 1964; Bock, 1969a; Swinton, 1958, 1960, 1964; Piveteau, 1950, 1955; Welty, 1962; Romer, 1966, 1968; George & Berger, 1966; Van Tyne & Berger, 1959; Pettingill, 1970).

Today's high cost of publication prohibits a detailed review of the rise and fall of the various theories on the relationships of *Archaeopteryx* and the origin of birds (readers are referred to the bibliography at the end of this paper), but a brief summary is in order. As noted above, prior to the pseudosuchian theory, dinosaurian affinities were accepted by many. But the fragmentary fossil record

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* See Appendix for a summary classification of the taxa referred to herein.

and the less complete roster of then known dinosaurs* prompted Mudge (1879) to observe that:

> "The dinosaurs vary so much from each other that it is difficult to give a single trait that runs through the whole. But no single genus or set of genera, have many features in common with birds, or a single persistent, typical element or structure which is found in both." (Mudge, 1879: 226)

That was followed by Fürbringer's (1888) conclusion that direct descent of birds from any known type of dinosaur was not possible and all resemblances between dinosaurs and birds were "parallels" and "convergent analogies". Broom (1906) argued that birds had arisen "from a group immediately ancestral to the Theropodous Dinosaurs" and in 1913 he specified:

> "The Pseudosuchia, now that it is better known, proves to be just such a group as is required. In those points where we find the Dinosaur too specialized we see the Pseudosuchian still primitive enough." (Broom, 1913: 631)

Thus, the stage was set for Heilmann (1926). After comparing the skeletal anatomy of *Archaeopteryx* with that of various ancestral candidates, namely pterosaurs, ornithopods, coelurosaurian theropods and pseudosuchians, he found the closest resemblance to be with coelurosaurian dinosaurs. Yet, he rejected a coelurosaurian ancestry of birds *solely* because clavicles, the precursors of the avian furcula, were unknown in theropods. Following the suggestion by Broom, Heilmann, too, concluded that birds probably arose from pseudosuchians.

Not since Lowe (1935, 1944) has anyone denied the avian identification of *Archaeopteryx,* or its importance for avian origins. That is not to say, however, that everyone accepts it as *the* ancestral bird. Lowe (1935), Tucker (1938b), Swinton (1960) and George & Berger (1966), to cite just a few, considered *Archaeopteryx* to be an aberrant form, well removed from the main line of bird evolution. The extreme view was that of Lowe (1935) who believed *Archaeopteryx* to be a feathered dinosaur (!) while Swinton (1960) argued "there is no justification for making *Archaeopteryx* the progenitor of all subsequent birds", pointing out that it would be extremely improbable if the most ancient bird known to us also happened to represent any stage of the main avian lineage. Simpson (1946) and de Beer (1964) on the other hand, concluded that *Archaeopteryx* probably was on the direct line of evolution from reptilian ancestors to modern birds. Although I accept Swinton's logic (but not his conclusion), it must be pointed out that a "main line" position for *Archaeopteryx* is *not impossible.* Not one feature of the skeletons or of the plumage impressions of any of the known specimens precludes such a central ancestral position. No other contemporaneous or more ancient candidates are known (except possibly the indeterminate specimen of *Laopteryx;* see Marsh,

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* The roster of dinosaurian genera has more than trebled since 1879, according to White's (1973) *Catalogue of the Genera of Dinosaurs.* It should also be pointed out that the meaning of the term "dinosaur" has changed since that time. Prior to the turn of the century, although applied to many of the same taxonomic groups as in today's usage, the term seems to have been visualized as encompassing a much narrower and more closely related spectrum of taxa than is generally accepted today.

1881 and Simpson, 1926). Improbable though it may be, the possibility that *Archaeopteryx* actually was ancestral to all later birds still exists, and the critical question remains: What was the source of *Archaeopteryx*?

EVIDENCE ON THE ORIGIN OF *ARCHAEOPTERYX*

At the present time, three distinct reptilian groups may be considered as possibly ancestral to *Archaeopteryx*: The Ornithopoda (Order Ornithischia*, Theropoda (Order Saurischia†) and Pseudosuchia (Order Thecodontia‡). A fourth candidate, sphenosuchid crocodilomorphs, has been suggested by Walker (1972) as close to the origin of both birds and crocodiles. There is no evidence indicative of close phyletic relationships between *Archaeopteryx* and either pterosaurs or lizards, hence neither of these groups will be considered further here. The only relevant evidence available to us for deciding which (if any) of the above suborders is the true and immediate ancestral group consists of the skeletal anatomy preserved in all of the known representatives of these four groups and that of the five presently known specimens of *Archaeopteryx*. The following material is organized on that basis. The anatomy of modern birds, so highly specialized and so remote in time from the Class origins, is of no value in seeking the origins of *Archaeopteryx*, and is also excluded from further consideration here.

Precisely what constitutes valid evidence of close phyletic relationship between two or more taxa has been, and still is, the subject of intense debate (see Bock, 1969b,c,d; Brundin, 1968; Colless, 1967, 1969a,b; Cracraft, 1967; Ghiselin, 1969; Hennig, 1966; Hull, 1967; Maslin, 1952; Nelson, 1970; and many others). Nevertheless, structural similarity, whether it be at the genetic, molecular or anatomical level, is widely accepted as the most reliable index of phylogenetic affinity. The difficulty is not in recognizing the degree of resemblance, but in distinguishing between those resemblances that are homologous and those that are not. Unanimity is rarely achieved because of the difficulty or impossibility of proving to everyone's satisfaction either the homology or non-homology of similar features. Such "proof" requires evidence that is rarely, if ever, available—that is, full and complete knowledge of the entire phylogenetic series. In the absence of that kind of documentary evidence, the only reasonable working hypothesis remaining is that such resemblances are homologous in the absence of contrary evidence, and the more extensive and detailed the structural similarities, the closer the phylogenetic relationships. In Hennigian terms, the greater the frequency of derived characters in common, as opposed to primitive characters, the closer the relationship.

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* Order Ornithischia
Suborder Ornithopoda: Families; Fabrosauridae, Heterodontosauridae, Hypsilophodontidae, Iguanodontidae, Hadrosauridae.

† Order Saurischia
Suborder Theropoda (Infraorder Coelurosauria): Families; Procompsognathidae, Coeluridae, Segisauridae, Dromaeosauridae; Ornithomimidae, (Infraorder Carnosauria): Megalosauridae, Tyrannosauridae.

‡ Order Thecodontia
Suborder Pseudosuchia: Families; Euparkeriidae, Ornithosuchidae, Prestosuchidae, Scleromochlidae.

If ornithopods, theropods and *Archaeopteryx* include a pseudosuchian stage somewhere in each of their ancestries (which few authorities would challenge), the matter before us may be reduced to two possible alternatives. First, *Archaeopteryx* evolved directly from a pseudosuchian ancestor independently of the contemporaneous ornithopod and theropod lineages. Or, second, *Archaeopteryx* evolved from a pseudosuchian ancestry *by way of* an intermediate theropod or ornithopod stock. The second alternative concludes that the similar features of *Archaeopteryx* and theropods (or ornithopods) are homologues. The first alternative requires that such similarities be non-homologous and independently derived in parallel.

Parallel evolution may be defined as the similar response (adaptive change) of a common heritage in two or more related lineages to similar environmental conditions (selective pressures). Visualize, if you will, two "sibling" lineages diverging from a common ancestor. They possess certain shared primitive characters of their common ancestor, plus the latent, but as yet unexploited, potential to develop similar specialized adaptations (derived characters) as a result of experiencing the same or very similar environmental conditions and ecologic opportunities—in more or less the same sequence. The essential criterion of parallelism is that derived characters in common among related (sibling) descendant groups are *not* present in the common ancestor. In other words, the postulated relationship between "ancestor" and "descendant" lineages (species) is based entirely upon the occurrence of *primitive characters* in common, whereas the common occurrence of *derived characters* is taken to mean "sibling" relationship *only*. To express this yet another way: parallelism is a purely theoretical explanation to account for the *absence* in any known antecedent of certain derived characters that *are* present in the supposed parallel groups. While I accept the concept of parallel evolution, in my opinion, the easily explained gaps in the known fossil record do not validate the negative evidence upon which the concept of parallelism seems to rest.

It is conceivable that solitary specialized (derived) features, or even several component features of a single structural complex, may arise more than once in parallel. But the probability of multiple near-identical structures of several independent structural complexes evolving in parallel seems very remote indeed. It is quite illogical to me to dismiss a (phylo)-genetic explanation of multiple derived characters in common in favour of coincidental environmentally imposed likeness. The critical question before us is: Which of the three possible ancestral groups possesses the highest incidence of "*Archaeopteryx*-like" derived characters?

The ornithopod evidence

The only advocate of an ornithopod ancestry of *Archaeopteryx* was Baur (1883, 1884a), although Galton (1970) suggested a common ancestor for *Archaeopteryx* and ornithischians. Baur based his conclusions chiefly on the evidence of the tarsus and pelvis in various dinosaurs which he contended approached the condition found in modern birds. However, most of the taxa cited by Baur (*Amphisaurus, Zanclodon, Compsognathus, Ceratosaurus*) are now known to be saurischian rather than ornithischian! There was a tendency in some ornithopods (*Thescelosaurus, Laosaurus, Camptosaurus, Hypsilo-*

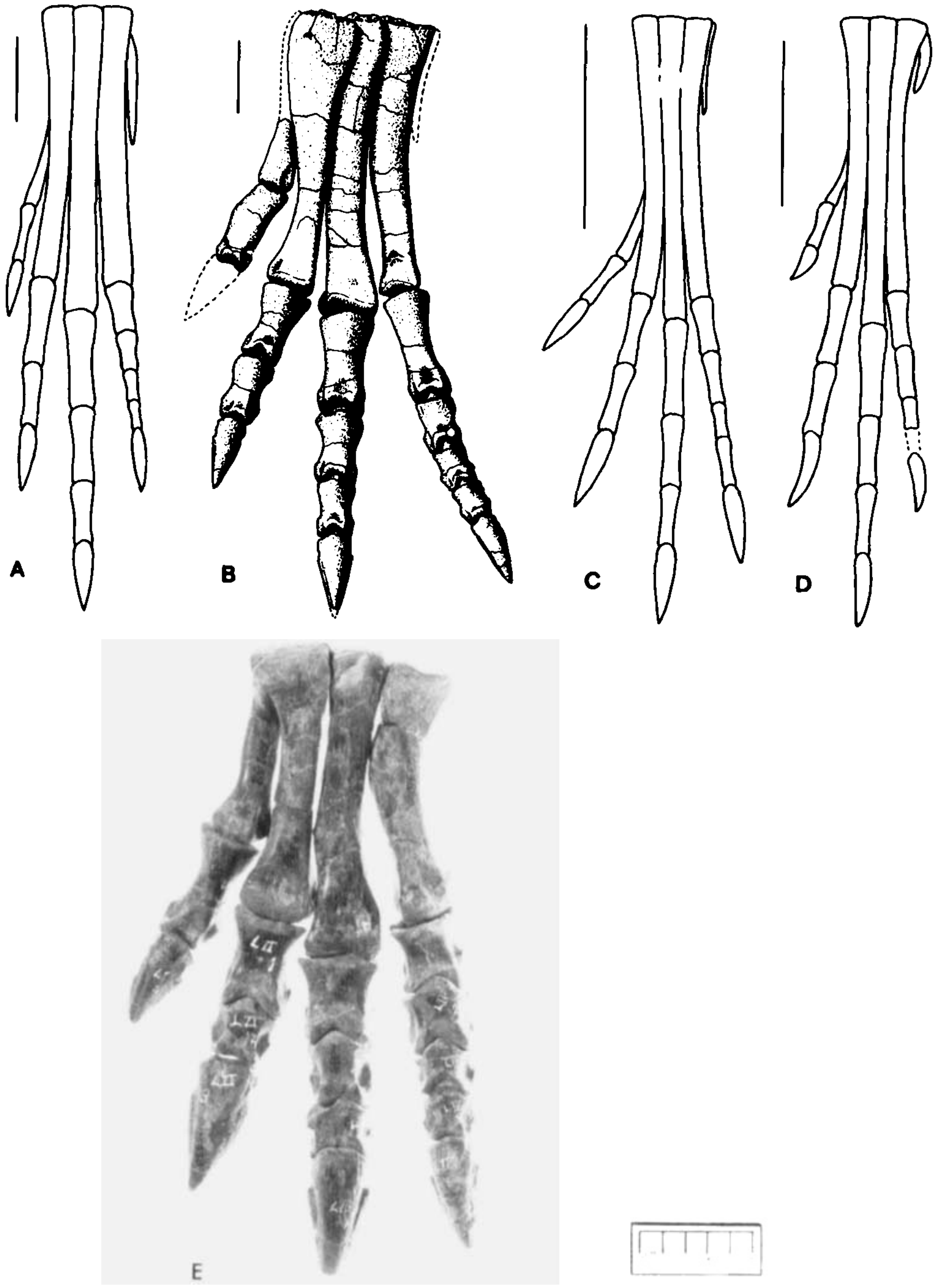

Figure 4. Comparison of the left foot and metatarsus in *Archaeopteryx* (C) with that of two ornithopod ornithischians, *Laosaurus consors*, Y.P.M. 1882 (B) and *Tenontosaurus tilleti**, P.U. 16338 (E). For added comparison, the feet of two coelurosaurian theropods are included; *Coelophysis longicolis*, A.M.N.H. 7224 (A) and *Compsognathus longipes*, Bayerische Staatssammlung, Munich (D). All specimens are reproduced to unit length of the metatarsus for easier comparison. Notice the more massive construction of the ornithopod feet, regardless of size, as compared with those of *Archaeopteryx* and the theropods. Notice also that the hallux (digit I) is not reversed in the ornithopod foot as it is in *Archaeopteryx* and theropods. Vertical scales = 3 cm. See also Fig. 15. A.M.N.H., American Museum; P.U., Princeton University; Y.P.M., Yale Peabody Museum.

*phodon, Tenontosaurus**) for reduction of the first toe, but the hallux was never reversed to a position behind digit II as occurs in *Archaeopteryx*, most modern birds and in nearly all theropods as well. As Fig. 4 shows, with the exception of the absence of digit V, there is little similarity between the pes of *Archaeopteryx* and those of typical ornithopods. The latter tend to be broader and more massive and while the tarsus does feature a mesotarsal ankle joint, the astragalus lacks an anterior ascending process.

The superficial resemblance of the ornithischian pelvis to that of modern birds (Fig. 5), and also perhaps to that of *Archaeopteryx* (but see later comments on this) has been the most important factor behind suggestions of close evolutionary relationships between birds and ornithischian dinosaurs. That similarity led Galton (1970), and others earlier, to equate the ornithischian postpubic rod (posterior ramus) with the posteriorly directed pubis of birds. The ornithischian prepubic process (absent in all Triassic and Early Jurassic ornithischians; see Fig. 5) Galton equated with the pectineal process of modern birds, which is developed on the ilium, but which is absent or only very weakly developed in *Archaeopteryx*. Galton related the backward shift of the ornithischian and avian pubis to the development of bipedal locomotion and suggested that this backward shift may have occurred only once. For this reason, he postulated a common ancestor for birds and

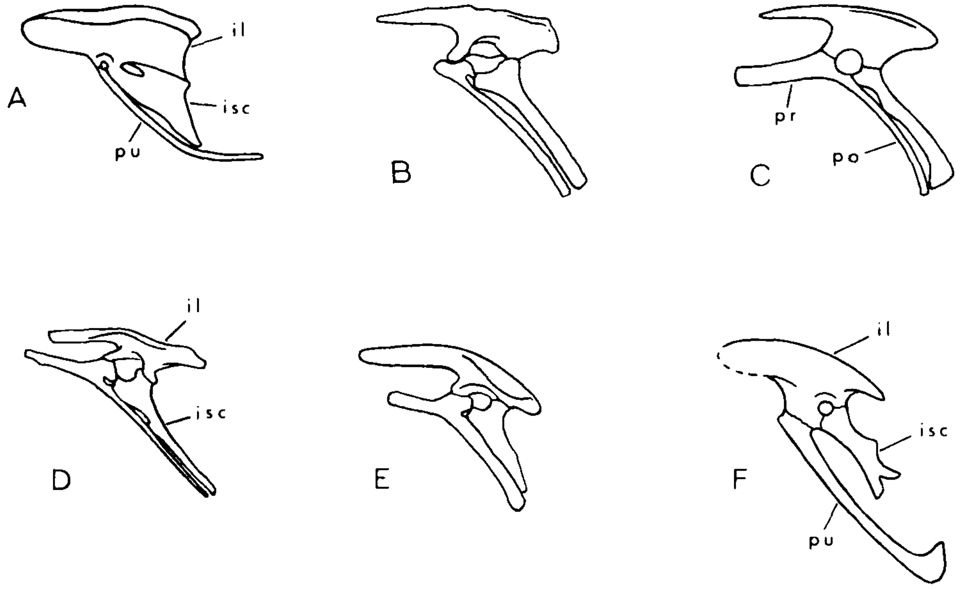

Figure 5. Pelves, in left lateral view, of several ornithischians compared with the pelvic organization of a modern bird (A) and that as *preserved* in the Berlin *Archaeopteryx* (F). The post-pubic rod (po) of ornithischians has been equated with the avian pubis (pu). The pre-pubic process (pr) is considered a new structure. A, *Columba*; B, *Scelidosaurus*; C, *Camptosaurus*; D, *Thescelosaurus*; E, *Stegosaurus*; F, *Archaeopteryx* (Berlin specimen). For the restored pubic orientation postulated for *Archaeopteryx*, see Fig. 8C. Sketches are not to scale. il, Ilium; isc, ischium; po, post-pubic ramus; pr, prepubic ramus; pu, pubis.

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* *Tenontosaurus* is an iguanodontid ornithopod recently described (Ostrom, 1970a) from the Early Cretaceous of western North America.

ornithischians, clearly acknowledging that birds could not be descendant from any presently known ornithischian. Galton also recognized that the very different pelvic arrangement in bipedal theropods posed some difficulties for his theory of bipedal locomotion in the origin of the avian and ornithischian pelvic arrangement, but he offered no further explanation. For additional discussion of the ornithischian (and archosaurian) pelvis, see the excellent paper by Charig (1972).

It now appears that the evidence of the pelvis is not so important after all. Despite the similarity in the orientation of the pubis in modern birds and ornithischian dinosaurs, there is substantial evidence, unrecognized until recently, that the pubis of *Archaeopteryx* almost certainly was not directed as sharply backward as the Berlin specimen seems to indicate. This, coupled with the absence of any other bird-like, or, more appropriately, *Archaeopteryx*-like, features in any known member of the Ornithischia (a fact which Heilmann stressed) greatly diminishes the probability of close phyletic relationship between ornithischians and birds. Galton attempted to explain the absence of any other avian features in ornithischians as the result of subsequent specializations and a shift to herbivory.

The Berlin specimen of *Archaeopteryx* seems to show the pelvic bones in natural articulation, with the pubis extending down and backward nearly parallel to the ischium, very similar to the condition in modern birds. The first indication that this "bird-like" arrangement might not be correct was suggested by the Teyler or Haarlem specimen, recognized as *Archaeopteryx* in 1970 (Ostrom, 1970b, 1972). As Fig. 6 shows, parts of the shaft and the distal extremities of the pubes in that specimen are preserved between the shafts of the femora in what appears to be natural position. However, there is no indication whatever of the ischium adjacent to these pubes as there should be if both elements were originally positioned as they are *preserved* in the Berlin specimen. Since all other bones of the Teyler specimen are preserved in articulation, it seems unlikely that the ischia only were disarticulated. Also important in this specimen is the orientation of the pubis. The pubic shaft and extremities form an axis that is nearly perpendicular to that of the posterior dorsal vertebrae (Fig. 6), in contrast to the 130° to 140° angulation preserved in the Berlin specimen (Fig. 7A). It is quite possible, of course, that either the pubes or the ischia of the Teyler specimen were displaced from their natural positions, but there is no evidence of disarticulation. More importantly though, other independent evidence exists which supports the non-avian pubic orientation in *Archaeopteryx*.

This evidence is to be found in the Berlin specimen, the Maxberg specimen, and in the recently described fifth specimen of *Archaeopteryx* (Mayr, 1973; Wellnhofer, 1974). Close examination of the Berlin specimen reveals a number of details that establish beyond any possible doubt that the two sides of the pelvis are displaced in relation to each other and that the right pubis is *not* preserved in a natural position. First, there is a distinct fracture across the proximal part of the right pubis (Fig. 7A). Secondly, as noted by Heilmann, there is a triangular area adjacent to that fracture that is not identifiable as bone, consisting of fine calcite crystals. Thirdly, the shaft and distal expansion of the right pubis are preserved at a higher level in the slab than the right ischium, and seem to be twisted with respect to the parasagittal plane defined

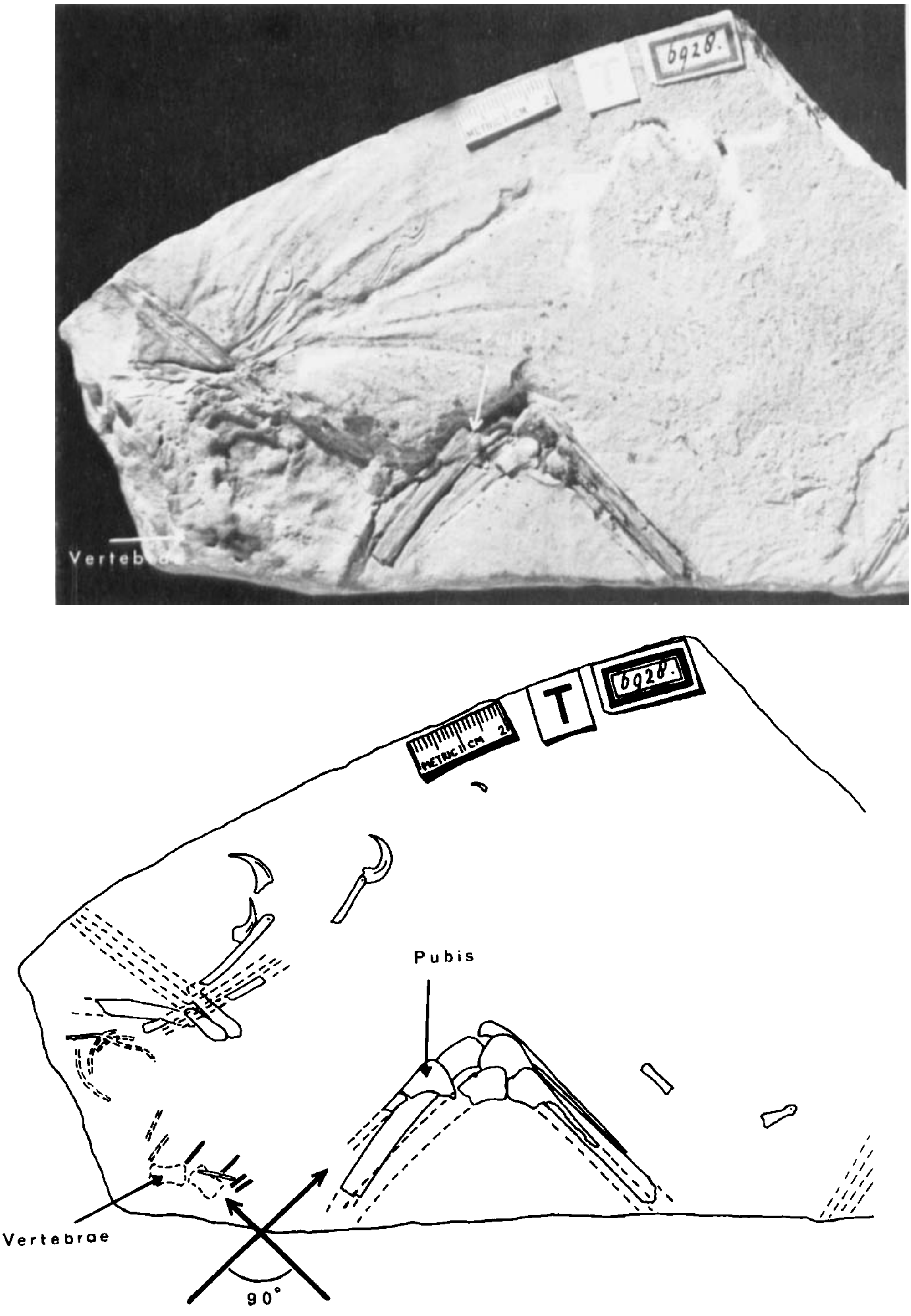

Figure 6. The main slab of the Teyler specimen of *Archaeopteryx* to show the angular relationship (approx. 90°) of the pubis to the posterior dorsal vertebrae. Notice that no sign of the ischium is preserved in the expected position. Compare with Figs 7 and 8.

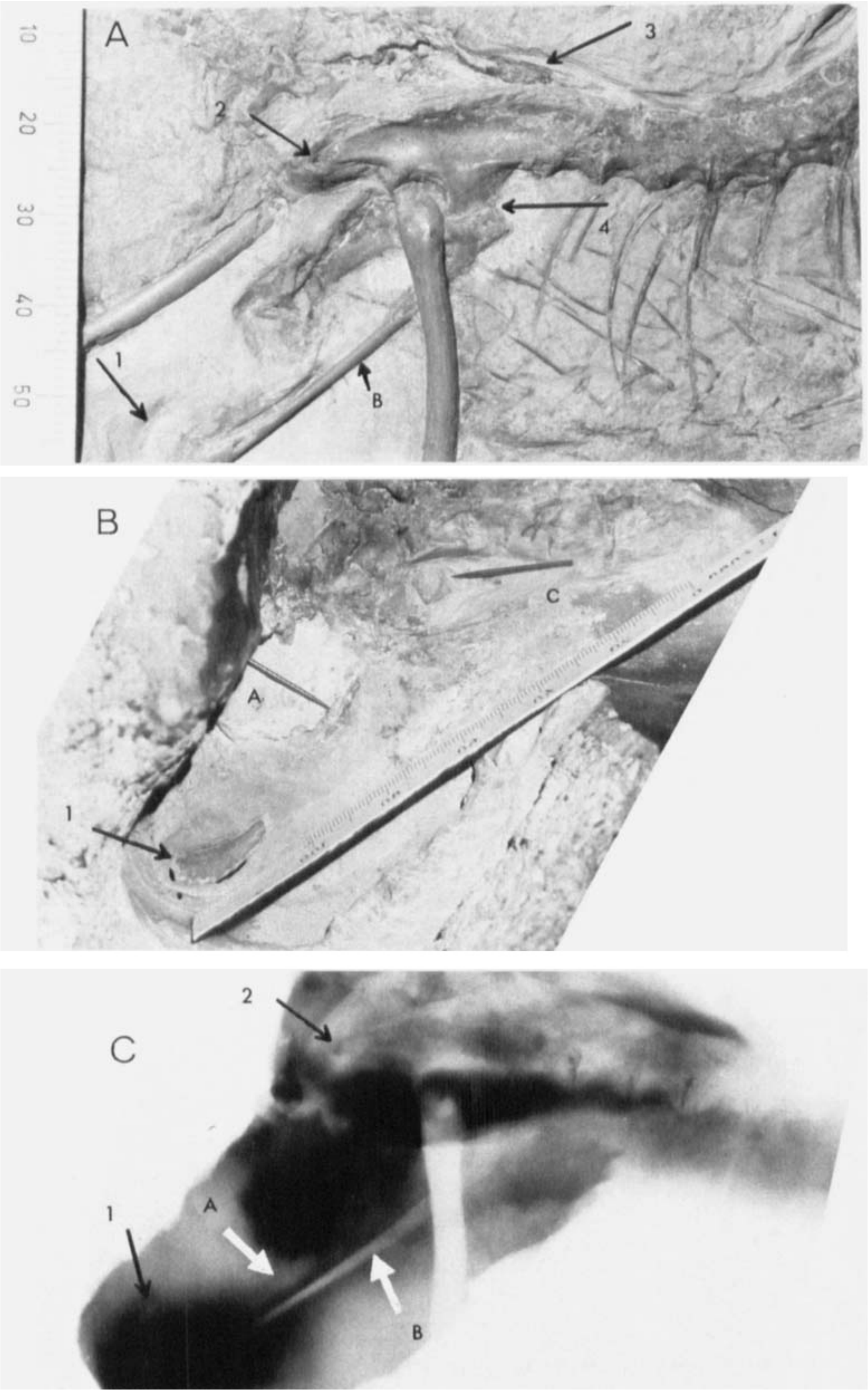

Figure 7

by the position of the right ilium. As shown by the London specimen, where both pubes are still joined, although disarticulated from the rest of the pelvis, there is a long pubic symphysis that would seem to require that the pubis in its natural position be situated medial to the ischium. Consequently, unless displaced, it should have been preserved at a lower level in the slab than is the case in the Berlin specimen. Finally, X-rays show that the left half of the pelvis in the Berlin specimen has been displaced upwards and backwards relative to the right, as is indicated by the position of the left femur and the dorsal edge of the left ilium (see Fig. 7A). Preparation of the underside of the Berlin specimen (Fig. 7B) has revealed that the distal end of the left pubis is still fused with that of the right pubis, but the two pubic shafts diverge upward to opposite sides of the right acetabulum. The X-rays (Fig. 7C) also show these discordant traces of the two shafts. Because of the firm union at the pubic symphysis, the upward and backward displacement of the left half of the pelvis appears to have pulled the right pubis (but not the ischium or ilium) up and backward also, fracturing it just below the ilium.

In the new Eichstätt specimen, the pubes are both present (Fig. 8A), but appear to be slightly rotated about a vertical axis. They are oriented at about 100° to 110° to the trace of the posterior dorsal vertebrae. This orientation is very close to that seen in the Maxberg specimen (the third specimen of *Archaeopteryx*), where, as shown in Heller's X-ray (1959, pl. 14-1), but not previously noted, the angle between the long axis of the ilium and the pubic shafts is also about 100° (see Fig. 8B). Thus, the last three specimens to be found all seem to confirm a displaced position of the pubis in the Berlin specimen.

It is not surprising that this condition was not recognized before, because obviously there is nothing surprising about a bird-like orientation of the pubis in an ancestral bird. In fact, it is improbable that post-mortem displacement coincidentally would have aligned this element in a bird-like orientation. The evidence is clear, however, that the pubis in the Berlin specimen has indeed been displaced, even though the natural position of the pubis cannot be reconstructed precisely. The fact that it has been displaced, and the absence of any positive evidence in any of the other specimens of *Archaeopteryx* that the

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Figure 7. The pelvic region of the Berlin *Archaeopteryx* specimen showing the different positions of the left and right pelves, evidence that the "bird-like" position of the right pubis in this specimen is not necessarily that of the original orientation in life. A. The upper surface of the main slab; arrow 1: the distal expansion of the pubis; arrow 2, the posterior extremity of the ilium; arrow 3, the dorsal margin of the left ilium clearly displaced upward relative to the right ilium; arrow 4, a fracture between the right pubis and ilium; arrow B, the shaft of the right pubis. B. Underside of the same specimen (printed in reverse for easier comparison with A); arrow 1 points to the distal expansion of the *left* pubis still fused to the right pubis (arrow 1 of A); pointer A indicates the *left* pubic shaft, and pointer C points to the head of the right femur still articulated in the acetabulum (as can be seen in A). The reversed printing of B clearly shows that the shafts of the left pubis (arrow A) and the right pubis (arrow B) diverge upward to opposite sides of the acetabulum. C. X-ray image of the same region (to approximately the same scale as A and B) showing the dissimilar positions of the two pubes. Arrows 1 and 2 respectively indicate the distal expansion of the pubes and the posterior extremity of the right ilium. Arrows A and B point to the shafts of the left and right pubes, respectively. Compare these photos with Figs 6 and 8. See text for further explanation. Scale divisions in A = 1.0 mm; in B = 0.5 mm. C is at the same magnification as A. X-ray provided through the courtesy of Dr H. Jaeger, Humboldt Museum für Naturkunde, East Berlin.

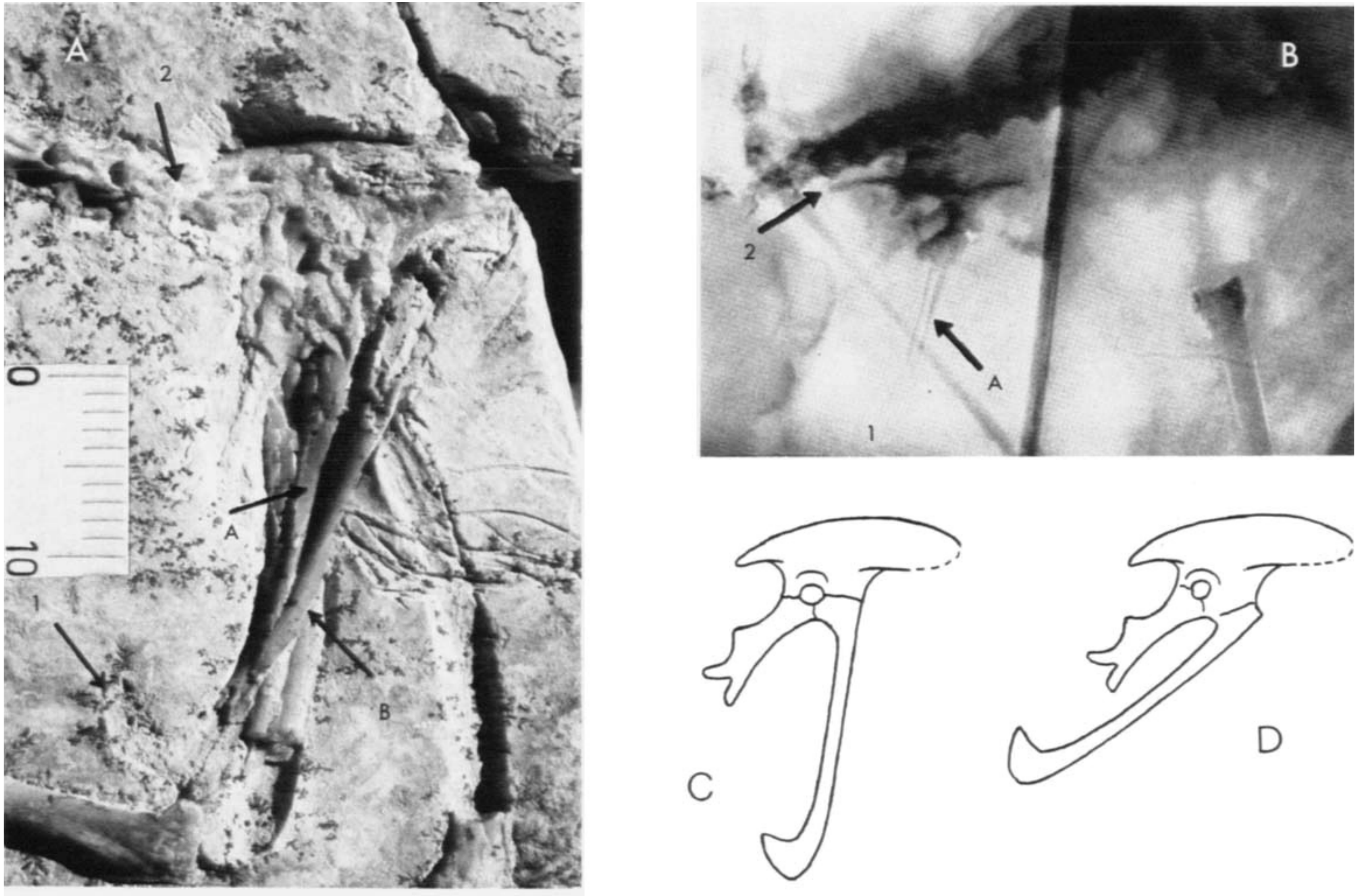

Figure 8

pubis had a bird-like (or ornithischian-like) orientation, nullifies the most important evidence of previous theories that related *Archaeopteryx* with ornithopod dinosaurs.

The theropod evidence

It has been stated (Colbert, 1969) that if it were not for the impressions of feathers, it is unlikely that the London and Berlin specimens of *Archaeopteryx* would have been identified as "bird" remains, but instead would have been labeled reptilian. (Recall the early debate about feathered reptile versus reptilian bird.) I would go even further than that. Were it not for those remarkable feather imprints, today both specimens would be identified unquestionably as coelurosaurian theropods. Notice that with the exception of the misleading orientation of the pubis in the Berlin specimen, there is only one skeletal feature that is *not* currently known in any theropod specimen. This single feature is the *fusion* of the clavicles into a furcula. More will be said about this later.

Some of the coelurosaurian characters of *Archaeopteryx*, particularly of the hand, have been discussed by several previous workers (see Lowe, 1935; Tucker, 1938b; Holmgren, 1955), but not since Heilmann (1926) has there been a comprehensive review of all the evidence. The fact is that there is much more evidence for the theropod affinities of *Archaeopteryx* than has generally been recognized. This evidence has been augmented by the three recently recognized specimens of *Archaeopteryx*, but in past years it has been largely overlooked because of frequently invoked suppositions of convergence and parallelism. Another critical factor has been the discovery of a variety of new theropods since Heilmann's time. All these discoveries make it necessary to re-examine the question of *Archaeopteryx* and bird origins. The following data and interpretations are based on my own extensive studies of the five specimens of *Archaeopteryx* and of nearly all the theropod taxa cited herein.

Manus and forelimb

Although sometimes described as "bird-like", the hand and forelimb of *Archaeopteryx* actually are not like those of modern birds at all, but they are remarkably similar in a number of details to those of certain small theropods, namely *Ornitholestes, Deinonychus, Velociraptor, Chirostenotes* and probably *Stenonychosaurus* and *Saurornithoides*. Some of these similarities have repeatedly been explained as adaptive only and of no phylogenetic

Figure 8. A. The pelvic region of the Eichstätt specimen of *Archaeopteryx*, showing the preserved pubis orientation nearly perpendicular to the long axis of the ilium, very close to the orientation preserved in the Teyler specimen (see Fig. 6); arrow 1, distal expansion of the pubes; arrow 2, posterior extremity of the left ilium; arrows A and B, left and right pubes lying on top of the left femur. B. X-ray image of the pelvic region of the Maxberg *Archaeopteryx* (from pl. 14-1, Heller, 1959); 1 indicates the distal expansion of the pubes; arrow 2 points to the posterior process of the ilium; arrow A points to the parallel shafts of the pubes, oriented nearly perpendicular to the long axis of the ilium, as in the Eichstätt specimen (A) and the Teyler specimen (Fig. 6). C. My best estimate of the reconstructed natural position of the pubis in *Archaeopteryx*, based on analysis of all five skeletal specimens. D. Past traditional interpretation of the pelvis in *Archaeopteryx*, based on the right side of the Berlin specimen. Scale divisions in A = 1.0 mm.

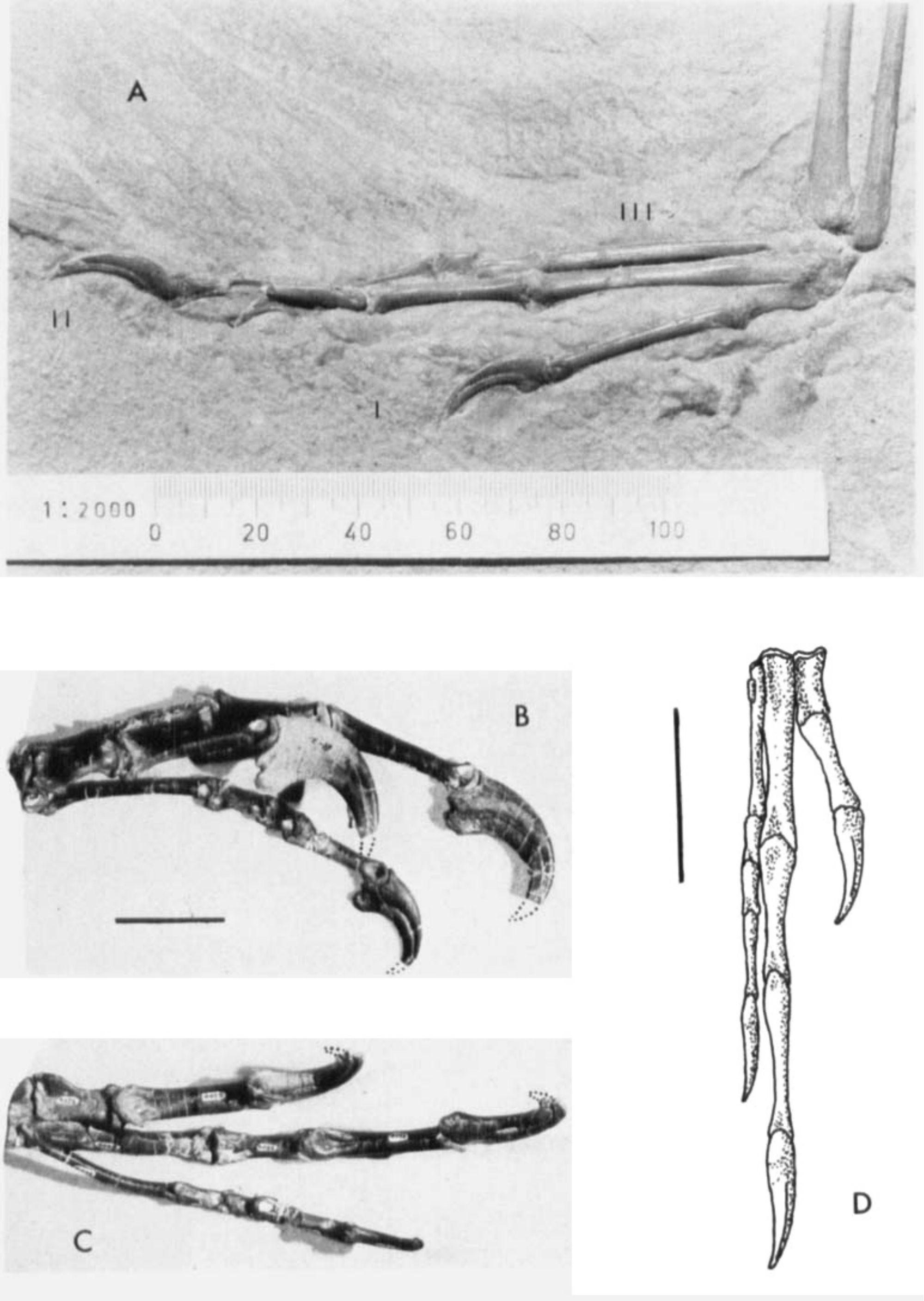

Figure 9. Comparison of the (right) hand and metacarpus of the Berlin *Archaeopteryx* specimen (A) with those (lefts) of the theropods *Deinonychus antirrhopus* (B & C), Y.P.M. 5206, and *Ornitholestes hermanni* (D), after Osborn (1917). Notice the relative lengths of the three fingers and metacarpals in all three. Similar construction of the hand and metacarpus is also found in *Velociraptor mongoliensis*, as is illustrated in Fig. 10C. Compare these data with Fig. 24. Scale divisions in A = 0.5 mm; scale lines in B, C, D = 5 cm.

signficance—in other words, due to convergent or parallel evolution (Tucker, 1938b; Simpson, 1946; de Beer, 1954b). Elsewhere (Ostrom, 1974a), I have challenged that explanation and more will be said about this later.

Manus. The manus of *Archaeopteryx* (Fig. 9A) consists of three fingers, digits IV and V having been lost. Digit I is the shortest, II the longest and III is intermediate in length. Digits I and II are the more robust and digit III is slender and more delicate. The phalangeal formula is primitive (2-3-4), but the phalangeal proportions are not. The penultimate phalanx is the longest in each finger, rather than the proximal phalanx (the primitive condition), and that of the first finger is especially long as compared with the terminal phalanx.

This same configuration occurs in several small to moderate sized theropods (Figs 9C, D and 10C), such as *Ornitholestes hermanni* (Osborn, 1903, 1917), *Deinonychus antirrhopus* (Ostrom, 1969), *Velociraptor mongoliensis* (see pl. 2, fig. 2 of Kielan-Jaworowska & Barsbold, 1972) and *Chirostenotes pergracilis* (Gilmore, 1924a). The chief difference between these theropod hands and those of *Archaeopteryx* is one of size, all of the theropods being larger. Also, the fingers are relatively shorter in the theropods.

The phalangeal formulae clearly indicate that the fingers retained in both *Archaeopteryx* and the theropods mentioned above, as well as in many other theropods, are the first three. Any other interpretation would require that digits I and V were lost completely in all these taxa and the remaining fingers reduced by one and only one phalanx *each*, or that digits I and II were lost without trace and the third and fourth fingers *only* were reduced by two phalanges each. Retention of a splinter-like metacarpal remnant at the fourth position in *Ornitholestes* and a reduced finger at that position in *Coelophysis* rule out the last explanation, for those taxa at least. Since there is no clear evidence of reduction of the first finger in any archosaur, the conservative interpretation is that these fingers represent I, II and III. The same is true of *Archaeopteryx*, and probably therefore, of modern birds as well (*contra*, Montagna, 1945; Holmgren, 1955, who interpreted the modern bird digits as II, III and IV, on the basis of embryological evidence).

Metacarpus. The metacarpus of *Archaeopteryx* consists of three metacarpals (Fig. 9A) with no sign of any other elements being preserved in any of the presently known specimens. Metacarpal I is very short and robust, while the second and third are very long (more than three times the length of the first) and subequal in length. The first two metacarpals are tightly appressed proximally (Fig. 10A), but are slightly divergent distally. Metacarpal III is more slender than the others and not so closely appressed against metacarpal II. The first and second metacarpals may have been fused since they are preserved in contact in one or both hands in the Berlin, Eichstätt and Maxberg specimens, and perhaps in the Teyler specimen too. In the London specimen, however, the left metacarpals II and III are preserved together, but metacarpal I is missing, suggesting that it was not co-ossified with metacarpal II in this, one of the largest of the five specimens. Heilmann (1926) thought that the second and third metacarpals might have been fused proximally, but the Maxberg specimen (the next largest) clearly shows that they were separate. The left metacarpal III is lacking in that specimen and that of the right side is separated by more than 2 mm from metacarpal II. The larger dimensions of the Maxberg and London specimens indicate that they were not immature, as compared with the smaller

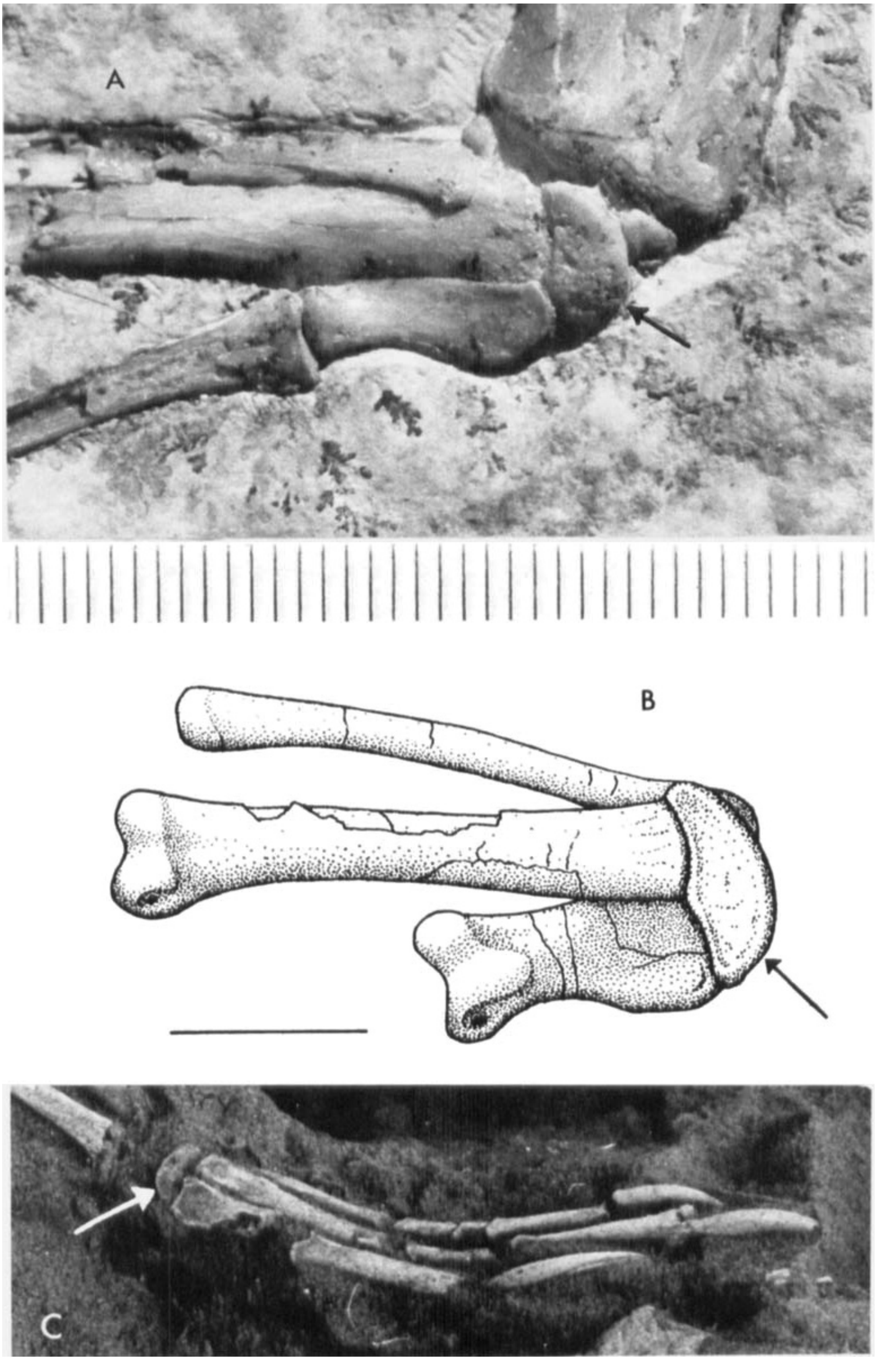

Figure 10

Berlin specimen which may be, so we must conclude that the three metacarpals were not normally co-ossified in the adult *Archaeopteryx.*

Several theropods display this same basic construction of the metacarpus, most notably, *Ornitholestes, Deinonychus* and *Velociraptor. Chirostenotes* may also have had a similar arrangement, although metacarpal III is not known. In each instance, the proportions are approximately the same as in *Archaeopteryx* and metacarpal III is more slender than the others. Most significant, however, is the form and closely appressed placement of the first metacarpal in all. In particular, notice the distinct proximal external facet for contact with metacarpal II and the internal basal expansion on metacarpal I of *Deinonychus* (Fig. 10B) and apparently also in *Velociraptor* (Fig. 10C). These compare very closely with similar features in the first metacarpal of *Archaeopteryx.*

Carpus. The carpus of *Archaeopteryx* appears to be composed of just three elements, one large semi-lunate distal carpal and two small ossicles. Petronievics (1923) first distinguished two carpals which he identified as the radiale and ulnare. Later (1925) he suggested that the "radiale" was composed of two fused distal carpals. Heilmann (1926) thought he could distinguish four separate carpals in the left wrist of the Berlin specimen, but this is far from evident in that specimen, nor does the new Eichstätt specimen substantiate this suggestion. The large semi-lunate distal carpal (the radiale of Dames, 1884, and Petronievics, 1923) articulates very precisely with metacarpals I and II, but has no contact with metacarpal III. This condition is very clearly shown in the right carpus of the Eichstätt specimen (Fig. 10A) and the left wrist of the Berlin specimen. A smaller carpal is preserved at the proximal end of the third metacarpal in the Eichstätt specimen, but whether it represents a proximal or a distal carpal cannot be established. Heilmann (1926) interpreted this as a centrale in the Berlin specimen, but I suspect that it is the ulnare. Another small element is preserved between the semi-lunate carpal and the radius in both wrists of the Berlin and Eichstätt specimens. It, presumably, is the radiale.

Among theropods, a very similar carpal construction is known in *Deinonychus* (Fig. 10B) and apparently in *Velociraptor* (Fig. 10C), and a comparable semi-lunate carpal has been found in *Stenonychosaurus* (Russell, 1969) and the Yale specimen of *Coelurus* (= *Ornitholestes*?). The semi-lunate carpal of *Deinonychus* has exactly the same relationships and form as in *Archaeopteryx.* Also, there is a smaller carpal between metacarpal III and the ulna, just as in the Eichstätt specimen.

Radius and ulna. These bones provide little detailed evidence for or against an *Archaeopteryx*—theropod relationship. Both elements are long and very slender, and distinctly bird-like, but in general proportions they are more similar to those of "long-armed" theropods such as *Deinonychus, Ornitholestes* and *Struthiomimus* than anything else (see Fig. 12). They are shorter than

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Figure 10. Carpus and metacarpus of *Archaeopteryx* (A), the Eichstätt specimen, compared with those of *Deinonychus antirrhopus* (B), Y.P.M. 5205, and *Velociraptor mongoliensis* (C). Arrows point to the distinctive half-moon-shaped distal carpal in each, a feature that is unique to certain theropods and *Archaeopteryx.* That condition, coupled with the equally distinctive short form of the first metacarpal, also illustrated here, is considered of critical phyletic importance. A and B represent right wrists, C shows the left wrist and hand. Scale divisions in A = 0.5 mm; scale line in B = 3 cm. Photo C provided through the courtesy of Dr Z. Kielan-Jaworowska and reproduced by permission of Dr R. Barsbold.

either the manus (digit II) or the humerus, a condition that occurs in the above theropods and some others, but not in most modern birds or pseudosuchians.

Humerus. Although rather bird-like in its general morphology, the humerus of *Archaeopteryx* also closely resembles those of several of the small theropods (Fig. 11), such as *Coelurus*, *Ornitholestes*, *Deinonychus* and perhaps *Velociraptor*. The shaft in all is long, slender and slightly curved. There is a long, high and well-defined deltopectoral crest, but little or no development of internal or external tuberosities or of a bicipital crest, as occur in modern birds. These same features are also lacking in the theropod humerus.

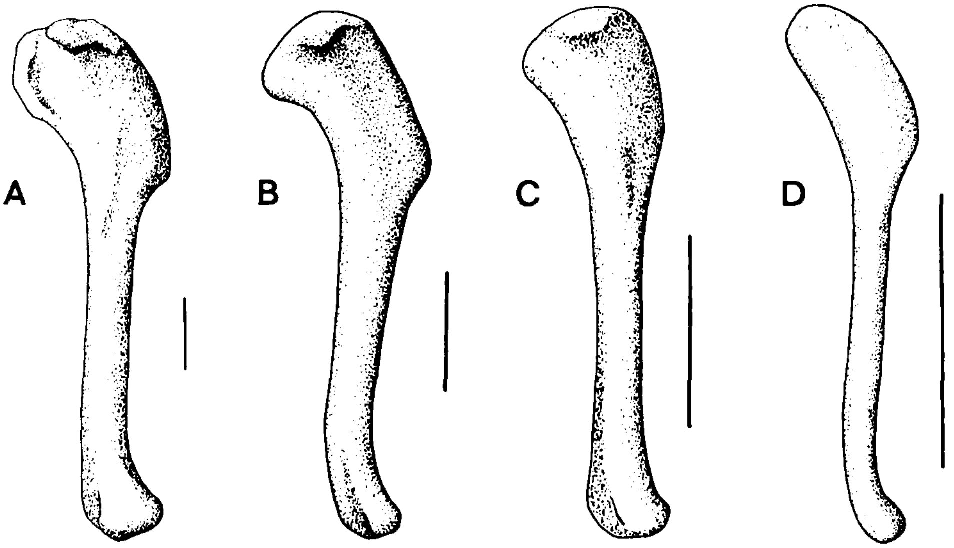

Figure 11. Comparison of humeral morphology of *Archaeopteryx*, Berlin specimen (D); and theropods *Deinonychus antirrhopus*, A.M.N.H. 3015 (A); *Ornitholestes hermanni*, A.M.N.H. 619 (B); and *Microvenator celer**, A.M.N.H. 3041 (C). All humeri are right elements viewed in dorsal aspect and drawn to the same length for better comparison. Relative sizes are indicated by the vertical scale lines which equal 3 cm. Compare with Fig. 25.

Forelimb summation. Individually, each of the forelimb components in *Archaeopteryx* shows some degree of morphological resemblance to the corresponding elements in certain theropods. This resemblance, as we have seen above, is most pronounced in the distal elements, which presumably are the more specialized components of the forelimb. Considered collectively, the resemblance still holds and is strengthened by dimensional aspects and intermembral proportions (Fig. 12). Tucker (1938b) and others have argued that an invariable trend among bipeds is a reduction of forelimb length, referring in particular to theropod dinosaurs—which, according to Tucker, obviously could not then have had any evolutionary connection with *Archaeopteryx* and bird origins. It is indeed well known that certain theropods, such as *Tyrannosaurus*, *Tarbosaurus*, *Albertosaurus* (=*Gorgosaurus*), and *Daspletosaurus*, possessed greatly shortened forelimbs, but it should be evident now

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* *Microvenator celer* is a small coelurid theropod recently described (Ostrom, 1970a) from the Early Cretaceous of Montana.

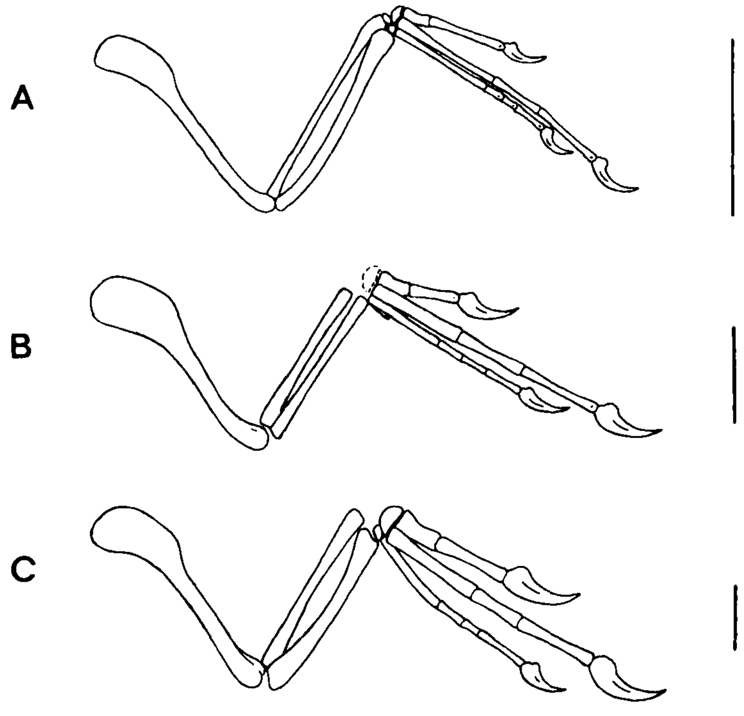


Figure 12. Outline sketches of the right forelimb skeleton of *Archaeopteryx* (A) compared with those of theropods *Ornitholestes* (B) and *Deinonychus* (C). Humeri are drawn to the same length to minimize size-related differences, sizes being indicated by the vertical scale lines which equal 5 cm. Notice the extreme relative lengths of the hands compared with those illustrated in Fig. 26.

from the abundant remains of *Ornitholestes*, *Deinonychus*, *Velociraptor*, *Ornithomimus*, *Struthiomimus*, *Dromiceiomimus*, *Gallimimus*, *Deinocheirus*, and others, that elongated forelimbs were characteristic of a number of theropods—all of which were bipedal. Forelimb length in *Deinonychus* and *Ornitholestes* is estimated at about 75% of presacral vertebral length. That compares with approximately 120% in the Berlin *Archaeopteryx* and nearly 140% in the Eichstätt specimen, as contrasted with only 40% to 50% in pseudosuchians.

Pectoral girdle

The pectoral girdle, like the manus and forelimb, is remarkably similar in *Archaeopteryx* and various small theropods, a fact that has not been generally recognized before. In fact, the only non-theropod feature of the pectoral girdle of *Archaeopteryx* is the furcula, which is well preserved in the London specimen (Fig. 23) and is partially preserved in the Maxberg and Berlin specimens. Independent of the plumage impressions, the presence of a furcula may be considered important substantive evidence of the avian affinities of *Archaeopteryx*, but it also has been alluded to (Heilmann, 1926) as *the* critical evidence against theropod relationships. Heilmann dismissed theropods as possible ancestral stock of *Archaeopteryx* solely on the grounds that they lacked clavicles—the presumed precursors of the avian furcula. The supposed absence of clavicles in theropods is negative evidence only, and thus inconclusive. But more important is the discovery that clavicles were present in at least some theropods, as will be discussed later.

Scapula. The scapula of *Archaeopteryx* is long and very narrow or strap-like (Fig. 13A). The posterior end flares only slightly or not at all, as is shown by

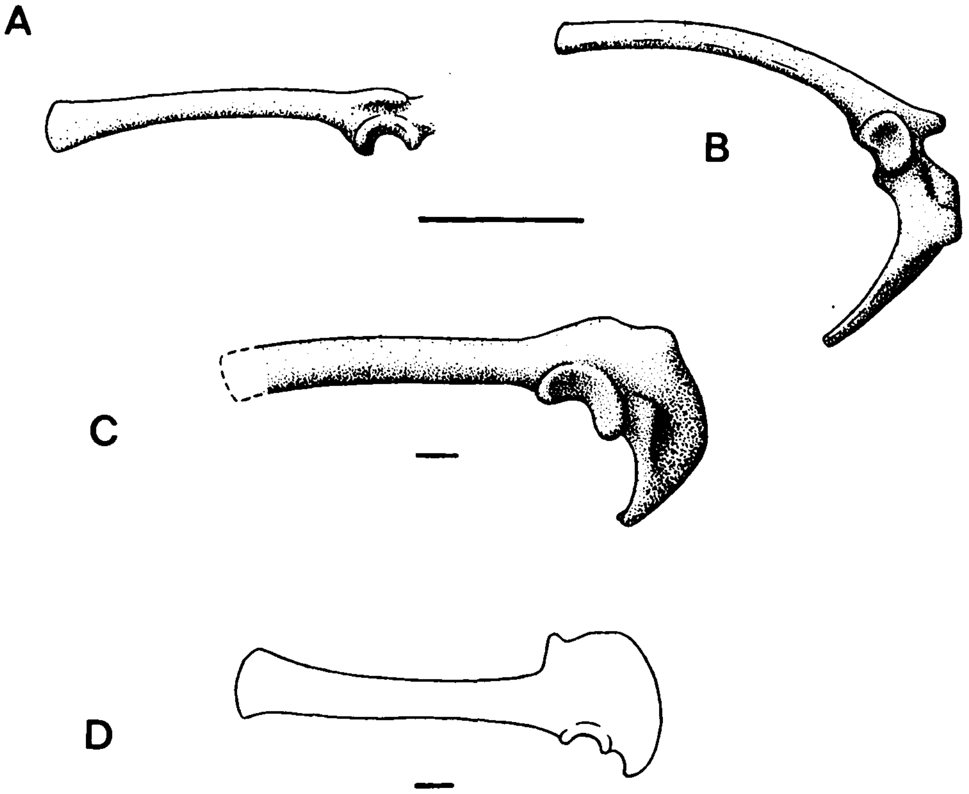


Figure 13. Pectoral girdle of *Archaeopteryx* (A and B), as reconstructed (by the author) from the London and Berlin specimens, compared with those of theropods *Deinonychus* (C), and *Allosaurus* (D). A is viewed perpendicular to the plane of the scapular blade (dorsal ?). B, C and D are viewed in lateral aspect. Compare this illustration with Fig. 27. Scapulae are drawn to the same length, relative sizes are indicated by the horizontal scale lines that equal 5 cm. Notice the distinctive strap-like form of the scapulae.

the London, Berlin and Maxberg specimens, contrary to the flared condition of most reptilian (other than theropod) scapulae, nor does it taper posteriorly as in modern birds. Its form is remarkably similar to the scapulae of *Struthiomimus, Ornitholestes, Deinonychus, Velociraptor* and most other theropods. As far as I know, this narrow, parallel-sided, strap-like scapular form occurs only in *Archaeopteryx* and theropod dinosaurs, and in slightly modified form in modern birds.

Coracoid. The coracoid is preserved apparently co-ossified or very firmly articulated with the scapula in the first three specimens of *Archaeopteryx*. This firm union is best indicated by the right scapulo-coracoid (unnoticed by Heller, 1959) in the Maxberg specimen, where it is preserved still united, although displaced some 8 or 9 cm from the pectoral region and the rest of the skeleton.

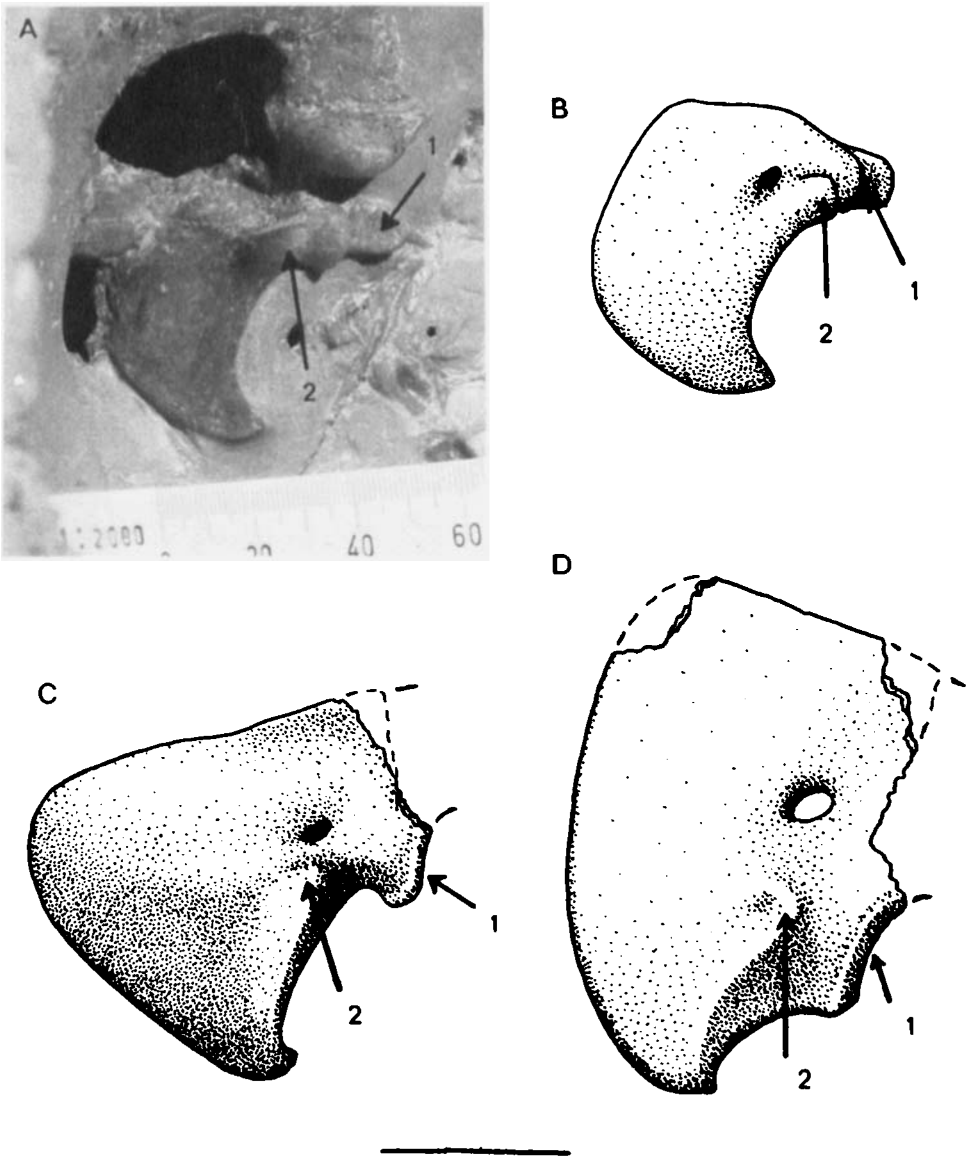


Figure 14. A, Left coracoid of *Archaeopteryx lithographica* (London specimen, underside of main slab; B, same-scale reconstruction of the same coracoid seen in anterior view. For comparison, theropod coracoids, all viewed in antero-lateral aspect; C, *Deinonychus antirrhopus*, Y.P.M. 5236 (drawn reversed for comparison); D, *Allosaurus* sp., Y.P.M. uncatalogued. Arrow 1 indicates the glenoid and arrow 2 points to the "biceps tubercle". Scale divisions in A = 0.5 mm; scale line in C and D = 5 cm.

Coracoid morphology is best seen in the left coracoid of the London specimen, well exposed on the underside of the main slab (Fig. 14A, B). As preserved there, the coracoid is relatively large, subrectangular and plate-like and is shaped very much like that of theropods. It is not elongated into the stout, strut-like form of modern birds. Just anterior to and below the glenoid portion and below and lateral to the supracoracoid foramen, there is a prominent tubercle or process. This feature, referred to as the biceps tubercle (Walker, 1972), is also well developed in many theropods, including *Deinonychus*, and has been interpreted as the probable site of origin of M. biceps brachii (Ostrom, 1974b, 1976). Figure 14 shows the strong resemblance between the coracoids of *Archaeopteryx* and some theropods.

Hindlimb and pes

Like the hand and forelimb, the foot and hind leg of *Archaeopteryx* have been compared with those of theropods (see especially Heilmann, 1926). There is also a marked similarity to the hind leg and foot of modern birds, which, together with the plumage and the (false) avian pattern of the pelvis, has been taken as strong evidence for the avian identification of these specimens.

Pes. Parts of the pes are preserved in all five skeletal specimens of *Archaeopteryx*, but the most complete and best examples are in the new Eichstätt specimen and the Berlin specimen. The pes is a four-toed structure in which the fifth toe has been lost and the first toe has been reversed to a posterior position, opposing the other toes (Fig. 15A). The principal supporting digits are II, III and IV, with the third the longest and the other two somewhat shorter and subequal in length. Digit I, the hallux, is much shorter than the others and is somewhat elevated on the metatarsus. The phalangeal formula is primitive (2-3-4-5) both in *Archaeopteryx* and in all adequately known theropods. The relative lengths of the phalanges are also primitive, with the proximal phalanx being the longest in all toes, in contrast to the phalanges of the hands. Similar phalangeal proportions are found in theropods and in most birds (exceptions are birds of prey, including owls, in which the penultimate phalanges are the longest—as in the hand of *Archaeopteryx*). Figure 15 shows these similarities between *Archaeopteryx* and certain theropods.

Metatarsus. The metatarsus of *Archaeopteryx* consists mainly of three complete elements, metatarsals II, III and IV. The first metatarsal is reduced to a very short wedge-like bone located distally, thus having no contact with the tarsus. It is closely appressed to, but not fused with, the postero-medial surface of the second metatarsal. Until discovery of the Eichstätt specimen, no vestige of metatarsal V had been recognized, but in the left metatarsus (on the main slab) of that specimen there is a very thin (less than 0.5 mm) splinter of bone about 6.5 mm long, extending from the tarsus down the posterior surface of the fourth metatarsal (Fig. 16A). The shaft tapers very slightly distally and the proximal end is somewhat expanded into what appears to be an articular head. If this actually is a remnant of the fifth metatarsal, as Wellnhofer (1974) also believes, then the metatarsal condition in *Archaeopteryx* is much more similar to that in a variety of theropods, such as *Coelophysis, Composognathus* (Fig. 16B), *Deinonychus, Velociraptor,* and *Stenonychosaurus,* than it is to either modern birds or pseudosuchians.

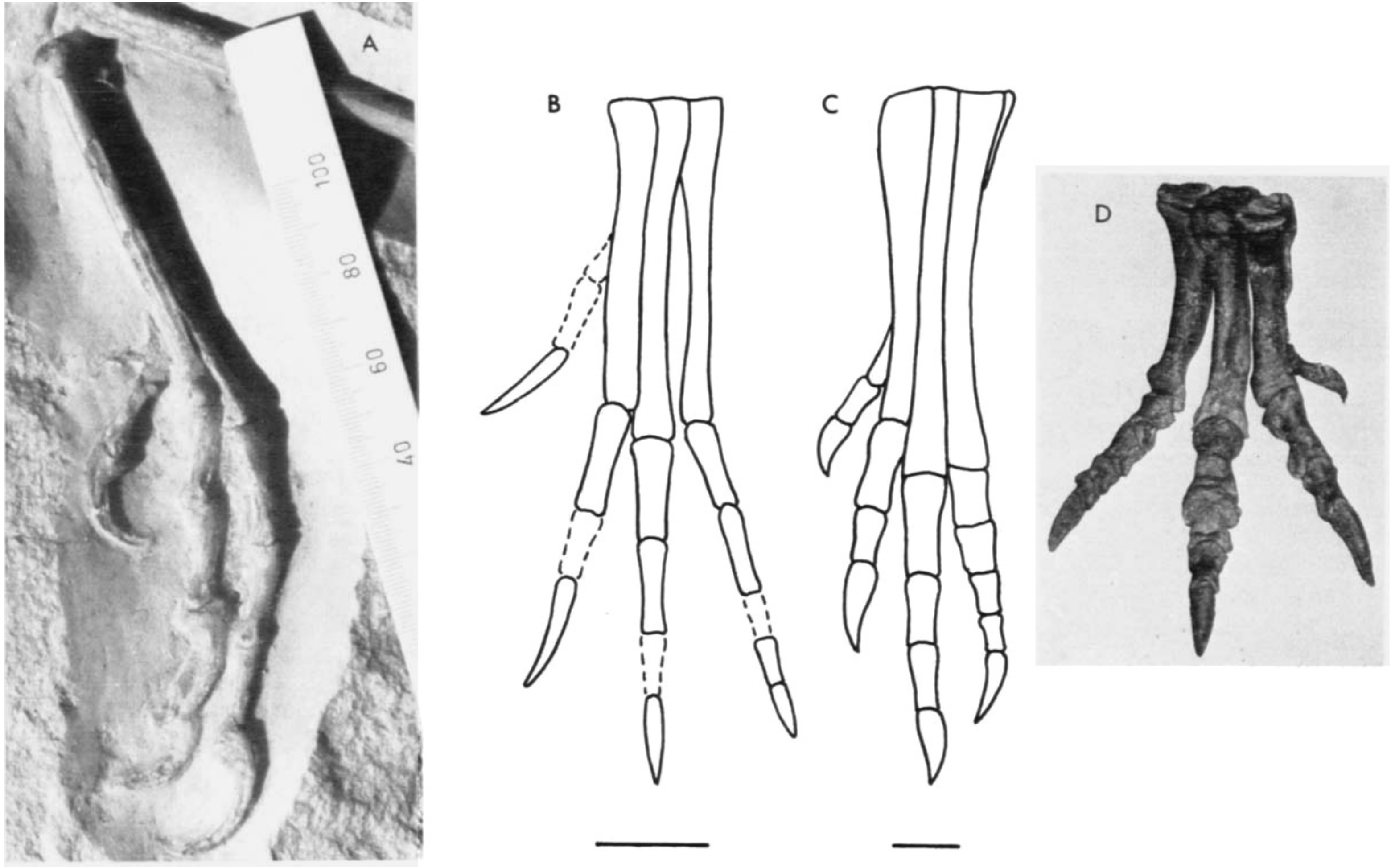


Figure 15. The left pes and metatarsus of *Archaeopteryx lithographica* (A), London specimen, in lateral view, compared with those of *Ornitholestes hermanni* (B), in anterior view; *Stenonychosaurus inequalis* (C), in anterior view; and *Allosaurus fragilis* (D), right foot in anterior view. Notice the reversed hallux, as contrasted with the condition characteristic of ornithopods (see Fig. 4B, E). Scale divisions in A = 0.5 mm; horizontal scale lines in B, C and D = 4 cm. Compare these structures with those of Fig. 28.

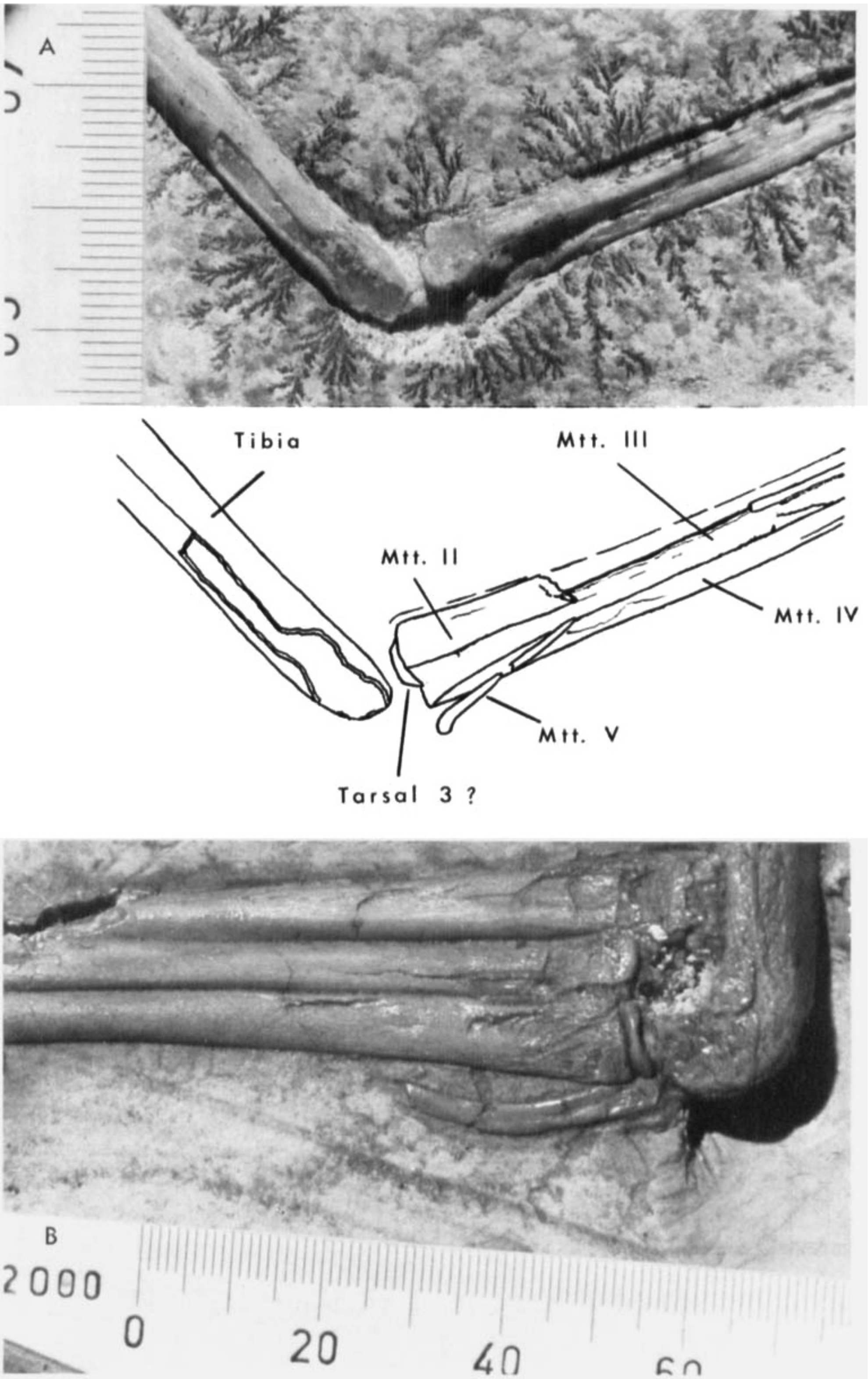


Figure 16

Over the years there have been different opinions as to whether the three main metatarsals of *Archaeopteryx* were fused or not (Owen, 1863; Marsh, 1881b; Dames, 1884; Petronievics, 1925; Heilmann, 1926; de Beer, 1954b; Heller, 1959). It is possible that the metatarsus is not fused in all of the specimens, although evidence against this is the fact that there is no physical separation or displacement of *any* of the three main metatarsals preserved in *any* of the specimens of *Archaeopteryx*. Moreover, the Maxberg specimen, as reported by Heller (1959), reveals no discernible physical separation or suture between the proximal ends of the three main metatarsals. X-rays indicate fusion of these elements proximally, but not distally (Heller, 1959: pl. 13-1). Wellnhofer (1974) concluded that the metatarsus was not fused in the new Eichstätt specimen, but that specimen is almost certainly an immature individual. Fusion of the metatarsals, even if only partial and variable, is the most significant difference between the metatarsus of *Archaeopteryx* and that of most theropods. With the exception of *Syntarsus* (Raath, 1969) and *Ceratosaurus* (where it may be pathological), fusion of the metatarsus is not known in theropods. (Neither is it known in ornithischians or pseudosuchians.)

Despite the bird-like fusion (even if incomplete), the metatarsus of *Archaeopteryx* is distinctly non-avian in another feature. There is no sign whatever of the prominent posterior crests of the hypotarsus (entocalcaneal and ectocalcaneal ridges) on the proximal posterior surfaces. This condition is likewise characteristic of all theropod metatarsi. Considering the prominence of the hypotarsus in modern birds, we can presume that the condition in *Archaeopteryx* and theropods reflects relatively poor leverage for the M. gastrocnemius and probably is a primitive condition.

Tarsus. The tarsus is not clearly preserved or fully discernible in any of the specimens of *Archaeopteryx*, but it appears to consist of two proximal elements, astragalus and calcaneum, which are co-ossified with the tibia and fibula, and two or perhaps three distal tarsals which are fused to the metatarsus. Thus *Archaeopteryx* would appear to have had at least an incipient tarsometatarsus, although not yet fully avian. Consequently, the ankle joint is a mesotarsal joint, as in modern birds, and also as in theropods and ornithopods. The astragalo-calcaneum is recognizable in all but the Teyler specimen, but is most distinct in the London and Berlin specimens. Both of the last, and the Eichstätt specimen, clearly show a well developed ascending process of the astragalus closely applied to the anterior surface of the tibial shaft (see Fig. 17A, B). This same feature is present in all adequately known theropods, except *Syntarsus* (Raath, 1969). It also occurs in very early developmental stages of many birds, but is not recognizable in mature individuals. An anterior ascending astragalar process is not known in any ornithopod, despite their having a mesotarsal joint, nor is it known in any pseudosuchian.

The Eichstätt specimen provides the best evidence concerning the distal tarsals, although the details are not beyond challenge. The left ankle, preserved

Figure 16. Left metatarsus and tarsus of the Eichstätt specimen of *Archaeopteryx* (A) showing the splint-like fifth metatarsal, compared with the same features of the right foot of *Compsognathus longipes* (B). Scale divisions = 0.5 mm. Mtt, Metatarsal.

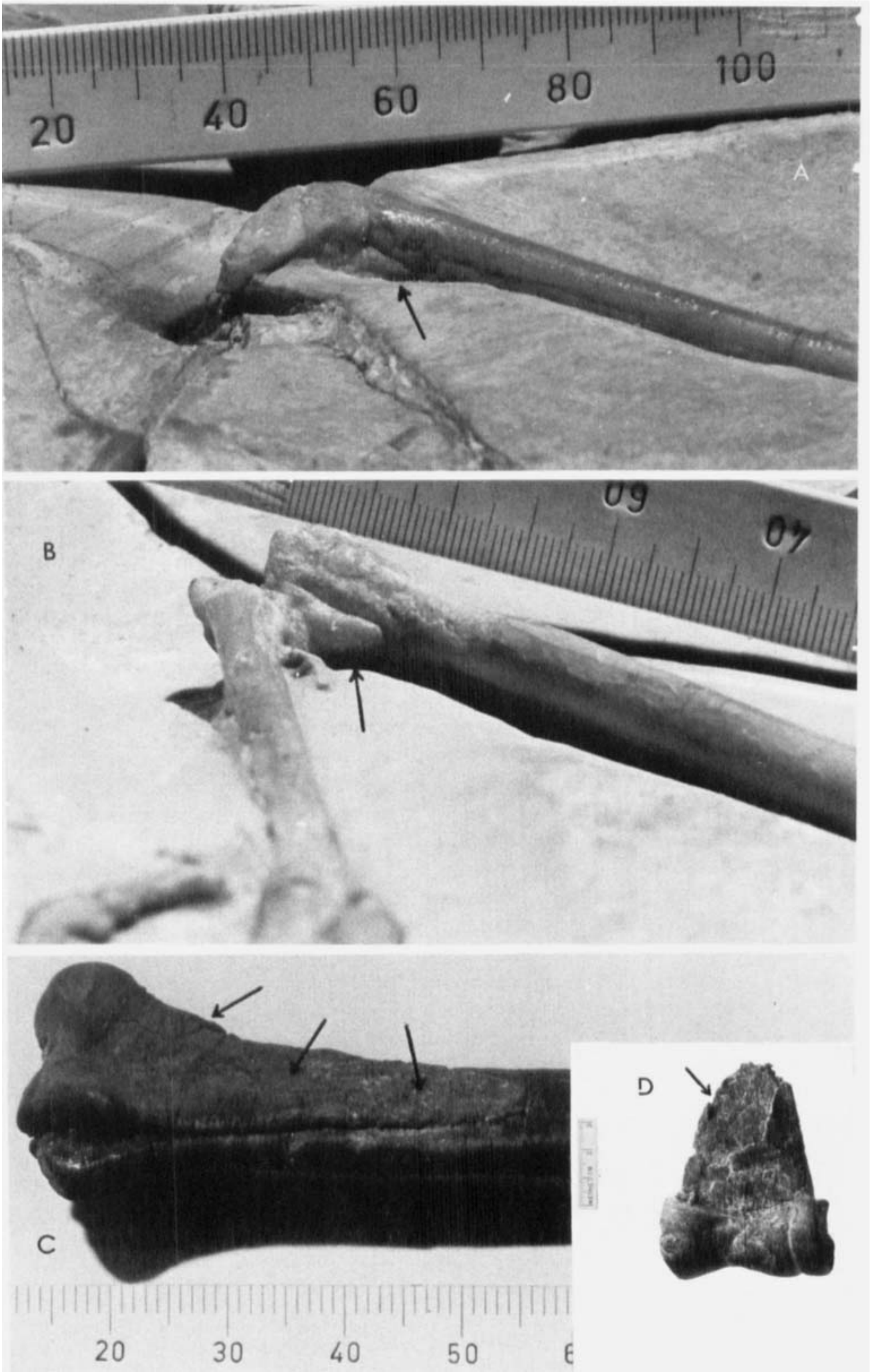


Figure 17

on the main slab, shows two distinct cap-like distal tarsals tightly appressed against the proximal ends of metatarsals II and III. In the Maxberg specimen, metatarsals III and IV are capped by a distal tarsal, whether by one or two cannot be determined. Probably, this represents the same element that caps metatarsal III in the Eichstätt specimen. From this we can conclude that the tarsus of *Archaeopteryx* had a minimum of at least two distal tarsals and perhaps as many as three. Wellnhofer (1974) suggests that a third tarsal may cap the fifth metatarsal. Perhaps the most important feature, however, is that some distal tarsals, whatever their number, were at least partly fused to the metatarsus, as is clearly shown by the Maxberg and Eichstätt specimens.

The partial fusion of tarsals to metatarsals, and probably of the main metatarsals to each other, approaches the condition of the modern avian tarsometatarsus more than that of any other group. In theropods, distal tarsals are preserved in *Syntarsus*, two of which are fused with the second and third metatarsals. Only two distal tarsals (unfused) are known in *Deinonychus* (capping metatarsals II, III and IV) and *Allosaurus* (capping metatarsals III and IV only). *Struthiomimus* has three distal tarsals applied to the proximal ends of metatarsals II and IV.

No final judgement can be made at this time as to the exact nature of the distal tarsalia of *Archaeopteryx*, but they appear to approach the theropod condition more closely than that of pseudosuchians. This is consistent with the theropod-like foot, the nature of the proximal tarsals, and the mesotarsal joint.

Tibia and fibula. These elements are perhaps less distinctive than other elements of the hindlimb, but nevertheless collectively they are intermediate between those of theropods and later birds. Both bones are relatively more slender than in theropods, even the very small forms like *Compsognathus* and *Microvenator*, but are more robust than in most later birds. The fibula is complete, extending from the knee to the tarsus, and is not fused to the tibia, although it is closely applied to the tibia throughout its length, reminiscent of the condition in some theropods (*Compsognathus, Deinonychus, Struthiomimus*). In most modern birds the fibula does not reach the tarsus. and is rarely fused to the tibia except distally. In their relative lengths these two bones are more bird-like than theropod-like, being about 35% longer than the femur. Among theropods, only in ornithomimids, *Microvenator, Compsognathus*(?), *Saurornithoides* and *Deinonychus* (Ostrom, in press) is the length of the tibia known to exceed that of the femur, but never by more than 15%, whereas this condition is virtually universal among modern birds. The tibia of *Archaeopteryx* bears a prominent internal cnemial crest, as in both birds and theropods, but unlike modern birds it has no external cnemial crest.

Femur. The femur of *Archaeopteryx*, like the epipodials, appears to be intermediate in its morphology between those of theropods and modern birds.

Figure 17. Comparison of the tarsus in *Archaeopteryx* and two theropods. A, Berlin specimen of *Archaeopteryx*, left tarsus in anterò-medial aspect; B, London specimen of *Archaeopteryx*, left tarsus in antero-medial view; C, *Microvenator celer* (A.M.N.H. 3041), left tibia and astragalus in antero-lateral aspect; D, *Deinonychus antirrhopus* (Y.P.M. 5226), left astragalus and calcaneum in anterior view. Arrows mark the prominent ascending process of the astragalus, a feature found only in theropods, *Archaeopteryx* and early stages of modern bird ontogeny. Scale divisions in A and B = 0.5 mm; in C and D = 1.0 mm.

Although shorter than the tibia, it is relatively longer and more slender compared with that of many birds and all larger theropods. It is also longer and more slender than that of some small theropods, such as *Compsognathus*. Perhaps its most distinctive character is the pronounced antero-posterior, non-sigmoidal curvature that is well preserved in all specimens (Fig. 18). Similar curvature occurs in most birds and all small theropods (*Compsognathus*, *Coelurus*, *Ornitholestes*, *Microvenator* and struthiomimids), but not in the larger forms. This may be a reflection of normal femur position—nearly vertical in the heavy bipeds such as *Allosaurus*, versus an extended, nearly horizontal, parasagittal attitude in the smaller theropods, as in living birds.

As for structural details, the head is sharply offset from the shaft at about 90°, but is angled slightly forward of the transverse plane. The Berlin (underside) and Eichstätt (main slab) specimens seem to show that the head is nearly hemispherical in form. Lateral to the head, two distinct but poorly defined prominences are well preserved in both the London and Berlin specimens (Fig. 18D). The larger and uppermost of these prominences lies just lateral to, and slightly behind the head and may correspond to the trochanter major of modern birds. On the other hand, it corresponds better to the "greater trochanter" of theropod femora (see the femur of *Microvenator*, Fig. 18D, E). Situated where it is, below, as well as behind and lateral to the head, there seems to be no way in which this structure could have articulated against an "anti-trochanter" of the ilium, as in modern birds. Hence we may presume that in *Archaeopteryx* it served exclusively for insertion of the "gluteal" muscles.

Below, lateral and anterior to this "greater trochanter" is a smaller and less well defined prominence or swelling. No comparable feature is located in this area in modern birds (unless it is the anterior part of the trochanter major), but theropod femora often bear a small to moderate process here, sometimes as a high flange and sometimes as a low knob. This feature is commonly referred to as the "lesser trochanter". Neither of these "trochanters" is the true homologue of mammalian trochanters, and they may not be homologous with theropod "trochanters" either, but the similar location in *Archaeopteryx* and known theropods is suggestive, to say the least.

A distinct knob also occurs below and posterior to the "lesser trochanter" in *Archaeopteryx*, on the external posterior surface of the shaft. A similar feature occurs at this site in *Microvenator* and *Deinonychus* (Ostrom, in press) and various other theropods. The functional significance of this structure (here termed the posterior trochanter), is not known.

Hindlimb summation. As with the forelimb, each of the hindlimb elements in *Archaeopteryx* has striking morphological resemblances to the same elements in various theropods. Considered as a whole, the hindlimb is perhaps more bird-like than theropod-like, particularly because of the slender form and the respective proportions of the several segments. Compared with total forelimb length, hindlimb length is also more avian than theropodian, but is closer to the latter than to most pseudosuchians (see Fig. 31).

Pelvic girdle

Reference has already been made to the importance attributed by past workers to the pelvis, particularly because of the apparent bird-like orientation of the pubis as it is preserved in the Berlin specimen. As I demonstrated earlier,

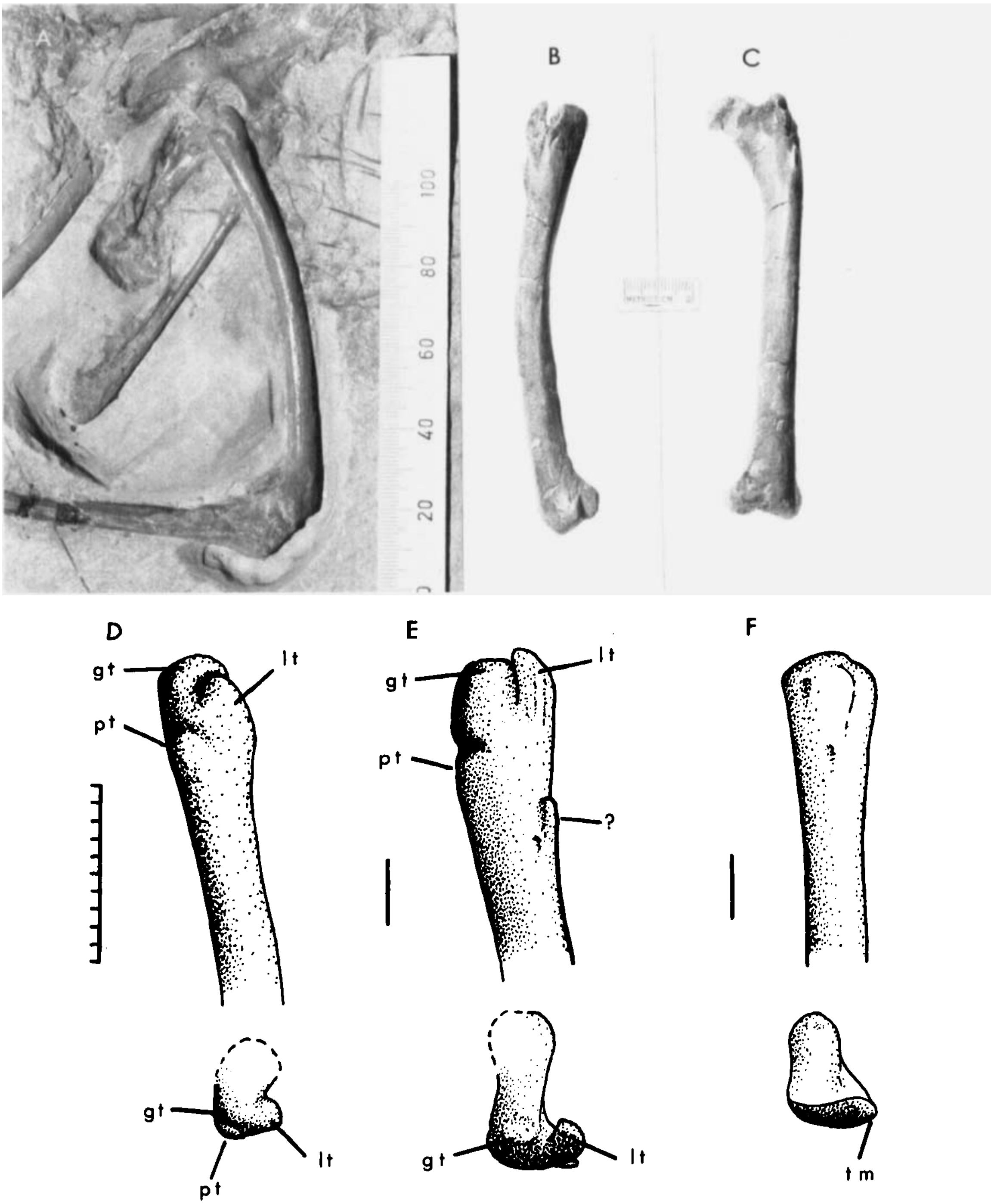


Figure 18. Right femur, Berlin specimen of *Archaeopteryx* (A) compared with the left femur of *Microvenator celer* in lateral (B) and anterior (C) views. Notice the simple fore-aft curvature in both. D, E and F contrast the proximal ends in lateral (upper series) and proximal (lower series) views of the right femora of *Archaeopteryx* (D), *Microvenator* (E), and a modern carinate, *Cathartes* (F). Scale divisions in A = 0.5 mm, in C and D = 1.0 mm. Vertical scale lines = 10 mm. gt, Greater trochanter; lt, lesser trochanter; tm, trochanter major; pt, posterior trochanter. See Fig. 30.

there is considerable evidence (see pp. 102-9) that establishes beyond any doubt that the pubic position preserved in that specimen is not the natural position. Hence the supposed similarity to the ornithischian pelvis cannot be verified in this or in any of the other specimens of *Archaeopteryx*. The original pubic position cannot be determined with certainty either, but it appears probable that in the Eichstätt specimen the preserved position approximates the natural position. This orientation is intermediate between the modern avian condition and that of theropods.

Pubis. The pubes are best preserved in the Eichstätt, Berlin and London specimens, with only fragments preserved in the other two. The London specimen establishes the presence of a long symphysis uniting the pubes distally (Fig. 20A) and extending over nearly half their total length. A pubic symphysis is a distinctly reptilian condition, in contrast to birds where the pubes are fused only in the ostrich.

The pubis of *Archaeopteryx* is very long, almost as long as the femur, with a narrow cylindrical shaft. The distal extremity is enlarged in the sagittal plane into a backwardly directed foot-like expansion (Fig. 19D, E). The London specimen seems to show this feature expanded transversely, as well as longitudinally, but such is definitely not the case in the Berlin, Eichstätt or Teyler specimens. The size and shape of the distal expansion vary somewhat among these last three specimens, perhaps because of varying degrees of preservation of associated cartilaginous tissue (see this region in the Eichstätt counterpart slab, Fig. 19E). Proximally the shaft expands moderately in an anterior-posterior direction. The Berlin specimen seems to show a sharp angular forward projection (Fig. 20B) just below the pubic peduncle of the ilium. However, the Eichstätt specimen clearly lacks any such projection, and in view of the dislocation of the pubis in the Berlin specimen, that feature is perhaps best considered as an artifact. Indeed, if the pubis is rotated forward, as I have suggested (see Fig. 8C), an orientation approaching the condition preserved in the Eichstätt, Maxberg and Teyler specimens results, and this anterior projection of the pubic peduncle disappears, becoming part of the junction between the pubis and the ilium.

The morphology of the pubis of *Archaeopteryx* is obviously similar to the pubic form in a variety of theropods, especially in its long narrow shaft, the foot-like distal expansion, the long symphysis and the great length relative to that of the femur. Compare this morphology with that of *Struthiomimus*, *Coelurus*, *Compsognathus*, *Microvenator* or, in fact, that of any theropod large or small (Fig. 19A, B, C, F). Virtually every theropod known from adequate material possesses this distinctive form of the pubis, there being only small differences in the shape or size of the distal expansion. To the best of my knowledge, this type of pubis is unique to theropods and *Archaeopteryx*.

Ilium. The ilium is not complete in any of the present specimens of *Archaeopteryx*, but a composite reconstruction is possible, using the Berlin, Eichstätt and London specimens (see Fig. 20). This reconstruction indicates a long, low blade with a gently convex dorsal border, a short and sharply tapered posterior process and a longer and more rounded anterior process. The London specimen suggests the presence of a slight downward expansion of the inferior margin of the anterior process at about mid-length, but this is not verified by the other specimens. The acetabulum, which is open as in all higher archosaurs,

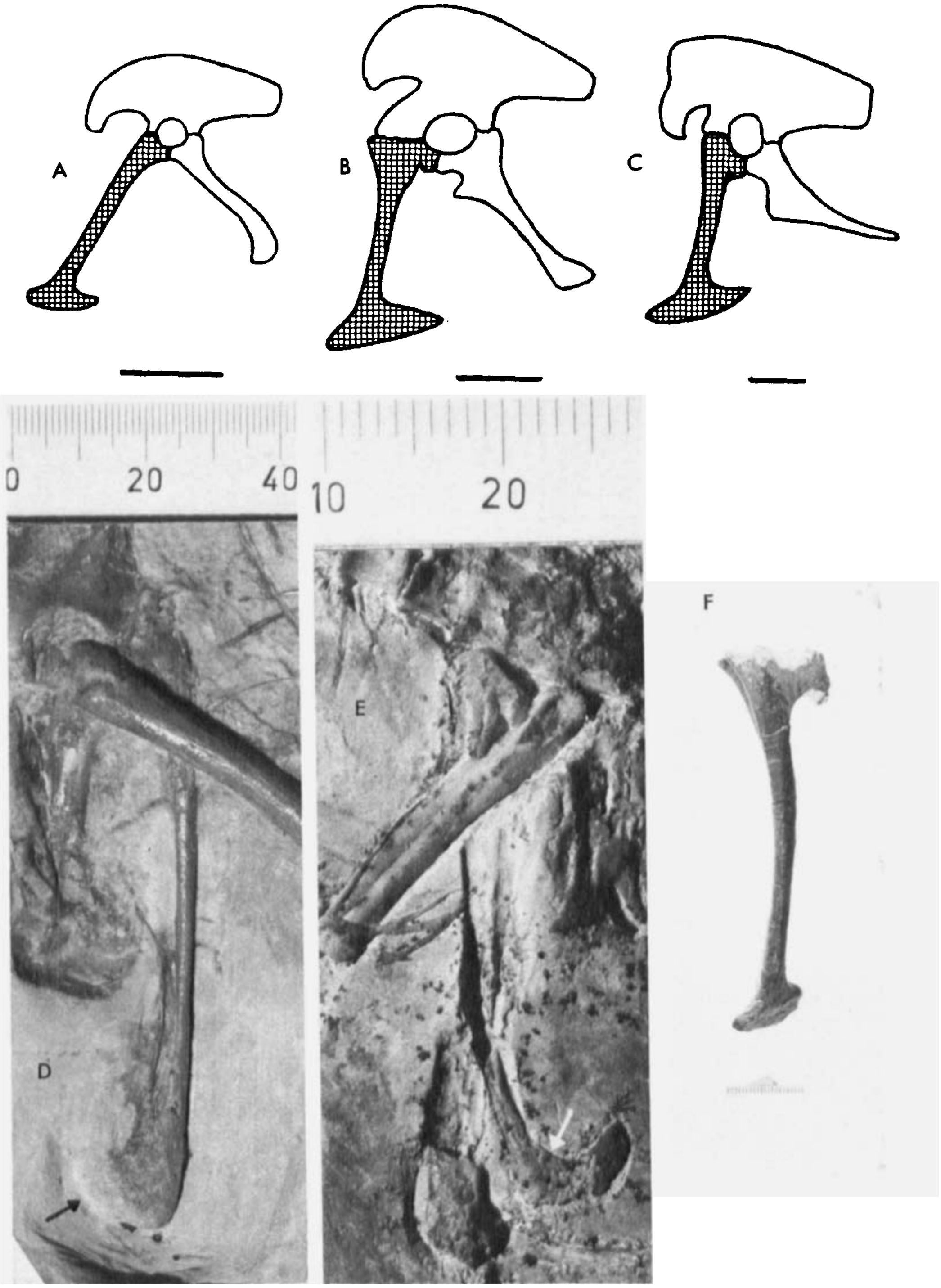
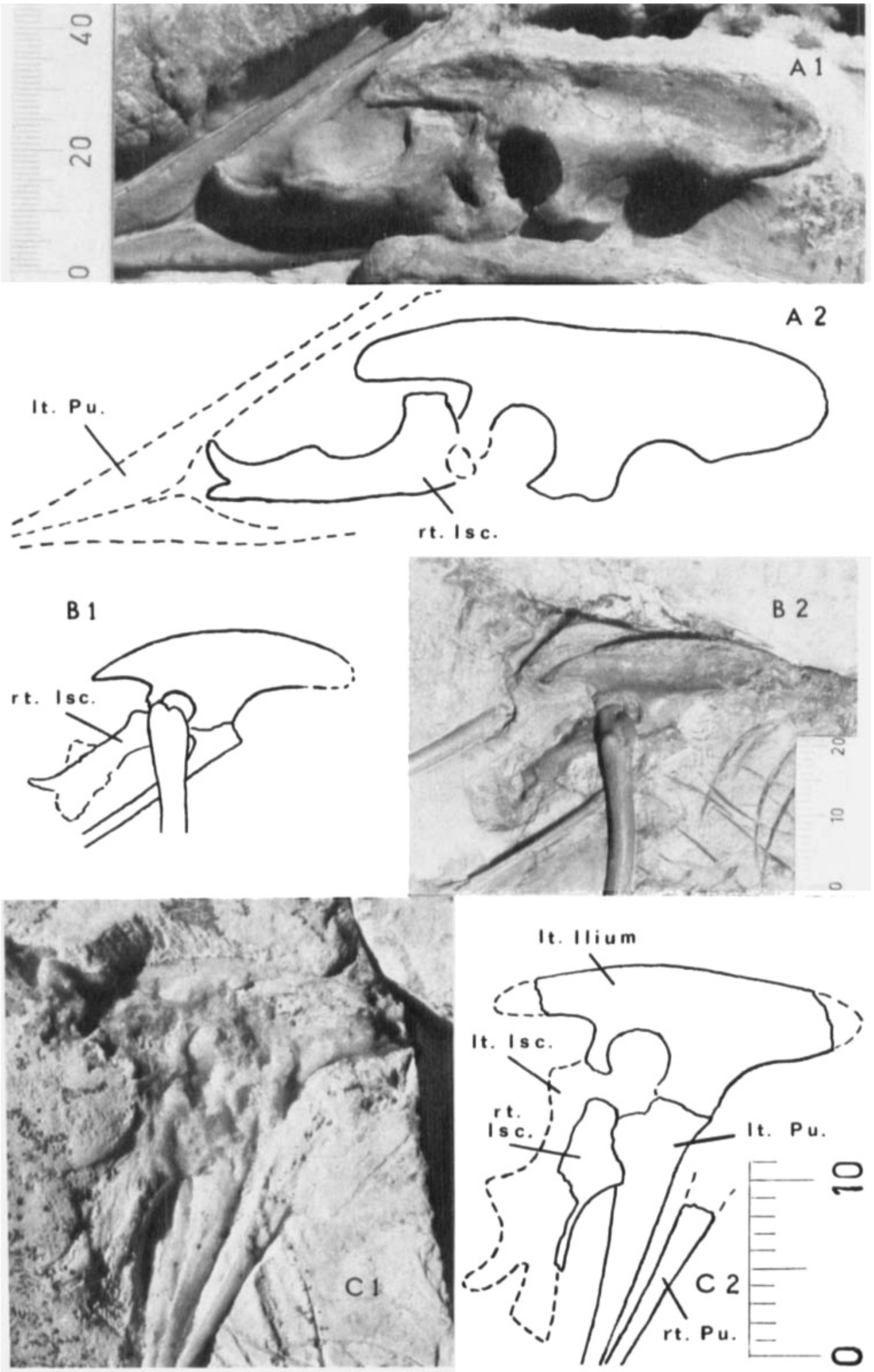


Figure 19. Comparison of pubic morphology in some theropods (*Struthiomimus*, A; *Allosaurus*, B; *Gorgosaurus*, C; and *Microvenator*, F) with that of the Berlin (D) and Eichstätt (E) specimens of *Archaeopteryx*. Long narrow pubic shafts and prominent distal expansions (arrows in D and E) are features that are known only in the pubes of theropods and *Archaeopteryx*. Horizontal scale lines in A, B and C = 20 cm; scale divisions in D = 0.5 mm; E and F = 1.0 mm. Compare with Fig. 32.


A1
40
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A2
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B1
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B2
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C1
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lt. Isc.
rt. Isc.
lt. Pu.
10
C2
rt. Pu.
0

Figure 20

is situated behind the mid-point of the ilium. The pubic peduncle is much more robust than the ischiadic peduncle, a typical saurischian condition, but there is no indication of any expansion that might be equated with a pectineal process. (The anterior "projection" of the pubis in the Berlin specimen, mentioned above, might be construed as a pectineal process, but, as I have shown, this feature is probably an artifact of the dislocation of the pubis and not a real process at all.) There is no anti-trochanter.

In its general shape, the ilium of *Archaeopteryx*, like the pubis, is strongly reminiscent of those of theropods. The most conspicuous differences are in the relative lengths of the anterior and posterior processes (the posterior process is generally the longer of the two in theropods), the posterior position of the acetabulum (a reflection of the short posterior process) and the lower total height of the ilium in *Archaeopteryx*. Nevertheless, the theropod ilium is much closer to that of *Archaeopteryx* than is that of any other reptile—or of any modern bird.

Ischium. This bone is best revealed, although incompletely, in the Eichstätt specimen. The form is unique (Fig. 20), but it is confirmed by the poorly preserved but similar ischium of the London specimen. There appears to have been a rather stout peduncle buttressed against the posterior proximal portion of the pubis (this part perhaps corresponds to the pubic side of the "fracture" line between the pubis and ilium in the Berlin specimen). Along the posterior border there are two sharp triangular projections, one proximal just beneath the iliac articulation and the other near mid-length. The most distinctive feature is the distal extremity which is bifurcated into a narrow, curved posterior process and a more robust anterior projection. The functional significance of this strange configuration is not known, especially since nothing comparable has been recognized in any other taxon. This unique morphology may be related to one other surprising aspect of the ischium in *Archaeopteryx*: its greatly abbreviated length as compared with that of the pubis, and the much greater relative length of the ischium in all theropods (but see below), pseudosuchians and modern birds. For example, there is no evidence on the proximo-ventral border of an obturator process, as occurs in theropods. Is it possible that the more anterior of the two processes at the distal extremity might be the obturator process on a greatly shortened ischium? Whatever the ancestry of *Archaeopteryx*, the ischium appears to have been greatly shortened and that may obscure the identity of the several seemingly unique processes. Although the morphology is different, it is interesting that the ischium of *Deinonychus* also is extremely short relative to the pubis (Ostrom, in press).

None of the specimens of *Archaeopteryx* provides any information about the ischiadic symphysis. Presumably this primitive condition was retained, in view of the very long pubic symphysis that is visible in the London specimen. However, the peculiar form of the ischium, especially of the distal processes and the posterior projection at mid-length, and the short length suggest that the

Figure 20. Morphology of the ilium and ischium in *Archaeopteryx*, as preserved in the London (A1 and 2), Berlin (B1 and 2) and Eichstätt (C1 and 2) specimens. Compare the shape of the ilium as preserved in these specimens with those of some theropods, as shown in Fig. 19A, B and C, and certain thecodontians (Fig. 32). Scale divisions in A = 0.5 mm; in B, C = 1.0 mm. isc, Ischium; lt, left; pu, pubis; rt, right.

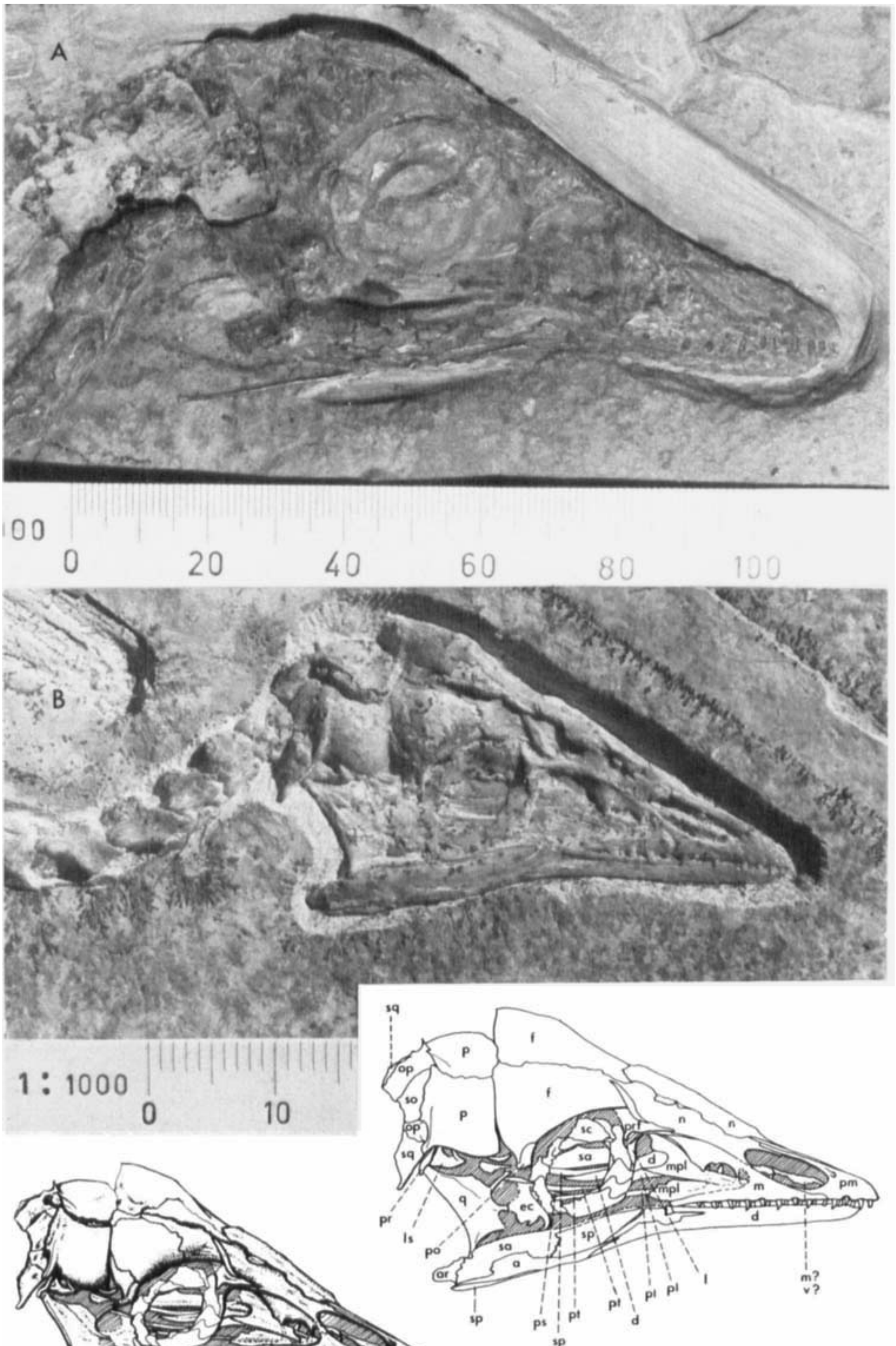
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Figure 21

ischiadic symphysis may have been reduced or entirely lost. The latter, of course, is an avian condition unknown in theropods.

Skull and jaws

Heilmann (1926) presented a rather detailed reconstruction of the skull and jaws of *Archaeopteryx* based entirely on the Berlin specimen (see figs 4, 5c, 105-2, 118-4, and 133c of Heilmann, 1926). Despite the details shown there, the actual specimen does not permit such detailed and precise conclusions. It is badly crushed and the bones are extensively fractured, chipped and distorted—to the extent that very few cranial or mandibular sutures are unmistakably identifiable (Fig. 21A). Heilmann's reconstruction has been republished by many authors and subsequent interpretations and hypotheses have been based on it (for example, see Bock, 1964). Quite probably, some authors have been unaware of the inadequate basis of Heilmann's reconstruction, and understandably so unless they have had the opportunity to examine the Berlin specimen itself. Bock (1964) pointed out the damaged condition of the Berlin skull and warned about the false "authenticity" that had resulted from the repeated publication of Heilmann's interpretation of that skull. Nevertheless, Bock accepted that reconstruction as "a reasonable one". Fortunately, the Eichstätt specimen now provides a comparative basis for evaluating and correcting past reconstructions of the Berlin skull (Fig. 21B).

Prior to examining the Eichstätt specimen, I had concluded, after many hours of microscopic inspection of the Berlin specimen, that the only indisputable features preserved there are the following:

(a) The skull is triangular in profile with a sharply tapered snout and a relatively deep and expanded temporal region.

(b) Only three major skull openings are visible in lateral aspect: a narrow, elliptical and obliquely oriented external naris; an intermediate-sized triangular antorbital fenestra; and a relatively enormous circular orbit containing a sclerotic ring composed of an indeterminate number of plates. The temporal region is imperfectly preserved, although clearly inflated, so despite the general conformation of the preserved regions which suggests the presence of one or more temporal fenestrae, the existence of the latter cannot be established from this specimen—all previous statements to the contrary notwithstanding.

(c) Teeth are present, apparently set in sockets, more or less isodont and of inflated conical form. The tooth row apparently did not extend behind the midpoint of the antorbital fenestra.

(d) The mandible is long and very shallow, and bears teeth which, like those in the maxilla, also seem to be thecodont. There seems to be a relatively long retroarticular process and there may be an external mandibular fenestra, as suggested by Heilmann (1926), but this last is far from certain (see later comments).

Figure 21. Skulls of the Berlin *Archaeopteryx* (A) and the new Eichstätt *Archaeopteryx* (B). Line drawings below (from Wellnhofer, 1974) interpret the details preserved in the Eichstätt skull. For a reconstruction of the Eichstätt skull, see Fig. 33C. Scale divisions in A = 0.5 mm; in B = 1.0 mm. Compare the skull morphology preserved in these two specimens with that illustrated in Fig. 22.

(e) The quadrate–squamosal region is badly damaged, but judging from the backward extension of the parietal area relative to the preserved position of the jaw articulation, and the coincidence of the anterior extremities of upper and lower jaws, the suspensorium was probably inclined forward (descended anteriorly).

(f) Associated with the lower jaw are two delicate, rod-like bones, 0.5 mm in diameter, that are probably part of the hyoid apparatus.

Without dwelling on the unverifiable positions and courses of the cranial sutures reconstructed by Heilmann, I should call attention to just one recent interpretation that has resulted from Heilmann's restoration. This is the suggestion by Cracraft (1970) that the mandible of *Archaeopteryx* provides an example of mosaic evolution. Cracraft's point is that *Archaeopteryx* (according to Heilmann's reconstruction) possessed an external mandibular fenestra bordered below by the dentary, as in birds, rather than by the angular as in reptiles. The toothed mandible thus features both reptilian and avian characters. Much as I would like to accept this interpretation, the highly fractured condition of the lower jaw bone (or bones) that borders the supposed mandibular fenestra, either below or above, makes it impossible to certify their identifications. In fact, the fractured upper margins of the supposed fenestra leave considerable doubt as to the very existence of a "fenestra"—a doubt which has not been removed by the new Eichstätt specimen.

The Eichstätt specimen (Wellnhofer, 1974) includes a much more complete and better preserved skull which undoubtedly will permit more reliable interpretations. This skull, together with Wellnhofer's interpretation of it, and the Berlin skull are illustrated in Fig. 21. Here it can be seen that the major features listed above are verified by the new specimen. Wellnhofer's study (1974) has already produced a number of new details, as well as confirming some of Heilmann's interpretations. Most significant for the present study, the two skulls together establish the presence of a variety of features that are also known (though not exclusively in all cases) in some small theropods such as *Ornitholestes*, *Compsognathus*, *Velociraptor*, perhaps *Saurornithoides*, and in some struthiomimids (Fig. 22). These features are:

(a) A sharply tapered snout.

(b) Long elliptical external naris bounded almost exclusively above and below by the premaxilla.

(c) A large triangular antorbital fossa which contains two small anterior openings and a large triangular posterior fenestra.

(d) A slender, nearly vertical preorbital bar separating the antorbital fossa and the orbit.

(e) A large circular orbit which contains a large sclerotic ring.

(f) A thin straight jugal bar.

(g) A stout quadrate of moderate length which is inclined forward (i.e., descends anteriorly).

(h) A lower jaw which is unusually shallow and has a conspicuous downward bend behind the tooth row.

(i) A long retroarticular process.

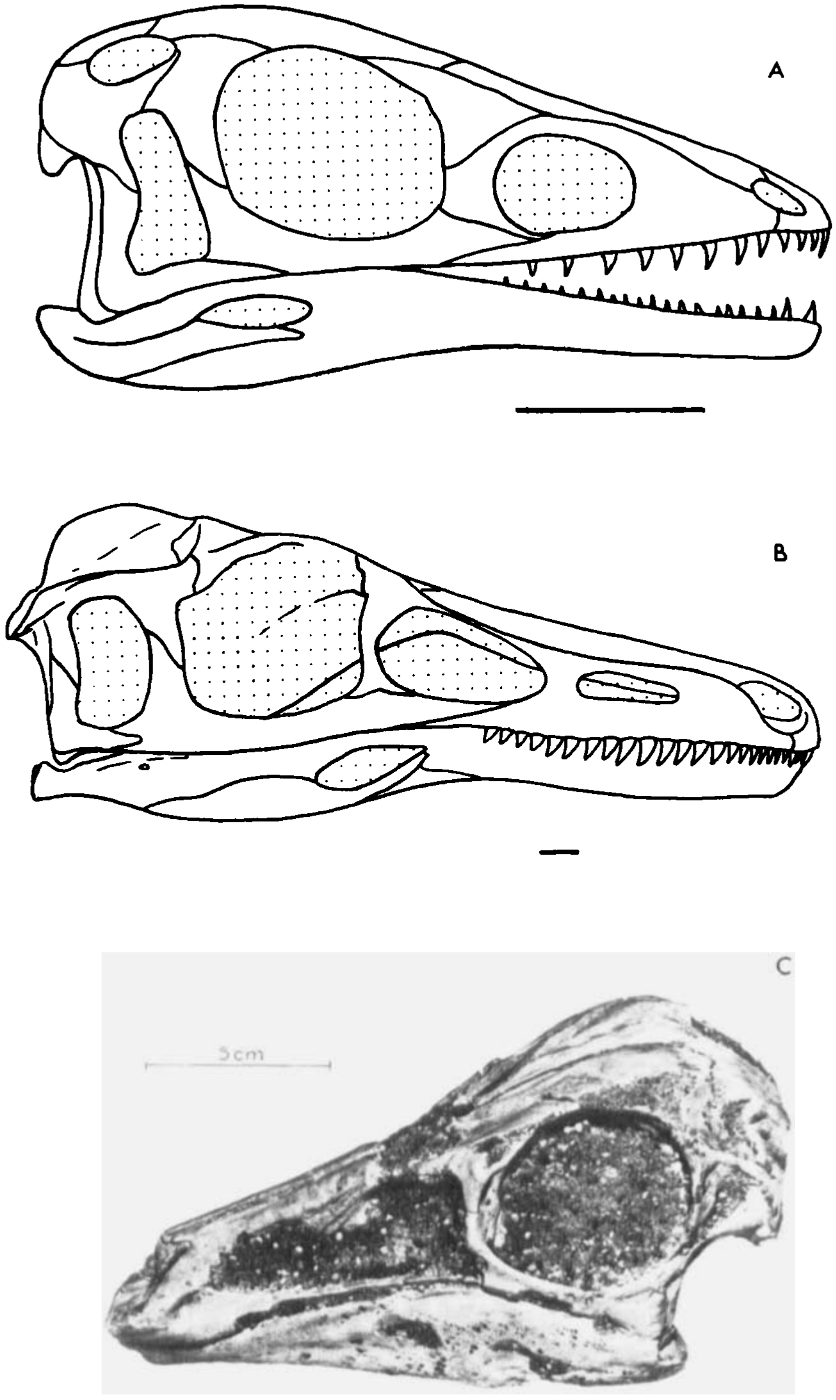

Figure 22. Skulls of A, *Compsognathus longipes* (partly after Heilmann, 1926); B, *Sauromithoides mongoliensis* (after Russell, 1969); C, *Gallimimus bullatus* (from Osmólska, Roniewicz and Barsbold, 1972). Horizontal scales in A and B = 10 mm. Compare these skulls with those illustrated in Figs 21, 33 and 34.

Important features that have not yet been recognized or confirmed in either specimen are:

(a) The positive existence of either temporal fenestra, although the quadrate apparently did not cover the entire temporal region and the general conformation of the temporal region suggests the presence of fenestrae.

(b) Positive existence of an external mandibular fenestra.

(c) A complete bony postorbital bar separating the orbit from the temporal region.

The last item is particularly important because it bears on the questions of kinesis and a streptostylic quadrate, both of which are considered critical conditions in bird ancestry (Versluys, 1912; Simonetta, 1960; Beecher, 1962; Bock, 1964). Bock, for example, has theorized that *Archaeopteryx* was probably both mesokinetic and streptostylic. The Eichstätt specimen seems to support Bock's speculations on both counts. Notice especially the distinct discontinuity between the parietals and frontals in that skull (Fig. 21B). Beecher (1962), on the other hand, believed that there was no evidence (and there was none in 1962) for mesokinesis and that for this reason *Archaeopteryx* must have been a side branch off the main path of avian evolution. (It is not clear to me why avian kinesis could not have developed *after Archaeopteryx*.) Wellnhofer (1974) is convinced that the Eichstätt skull was both kinetic (possibly mesokinetic) and streptostylic.

As for theropod kinesis, Versluys (1910, 1912) believed that most dinosaurs, including theropods, were kinetic. In a recent study, Colbert & Russell (1969) postulated that the small theropod *Dromaeosaurus* probably had a mesokinetic skull. On circumstantial evidence I suggested that the skull of *Deinonychus* might also have been kinetic (Ostrom, 1969). In any case, as Bock (1964) observed, there is no direct proof of mesokinesis in *Archaeopteryx* (that is still true), and this holds for all theropods as well.

For some, the possible absence of an external mandibular fenestra in the Eichstätt specimen may come as a disturbing surprise. After all, most modern birds and nearly all archosaurs, including thecodonts and theropods, possess this fenestra. I cannot testify to its universal occurrence in pseudosuchians, but it is variable in theropods, being absent in *Ornitholestes, Velociraptor* and perhaps *Compsognathus*. It is also not universally present in modern birds! Its presence or absence in *Archaeopteryx*, however, is not crucial for the simple reason that the question is beyond resolution—at least until such time as the reverse (left) side of the new Eichstätt specimen can be prepared. The region of the external mandibular fenestra is not intact on the right side of that specimen. The posterior parts of the dentary and the adjacent regions of the surangular and angular were apparently lost when the Eichstätt slabs were split, so that the inner surface of the splenial is exposed (Wellnhofer, 1974), rather than the external mandibular surface.

Some of the features listed above are not exclusive to *Archaeopteryx* and theropods and thus cannot be used as arguments in favor of a theropod ancestry (i.e., sclerotic ring, tapered snout, circular orbit), but they do add to the general "theropod-like" appearance of *Archaeopteryx*. On the other hand, there are a number of features that are not known in pseudosuchians but which are typical of theropods, such as elliptical naris, triple antorbital fenestrae, the anterior inclination of the quadrate, long retroarticular process, and shallow mandible with a downward bend*. These clearly argue in favor of theropod affinities and militate against a close relationship with pseudosuchians.

Another important cranial feature that by itself does not favour either theropod or pseudosuchian ancestry is the elevated posterior position of the occipital condyle and foramen magnum; this can be inferred from the position of the cervical series, well above the dorsal end of the quadrate (see the Berlin and Eichstätt skulls, Fig. 21). This primitive condition is characteristic of both pseudosuchians and theropods, in contrast to all later birds where the occipital condyle and foramen magnum are at the base of the skull, well below the level of the upper extremity of the quadrate. In this feature, *Archaeopteryx* was far from avian.

Vertebral column

Little precise anatomical information pertinent to the question under consideration here is obtainable from the vertebrae preserved in the various specimens of *Archaeopteryx*. In most respects the column appears more or less primitive. For example, it is generally agreed that the vertebrae lack the saddle-shaped articulations of the centrum that are characteristic of modern birds. The two or three surfaces of centra that are exposed in the London specimen seem to be slightly concave and several authors accordingly have reported the vertebrae of *Archaeopteryx* to be amphicoelous. X-rays of the Maxberg and Berlin specimens seem to substantiate this condition for some parts of the column, but the question is still open for other vertebral regions. If the vertebrae of the entire column were amphicoelous, this would be consistent with either theropod or thecodontian affinities and would prove nothing about bird origins. One possibly noteworthy feature is the apparent presence of small pleurocoels on some of the posterior dorsal vertebrae in both the London and Berlin specimens. Such pleurocoels are not known in pseudosuchians or ornithischians, but they are a common feature among theropods. The caudal vertebrae of *Archaeopteryx*, as is revealed most clearly in the Eichstätt specimen, are typical of long-tailed reptiles (theropods included) both in their form and in their progressive change in length and morphology along the tail. Of greatest interest, though, is the peculiar elongated form of the zygopophyses of the last 15 to 16 vertebrae. While not so extreme as in the dromaeosaurids *Deinonychus* or *Velociraptor*, or in the rhamphorhynchoid pterosaurs, their form is very reminiscent of the condition in struthiomimid theropods. Similarly, the chevrons behind the seventh caudal are also greatly elongated antero-posteriorly and severely flattened dorso-ventrally, as in both struthiomimids and dromaeosaurids. To the best of my knowledge, these conditions are not known in any pseudosuchian, or in any other reptile other than the theropods cited and rhamphorhynchoids.

According to my own count, which agrees with that of Dames (1884), the vertebral count of the Berlin specimen shows a minimum of 22 presacral vertebrae including an indistinguishable atlas. Twelve of these are clearly

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* Another, less direct, but very interesting piece of evidence that bears on theropod–avian relationships as advocated here is the similarity of the intramandibular joint of *Hesperornis* and *Ichthyornis* (Gingerich, 1973; Gregory, 1951) to those of *Deinonychus* and *Dromaeosaurus* and the similarity of the surangular–articular relationships in *Hesperornis* and *Deinonychus*.

recognizable as dorsals or trunk vertebrae, according to Dames, but I believe at least 13 and possibly 14 dorsals are present. Including a small undected atlas, the cervical count is then 8 or 9. The vertebrae of the London specimen are somewhat displaced and an unknown number are missing. According to de Beer (1954a,b), 20 precaudals are preserved in a continuous series. Five of these are definitely sacrals (de Beer included an unfused sixth, "T-15"). Of the remaining 15, all appear to be trunk elements, but the first is so poorly exposed and preserved that its identification is extremely doubtful and several others ("T-6" and "T-7", by de Beer's designation) similarly cannot be positively identified even as vertebrae. The Eichstätt specimen shows 22 distinct presacrals, eight of which appear to be cervicals. Adding one more for the undetected atlas, the Eichstätt vertebral column consists of nine cervicals and 14 dorsals. Wellnhofer (1974) recognized a fragment of the neural arch of the atlas and independently arrived at this same presacral count.

Dames (1884) estimated that seven sacral vertebrae are concealed beneath the right ilium of the Berlin specimen, but if the length of the last exposed dorsal is used as an index of sacral vertebral length, no more than six, and probably only five segments lie beneath the ilium. X-rays clearly show five, but the posterior end of the fifth is indistinct, so there might possibly have been a sixth even though there seems to be insufficient space for it. The London specimen, as already noted, seems to have five also, but the preservation is very poor in that region. The Eichstätt specimen clearly has five sacrals by my count—a number verified by Wellnhofer (1974). The caudal series in the London and Berlin specimens have been reported at 20 segments in each, but I think the Berlin specimen may have 21. The Eichstätt specimen positively includes no less than 22 caudal vertebrae. Wellnhofer counted 23. Thus, from these three skeletons, the vertebral formula of *Archaeopteryx* seems to be 9 cervicals, 14 dorsals, 5 (or 6?) sacrals and 20 to 23 caudals. A comparison of the vertebral counts in the various relevant taxa is as follows:

Archaeopteryx	Coelurosaurs	Pseudosuchians	Ornithopods
Cervicals 9 (inc. atlas)	9-10	7-8	9-13
Dorsals 14	13-14	13-18 (typically 17)	14-17
Sacrals 5	4-5	2-4 (typically 2)	4-8
Caudals 20-23	30-40	30-40	40-60

While not conclusive, there can be little disagreement that the vertebral count in *Archaeopteryx* conforms most closely to that of coelurosaurian theropods.

The vertebral count *per se* cannot be considered as strong evidence one way or the other, regarding the question of ancestry. However, another feature of the column that may be important is the nature of the cervical series. Both the Berlin and Eichstätt specimens show that the neck was both long and flexible. The strongly arched cervical series in both specimens indicates a high degree of flexibility and its great length sharply delineates the neck from the trunk region. The resulting picture is that of an animal with a nearly horizontal trunk and a well-defined, mobile, arched neck, supporting an elevated head. This image is reinforced by the elongated, angled form of the cervicals, as preserved in the Eichstätt specimen, which also suggests high flexibility. A long arched cervical series is one of the distinctive characters of "coelurosaurian", as opposed to "carnosaurian", theropods. Notice that this coelurosaurian-like neck extended back from the rear of the skull in *Archaeopteryx*—as it does in coelurosaurs, rather than from beneath as in later birds. The pseudosuchian neck also extends from the rear of the cranium, but here the neck consistently is short and poorly differentiated from the trunk in all presently known forms. Also, there is no evidence that the pseudosuchian neck was particularly flexible.

Quite probably the long flexible neck in *Archaeopteryx* and coelurosaurs was linked functionally with an active, obligatory bipedal habit. High mobility of the neck and head would be advantageous in locating and catching prey, but it also could have contributed to dynamic stability in a biped by producing small, but quick, shifts of weight in front of the center of gravity, countered by tail movements on the opposite side of the bipedal pedestal. In this sense, the short, relatively inflexible neck of pseudosuchians is consistent with our traditional conception of the most advanced pseudosuchians being only facultative bipeds, in which a bipedal posture could be maintained only while in rapid motion, as a result of inertia. In coelurosaurs, the cervical series constitutes 45% to 55% of the presacral column, whereas in pseudosuchians it seems to range from 25% to 35%. In *Archaeopteryx* it equals 45%.

Other skeletal elements

Sternum. De Beer (1954b) identified a fragment of the London specimen as the sternum. The object is so poorly preserved that it defies accurate description, let alone positive identification. By eliminating all the other missing elements of the skeleton, de Beer concluded that this fragment must be the sternum, figuring it as a narrow rectangular transverse bone. De Beer recounted past interpretations and speculated that this was the object which Marsh (1881) claimed was "a well-ossified, broad sternum". Whatever Marsh saw is unknown now, for he did not figure it. Of the several other missing elements dismissed by de Beer, it could just as easily be one or two badly preserved vertebrae. The X-ray published by de Beer (pl. VI-2) shows it to be a relatively dense ossification, which seems inconsistent with the thin plate-like form expected of a sternum. In view of this evidence and the condition in the other specimens which have no identifiable sterna, I believe that this object probably represents one or more vertebrae.

If the London sternum is in doubt, there can be no doubt about the condition in the Berlin and Eichstätt specimens. Dames (1897), after preparation of the underside of the main slab of the Berlin specimen, claimed that the sternum was present, at least in part (see his Fig. 1). Thanks to X-rays kindly supplied to me by Dr H. Jaeger of the Humboldt Museum für Naturkunde, the bone which Dames believed to be the sternum can now be seen to be the right coracoid oriented upright and still articulated with the right scapula. The left coracoid, which was correctly identified by Dames, has collapsed under sediment compaction and lies in the plane of the slab. Other fragments occur in this region, but none appears to represent any part of the sternum. The Eichstätt specimen, because it is small and thus probably immature, may not settle the question once and for all, but it contains no evidence whatever of an ossified sternum. The same is true of the much larger Maxberg specimen as well.

In view of the above, it must be concluded that there was no ossified sternum in *Archaeopteryx.* This has far-reaching implications for the flying ability of *Archaeopteryx,* as I have discussed elsewhere (Ostrom, 1974a). It has less significance, perhaps, for the question of the origins of *Archaeopteryx.* With the possible exception of one specimen of *Velociraptor* (Kielan-Jaworowska & Barsbold, 1972; pl. II-2), ossified sterna apparently are not known in theropods, despite the fact that they do occur in other saurischians. More surprising though is the fact that the sternum is also unknown in thecodontians! By that token, following Heilmann's example, we should perhaps exclude pseudosuchians from the ancestry of all later archosaurs, since sauropods, ornithischians, pterosaurs and crocodilians (as well as modern birds!) all possess sterna. This would appear to be doubly justified since the sternum is an endochondral element. However, it is obvious that we should not make any such rash conclusion on negative evidence only.

Clavicle–furcula question. The London specimen of *Archaeopteryx* includes a symmetrical "boomerang"-shaped bone (Fig. 23) which all previous investigators have identified as a furcula. It is situated in the anterior part of the trunk region between, but not in contact with, the two scapulae. It is a robust element with nearly uniform dorso-ventral breadth (about 4.0 mm) throughout. The exposed surface is convex. A similar bone is partially preserved in the two slabs of the Maxberg specimen. The dimensions are approximately the same, but impressions indicate that one side, probably the posterior surface, is concave. In neither specimen is there any indication of

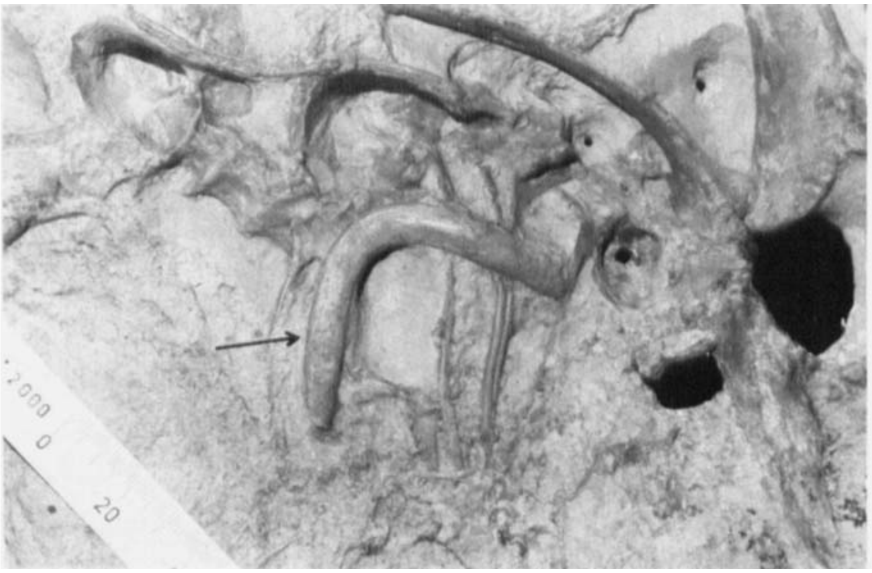

Figure 23. The furcula (arrow) in the London specimen of *Archaeopteryx.* A similar but fragmentary furcula is preserved in the Maxberg specimen, and several fragments in the Berlin specimen may represent parts of the same element. Scale divisions = 0.5 mm.

what might be considered a hypocleideum. Compared with most modern carinates, the angle between the rami of this furcula is quite broad, approximately 80°. In the Berlin specimen, fragments of bone adjacent to the coracoids have been considered as part of the furcula by several previous workers. I am inclined to agree with this identification, although it cannot be proved. In view of its presence in these three specimens, it is something of a surprise to find that there is no sign of a furcula in the very well preserved Eichstätt specimen. Its apparent absence may be an artifact of preservation, but a more likely explanation is that, because of the small size and probable immaturity of this specimen, the furcula had not yet ossified. (Is its absence here any less or more significant than its supposed absence in theropods?).

The presence of what appears to be a well developed furcula in the London and Maxberg specimens confirms the avian status of *Archaeopteryx* indicated by the feather impressions. It also has critical significance regarding the origin of *Archaeopteryx* and the specific ancestry of birds. Inasmuch as the furcula is widely accepted as the coalesced clavicles (but see p. 166), it follows that the immediate ancestor of *Archaeopteryx* must have possessed either paired or fused clavicles. Broom (1913) did not specify his reasons, but in all probability the supposed absence of clavicles in all theropods then known is what led him to conclude that dinosaurs were too specialized, but that pseudosuchians were "still primitive enough" to include bird ancestors. Heilmann (1926) presented an impressive comparison of the numerous similarities between birds and *Archaeopteryx* on the one hand and coelurosaurian theropods on the other. And after comparison with other potential ancestral groups, he concluded:

> "From this it would seem a rather obvious conclusion that it is amongst the Coelurosaurs that we are to look for the bird-ancestor. And yet, this would be too rash, for the very fact that the clavicles are wanting would in itself be sufficient to prove these saurians could not possibly be the ancestors of the birds." (Heilmann, 1926: 183)

On the basis of that single piece of negative evidence, Heilmann completely dismissed an impressive array of data and thereby effectively stilled all but a few advocates of a coelurosaurian ancestry of birds.

Although this will be discussed at length later, it is important to point out here that the *only evidence* that has been advanced so far that is contrary to a theropod ancestry of *Archaeopteryx* is the supposed absence of clavicles in theropods. This is negative evidence only and therefore inconclusive (like the absence of a sternum in all known thecodonts). Unless found in perfect articulation with the scapulocoracoid, the clavicle could easily be mistaken for a rib fragment. But even more significant is the discovery by Camp (1936) of the unmistakable presence of a clavicle in articulation with the scapula and coracoid in the small Triassic coelurosaur *Segisaurus*. Also, Osborn (1924) reported the presence of what appears to be a fused clavicle and interclavicle in the Cretaceous Mongolian coelurosaur *Oviraptor*. A remarkable specimen of *Velociraptor* reported by Kielan-Jaworowska & Barsbold (1972) also possesses what appears to be a clavicle in natural articulation. From these few specimens, it would seem that the clavicle is *not* lacking in all theropods and I suspect that a careful search would uncover others.

Gastralia. Gastralia, or dermal abdominal ribs, are present in all five skeletal specimens of *Archaeopteryx*, but they are best preserved in the Berlin and Eichstätt specimens. They are delicate hair-like bones, at least some of which are "V" or chevron-shaped. Their exact arrangement cannot be reconstructed with certainty, but they appear to have been rather widely spaced extending up and backward at a wide angle to the dorsal ribs, very much like the widely spaced arrangement preserved in *Struthiomimus altus* (see pl. 24, Osborn, 1917). Gastralia are present in a variety of reptiles including pseudosuchians and theropods. Their presence in all of the specimens of *Archaeopteryx* may be considered as evidence of reptilian origins, but it does not necessarily support either theropod or pseudosuchian affinities, although the resemblance is closer to the theropod pattern. It does, however, add evidence against the ornithischian affinities of *Archaeopteryx* since gastralia apparently are absent in all ornithopods*.

The presence of gastralia in *Archaeopteryx* and their absence in all modern birds presumably correlate with the unossified sternum that supposedly existed in the former and with the greatly enlarged and well-ossified sterna that are present in all the latter. In fact, the gastralia provide positive evidence that the sternum, whatever its condition in *Archaeopteryx*, must have been relatively small. Obviously, the absence of gastralia in modern birds has no significance relative to the avian affinities of *Archaeopteryx*.

Summary of theropod evidence

In summary, a considerable amount of evidence points to a close phyletic relationship between theropods and *Archaeopteryx*. The only derived characters for birds that are present in *Archaeopteryx* are the furcula and the evidence of feathers. By contrast, the specimens of *Archaeopteryx* possess a large number of derived characters for coelurosaurian theropods: tridactyl manus and metacarpus design, construction of the carpus, elongated forelimb, morphology of the scapulo-coracoid, construction of the pes and metatarsus with a short elevated hallux, mesotarsal joint with an anterior ascending process of the astragalus, morphology and orientation of the pubis, morphology of the ilium, obligate bipedal posture. These must be considered as *prima facie* evidence of very close phylogenetic relationship between *Archaeopteryx* and coelurosaurian theropods. To date, the only *evidence* that has been offered against a theropod ancestry of birds, the supposed absence of clavicles in the theropods, is now known to be false. Consequently, no longer is there any logical reason to dismiss the Theropoda as the most probable immediate ancestral stock of *Archaeopteryx* and higher birds.

The pseudosuchian evidence

Most advocates of a pseudosuchian ancestry of birds have followed Heilmann's (1926) example and discussed this with specific reference to *Euparkeria* and/or *Ornithosuchus* (see for example Tucker, 1938b; Simpson,

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* Gilmore (1924b) illustrated several isolated splint-like bones of *Stegoceras* (=*Troodon*), which he interpreted as abdominal ribs, but I believe them to be ossified caudal tendons. They were associated with such tendons (which are characteristic of nearly all ornithopods) and they are almost identical in form to ossified caudal tendons preserved in place in the pachycephalosaurid *Homalocephale* described by Maryánska & Osmólska (1974).

1946; de Beer, 1954b; Swinton, 1960, 1964; and Brodkorb, 1971), implying at least that these taxa were representative of the supposed pseudosuchian stage in bird ancestry. At the moment, though, the term Pseudosuchia means different things to different people. This is due in large measure to the many important thecodontian discoveries made in South America, Africa and elsewhere in recent years and the fact that no general consensus has been reached as yet concerning the relationships between these and previously known forms such as *Euparkeria, Ornithosuchus, Sphenosuchus* and others. Despite the fact that most authorities had come to accept the idea that all higher archosaurs and birds were probably descendant from pseudosuchian thecodontians, very little was actually known about pseudosuchians other than those mentioned above, and a few others. Acceptance of that theory is understandable though, because Broom (1913) and Heilmann (1926) both observed that the "pseudosuchians" then known were similar in some ways to *Archaeopteryx* or later archosaurs, yet were still primitive in many other features. Today, the picture is complicated by various new discoveries and it may be some time before the full significance and relationships of all the new specimens are understood and can be expressed in a "consensus" classification. For that reason, this section (which as a result may be somewhat premature) will deal with pseudosuchians in general (and occasionally with non-pseudosuchian thecodontians), rather than with a particular kind, to show that the basic coelurosaurian features of *Archaeopteryx* are not present in these reptiles as they are presently known. I hope to demonstrate that the relationship between *Archaeopteryx* and pseudosuchians is remote.

In recent years, several important events have occurred which have contributed further to the present confusion over what is or is not pseudosuchian. In 1964, A. D. Walker came to the conclusion that *Ornithosuchus* (long recognized as an advanced pseudosuchian and often referred to as *the* classic example of the pseudosuchian state) was not a pseudosuchian at all, but a primitive carnosaurian theropod; this conclusion is not generally accepted. Later, Walker (1970) proposed a revision of the traditional Order Crocodilia, recognizing a new Order Crocodylomorpha composed of two suborders, the Paracrocodylia and Crocodylia. The latter included all proper crocodilians plus various long-recognized primitive forms (Protosuchia). To the Paracrocodylia Walker assigned a variety of taxa which have certain crocodilian tendencies, but which seem to be removed from the main crocodilian lineage. Among these, Walker included *Sphenosuchus* from the Late Triassic of South Africa, which over the years has usually been classified as a pseudosuchian, even though its affinities with crocodilians have long been recognized (von Huene, 1925; Broom, 1927).

Bonaparte (1971a), in describing some of the new Triassic reptiles from Argentina, presented a new classification of all currently known thecodontians in which he recognized three pseudosuchian infraorders: Ornithosuchia (including *Ornithosuchus* and *Euparkeria*), Sphenosuchia (including with *Sphenosuchus* one of the new Argentine forms, *Pseudhesperosuchus*, and also *Triassolestes*) and Proterochampsia (including *Cerritosaurus* and the proterochampsids). Subsequently, Romer (1972c) published his first attempt at classifying the new and the old thecodontians, placing *Euparkeria* and *Ornithosuchus* in two, of three, separate families of the Pseudosuchia. He placed *Sphenosuchus* (and *?Pedeticosaurus* and *Hemiprotosuchus*) in the crocodilian suborder Protosuchia, which consisted of two families, Protosuchidae and Sphenosuchidae. Also included *incertae sedis* in the Protosuchia was Bonaparte's *Pseudhesperosuchus.* Romer regarded *Cerritosaurus* and other proterochampsids as proterosuchians rather than pseudosuchians.

Except for shuffling some possibly relevant taxa (not all have been mentioned here) in and out of the potentially ancestral "Pseudosuchia", these events would seem to have little bearing on the question at hand. That would be true except for two other papers by Walker (1972, 1974), in which he argues that *Sphenosuchus*, in addition to being close to crocodilian origins, is also close to the origin of birds.

Some authors may still prefer to consider *Sphenosuchus* as a thecodontian, perhaps even a pseudosuchian. But in deference to Walker's theory, I will not include *Sphenosuchus* in the following discussion dealing with the evidence for a pseudosuchian origin of birds. This should not be taken to mean that I either accept or reject Walker's taxonomic assignments. Romer (1972c), has summarized his views on the alignment of the Pseudosuchia, but these have not received general acceptance either. Romer's classification is as follows:

Order Thecodontia
  Suborder Pseudosuchia
      Family Euparkeridae: *Euparkeria (Browniella), ?Wangisuchus.*
      Family Ornithosuchidae: *Ornithosuchus (?Dasygnathus, Dasygnathoides), Gracilisuchus, Venaticosuchus, Riojasuchus, ?Parringtonia, ?Dyoplax.*
      Family Scleromochlidae: *Scleromochlus, ?Lagerpeton.*
      Pseudosuchia, presumably representing a number of distinct families: *Lagosuchus, Hesperosuchus, Lewisuchus, Saltoposuchus, Strigosuchus, Dibothrosuchus, Teleocrater, Erpetosuchus (Herpetosuchus), Triassolestes*.*

I also consider *Rauisuchus, Ticinosuchus* and *Hesperosuchus* as probable pseudosuchians.

Yet another alignment of thecodontians is that of Charig, Krebs, Süs & Westphal (in press), which I have adopted here (see Appendix).

Despite these uncertainties in classification, there is widespread agreement that "pseudosuchian type" thecodontians are more primitive in almost all characters than are all other non-thecodontian archosaurs and birds. And, although Krebs (1963, 1965, 1974) does not agree, it is generally held that as a group, they probably did give rise to all non-thecodont archosaurs and birds. But the question that still remains: Is there any reason to believe that *Archaeopteryx* arose directly from a pseudosuchian rather than from a coelurosaur? In the absence of any contrary evidence from coelurosaurs, we must determine if there is *any* concrete evidence in presently known

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* Charig & Reig (1970) considered *Saurosuchus, Prestosuchus, Mandasuchus* and *Ticinosuchus* to be pseudosuchians. Krebs (1965) had originally assigned *Ticinosuchus* to the Pseudosuchia (family Rauisuchidae) and in 1973 offered new tarsal evidence for a pseudosuchian placement of *Rauisuchus.* Although Romer (1972c) placed *Ticinosuchus* (and the other taxa above) in the Proterosuchia (Prestosuchidae), *Ticinosuchus* is included in the following discussion of pseudosuchian evidence.

pseudosuchians to substantiate a closer relationship between birds and pseudosuchians than between birds and coelurosaurian theropods.

Manus and forelimb

The pseudosuchian manus and forelimb are primitive and unspecialized in virtually every respect. Accordingly, it is conceivable that these structures could have been modified to the specialized condition of *Archaeopteryx*, just as they are supposed to have given rise to the equally specialized manus and forelimb of coelurosaurs. It must be emphasized, however, that there is nothing about the manus or forelimb, insofar as they are presently known in any pseudosuchian, that even remotely resembles features in either *Archaeopteryx* or any theropod. Independent derivation of two such strikingly similar appendages from a dissimilar, albeit primitive, ancestor is at least twice as improbable as a common derivation from a single lineage.

Manus. The pseudosuchian manus in all cases appears to have consisted of no less than four digits, and probably five. In *Euparkeria*, the hand is incompletely known, but Ewer (1965) reported parts of four metacarpals in two specimens. Similarly, a complete manus is not known in existing specimens of *Ornithosuchus.* Walker (1964), however, identified metacarpals I to IV and presumed that a fifth was present. Colbert (1952) reported fragments of five metacarpals in *Hesperosuchus* and Krebs (1965) reconstructed five complete digits in *Ticinosuchus* from disarticulated elements of both hands. As a "typical" pseudosuchian, *Ticinosuchus* seems to provide the best available evidence on the pseudosuchian manus. As pieced together by Krebs, the manus consisted of five complete digits (Fig. 24) with a primitive formula (2-3-4-5-3). The fingers are relatively short, apparently only a little longer than the respective metacarpals. The proximal phalanx is the longest in each finger and digit III is the longest finger.

This structure differs significantly from that of *Archaeopteryx* and most coelurosaurs. Conversion into either would require the loss of digits IV and V, great elongation of all remaining digits relative to their metacarpals, and elongation of all penultimate phalanges relative to the proximal elements. While digit V may have been reduced or lost in *Euparkeria* and *Ornithosuchus* and perhaps other genera as well, there is no certain evidence of this, nor is there evidence of reduction of digit IV in any pseudosuchian.

Metacarpus. As noted above, five metacarpals are present in *Ticinosuchus* and *Hesperosuchus.* Only four are known in *Euparkeria* and *Ornithosuchus*, although Walker (1964) supposed a fifth to be present. Bonaparte (1971b) identified five metacarpals in *Riojasuchus*, although the second to fifth were all incomplete. He described the first two as the more robust. In *Euparkeria*, metacarpal I appears to be the shortest, suggestive of the conditions in *Archaeopteryx* and many theropods, whereas V is the shortest in *Ticinosuchus* while IV (V is not known) is the shortest in *Ornithosuchus.* Metacarpal III (not II, as in *Archaeopteryx* and theropods) apparently is always the longest. None of the five metacarpals is complete in the only specimen of *Hesperosuchus*, but their slender construction, even of metacarpal I, suggests a greater relative length for the metacarpus in this genus.

Available evidence indicates a short, primitive construction of the pseudosuchian metacarpus, with five elements present in some and possible

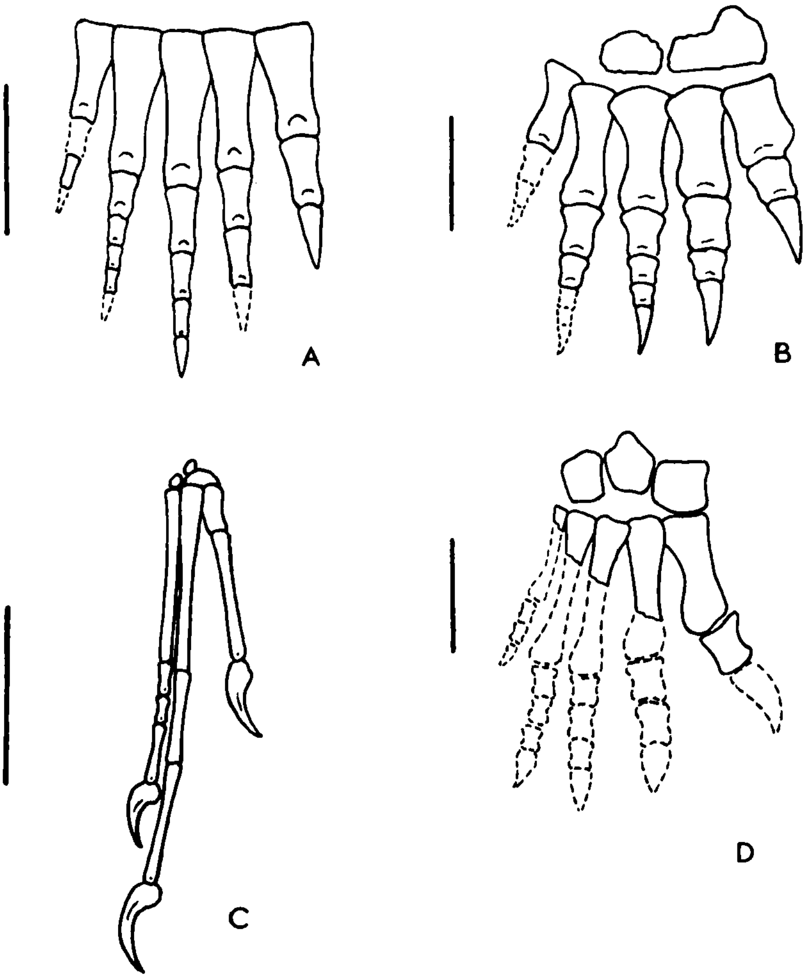

Figure 24. Comparison of some thecodontian hands with that of *Archaeopteryx*. A, *Ticinosuchus* (after Krebs, 1965); B, the aetosaur *Stagonolepis* (after Walker, 1961); C, *Archaeopteryx* (Berlin specimen); D, *Riojasuchus* (after Bonaparte, 1971b). All are right hands, but not drawn to the same length. Vertical scales = 3 cm. Contrast the pronounced differences from *Archaeopteryx* with the strong similarities illustrated in Fig. 9.

reduction to four in *Euparkeria* and perhaps *Ornithosuchus*. *Ticinosuchus* with metacarpal V the shortest, coupled with *Ornithosuchus* where IV is the shortest and no evidence of a fifth exists, might be considered as indicative of a trend among some pseudosuchians toward the three-fingered manus of *Archaeopteryx*. However, *Ornithosuchus* has an elongated metacarpal I, whereas in *Euparkeria* the first is very short and theropod-like, but there is no evidence that metacarpal IV is undergoing reduction. The metacarpus of *Archaeopteryx* obviously *could* have been derived from any of these, but structural similarities between the metacarpi of *Archaeopteryx* and the Pseudosuchia are not obvious.

Carpus. The few carpals that are known in pseudosuchians are, for the most part, rather indistinctive ossicles of uncertain identity. No carpals are preserved in *Euparkeria*, but because of the space between the metacarpals and the epipodials, Ewer (1965) supposed them to have been cartilaginous. Von Huene (1914) recognized three carpals in *Ornithosuchus*, and, more recently, Walker (1964) identified a fourth. Walker was not able to identify which carpals were represented. Krebs (1965) found only two elements in *Ticinosuchus* which he labelled the radiale and ulnare. Bonaparte (1971b) reported three large and massive carpals (radiale, ulnare and an intermedium) in *Riojasuchus*.

None of these various patterns shows any particular resemblance to the carpus of *Archaeopteryx* (see Fig. 24). In that light, there is nothing to be gained from theorizing about transitional stages from one to the other. The *Archaeopteryx* pattern could have been derived from one of these, but at the moment there is no evidence of that.

Radius and ulna. The epipodials of pseudosuchians are not particularly distinctive, being more or less straight and cylindrical and of varying robustness. Those of *Hesperosuchus* are long and quite slender, while those of *Riojasuchus* and *Ticinosuchus* are shorter and more massive. A moderate to prominent olecranon on the ulna is present in all. In *Hesperosuchus* and *Ornithosuchus*, the radius and ulna appear to have been positioned close together, while in *Ticinosuchus* and *Riojasuchus* there was a significant intermembral space. Only in *Hesperosuchus* does the epipodial form approach the very long and slender form of the radius and ulna in *Archaeopteryx*.

Humerus. The pseudosuchian humerus is considerably more robust and much shorter relative to the dimensions of the animal as a whole, than in either *Archaeopteryx* or coelurosaurs. The shaft is essentially straight but flares prominently at both ends and thus has a narrow-waisted shaft profile. The deltopectoral crest projects prominently from the shaft, but is rather short and limited to the proximal quarter of humeral length. Considerable variation exists in the relative massiveness of the pseudosuchian humerus (Fig. 25). That of *Hesperosuchus* is very slight, even delicate, as compared with that of *Ticinosuchus* or *Riojasuchus*. Apart from being straighter and more robust, the most conspicuous difference between typical pseudosuchian humeri and that of

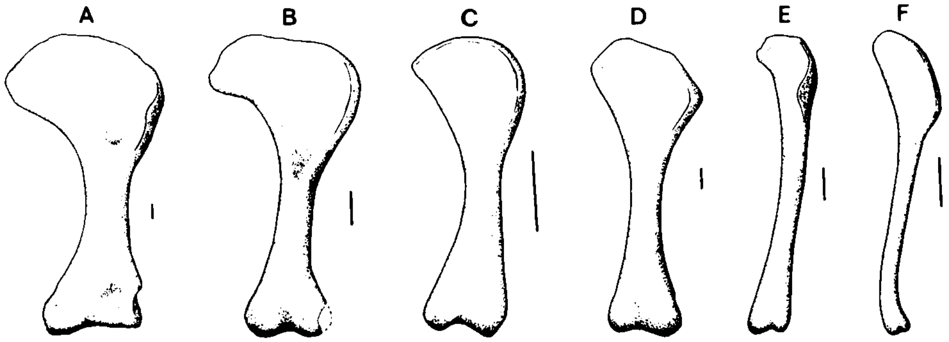

Figure 25. Comparison of various thecodontian humeri with that of *Archaeopteryx*. A, The aetosaur *Stagonolepis* (after Walker, 1961); B, *Riojasuchus* (after Bonaparte, 1971b); C, *Euparkeria* (after Ewer, 1965); D, *Ticinosuchus* (after Krebs, 1965); E, *Hesperosuchus* (after Colbert, 1952); F, *Archaeopteryx* (Berlin specimen). All are left humeri viewed in ventral aspect and drawn to unit length. Vertical scales = 10 cm. Compare these humeri with those of Fig. 11.

Archaeopteryx is the much shorter length of the shaft in pseudosuchians distal to the deltopectoral crest and the more massive distal extremity.

Forelimb summation. The pseudosuchian forelimb is relatively much shorter and more massive than that of *Archaeopteryx* or coelurosaurs (Fig. 26), and the hand constitutes only a small fraction of forelimb length. Total forelimb length ranges from about 40% to 50% of presacral vertebral length in most pseudosuchians and reaches a maximum of about 60% in *Hesperosuchus*, compared with about 75% in *Ornitholestes* and 120% in *Archaeopteryx*. Considerable variation exists among pseudosuchians in the ratio of humerus to epipodial lengths, with the humerus length exceeding that of the radius by about 10% in *Euparkeria* and *Hesperosuchus*, and by 20% in *Ornithosuchus*, whereas the radius is 5% longer than the humerus in *Ticinosuchus* and the two elements are equal in *Scleromochlus*. While the ratio in *Euparkeria* and

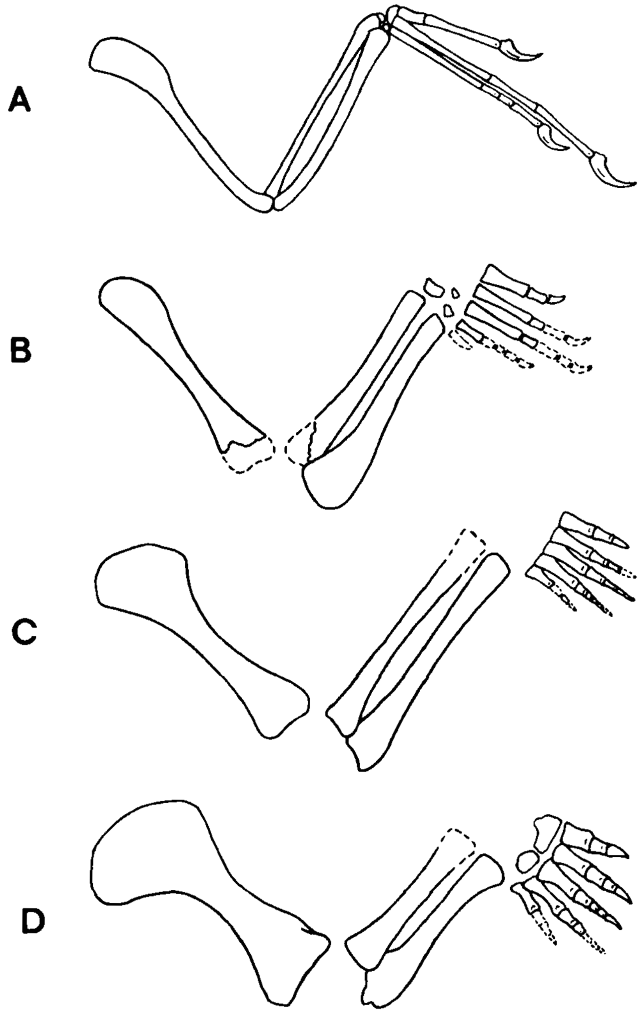

Figure 26. The right forelimb skeleton of *Archaeopteryx* (A) contrasted with that of several thecodontians; *Ornithosuchus* (B); *Ticinosuchus* (C); and *Stagonolepis* (D). For convenient comparison, all humeri 'are drawn to the same length to show differences in component proportions and robustness. Vertical scales = 5 cm. Compare with Fig. 12.

Hesperosuchus approximates that of *Archaeopteryx*, the proportionately much shorter total limb length is in strong contrast. Likewise, the short massive hand is completely different in design and proportions from that of *Archaeopteryx*. In summary, the forelimb and hand as known in pseudosuchians are sufficiently primitive in all features for both the *Archaeopteryx* and coelurosaurian conditions to have been derived from them, but there are no strong similarities to either of the latter.

Pectoral girdle

The scapulo-coracoid, known in a variety of pseudosuchians, appears to have been fairly uniform in design and bears only superficial resemblance to that of *Archaeopteryx* and theropods. In some specimens, a well-ossified clavicle and interclavicle have been noted.

Scapula. The scapula consists of a narrow to moderately wide blade which flares to a variable extent at its posterior extremity (Fig. 27). Proximally there is a very large and long acromial expansion projecting away from the glenoid. The blade appears to have been oriented at nearly right angles to the vertebral column or inclined slightly backward, instead of nearly paralleling the vertebral

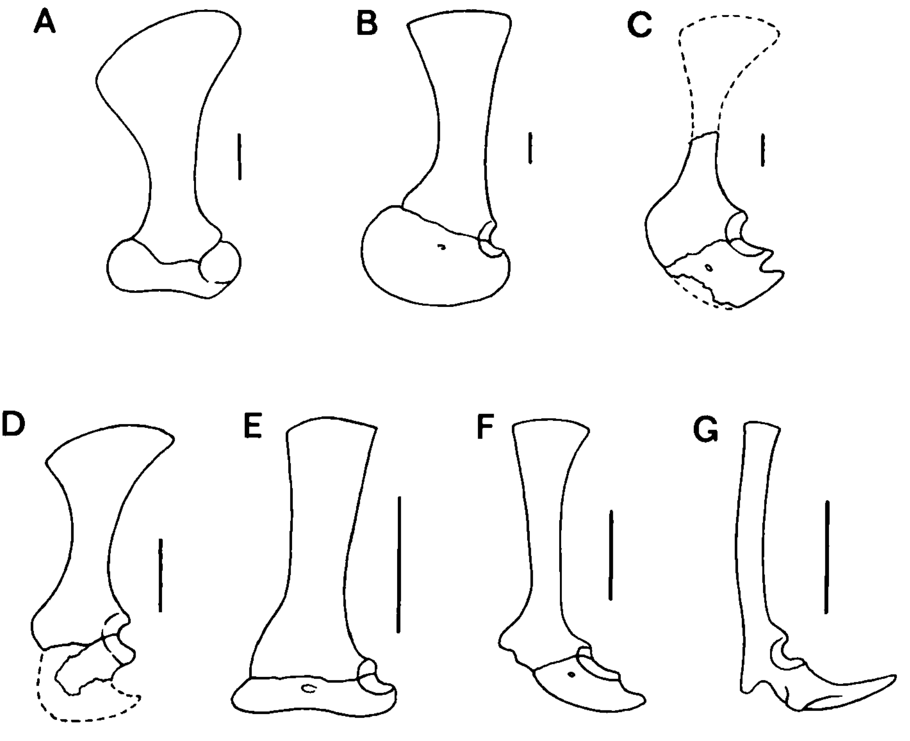

Figure 27. Outline drawings of the left scapulo-coracoids of various thecodontians compared with that of *Archaeopteryx* (G). All figures are viewed normal to the scapula with corresponding distortion of the coracoid outlines. Notice the broad, flaring form of the posterior extremity which is typical of the thecodontian scapula. A, The aetosaur *Stagonolepis* (after Walker, 1961); B, *Ticinosuchus* (after Krebs, 1965); C, *Riojasuchus* (after Bonaparte, 1971b); D, *Hesperosuchus* (after Colbert, 1952); E, *Euparkeria* (after Ewer, 1965); F, *Ornithosuchus* (after Walker, 1964); G, *Archaeopteryx* (reconstructed from the Berlin and London specimens). Scapulae are all drawn to the same length. Vertical scales = 2 cm. Contrast these data with those illustrated in Fig. 13.

column as seems to have been the case in *Archaeopteryx* (see, for example, the Berlin specimen). The glenoid region is robust and lies well behind the blade axis.

Coracoid. The coracoid of pseudosuchians is crescentic in shape with a strongly curved antero-ventral margin. The coracoid part of the glenoid is much larger than the scapular part and extends well behind it. Below that is a long posterior extension of the ventral coracoid edge which reaches far behind the glenoid. A faint to strong ridge is present in *Ornithosuchus,* extending from the glenoid rim down and back to the end of this posterior extremity. Some part of this ridge may correspond to the "biceps tubercle" of *Archaeopteryx* and coelurosaurs, but its form and location are significantly different. Perhaps a better comparison can be made with what appears to be an external swelling between the glenoid and the supracoracoid foramen in *Euparkeria,* as figured by Ewer (1965, fig. 9).

Clavicle and interclavicle. These dermal elements of the pectoral girdle have been identified in several pseudosuchians, namely in specimens of *Euparkeria, Ornithosuchus, Saltoposuchus, Ticinosuchus* and perhaps more. The clavicle appears to have been a thin, curved rod-like element adjacent to the anterior margin of the coracoid and the acromial border of the scapula. As reconstructed by Ewer (1965), the interclavicle in *Euparkeria* is a thin spatulate bone that was situated between the medial or inferior borders of the two coracoids. No interclavicle has been recognized as such in *Archaeopteryx,* but Osborn (1924) recognized an interclavicle in *Oviraptor,* as did Camp (1936) in *Segisaurus.* Clavicles have also been identified in both of these genera and may also be present in a specimen of *Velociraptor,* as was noted above. There is no obvious similarity between known pseudosuchian clavicles and the furcula preserved in two of the *Archaeopteryx* specimens.

Sternum. As noted earlier, the sternum is not known in any pseudosuchian. We may safely assume that it was present in a cartilaginous state, since it occurs, usually in an ossified state, in all other major archosaurian groups, including birds, of course, although apparently not in *Archaeopteryx* or most theropods.

Hindlimb and pes

The pseudosuchian pes and hindlimb are much better known than the forelimbs, with well preserved remains available in *Euparkeria, Ornithosuchus, Gracilisuchus, Riojasuchus, Scleromochlus, Hesperosuchus* and *Ticinosuchus,* plus the potentially very important new South American forms *Lagosuchus* and *Lagerpeton.* For the most part, the rear appendage is primitive for an archosaur, although clearly advanced over the lepidosaurian condition, and is potentially a good structural precursor to the condition in *Archaeopteryx* and that of all theropods. There are some difficulties, however, concerning the evolutionary significance of the typical pseudosuchian tarsus. These difficulties have been most clearly elucidated by Krebs (1963, 1965, 1974). The recent discoveries of the South American genera *Lagosuchus* and *Lagerpeton* (Romer, 1971, 1972b) may provide important evidence for resolving this problem.

Pes. Where adequately known, the pseudosuchian foot is composed of at least four and usually five digits with a primitive phalangeal formula of 2-3-4-5-(3), (see Fig. 28). Digit V is present in *Euparkeria, Ornithosuchus,* *Hesperosuchus, Riojasuchus* and *Ticinosuchus,* but is reduced to a splint-like vestige of the metatarsal in *Lagosuchus, Gracilisuchus, Lagerpeton* and apparently (Woodward, 1907) in *Sclermochlus.* In *Riojasuchus,* the fifth toe may have been reduced to two phalanges. Except for *Lagerpeton,* where the fourth toe is the longest, and III, II and I are successively shorter, the third toe is the longest in all known pseudosuchians. The fifth (when present) and first digits are the shortest and subequal in length, and the second is generally slightly shorter than the fourth. In all instances, the proximal phalanx is the longest in each toe. The foot is relatively short and broad in *Euparkeria* and *Riojasuchus,* as compared with those of *Ornithosuchus* and *Hesperosuchus.* By contrast, those of *Lagerpeton* and *Lagosuchus* are surprisingly long and slender.

The reduced feet of *Lagosuchus* and *Gracilisuchus* are of special interest because with the loss or reduction of the fifth toe, together with the slender and nearly symmetrical construction, they approach the condition in *Archaeopteryx* and various coelurosaurs much more closely than does any other pseudosuchian. The unreversed hallux is the most obvious difference from *Archaeopteryx.*

Metatarsus. Five metatarsals are present in all adequately known pseudosuchians (Fig. 28) but the fifth is reduced to a splint-like vestige in *Lagosuchus, Gracilisuchus* and *Lagerpeton* and perhaps in *Scleromochlus. Euparkeria* and *Riojasuchus* are judged to have the most primitive metatarsi in that these are relatively short, none of the elements seems to be reduced and the fifth metatarsal is distinctly hook-shaped, as in lepidosaurs. The metatarsus of *Ticinosuchus* is similar. In *Euparkeria* the metatarsals are quite short, approximating the length of the corresponding toe*. The metatarsals are longer than the digits in *Hesperosuchus,* and very much longer in *Lagosuchus, Lagerpeton* and perhaps *Gracilisuchus* where the entire foot including the metatarsus is very long and narrow. Where the fifth metatarsal is not reduced, the metatarsus is nearly symmetrical, with III the longest, II and IV of shorter subequal lengths and I and V the shortest and also subequal. Exceptions to this form are found in *Riojasuchus,* where the fourth metatarsal is about the same length as the third, and in the incompletely known *Lewisuchus* where the second and third metatarsals are of equal length. *Lagerpeton* has the most specialized design, the metatarsus being asymmetrical with metatarsal IV the longest and III, II and I successively shorter.

The reduced metatarsus with a splint-like vestige of the fifth is reminiscent of coelurosaurian metatarsi, like those of *Coelophysis, Compsognathus, Ornitholestes* and others. The metatarsus of the Eichstätt specimen of *Archaeopteryx* is also similar in this respect. But the reduced metatarsi of the new South American forms, and of pseudosuchians in general, are distinct from that of *Archaeopteryx* and all theropods in that the first metatarsal is never reduced (in fact it is very long in every pseudosuchian except *Lagerpeton*), nor is it positioned behind metatarsal II. The avian and theropod metatarsi are easily derivable from the generalized pseudosuchian condition, but, except for reduction of the fifth toe in some, there is no obvious trend toward this condition in known pseudosuchian material.

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* Charig (1972) has pointed out that, in most instances, greater relative lengths of metatarsals compared with digit lengths is probably a consequence of phalangeal shortening rather than of metatarsal elongation.

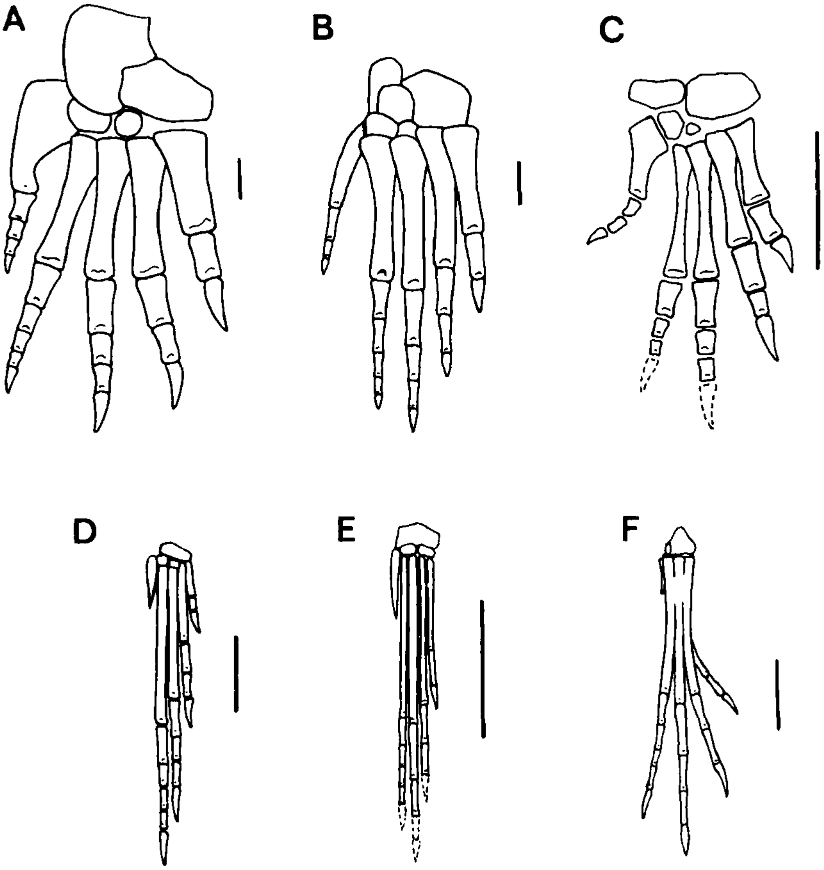

Figure 28. Outline drawings of the right pes, metatarsus and tarsus of various pseudosuchians compared with those of *Archaeopteryx* (F) and the aetosaur *Stagonolepis*. All views are dorsal (anterior) and are to the same length to eliminate size differences and facilitate comparison. A, *Stagonolepis* (after Walker, 1961); B, *Ticinosuchus* (after Krebs, 1965); C, *Euparkeria* (after Ewer, 1965); D, *Lagerpeton* (after Romer, 1971); E, *Lagosuchus* (after Romer, 1971); F, *Archaeopteryx*. Vertical scales = 2 cm. Compare with Fig. 15.

Tarsus. The pseudosuchian tarsus, where adequately known, consists of two large proximal elements, the astragalus and calcaneum, and two smaller distal tarsals that are usually identified as the third and fourth. The distal elements appear to have been positioned at the proximal ends of the third and fourth (and sometimes the fifth) metatarsals. A slightly different arrangement apparently existed in *Gracilisuchus* in which the calcaneum articulated directly with the fourth and fifth metatarsals and the two distal tarsals occupied positions between the astragalus and the first three metatarsals, according to Romer's (1972a) reconstruction. In nearly all pseudosuchians, the calcaneum bears a prominent "heel" or backwardly projecting tuber, which like that of crocodilians probably provided leverage for extensor muscles of the foot. Figure 29 compares the proximal tarsals of *Ticinosuchus* with those of *Deinonychus* and *Archaeopteryx*. Notice that there is no calcaneal tuber in the last two and no ascending process of the astragalus in the first.

As shown, the typical pseudosuchian tarsus differs markedly from that in

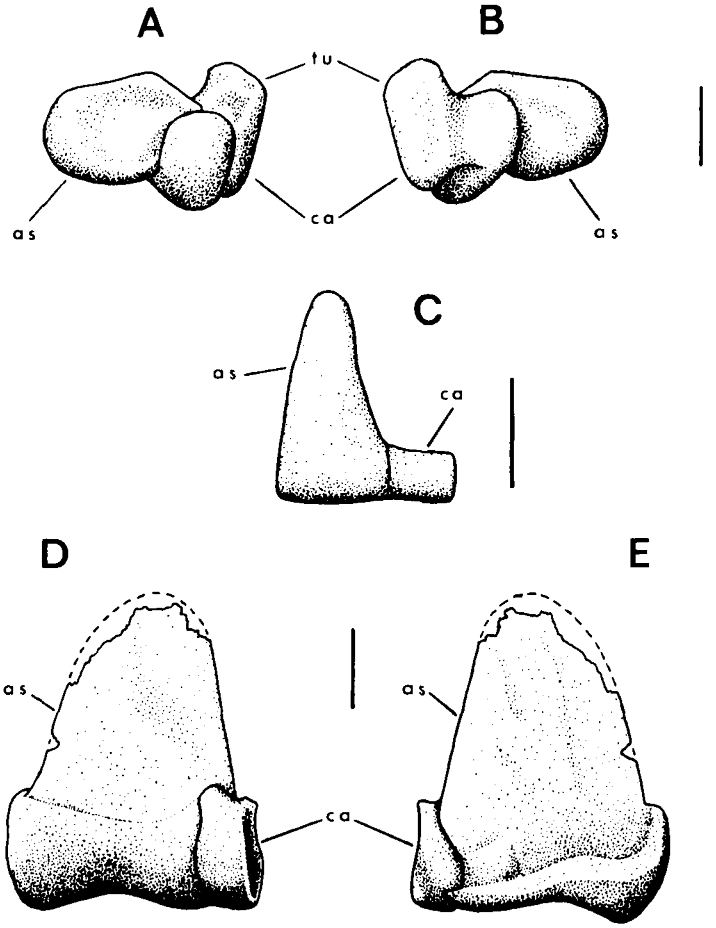

Figure 29. Pseudosuchian proximal tarsals (A and B) contrasted with those of *Archaeopteryx* (C) and a small theropod dinosaur (D and E). A and B, anterior and posterior views, respectively, of the astragalus and calcaneum of *Ticinosuchus*, as reconstructed by Krebs (1965). C, Anterior view of the proximal tarsals as reconstructed by the author from the Berlin, London and Eichstätt specimens of *Archaeopteryx* (see Fig. 17). D and E, anterior and posterior views, respectively, of the same proximal tarsals in *Deinonychus antirrhopus* (Y.P.M. 5226). Of special importance is the prominent dorsal or ascending process of the astragalus in *Archaeopteryx* and theropods, a blade-like dorsal flange that overlaps the lower anterior surface of the tibia. Also important is the prominent posterior tuber of the pseudosuchian calcaneum, a feature that is unknown in theropods and *Archaeopteryx*. Vertical scales in C = 2 mm; in A, B, D and E = 2 cm. as, Astragalus; ca, calcaneum; tu, calcaneal tuber.

Archaeopteryx and theropods, in which the tarsus forms a simple roller-bearing or hinge-like mesotarsal joint between the foot and the crus, with the two proximal tarsals firmly joined to the crus and the distal tarsals united with the metatarsals. As Charig (1972) and others have noted, the mesotarsal joint is correlated with digitigrade posture, upright parasagittal limb orientation and sometimes with bipedality. The typical condition in pseudosuchians is a crurotarsal joint in which the calcaneum is structurally part of the foot and the astragalus is part of the crus, as in modern crocodilians. This organization is associated with a plantigrade condition and semi-erect or sprawling posture. Contrary to the mesotarsal joint where nearly all of the movement takes place between the distal tarsals on one side and the astragalus and calcaneum on the other, in the pseudosuchian tarsus the principal movement takes place at a complex ball-and-socket articulation between the astragalus and calcaneum. The function of the calcaneal tuber is clearly to provide increased leverage for extension (backward thrust) of the plantigrade foot. In the mesotarsal ankle, this thrust is provided to the digitigrade foot through the digital flexors, hence no calcaneal tuber is necessary.

Krebs (1963, 1965, 1974) has argued persuasively that the mesotarsal condition cannot have been derived from the crocodiloid or crurotarsal condition typical of pseudosuchians. His principal argument: it is difficult to visualize the transfer of the calcaneum from the pes to the crus without disrupting the primary ankle functions of flexion and extension. Charig (1972) acknowledged the difficulties cited by Krebs, but he did not consider them insurmountable. He postulated that the mesotarsal joint might have evolved by way of a small, unknown pseudosuchian in which "because of its lightness, the development of a complex 'crocodiloid' tarsus with a massive calcaneal tuber was unnecessary".

It now appears that Charig may have been correct and that Krebs' arguments are purely academic. Several specimens of two new Argentine pseudosuchians, *Lagerpeton* and *Lagosuchus* (Romer, 1971, 1972b), both small, have what appear to be fully developed mesotarsal joints. In both, the astragalus and calcaneum are united and closely applied to the tibia and fibula. Two distal tarsals are present, capping metatarsals III and IV in *Lagerpeton* and I to IV in *Lagosuchus*. Of special interest in *Lagosuchus* is a small bony process that projects backward from the fibular region of the astragalo-calcaneum. If this structure does not represent a vestige of the calcaneal tuber, it certainly is remarkably coincidental in its position and construction. No such feature is preserved in *Lagerpeton*. In *Lagerpeton*, an ascending process of the astragalus occurs on the flexor surface of the tibia, rather than on the extensor or anterior surface.

Neither of these genera can be directly ancestral to later dinosaurs or birds because of the specializations of the astragalus in *Lagerpeton* and the peculiar form of the ilium in *Lagosuchus*, but they do indicate that some pseudosuchians possessed a mesotarsal ankle joint, thus obviating the problem raised by Krebs of converting the much more common pseudosuchian crurotarsal joint. The tarsus of *Lagosuchus* is even more interesting for the question at issue here, because, as was noted above, the pes and metatarsus also approach the pattern of *Archaeopteryx* and coelurosaurs much more closely than do those of any other known pseudosuchian. As Fig. 28 shows, the toes and metatarsals are long and slender and the relative lengths of all are similar to those of *Archaeopteryx*. The most significant difference is the unreversed hallux in *Lagosuchus*.

Tibia and fibula. These elements provide little evidence for resolving the question of the origin of *Archaeopteryx* one way or the other. Proportions and relative lengths differ slightly among pseudosuchians, but the morphology typically is that of nearly straight, cylindrical bones with expanded extremities. A cnemial crest is present in some but is never prominent (ridge would be a more appropriate term). In *Riojasuchus* and *Ticinosuchus* there is a prominent anterior expansion near mid-shaft on the fibula. Although incompletely preserved, the fibulae of *Euparkeria* and *Ornithosuchus* do not seem to possess a similar feature, nor has it been recognized in other pseudosuchians that I am aware of. In the new South American forms *Lagosuchus*, *Lagerpeton* and *Gracilisuchus* the tibia and fibula are long and slender. In *Euparkeria*, *Ornithosuchus*, *Ticinosuchus* and *Riojasuchus* they are relatively shorter and more massive. The fibula is never splinter-like as in *Archaeopteryx*.

Femur. The pseudosuchian femur is distinctly crocodilian in form, slightly sigmoidal with a stout, compressed cylindrical shaft (Fig. 30). It is distinctly non-avian, unlike the femur of *Archaeopteryx*. The proximal end bends medially and anteriorly, the head being only slightly offset from the shaft with no distinct neck. The head tends to be elliptical rather than hemispherical. There is no sign whatever of a "greater trochanter", but a conspicuous external protuberance occurs slightly below the level of the femoral head in *Ornithosuchus* and *Riojasuchus*. This was labelled the "lesser trochanter" by Walker (1964) and Bonaparte (1971b). A much less prominent swelling or ridge is present in *Hesperosuchus* and *Euparkeria*, and perhaps also in *Lagerpeton*, according to Romer's (1972b) restoration. A probable fourth trochanter is also present in *Riojasuchus*, where it is very prominent, and in *Ornithosuchus*. As Fig. 30 illustrates, there is very little resemblance between pseudosuchian femora and that of *Archaeopteryx*.

Hindlimb summation. Individually, the hindlimb components in classical pseudosuchians (e.g., *Euparkeria*, *Ornithosuchus*, *Hesperosuchus*) bear little resemblance to those of *Archaeopteryx*. The femur is distinctly crocodilian-like and longer than the tibia, and the distal elements are relatively shorter and much more massive. Taken as a whole, the hindlimb proportions also differ greatly from *Archaeopteryx* (see Fig. 31). The new South American forms *Lagosuchus* and *Lagerpeton*, and also *Scleromochlus*, however, do show tendencies toward the conditions in *Archaeopteryx*. The femur is straighter and

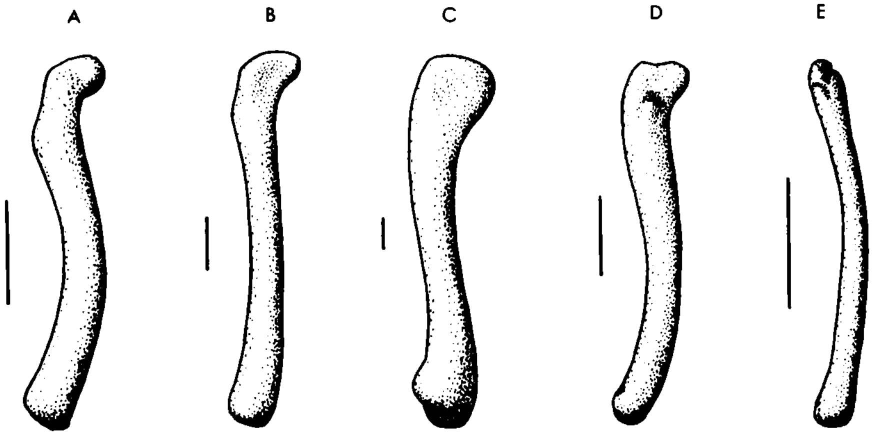

Figure 30. Comparison of right femora in lateral aspect, of various pseudosuchians with that of *Archaeopteryx* (E). Notice that, in addition to being more slender, the femur of *Archaeopteryx* displays a simple fore-aft curvature, in contrast to the sigmoidal curvature of pseudosuchian femora. A, *Lagerpeton* (after Romer, 1971); B, *Hesperosuchus* (after Colbert, 1952); C, *Ticinosuchus* (after Krebs, 1965); D, *Ornithosuchus* (after Walker, 1964); E, *Archaeopteryx* (see Fig. 18). All elements are drawn to the same length; relative scales are indicated by the vertical scales which equal 2 cm.

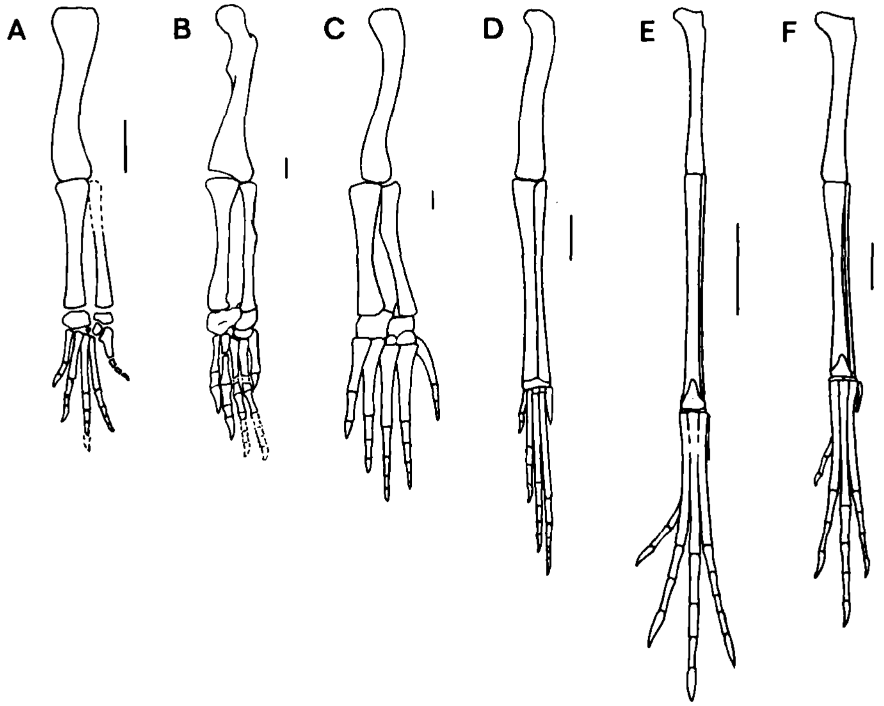

Figure 31. Outline drawings of the left hindlimb skeleton of *Archaeopteryx* (E) contrasted with those of various pseudosuchians (A-D) and that of a small theropod (F). All figures are views of the anterior aspect with femora drawn to the same length in order to minimize differences due to size. A, *Euparkeria*; B, *Riojasuchus*; C, *Ticinosuchus*; D, *Lagerpeton*; E, *Archaeopteryx*; F, *Compsognathus*. Vertical scales = 2 cm.

more slender, the fifth digit is reduced and the epipodials, metatarsus and foot are elongated and slender. Furthermore, the hindlimb proportions of these genera are quite close to those of the several specimens of *Archaeopteryx*, with the tibia approximately 20% to 30% longer than the femur, compared with 30% to 40% in *Archaeopteryx*, and the metatarsus constituting a similar fraction of total hindlimb length.

Pelvic girdle

Pelvic form seems to have been relatively conservative within the Pseudosuchia. All possess comparatively low and short ilia with very short anterior processes and a posterior process of long or only moderate length (Fig. 32). The acetabulum is large and closed (except for an incipient perforation in *Ornithosuchus*) and a long vertical suture joins the pubis and ischium beneath the acetabulum. A robust ischium projects almost straight backward and slightly downward. The pubis, only slightly less robust, projects antero-ventrally in its proximal part, but then turns sharply downward distally. This latter feature has been noted by Heilmann (1926) and others as possibly indicative of an initial stage in the backward rotation of the pubis toward the avian condition—a possibility that I reject in view of the total dissimilarity between avian and pseudosuchian pubes. There is little resemblance between

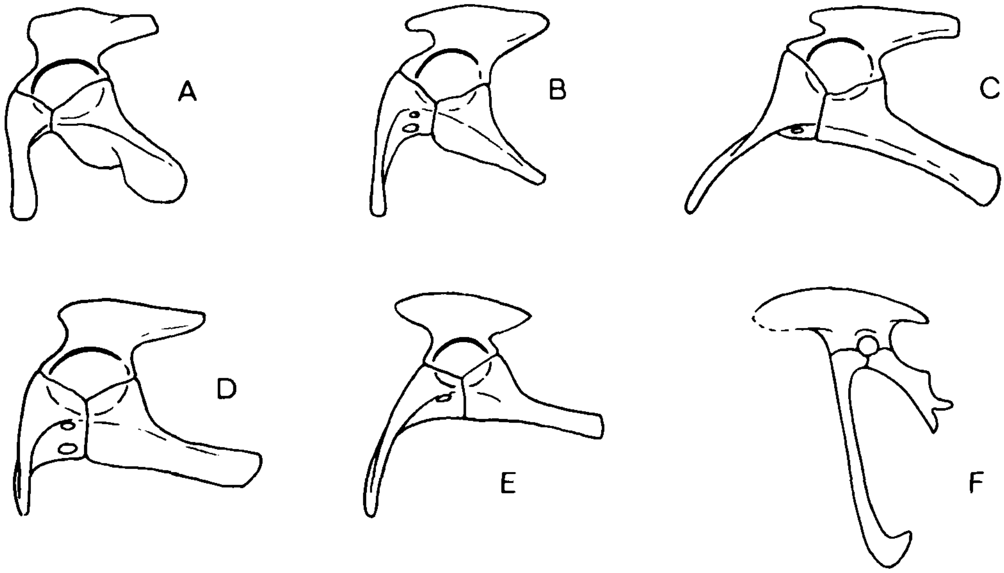

Figure 32. Thecodontian pelves compared with that of *Archaeopteryx* (F). All figures are of left pelves in lateral view, but not to the same scale. A, *Erythrosuchus* (a proterosuchian); B, *Stagonolepis* (an aetosaur); C, *Ticinosuchus* (a pseudosuchian) D, *Euparkeria* (a pseudosuchian); E, *Ornithosuchus* (a pseudosuchian); F, *Archaeopteryx* (as reconstructed by the author from all five skeletal specimens).

the pelvis (as a whole) of any known pseudosuchian and that of *Archaeopteryx*.

Pubis. The pseudosuchian pubis is distinctly primitive in its morphology, as is well illustrated by those preserved in *Euparkeria, Ornithosuchus* and *Ticinosuchus.* From an extensive dorsal union with the ilium, a robust longitudinal and nearly horizontal bony plate of the pubis curves downward beneath and medial to the acetabulum into a broad transverse and nearly vertical plate distally. There is no mid-length constriction into a long slender cylindrical shaft as in coelurosaurs and *Archaeopteryx.* A long symphysis joins the two pubic plates in front of and beneath the sacrum into a wide transverse apron which extends up and backward to the inferior junction with the ischia. In *Euparkeria* two distinct foramina are present below the acetabulum—an obturator foramen below and a smaller thyroid foramen above. Only the obturator foramen can be recognized in *Ornithosuchus.* Neither of these occurs in *Archaeopteryx,* the obturator foramen being represented by an open notch as in most theropods and birds. The broad transverse pubic apron is also markedly different from the narrow longitudinal distal expansion of the pubes in theropods and *Archaeopteryx.*

Ilium. Most pseudosuchian ilia are constructed on a similar plan, being relatively low and short vertical blades with nearly straight or gently convex upper margins. The anterior process is very short or almost non-existent (see, for example, *Euparkeria,* Fig. 32D), and rarely extends much in front of the acetabulum (*Ornithosuchus,* Fig. 32E). The posterior blade, on the other hand, is a moderate to lengthy extension behind the acetabulum (see *Ticinosuchus,* Fig. 32C). In a general way, these relative proportions resemble those in a variety of theropods, except that there the ilium is usually much deeper. This contrasts sharply with the proportions in *Archaeopteryx* where the anterior process is the longer. Another similarity between pseudosuchian and theropod ilia is the sharply defined notch between the pubic peduncle and the anterior process, immediately above the anterior rim of the acetabulum. No such notch exists in any of the specimens of *Archaeopteryx*. Compared with *Archaeopteryx*, the pseudosuchian acetabulum is enormous relative to the ilium; the greater relative iliac length in *Archaeopteryx* suggests much greater leverage for the ilio-femoralis muscles along the longitudinal axis, which may presumably be correlated with the upright posture and parasagittal limb excursion. The typical brachyiliac condition of pseudosuchians could have evolved into the more elongated iliac condition of birds, but there is no indication of such a tendency among known specimens.

Unfortunately the pelves of *Lagerpeton* and *Lagosuchus*, which might be expected to approach the avian condition more closely than those of other pseudosuchians, are incompletely known. The ilium of each, however, is known from two specimens. That of *Lagerpeton*, as figured by Romer (1972b), appears to have been short and of the general pseudosuchian configuration, with the posterior process much longer than the anterior process. The ilium of *Lagosuchus* is quite a different matter, but nevertheless it does not seem to strengthen the evidence for close pseudosuchian-avian relationships. It is of peculiar form, reminiscent of a "problematical" bone reported by Colbert (1952) in *Hesperosuchus*; it consists of two vertical blades, separated by a broad trough, which join to form a hook-like posterior process. The "anterior" process is a very short blunt nubbin that projects anterolaterally. So despite the somewhat *Archaeopteryx*-like construction of the hindlimb of *Lagosuchus*, the ilium of the latter has no resemblance whatever to that of *Archaeopteryx* or of any known theropod.

Ischium. The paired ischia of *Ornithosuchus* and *Euparkeria* appear to have been united over much of their length by a long sagittal symphysis. Thus the pubo-ischiadic plate was primitively continuous, except that instead of being nearly flat and horizontal, it bowed upward in the region of the pubo-ischiadic suture. It is not certain, but apparently the ischia of *Archaeopteryx* were not joined medially, or at the very most had contact only near their extremities. From the robust lower margin of the acetabulum, the pseudosuchian ischium extends back and slightly downward as a broad, nearly horizontal transverse plate. Newton (1894) observed an obturator process on the proximal inferior margin in *Ornithosuchus*, but no comparable feature has been reported in other pseudosuchian genera, as far as I know. An enlarged obturator process is present in many theropods, but appears to have been absent in *Archaeopteryx*, although the unique form and short length of its ischium may obscure identification of the obturator process.

Clearly, there is no obvious similarity between the ischium of *Archaeopteryx* and that of any pseudosuchian, where it is known. Unfortunately the ischium is not known in the new South American genera.

Skull and jaws

Good cranial and mandibular materials exist for a number of pseudosuchian genera, such as *Euparkeria*, *Ornithosuchus*, *Riojasuchus*, *Venaticosuchus* and

Gracilisuchus. Detailed studies of these specimens by Ewer (1965), Walker (1964) Bonaparte (1971b) and Romer (1972a) provide a good picture of the general nature of the pseudosuchian skull and jaws—a picture that perhaps is better than we may ever have for *Archaeopteryx* even with the remarkable Eichstätt specimen. As several authors have noted before, the pseudosuchian skull is primitively archosaurian, featuring a number of characters that are retained in later, more advanced archosaurs: the large antorbital fenestra, sclerotic ring, large naris bounded by the premaxilla and nasal, and a diapsid condition. All but the last are certainly present in *Archaeopteryx*, which may have possessed the diapsid condition also. As Fig. 33 shows, however, the general configuration of the pseudosuchian skull and jaws is quite different from that of *Archaeopteryx*, with a number of cranial and mandibular features that are not found in the latter. Some of these features are:

(a) There is a single antorbital fenestra, but no sign of smaller accessory fenestrae at the front of the antorbital fossa.

(b) The orbit tends to be triangular and elevated, with both the preorbital and postorbital bars converging to a junction beneath the orbit. In both *Ornithosuchus* and *Riojasuchus* the lower temporal fenestra and the antorbital fenestra extend beneath the orbit.

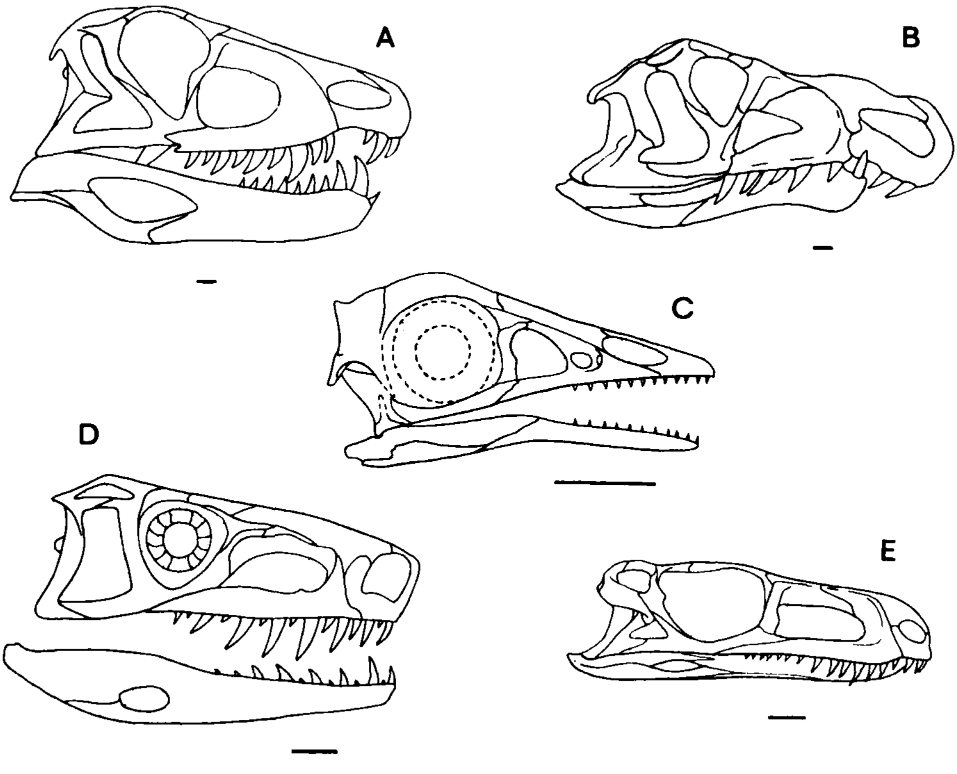

Figure 33. Pseudosuchian skulls (restored) compared with that of *Archaeopteryx* (C), also restored. All skulls are drawn to the same length, with relative sizes indicated by horizontal scales which equal 10 mm. A, *Ornithosuchus* (after Walker, 1964); B, *Riojasuchus* (after Bonaparte, 1971b); C, *Archaeopteryx* (after Wellnhofer, 1974); D, *Euparkeria* (after Ewer, 1965); E, *Gracilisuchus* (after Romer, 1972a).

(c) The snout is short and the premaxillary portion tends to bend downward in front of the mandibles. This is particularly evident in short-jawed genera such as *Ornithosuchus, Riojasuchus* and *Venaticosuchus.*

(d) The dentition is heterodont, consisting of relatively few teeth which are unusually large, often tusk-like, compared to the size of the skull. A distinct diastema is commonly present at the maxillary–premaxillary suture, corresponding to the position of a very large lower tusk near the extremity of the lower jaw.

(e) The suspensorium slopes (descends) backward and the articulation is situated farther back than the occipital condyle. The quadrate is over-lapped superficially by a large quadratojugal and squamosal which project forward into the lower temporal fenestra, greatly constricting that opening in *Gracilisuchus* and *Ornithosuchus.* A deep posterior notch (the otic notch?) is formed by a posterior extension of the upper part of the squamosal.

(f) The mandible is short and deep, especially in those taxa with an overhanging premaxilla. A large, long external mandibular fenestra is present in all presently known pseudosuchians.

It cannot be stated that any of these features would exclude pseudosuchians from the ancestry of *Archaeopteryx,* but neither do they weigh in favour of close relationships.

Vertebral column

Complete vertebral series are not known in many pseudosuchians, but the typical column seems to consist of from 21 to 25 presacrals, two (rarely up to four) sacrals and a long caudal series of up to 55 segments, according to the data reported for the genera listed below. In most specimens there is no clear distinction between the cervical region and the dorsals, the division by various authors often being arbitrary or based on the assumption of seven or nine cervical vertebrae. The neck is never long, constituting only 30% or less of the presacral length. Unlike *Archaeopteryx* and many coelurosaurs, there is no indication of any high degree of flexibility in the neck region. All vertebrae are amphicoelous, relatively short, and of simple construction without pleurocoels. Vertebral lengths and neural spine heights are nearly uniform throughout much of the precaudal series.

The most pronounced difference between the pseudosuchian vertebral column and that of *Archaeopteryx* is the lesser degree of differentiation in the presacral series and the shorter, apparently inflexible neck region in pseudosuchians. A summary of pseudosuchian vertebral counts is as follows:

	Cervicals + Dorsals	Sacrals	Caudals
Euparkeria	22	2	30-40
Ornithosuchus	24	3	25+
Scleromochlus	21	4	40-50
Gracilisuchus	23	2	?
Ticinosuchus	24 or 25	2	55+
Riojasuchus	24	3	?
Archaeopteryx	23	5	20-23

Other skeletal elements

Gastralia. It was noted above that gastralia are usually present in pseudosuchians and perhaps the best example is the type specimen of *Euparkeria* (see fig. 20, Ewer, 1965), where they appear to be completely undisturbed. In this specimen the gastralia consist of numerous closely spaced chevron-shaped or straight rod-like bones which form a long cuirass extending from the anteriorly positioned interclavicle all the way back to the pelvic region. This same close spacing was apparently true of the cuirass in *Ornithosuchus* and *Scleromochlus.* The gastralia in the specimens of *Archaeopteryx* have been slightly disarrayed, but the Berlin and Eichstätt specimens show a similar chevron-like form. However, far fewer elements seem to be involved, and, as preserved, they are much more widely spaced. Because it is a primitive condition, the presence of gastralia alone has no significance in relation to the origin of *Archaeopteryx.* Also, the significance of the smaller number of gastralia and their wider spacing in *Archaeopteryx* is not known, because the precise original arrangement cannot be established. However, it does resemble the pattern preserved in some theropods like *Struthiomimus* (A.M.N.H. 5339; see Osborn, 1917: pl. 24) and *Allosaurus* (U.S.N.M. 4734), more closely than that of pseudosuchians.

Scutes. Dermal ossifications are characteristic of various thecodontians, but their presence in pseudosuchians cannot be considered a primitive state. No dermal scutes are preserved in the most primitive thecodontians, nor in any of the specimens of *Archaeopteryx.* Dermal ossifications have been reported in theropods (Gilmore, 1920), but seem to be minor, or isolated occurrences. Hence these elements are considered irrelevant to the question at issue, (until such time as they are detected in a future specimen of *Archaeopteryx*).

Summary of pseudosuchian evidence

Beyond the generally accepted fact that pseudosuchians are indeed "primitive enough" to have given rise to birds, as Broom and Heilmann both observed, there are few reasons for postulating a close evolutionary relationship between them. There are very few close anatomical resemblances between *Archaeopteryx* and any pseudosuchian. In fact, only in *one* feature does *any* pseudosuchian resemble *Archaeopteryx* more closely than does any theropod, this being the tibia to femur ratio in *Scleromochlus, Lagosuchus* and *Lagerpeton,* where the tibia is from 20% to 30% longer than the femur. Among theropods, only in struthiomimids, *Compsognathus, Microvenator* and *Deinonychus** is the tibia longer than the femur but by only 10% to 15%. In *all other features,* the closest resemblance to the morphology preserved in *Archaeopteryx* is found in coelurosaurian theropods. On the basis of the degree of anatomical similarity, *Archaeopteryx* must be considered much more closely related to coelurosaurian theropods than to pseudosuchians.

The Sphenosuchus *evidence*

The question of bird origins has been complicated in recent years by a new hypothesis put forward by Walker (1972, 1974) in which it is suggested that

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* A new specimen of *Deinonychus* (now under study by the author) provides the only known femora for this genus. The femur is nearly 10% shorter than the tibia (Ostrom, in press).

birds arose from an unknown Middle or Late Triassic reptilian stock (which he refers to as "proavians") which also gave rise to crocodilians. On the surface of it, Walker's common-ancestor hypothesis would seem to be only a rephrasing of the long-held belief that thecodontians gave rise to crocodiles and birds (as well as dinosaurs and pterosaurs). But his thesis is more complex than that. On the basis of a single specimen of the South African Late Triassic thecodontian-like reptile *Sphenosuchus*, Walker believes that birds and crocodiles shared an immediate common ancestry above the thecodontian level of organization.

At first glance, *Sphenosuchus* appears to be a typical pseudosuchian not very different from *Euparkeria* (Fig. 34), and various authors (e.g., von Huene, 1925; Broom, 1927; Romer, 1956) have so classified it. However, *Sphenosuchus* also has certain crocodilian features, as do several other Triassic thecodontian forms (*Pedeticosaurus, Erythrochampsa, Notochampsa*). These crocodile-like "thecodonts" have been something of an enigma for many years. In 1966, Romer removed *Sphenosuchus* from the Pseudosuchia and placed it with primitive crocodilians (Protosuchia), a placement that he maintained in later years (1972c). Subsequently, Walker (1970) proposed his revised classification of crocodilians in which he allied *Sphenosuchus* with other aberrant, crocodile-like genera (*Pedeticosaurus, Saltoposuchus* and *Hesperosuchus*). More recently, Bonaparte (1971b) allied the new Argentine form, *Pseudhesperosuchus*, with *Sphenosuchus* and *Hesperosuchus* in his Infraorder

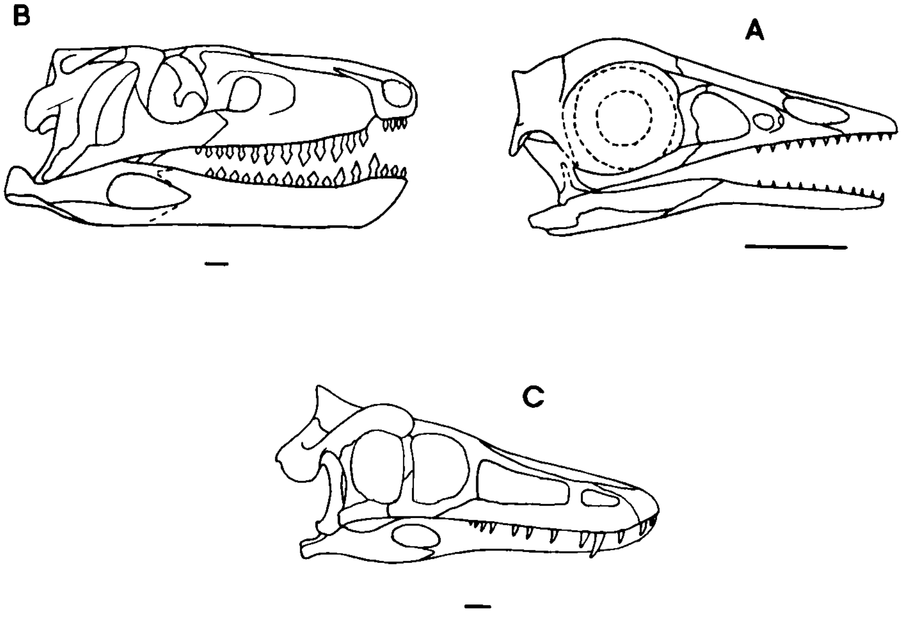

Figure 34. Comparison of the restored skulls of *Archaeopteryx* (A) and *Sphenosuchus acutus* (B). The *Archaeopteryx* restoration is by Wellnhofer (1974), based largely on the Eichstätt specimen (see Fig. 21B). The reconstruction of the skull of *Sphenosuchus* is by Walker (1972), based on the only known specimen. Also included is a restoration (by Bonaparte, 1971b) of the skull of *Pseudhesperosuchus jachaleri* (C), from the Upper Triassic of Argentina. It is included here for comparative purposes because both Bonaparte and Walker consider *Pseudhesperosuchus* to be a sphenosuchid, belonging to a family which, according to Walker, should be regarded as primitive crocodylomorphs. Bonaparte, however, places sphenosuchids in the suborder Pseudosuchia. Horizontal scales = 10 mm.

Sphenosuchia, but he considered these to be pseudosuchians, not crocodylomorphs. In 1972(c), Romer summarized some of the more important crocodilian-like features in the skull of *Sphenosuchus,* citing the forward inclination of the quadrate, reduced quadratojugal, small antorbital fenestra, loss of the postfrontal, fusion of the basipterygoid articulation, partial development of a secondary palate, and, in the incomplete post-cranial skeleton, the elongated form of the coracoid. There can be no question about the crocodilian nature or tendency of these conditions, but some of them (small or absent antorbital fenestra, absence of the postfrontal, and fusion of the basipterygoid articulation) are widespread among archosaurs and are not exclusively crocodilian. Of much greater importance here is Walker's (1972, 1974) claim that other cranial features of *Sphenosuchus* are also present in certain modern birds or closely resemble features thereof, and additional characters of *Sphenosuchus* preview (anticipate) other conditions of later birds.

Dr Walker was kind enough to show me what he believes to be evidence for *Sphenosuchus*—avian affinities, much of which he has published in the two papers cited above. In view of his announced intention to publish a monographic study of *Sphenosuchus,* I will list here only the more important details mentioned by Walker in those papers. It should be kept in mind that this listing is not necessarily the complete evidence recognized by Walker now, inasmuch as his studies are still in progress. The major items cited by Walker are:

(a) An anterior placement of the inner head of the quadrate, a condition that is present but masked in modern birds because of expansion of the brain case.

(b) An elongated cochlea of the inner ear, as in birds and crocodilians.

(c) A quadrate with all the essential features of the avian quadrate, including orbital and pterygoid processes and a curved articular facet for the quadratojugal.

(d) An indication of streptostyly and kinesis (character "C" above) in the juvenile (but not the adult) skull of *Sphenosuchus,* after the pattern of kinesis and streptostyly in modern birds.

(e) An extensive system of air spaces within the cranium, from which the pattern of pneumatic cavities in birds and crocodilians could be derived.

(f) A palatal configuration with a low position of the palatine—maxillary contact and a system of ridges on the palatines close to the mid-line (a preview of the avian hemipterygoids), all of which provide an ideal pattern from which to derive the schizognathous bird palate.

(g) A crescentic shape of the occipital surface, with short downwardly and backwardly directed paroccipital processes projecting well behind the quadrates to form the posterior walls of the tympanic cavities, as in some modern birds.

(h) Contours of the occipital surface with its pattern of low ridges and shallow depressions.

(i) A thin, transverse occipital crest with its paired dorso-lateral culminations, resembling that of some living birds.

(j) A well developed sagittal crest between large upper temporal fenestrae and a vertical orientation of the transverse (occipital) crest, in close resemblance to those of the Great Northern Diver (*Gavia immer*).

(k) The coracoid elongated like those of modern birds (and crocodilians).

The most important of these, apparently, is the evidence that Walker sees for bird-like kinesis and streptostyly at some stage immediately preceding *Sphenosuchus* (or in the juvenile *Sphenosuchus*). For example, in addition to the above features, Walker postulates the loss of the upper temporal arch and the postorbital bar during the post-*Sphenosuchus* evolution of birds. This loss presumably improved the kinetic mobility of the avian skull. Walker's interpretation is based on the upward and forward curvature of the upper temporal bar in *Sphenosuchus*, which he believes agrees with the positions of remnants of this bar that are retained in the modern bird skull.

Having myself seen some of Walker's evidence in *Sphenosuchus*, I am satisfied that his descriptions of *Sphenosuchus* are accurate and that his anatomical interpretations are reasonable. As for the similarities he cites between *Sphenosuchus* and certain modern birds, the important question to be answered is: Just what is their significance? I am concerned about the validity of equating a few anatomical features in a primitive archosaur of Late Triassic age(!) with similar anatomical features of a few modern birds (or modern crocodiles, for that matter) and concluding that they represent real evidence (homologous rather than homoplastic structures) of close evolutionary relationship. Separated as they are by more than 200 million years, it would seem to me that any modern bird is so far removed from any Late Triassic "proavian" that the significance of the above similarities must be very doubtful. For exactly these reasons, I remarked in an earlier section (p. 100) that there was no value whatever in referring to anatomical conditions of modern birds in our quest for the ancestral stock of *Archaeopteryx*. If we accept that *Archaeopteryx* is close to the ancestral stock of birds, then modern birds can tell us only what has happened *since* the *Archaeopteryx* stage, but nothing about what happened before.

It is unfortunate that the Berlin and Eichstätt skulls do not enable us to establish whether any of these "*Sphenosuchus*-bird" conditions were also present in *Archaeopteryx*—the earliest available stage of non-thecodontian *avian* evolution. It is hoped that further preparation of the underside of the Eichstätt specimen will be possible in the future and may reveal some of those features. My own examinations of the Eichstätt specimen have led me to the conclusion that the quadrate in *Archaeopteryx* probably was streptostylic, and this means that there may have been some kinesis, as theorized by Bock (1964) and Wellnhofer (1974). If these and other details cited above could be verified in *Archaeopteryx*, it would do much to validate the significance that Walker attributes to the similarities he finds between *Sphenosuchus* and some modern birds.

Aside from the features noted by Walker, other published data on *Sphenosuchus* (Haughton, 1915; von Huene, 1925; Broom, 1927) seem to indicate the same dissimilarities with *Archaeopteryx* that were noted above in pseudosuchians, namely:

(a) A single small antorbital fenestra with no indication of subsidiary fenestrae.

(b) Heterodont dentition consisting of relatively large teeth. A wide diastema at the premaxillary–maxillary suture, filled by a large tusk of the lower jaw.

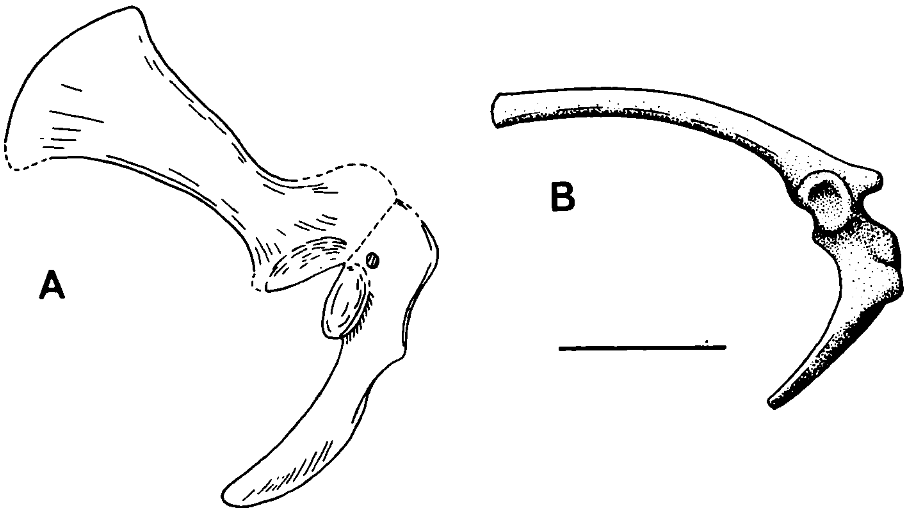

Figure 35. The right scapulo-coracoid of *Sphenosuchus acutus* (A) compared with that of *Archaeopteryx* (B). Both specimens are viewed in lateral aspect but are not drawn to the same scale. A is taken directly from Broom (1927), with no scale given. B is a reconstruction by the author based largely on the London and Berlin specimens. Horizontal scales = 2 cm.

(c) Suspensorium, although steeper, still sloping (descends) backward; jaw articulation still posterior to the occipital condyle.

(d) Mandible deep and slightly shorter than the upper jaw and bearing a large external mandibular fenestra.

In the post-cranium, the scapula (Fig. 35). expands distally into a broad flaring blade, quite unlike the narrow strap-like blade of *Archaeopteryx.* The coracoid is elongated after the fashion of modern crocodilians, but in no way does it resemble the peculiar elongated design of modern carinate birds. Any suggestion that it does so is entirely false. But, even more important, the great relative length of the coracoid in *Sphenosuchus* cannot possibly have any bearing on the elongation of the avian coracoid because in *Archaeopteryx,* which is more recent in time, and presumably much higher up the avian ladder than any sphenosuchid, the coracoid is relatively much shorter and more quadrangular (see Fig. 14A, B).

In their general configurations, neither the skull and jaws, nor the scapulo-coracoid of *Sphenosuchus* is remotely suggestive of affinities with *Archaeopteryx,* despite the possible streptostyly and kinesis that may have existed in both genera. Furthermore, the logic of a close relationship between *Sphenosuchus* and ancestral birds is greatly diminished by the enormous time gap between the Late Triassic *Sphenosuchus* and the living birds with which it has been compared.

EVIDENCE SUPPOSEDLY CONTRARY TO A THEROPOD ANCESTRY FOR *ARCHAEOPTERYX*

The pseudosuchian theory of bird origins is so widely accepted today that it would be foolish not to expect some strong reactions opposing the theropod ancestry proposed here. For this reason, it seems advisable for me to comment on some of the counter-arguments and criticisms that have been raised in the past, as well as others that are likely to come up in the future. Some of the criticisms that can be anticipated are:

(1) No theropod specimen of the proper geological age (pre-Kimmeridgian) is known that possesses all the features required of an immediate ancestor of *Archaeopteryx*.

(2) The anatomical evidence that I have presented represents a "conglomeration of parts" taken from a variety of coelurosaurian theropods to construct a makeshift and purely hypothetical bird ancestor.

(3) Nearly all the coelurosaurian evidence cited by me post-dates *Archaeopteryx*, or at the very best is contemporaneous (*Ornitholestes*, *Compsognathus*) and therefore cannot be related to ancestral forms.

(4) The predominant trend among theropods was a shortening of the forelimb, *not* elongation as would clearly be required in an *Archaeopteryx* ancestry.

(5) The bird-like orientation of the pubis in the Berlin specimen is *not* like that of coelurosaurian dinosaurs.

(6) The clavicle is absent in coelurosaurian dinosaurs.

(7) There is no ossified sternum known in theropods.

(8) The bird-like features of some coelurosaurs are most logically explained as parallelisms or convergent features.

Taking each of these in order, we must recognize the first criticism for exactly what it is—negative evidence only. The fact that no "suitable" coelurosaurian "pre-*Archaeopteryx*" is known to us is neither surprising nor significant. First of all, terrestrial vertebrate remains of Early and Middle Jurassic age are extremely rare, as compared with those known from later Jurassic or Late Triassic times. But even if an extensive fossil record of earlier Jurassic vertebrate life were known to us, discovery of the immediate antecedent of *Archaeopteryx* would be extremely improbable. The fact that such an ancestor has not been found (or recognized) as yet does not establish that it never existed. Obviously it did, whatever it was. We must be particularly cautious about drawing *absolute* conclusions from negative evidence. For example, an equally illogical alternative argument is that the absence of any known "suitable" intermediate form between Late Triassic pseudosuchians and *Archaeopteryx* is compelling evidence that birds could not have evolved from a pseudosuchian ancestor.

As for the second criticism, it is quite correct that I have assembled many *Archaeopteryx*-like anatomical features from a number of different theropods and that no theropod possesses all these features. The last is due in part to the fact that many of the taxa involved are known only from incomplete remains (in most instances, far less complete than most of the skeletal specimens of *Archaeopteryx*). For example, the carpus is not known in *Ornitholestes* (nor is the pubis or coracoid). The carpus is known, however, in *Deinonychus* and *Velociraptor* which have hands very much like those of *Ornitholestes*—and *Archaeopteryx*. The carpals of these genera *also* resemble those of *Archaeopteryx*. The fact that *each* of these many *Archaeopteryx*-like anatomical features occurs in *more than one* coelurosaur is extremely important, indicating that none is restricted in its occurrence and that all may have been widespread among coelurosaurs. We may regard them as general "coelurosaurian" traits.

The observant reader will have noticed that I have made few comparisons with Triassic coelurosaurs (e.g., *Coelophysis, Halticosaurus, Procompsognathus*) that might have been directly ancestral to *Archaeopteryx*. That much of the coelurosaurian evidence cited here is drawn from taxa post-dating *Archaeopteryx* is a valid criticism, except that I am not proposing any of these taxa as ancestral to *Archaeopteryx*. As with the first criticism, there is no evidence that these same features, or their precursors, did not exist prior to Late Jurassic times. These characters are considered as representing the "coelurosaurian state" and there is ample evidence (*Coelophysis, Segisaurus, Procompsognathus, Compsognathus, Ornitholestes, Coelurus*) that the "coelurosaurian state" existed long before *Archaeopteryx*. Triassic genera were not utilized in this analysis for the simple reason that they are more primitive in most features and less like *Archaeopteryx* than are many later coelurosaurs. With the possible exception of the fused clavicles and the unique form of the ischium, each character of the skeletal anatomy of *Archaeopteryx* can be found in *more than one* coelurosaur. Obviously, *Ornitholestes* cannot have been ancestral to *Archaeopteryx*, but *Archaeopteryx* and *Ornitholestes* could have had a common *coelurosaurian* ancestor. Any other explanation for the "coelurosaurian state" of *Archaeopteryx* seems contrived, to say the very least.

Tucker (1938a) and several other authors have observed that a major trend among (theropod) dinosaurs was the pronounced reduction of the forelimb, "tending to become non-functional". Tucker (1938b) even went to the extreme of suggesting that terrestrial bipeds (presumably all kinds) almost invariably undergo forelimb reduction. Both of those observations are only partly true. Forelimb reduction was typical of some, but not all, of the large carnosaurian theropods, and it was not true of most small or medium-sized coelurosaurian theropods*. In fact, forelimb elongation is clearly evident in *Ornitholestes, Velociraptor, Deinonychus* and all struthiomimids. Ample evidence now exists, much of it discovered since Tucker's time, to show that evolutionary trends in the forelimbs of theropods were not all contrary to that required in the ancestry of the very long-armed *Archaeopteryx*.

With regard to the fifth criticism predicted above, concerning the non-theropod-like orientation of the pubis preserved in the Berlin specimen of *Archaeopteryx*, it was demonstrated above that the pubis was preserved in an unnatural position. In my opinion, the evidence for this is beyond dispute, but for those who are unable to accept that evidence, it must be conceded that the pubis rotated back from a reptilian position *sometime* during the course of

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* Forelimb shortening in theropods has traditionally been correlated with large size (as in *Gorgosaurus = Albertosaurus, Tyrannosaurus, Tarbosaurus, Daspletosaurus*), but *Deinocheirus* (Osmólska & Roniewicz, 1969), with its nearly 9 foot-long forelimbs was certainly large, even if not clearly "carnosaurian". Furthermore, *Compsognathus*, the classic specimen of a "coelurosaur", which is almost exactly the same size as *Archaeopteryx*, possesses distinctly shortened forelimbs and hands very much like those of the large "carnosaurian" genera listed above. Forelimb shortening among theropods seems to have been universally correlated with two anatomical conditions other than that of absolute size: (1) a very large relative skull size combined with a relatively short neck, and (2) reduction of the manus to digits I and II. Except for *Deinocheirus*, in every one of the theropods mentioned above, (including *Compsognathus*), skull length is comparable to or greater than the total length of the forelimb, and the manus consists of only two fingers; in *Deinocheirus*, in any case, the skull is unknown.

avian evolution. Whether this rotation occurred before or after *Archaeopteryx* is not of crucial importance. Existing evidence suggests that pubic rotation had already begun before the *Archaeopteryx* stage, because in *Archaeopteryx* its position in life seems to have been intermediate between that of theropods and that of later birds.

The sixth point, discussed in some detail earlier, is the only specific evidence that has ever been raised for rejection of a coelurosaurian ancestry of birds: the supposed absence of clavicles in theropods. The avian furcula is currently believed to represent the co-ossified clavicles, and nearly all developmental biologists consider the clavicles to be dermal rather than endochondral ossifications. They are known to be somewhat variable in their degree of ossification, presumably varying in accordance with the kinds and intensities of stresses imposed on the shoulder joint and the degree of stability or mobility required there. Even among carinates, for example, the clavicles may be unfused or even greatly reduced, as was shown by Glenny & Friedmann (1954) and reported further by Van Tyne & Berger (1959). As dermal elements, their apparent absence in any particular theropod specimen might well be the result of their having existed in a membranous state, which would not be preserved as fossil evidence.

Another intriguing aspect of the clavicle-furcula problem is that raised by Lansdown (1968)*. He presented evidence that the furcula of the Japanese quail (*Coturnix c. japonica*) is endochondral, at least in part, rather than dermal in origin. This raises two important questions: first, is the avian furcula really derived from fusion of the paired clavicles? and second, are endochondral and dermal osteogenesis mutually exclusive? If the answer to the last question is yes, then the answer to the first must be no—and the putative absence of theropod clavicles has no bearing on the question of bird origins. The furcula would then be a *de novo* structure, inasmuch as neither the clavicles nor the interclavicle alone could have given rise to an endochondral element.

As with the supposed absence of clavicles, the lack of a certifiable sternum in theropods† is negative evidence and of no significance, especially since it apparently is lacking in *Archaeopteryx* also. The "proof" of this statement is the complete absence of a sternum in all known specimens of pseudosuchians—the almost unanimously accepted ancestral stock of all later archosaurs, all of which (crocodilians, pterosaurs, ornithischians, sauropods, birds, but perhaps not theropods) possess cartilaginous or well ossified sterna. If the absence of (dermal?) clavicles among the theropods is sufficient cause for discarding that group as ancestral to birds, then surely the absence of a (endochrondral) sternum in all known thecodontians is an equally valid reason for dismissing pseudosuchians from the ancestry of all later archosaurs—birds included. As for the ancestry of *Archaeopteryx*, the importance of a sternum is questionable, because no sternum has been identified positively in any of those specimens.

The final criticism listed at the beginning of this section, the parallel or convergent explanation of the "bird-like" features of some coelurosaurian dinosaurs, is likely to be the most frequently invoked argument against a

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* I am indebted to Mr John Attridge of Birkbeck College, University of London, for bringing Lansdown's work to my attention.

† Lambe (1917) described a poorly preserved bone in *Gorgosaurus* (=*Albertosaurus*) which he considered to be part of the sternum.

theropod origin of birds. Fürbringer (1888) was the first to raise this explanation and more recently it has been clearly and emphatically restated by Simpson (1946):

> "Almost all the special resemblances of some saurischians to birds so long noted and so much stressed in the literature, are demonstrably parallelisms and convergences. These cursorial forms developed strikingly bird-like characters here and there in the skeleton in one genus or another. They never showed a general approach to avian structure (as do *Archaeopteryx* and *Archaeornis*), some avian characters were not achieved or even hinted at in any of them, and they all retain the most conclusive marks of the reptilian nature." (Simpson, 1946: 94-5)

De Beer (1954b) followed suit; concluding that the dinosaurs could not be ancestral to the birds:

> ". . . for many of the points of resemblance which they appear to share with birds can easily be proved to be spurious, . . ." (de Beer, 1954b: 45)

These statements, and variations on the same theme, have been repeated so often that they are now generally accepted as fact. But the important and surprising fact that has been overlooked by everyone is that these and similar statements are not directed at the critical issue. They are not addressed to the question of the *origin* of *Archaeopteryx* and they do not explain the dinosaurian nature of *Archaeopteryx*.

Although there are differences of opinion as to whether *Archaeopteryx* is on the main line of descent to modern birds, there seems to be no difficulty for most in visualizing the evolutionary transition from an *Archaeopteryx*-like stage to the modern bird. The bird-like features of *Archaeopteryx* are accepted by all, and only once (Lowe, 1935) has any avian feature of *Archaeopteryx* (feathers) been attributed to multiple (parallel or convergent) origins. But inexplicably, instead of addressing the question to the source of the avian *and non-avian* characters of *Archaeopteryx*, queries have been directed at the irrelevant "bird-like" characters of some dinosaurs. Consider for a moment: If *Archaeopteryx was* derived from a coelurosaurian ancestor, as I believe, then it is understandable why *some* coelurosaurs *also* have a few bird-like features. This also accounts for the many coelurosaurian features of *Archaeopteryx*. In seeking the origin of *Archaeopteryx*, the crucial question is: Which Mesozoic reptiles are most similar to *Archaeopteryx?—not* which ones are most similar to modern birds. Rephrasing the above "explanation": Are we now to believe that those coelurosaurian-like characters of *Archaeopteryx* are just parallel or convergent features? Simpson (1961) observed that:

> ". . . intricately co-ordinated structures are less liable to *close convergence* and an aspect of that fact is that they tend to be less labile and to retain *ancestral conditions* longer." (Simpson, 1961: 100) (My italics)

Certainly this must apply to such functionally co-ordinated structures as the manus, carpus and forelimb, or pes, tarsus and hindlimb of *Archaeopteryx* and coelurosaurs. Given the incomplete nature of the fossil record, the almost simultaneous acquisition of so many coelurosaurian characters in *Archaeopteryx* and in coelurosaurs by means of parallel or convergent evolution is, in my judgement, infinitely less probable than by means of simple evolutionary descent from a common coelurosaurian stock.

Some other objections that might be raised to a theropod origin of *Archaeopteryx* are:

(a) The presence of a vestigial fourth metacarpal in some theropods (*Ornitholestes*) and of a complete fourth digit in the manus of some others (*Coelophysis, Ceratosaurus, Procompsognathus*).

(b) The presence of a vestigial fifth metatarsal in some theropods (*Ornithomimus, Struthiomimus, Deinonychus*).

(c) The supposed absence of sclerotic plates in theropods.

The existence of vestigial digits over and above the number present in *Archaeopteryx* hardly seems to be valid evidence against the affinities suggested here when it is obvious that the prevalent condition among theropods is the complete loss of the fourth and fifth fingers and the fifth toe—exactly as in *Archaeopteryx*. The retention of these structures in a few taxa is merely the retention of a more primitive state and neither precludes nor verifies phyletic relationship with *Archaeopteryx*. (It may be recalled from a preceding section that there is evidence of a vestige of the fifth metatarsal in the Eichstätt specimen; see Fig. 16A.) As for the absence of sclerotic plates in theropods, that too is invalid because they have been reported in the theropods *Struthiomimus* (Parks, 1928) and *Dromaeosaurus* (Colbert & Russell, 1969).

In summary, all the major criticisms that have been, and may still be, voiced against a direct evolutionary relationship between theropod dinosaurs and *Archaeopteryx* have been found to be inconclusive, incorrect or irrelevant. In my opinion, no conclusive evidence exists for rejecting coelurosaurs as the immediate ancestral stock of *Archaeopteryx*. On the contrary, this relationship is supported by a large body of positive anatomical evidence.

AFTER HEILMANN

Although it was first suggested by Broom (1913), Heilmann is properly credited with laying the foundation of the pseudosuchian or "common ancestor" theory of bird origins. However, it has been the opinions and evaluations of subsequent scholars that have established that theory as the prevailing view so widely held now by most ornithologists and paleontologists. Because the thesis presented here is contrary to that theory, it is appropriate to examine some of the more influential views that have been expressed since Heilmann—the remarks that have contributed to the increasingly favourable climate within which Heilmann's ideas have been examined.

One of the most important participants, and the first to digress from Broom's and Heilmann's theory, was Percy Lowe (1935, 1944), who maintained that *Archaeopteryx* and *Archaeornis* were not birds at all, but were feathered dinosaurs; that they also were not ancestral to birds; and that ratites (his Struthiones) were not descended from volant ancestors (a view contrary to that held then and now by most ornithologists), but had arisen instead from bipedal, coelurosaurian dinosaurs. His most important contribution was in recognizing that the skeletal anatomy of *Archaeopteryx* was not avian but rather was almost entirely coelurosaurian, the details of which he clearly enumerated. Those conclusions were largely ignored by the scientific community, probably because his other ideas were–in Lowe's own words–"a zoological transgression". Most ornithologists rejected Lowe's ideas on ratite origins; this rejection was later validated by de Beer (1956), who showed that ratite anatomy was inexplicable unless it had been derived from a flying ancestor. This presumably increased general scepticism about some of Lowe's other ideas, especially because his dinosaurian label for *Archaeopteryx* implied an unlikely diphyletic origin of feathers. Lowe's paper prompted a strong response from Tucker (1938a) in which it was noted that *Archaeopteryx* and *Archaeornis* were indeed extraordinarily reptilian, but that there was nothing in their organization that would not be expected in primitive birds just emerged from reptilian stock. I am in complete agreement with that statement. Tucker (1938b) further wrote:

> "The reptilian ancestry of birds is so self evident and so universally recognized by zoologists that it can be taken as axiomatic in any discussion. We shall further accept the view that the immediate reptilian ancestors of birds, if known, would have to be placed in or extremely close to the group Pseudosuchia. The direct derivation of birds from dinosaurs, favoured by some earlier writers, would probably not be advocated by any competent zoologist at the present day, but the many similarities between the two groups suggest a common origin." (Tucker, 1938b: 322)

Since Tucker's remarks, a wealth of new dinosaurian evidence has come to light which, I hope, removes all advocates of a dinosaurian origin of birds from the ranks of the incompetent. Lowe's second paper (1944) prompted an even stronger response by Simpson (1946):

> "*Archaeopteryx* and *Archaeornis* are intermediate between reptiles and birds in structure and their bearing on the origin of birds is unchanged by the purely verbal question of whether to call them reptiles or birds. . . . It is, indeed, an interesting point that these Jurassic birds (as I shall continue to call them) are more reptilian than might have been expected in an animal that had already developed a feathered wing–a point as strongly emphasized by Heilmann as by Lowe although Heilmann did not question the position of these animals near or, at least structurally, in the avian ancestry. The only logical conclusion is, I think, that the primary avian structure was the feathered wing which developed as a flying apparatus, a conclusion in no way negatived by its being as yet unperfected in the Jurassic, even if, as Lowe believes, the wing was then fit only for gliding rather than flapping flight." (Simpson, 1946: 94)

Simpson further found Lowe's designation of *Archaeopteryx* and *Archaeornis* as dinosaurs to be "nothing short of fantastic" (footnote p. 94).

After such strong reactions as these, it is not surprising that there have been so few critics of the pseudosuchian theory. But, in response to Simpson's footnote, the question must still be asked: How would those fossil remains have been identified—indeed, how would they *now* be classified, if no feather imprints had been preserved in any of those specimens? The skeletal anatomy of *Archaeopteryx*, as I have demonstrated, is almost entirely coelurosaurian (just as Lowe reported, and as Heilmann before him had concluded) and includes only one exclusively avian character—the furcula. In fact, it is only because of the distinct feather impressions preserved in two of the specimens of *Archaeopteryx* that we now have *any knowledge at all* about Jurassic birds or about the origin of birds. In the absence of those feather impressions, I do not believe that any of the specimens of *Archaeopteryx* would ever have been recognized as avian, or even as remotely related to birds. Regardless of how one

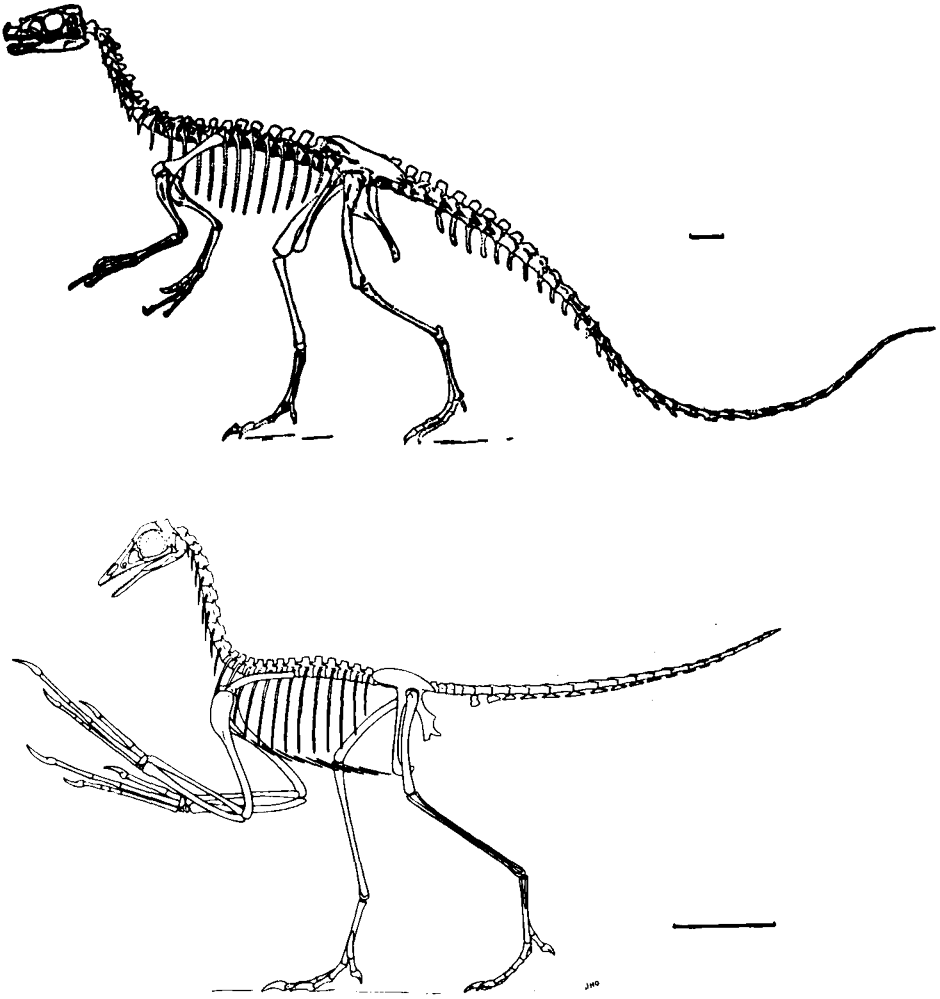

Figure 36. Skeletal reconstruction of two Late Jurassic bipedal predators; *Ornitholestes hermanni* (above), a coelurosaurian dinosaur from the Morrison Formation (Kimmeridgian age) of North America, and *Archaeopteryx lithographica* (below) from the Solnhofen Limestone (Kimmeridgian age) of Europe. Reconstruction of *Ornitholestes* is from Osborn (1903); that of *Archaeopteryx* is by the author based on the Berlin specimen. Scales = 5 cm.

assesses the importance of the systematic placement of *Archaeopteryx*, Lowe's dinosaurian label is not as fantastic as Simpson thought. Unfortunately, however, that designation by Lowe completely obscured the real significance of his observations.

Holmgren (1955) was another who found the resemblances between *Archaeopteryx* and coelurosaurian dinosaurs of special interest. He presented extensive embryological evidence (from *Struthio*, *Anser* and *Gallus*) which he compared with the anatomy of *Archaeopteryx* and various coelurosaurs, and concluded:

> "That the Coelurosaurs agree more closely with the Saururae [*Archaeopteryx* and *Archaeornis*] than the Pseudosuchians do and that there is thus better evidence that the birds have a coelurosaurian than a pseudosuchian ancestry. As the coelurosaurs are probably derived from Pseudosuchians, we arrive at the phylogenetic series Pseudosuchians–Coelurosaurs–birds. If we were to assume that the birds are direct descendants of Pseudosuchians, we would have to seek Jurassic connecting links between the Triassic Pseudosuchians and the Upper Jurassic Saururae. But no such links have hitherto been recorded." (Holmgren, 1955: 307)

It is unfortunate that so little attention has been given to Holmgren's paper, but it seems to have been largely ignored, perhaps because it was preceded the year before by de Beer's (1954b) monographic study of the London *Archaeopteryx*, which re-emphasized most of Simpson's (1946) conclusions. Or perhaps it was dismissed because Holmgren, like Lowe (1935, 1944) before him and Glutz von Blotzheim (1958) later, also believed in an independent origin of ratites from the larger Cretaceous coelurosaurs. But it must be noted here that Holmgren's work was published posthumously, and the introductory editorial comment clearly states that Holmgren considered the phylogenetic section as incomplete and only a tentative outline indicating the course that future research should pursue. In retrospect, though, it appears that all those who once argued in favour of a non-carinate origin (and especially a dinosaurian origin) of ratites have paid the price by having their other ideas rejected as well. The great debate over the separate origins of ratites and carinates was settled by de Beer (1956) who demonstrated that the structure of the ratite wing, pygostyle and cerebellum were inexplicable unless they had been retained from a flying ancestor.

In his discussion of the ancestry of *Archaeopteryx*, de Beer (1954b) also considered the supposedly "spurious" resemblances between dinosaurs and birds, noting the "lost" clavicles of dinosaurs, spurious similarities in the forelimb, and that the backwardly directed pubis of birds was unrelated to the post pubis of ornithischian dinosaurs. On these grounds, he re-affirmed the conclusions of Tucker (1938b) and Simpson (1946) and accepted the pseudosuchian theory of Broom and Heilmann, a position he continued to maintain in later years (1964). This same phylogeny has been adhered to by nearly everyone since, apparently without question (see Swinton, 1960, 1964; Welty, 1962; Romer, 1966, 1968; and Brodkorb, 1971, to mention only a few). Only Bock (1969a) qualified his acceptance of a pseudosuchian origin:

> "The pseudosuchians are generally accepted as the most probable reptilian ancestor of birds; however, acceptance of this group is more by default than by direct demonstration. Pseudosuchians may have been chosen because they also gave rise to the crocodiles, the living reptiles with which birds share the greatest number of characters. Although pseudosuchians have not been proven to be avian ancestors, they possess no features to discount this possibility." (Bock, 1969a: 1480)

Bock's final sentence above is absolutely correct, but the same can be said of coelurosaurs–only more so.

Most recently, two papers have appeared which, although accepting my coelurosaurian ancestry theory, in the long run may generate strong reactions unfavourable to my thesis on bird origins. Because of that possibility, I feel that some comment is appropriate here, despite the fact that neither paper is primarily concerned with the subject of bird origins. The papers in question are one by Bakker & Galton (1974) on dinosaur monophyly and a reply by Thulborn (1975) on dinosaur polyphyly. Bakker & Galton present very interesting evidence which they believe supports a monophyletic origin of the two dinosaurian orders (Saurischia and Ornithischia), which they elevate to subclass rank for inclusion in a proposed new vertebrate class, Dinosauria. Their new class is established primarily on purely speculative grounds that all dinosaurs were probably endothermic and possessed high levels of exercise metabolism. They then propose that the class Aves be reduced in rank to a subclass of their new class Dinosauria on the grounds that:

> "the avian radiation is an aerial exploitation of basic dinosaurian physiology and structure, much as the bat radiation is an aerial exploitation of basic primitive mammal physiology. Bats are not separated into an independent class merely because they fly. We believe that neither flight nor the species diversity of birds merits separation from dinosaurs on a class level." (Bakker & Galton, 1974: 171)

While I appreciate their acceptance of my conclusions about the ancestral affinities of *Archaeopteryx* and later birds, I reject the assertion by Bakker & Galton that the avian radiation is merely an aerial exploitation of basic dinosaurian physiology and structure, as well as their reasoning that birds should therefore be classified as dinosaurs. Bakker & Galton do not know what dinosaurian physiology was; no one does. And for them to suggest that the avian radiation was no more successful (by any criterion) than that of bats is patently false. The possibility (I would like to believe, probability) that *Archaeopteryx*, and presumably all subsequent birds, evolved from one particular group of dinosaurs does not justify such a radical departure from conventional classification schemes.

Thulborn (1975), in a well-phrased reply to Bakker & Galton, claims that there is no convincing evidence that dinosaurs were endothermic and challenges their evidence of dinosaurian monophyly with evidence of his own for polyphyly. But of interest here is Thulborn's proposed classification which transfers the ancestors of birds (the entire dinosaurian suborder Theropoda) to the class Aves.

I confess that I am unable to accept such theropods as *Tyrannosaurus* and *Allosaurus* as "birds", and therefore have little sympathy with this re-classification scheme either. Thulborn's approach is comparable to that of Reed (1960), who proposed the expansion of the class Mammalia to include all therapsids and sphenacodont pelycosaurs. As Simpson (1960, 1961) and others have repeatedly urged, classifications should be as stable and utilitarian as is consistent with the acquisition of new evidence and methodology. The new view that birds may be descendant from some group of theropod dinosaurs, rather than from pseudosuchian thecodontians, does not require (or justify) the radical systematics proposed by Bakker & Galton and by Thulborn. Nor are their classifications justifiable on utilitarian grounds.

SUMMARY

The question of the origin of birds can be equated with the question of the origin of *Archaeopteryx.* This last question evokes two possible answers, depending upon how one views the importance of "primitive versus derived characters" in assessing phylogenetic relationships. One possible answer is: *Archaeopteryx* is a direct descendant of some unknown, but presumably *Euparkeria*-like pseudosuchian. This answer is predicated on the belief that *Archaeopteryx* only parallels or converges with various coelurosaurs in certain skeletal similarities. This is the view now held by the majority of biologists— a view that I find unacceptable. The second possible answer is: *Archaeopteryx* is directly descendant from a small unknown *Ornitholestes*-like coelurosaurian dinosaur. This answer assumes that skeletal similarities between coelurosaurs and *Archaeopteryx* are derived from a common ancestor, itself a coelurosaur. This is the view advocated here.

There is no evidence to support an ornithischian ancestry of birds. The pubis of *Archaeopteryx* apparently was not reflected backward as in ornithischians and modern birds, and in any case, the ornithischian pubis is only superficially like that of living birds. Nor is the so-called ornithopod foot like that of birds.

Evidence of close theropod—*Archaeopteryx* relationships, however, is abundant: the presence of the same, multiple, specialized adaptations in both *Archaeopteryx* and various coelurosaurs (tridactyl manus, metacarpus and carpus morphology, forelimb and pectoral girdle structure, four-toed pes, reversed hallux, metatarsal morphology, mesotarsal joint, hindlimb construction, pelvic form, plus elongated forelimbs, bipedal posture, vertebral structure and formula, and basic cranial morphology).

The presence in *Archaeopteryx,* coelurosaurs and pseudosuchians of several primitive characters in common (thecodont dentition, sclerotic ring, possibly amphicoelous vertebrae, long caudal series, gastralia, pubic symphysis, short coracoids) indicates only a probable common ancestry. It does not establish that the Coelurosauria could not have given rise to *Archaeopteryx*—and higher birds. There is no evidence (outside of *Lagosuchus* and *Lagerpeton*) of shared derived characters to suggest a close evolutionary relationship between classic pseudosuchians and *Archaeopteryx.* Similarly, there is no clear-cut evidence in the form of shared derived characters to link *Archaeopteryx* with *Sphenosuchus.*

The absence of clavicles in theropods (now known to be false), once

considered as conclusive evidence against a coelurosaurian ancestry of birds, is no more significant than is the absence of a sternum in all known pseudosuchians as evidence against a pseudosuchian ancestry of all other archosaurs. The absence of any known "ideal" coelurosaurian pre-*Archaeopteryx* is only negative and inconclusive evidence, especially in view of our meagre and exceedingly deficient knowledge about Early and Middle Jurassic terrestrial vertebrates.

All available evidence indicates that the immediate ancestor of *Archaeopteryx* was a small coelurosaurian dinosaur and that the phylogeny of avian ancestry was: Pseudosuchia–Coelurosauria–*Archaeopteryx*–higher birds.

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ADDENDUM

After this study had been submitted to the Linnean Society, a copy of Ellenberger & de Villalta's (1974) preliminary note on *Cosesaurus aviceps* reached my desk. This note reports the discovery in Middle Triassic rocks of Spain of a tiny (15 cm length) tetrapod with what appears to be a very bird-like, tooth-bearing skull. Ellenberger & de Villalta interpret this specimen as a "protobird" and suggest that it is closer to true birds than are the specimens of *Archaeopteryx*. Not having seen the specimen, I am in no position to comment on that, but their published photographs and dimensions indicate an animal about the size and proportions of *Scleromochlus*. No feather impressions are reported and the post-cranial skeleton appears to lack all of the advanced characters shared by *Archaeopteryx* and coelurosaurs, and shows no derived characters of birds.

ADDENDUM REFERENCE

ELLENBERGER, P. & de VILLALTA, J. F., 1974. Sur la présence d'un ancêtre probable des Oiseaux dans le Muschelkalk supérieur de Catalogne (Espagne). Note préliminaire. *Acta Geol. Hisp.*, IX, 5: 162-8.

APPENDIX

Systematic list of taxa

For the convenience of those readers who may not be familiar with the systematic assignment of the various taxa referred to throughout this paper, the following listing is provided, together with the age and provenance of each taxon.

CLASS AVES

Subclass Archaeornithes (Saururae)
  Order Archaeopterygiformes
    Family Archaeopterygidae
      Archaeopteryx lithographica (=*Archaeornis siemensi*); Late Jurassic, Europe.
Subclass Neornithes
  Order Hesperornithiformes
    Family Hesperornithidae
      Hesperornis; Late Cretaceous, North America.
  Order Ichthyornithiformes
    Family Ichthyornithidae
      Ichthyornis; Late Cretaceous, North America.
AVES?: INCERTAE SEDIS
      Laopteryx priscus; Late Jurassic, North America.

CLASS REPTILIA

Subclass Archosauria
  Order Thecodontia
    Suborder Proterosuchia
      Family Proterochampsidae
        Cerritosaurus; Middle Triassic, South America.
      Family Erythrosuchidae
        Erythrosuchus; Early Triassic, South Africa.

- Suborder Pseudosuchia
    - Family Euparkeriidae
        - *Euparkeria;* Early Triassic, South Africa.
    - Family Ornithosuchidae
        - *Gracilisuchus;* Middle Triassic, South America.
        - *Ornithosuchus;* Late Triassic, Europe.
        - *Riojasuchus;* Late Triassic, South America.
        - *Venaticosuchus;* Late Triassic, South America.
    - Family Prestosuchidae
        - *Mandasuchus;* Middle Triassic, East Africa.
        - *Prestosuchus;* Middle Triassic, South America.
        - *Saurosuchus;* Middle-Late Triassic, South America.
        - *Ticinosuchus;* Middle Triassic, Europe.
    - Family Scleromochlidae
        - *Lagerpeton;* Middle Triassic, South America.
        - *Scleromochlus;* Late Triassic, Europe.
- Pseudosuchia Incertae Sedis
    - *Hesperosuchus;* Late Triassic, North America.
    - *Lagosuchus;* Middle Triassic, South America.
    - *Lewisuchus;* Middle Triassic, South America.
    - *Rauisuchus;* Middle Triassic, South America.
    - *Saltoposuchus;* Late Triassic, Europe.
    - *Triassolestes;* Middle-Late Triassic, South America.
- Suborder Aetosauria
    - Family Aetosauridae
        - *Stagonolepis;* Late Triassic, Europe.

Thecodontia Incertae Sedis

- *Longisquama;* Early Triassic, Eurasia.

Order Crocodilia

- Suborder Protosuchia
    - Family Notochampsidae (Protosuchidae)
        - *Erythrochampsa;* Late Triassic, South Africa.
        - *Notochampsa;* Late Triassic, South Africa.
    - Family Pedeticosauridae (Sphenosuchidae)
        - *Hemiprotosuchus;* Late Triassic, South America.
        - *Pedeticosaurus;* Late Triassic, South Africa.
        - *Sphenosuchus;* Late Triassic, South Africa.
- Protosuchia Incertae Sedis
    - *Pseudhesperosuchus;* Late Triassic, South America.

Order Ornithischia

- Suborder Ornithopoda
    - Family Hypsilophodontidae
        - *Hypsilophodon;* Early Cretaceous, Europe.
        - *Laosaurus;* Late Jurassic, North America.
        - *Thescelosaurus;* Late Cretaceous, North America.
    - Family Iguanodontidae
        - *Camptosaurus;* Late Jurassic, North America.
        - *Tenontosaurus;* Early Cretaceous, North America.

  - Suborder Pachycephalosauria
      - Family Pachycephalosauridae
        - *Homalocephale;* Late Cretaceous, Asia.
        - *Stegoceras* (=*Troodon*); Late Cretaceous, North America.
  - Suborder Stegosauria
      - Family Stegosauridae
        - *Scelidosaurus;* Early Jurassic, Europe.
        - *Stegosaurus;* Late Jurassic, North America.
- Order Saurischia
  - Suborder Theropoda
    - Infraorder Coelurosauria
      - Family Procompsognathidae
        - *Coelophysis;* Late Triassic, North America.
        - *Compsognathus;* Late Jurassic, Europe.
        - *Procompsognathus;* Late Triassic, Europe.
        - *Syntarsus;* Late Triassic, Africa.
      - Family Segisauridae
        - *Segisaurus;* Late Triassic, North America.
      - Family Coeluridae
        - *Coelurus;* Late Jurassic, North America.
        - *Microvenator;* Early Cretaceous, North America.
        - *Ornitholestes;* Late Jurassic, North America.
      - Family Dromaeosauridae
        - *Chirostenotes;* Late Cretaceous, North America.
        - *Deinonychus;* Early Cretaceous, North America.
        - *Dromaeosaurus;* Late Cretaceous, North America.
        - *Saurornithoides;* Late Cretaceous, Asia.
        - *Stenonychosaurus;* Late Cretaceous, North America.
        - *Velociraptor;* Late Cretaceous, Asia.
      - Family Ornithomimidae
        - *Archaeornithomimus;* Late Cretaceous, Asia.
        - *Deinocheirus;* Late Cretaceous, Asia.
        - *Dromiceiomimus;* Late Cretaceous, North America.
        - *Gallimimus;* Late Cretaceous, Asia.
        - *Ornithomimus;* Early-Late Cretaceous, North American and Asia.
        - *Oviraptor;* Late Cretaceous, Asia. (*Oviraptor* may not be an ornithomimid, but it is a coelurosaur. See Russell, 1972.)
        - *Struthiomimus;* Late Cretaceous, North America and Asia.
    - Infraorder Carnosauria
      - Family Megalosauridae
        - *Allosaurus;* Late Jurassic, North America.
        - *Ceratosaurus;* Late Jurassic, North America.
      - Family Tyrannosauridae (Deinodontidae)
        - *Albertosaurus (=Gorgosaurus)* Late Cretaceous, North America.
        - *Daspletosaurus;* Late Cretaceous, North America.
        - *Tarbosaurus;* Late Cretaceous, Asia.
        - *Tyrannosaurus;* Late Cretaceous, North America.
    - Carnosauria Incertae Sedis
        - *Zanclodon;* Late Triassic, Europe.

- Suborder Sauropodomorpha
  - Infraorder Prosauropoda
    - Family Anchisauridae (Thecodontosauridae)
      - *Amphisaurus* (=*Anchisaurus*); Late Triassic, North America.