

New Light on the Origin of Birds and Crocodiles

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Detailed evidence from the skull of *Sphenosuchus*, and from embryological and other resemblances between birds and crocodiles, suggests that these two groups are much more closely related than has been realized.

It has long been recognized that birds are more closely related to crocodiles than to other living reptiles. Many features of the anatomy of the two groups testify to this relationship—for example, the structure of the heart in crocodiles represents an advanced stage on the way to the bird type, by contrast with the more primitive conditions found in other living reptile groups¹. In the skull, also, the ossified laterosphenoids and the occurrence of mandibular and antorbital fenestrae (the latter present in early crocodylians) provide further evidence of affinity. These and other resemblances are usually assumed to be the result of independent descent from the Thecodontia, a group of Triassic reptiles which is also believed to have given rise to the two orders of dinosaurs and the flying reptiles, and which, largely by inference, is thought to have possessed all these features. But detailed study and dissection of bird and crocodylian skulls, and comparison with that of *Sphenosuchus*, a crocodile from the Upper Triassic Red Beds of South Africa, throws doubt on this basic assumption and suggests, on the contrary, that birds and crocodiles form essentially one stock.

Probably the most important feature of the crocodylian skull, and one which has received little attention, is the forward position of the primary or original head of the quadrate. This has moved forward and inward along the paroccipital process so that it no longer articulates with the opisthotic, and is prevented from doing so by a process from the prootic. Thus the head of the quadrate in the Crocodylia articulates essentially with the squamosal and prootic, whereas in all other archosaurs (thecodonts and their descendants, Fig. 1a), it rests in a cup formed by the squamosal and opisthotic and does not touch the prootic. That this is an ancient condition in the "orthodox" crocodylian stock is demonstrated by the skull of a small protosuchian crocodile from the Red Beds of Lesotho, BM(NH) R 8503, in which the suture between prootic and opisthotic is clearly visible passing behind the head of the quadrate. The condition in birds (Fig. 1c) is basically the same as that in crocodiles, but two principal factors have conspired to conceal this fundamental resemblance—first, the great development of secondary contacts between the crocodylian quadrate and the braincase, virtually blocking the cranio-quadrate passage, and, second, the inflation of the bird cranium because of the increased size of the brain, which has forced the upper articulation laterally, obscuring the fact that it is morphologically more medial and anterior than in typical reptiles. To some extent bone added to the exoccipital in birds has also enclosed some of the nerves and vessels in a rather crocodylian manner.

The inward and forward movement of the quadrate head is very clearly seen in *Sphenosuchus* (Fig. 1b), in which there were, as yet, no firm connexions with the side of the brain-

case. It is difficult to visualize the migration of the upper quadrate articulation taking place otherwise than at a time when the bone was freely movable (that is, streptostylic), and this assumption is borne out by the complete absence in *Sphenosuchus* and other crocodiles of the descending process from the squamosal which, in typical archosaurs, meets the quadratojugal halfway down the lateral temporal fenestra. The loss of this stabilizing process in lizards, also in the context of the development of streptostyly, has been pointed out by Robinson².

One of the most striking characteristics of the bird skull is precisely this streptostylic quadrate (Fig. 2a), part of a kinetic system whereby forward movement of the lower end of the bone operates a "push rod" arrangement of bony bars which has the effect of elevating the beak; upward bending takes place at a region of flexible bone in front of the orbits. The whole palate and beak are thus movable relative to the cranium. There are indications that a similar, but more primitive streptostylic-kinetic system had only recently ceased to operate in the skull of *Sphenosuchus* (Fig. 2b). The head of the quadrate rests for the most part in a smooth socket, but over a small area it is fused to the squamosal. The upper part of the quadratojugal has only smooth groove-and-tongue contacts with the squamosal and quadrate and has every appearance of being a new extension, recently evolved to prevent streptostyly. Other such devices are present in the skull—thus the quadrate and pterygoid form a deep lamina in close proximity to the side wall of the braincase, and the basal articulation of the pterygoid is immovably fixed. The reason for this loss of kinesis is, with little doubt to be found in the size and powerful build of the maxilla and its dentition, and it seems reasonable to infer that the nasals and certain other bones have, in consequence, been thickened. It is thus not easy to be certain of all the former positions of relative movement. A pivot joint with the quadrate is still present within the lower end of the quadratojugal, however, and bending probably formerly occurred at a depression and change of slope on the nasals in a position comparable with the hinge in the bird skull. The fourth pivot is most likely to have been at the overlap between jugal and maxilla. Sliding was still clearly possible at bone overlaps as shown in Fig. 2. Some flexibility of the postfrontal/jugal bar may also have been necessary; significantly, this is the most slender of all the "arches" at the postulated position of bending.

A kinetic system of this type would necessarily involve movement of the entire palate by way of the pterygoids. The bird palatine is extremely elongated, the anterior end passing below a short shelf from the maxilla (Fig. 3b) to reach the premaxilla. It is thus able to transmit the forward thrust from the quadrate and pterygoid in a direct line to the beak. Significantly, the anterior end of the palatine in *Sphenosuchus* (Fig. 3a) is elongated along the outside of the choana and it meets the maxilla very low down, below the level of the short secondary palate formed by the maxillae, concealing the interdental plates and almost touching the teeth. It was thus well placed to transmit the forward push from the pterygoid because it has the maximum possible moment-arm about the nasal hinge (Fig. 2b). If kinesis had continued, the anterior end of the palatine would have tended to migrate forwards, as this would bring the direction of thrust more nearly parallel to the mid-line.

In doing so it would have passed below the maxillary shelf. The long axis of the palatine is further forward, and less oblique to the mid-line, than that of the ectopterygoid, and would thus tend to supplant the latter, a process which has led to the loss of the ectopterygoid in birds.

Furthermore, the *Sphenosuchus* palatine has a short, almost vertical trough at the rear end of the choana, supported by a branching ridge-system (Fig. 4), the whole bearing a striking resemblance to that which occurs in birds. The fulmar (*Fulmarus glacialis*) and other petrels, which are commonly regarded as among the most primitive of non-ratite birds, show especially close similarity in this respect, and to some extent in the vomer also. In birds,

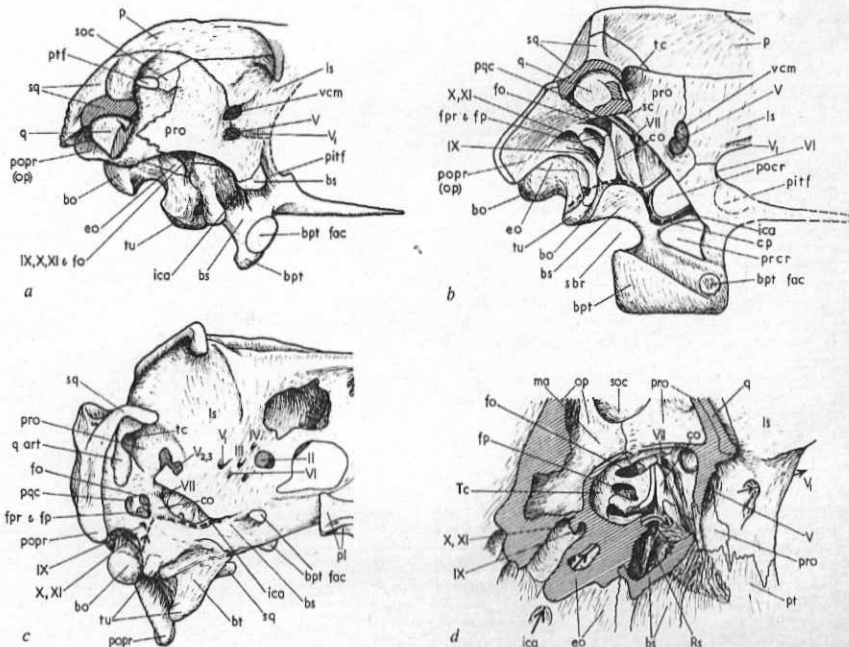


Fig. 1 *a*, The typical archosaurian upper quadrate articulation in the Upper Triassic thecodont *Stagonolepis*³. The paroccipital process is inclined too strongly backward, because of distortion ($\times 3/8$); *b*, preliminary restoration of the right side of the braincase of *Sphenosuchus*, with distortion corrected ($\times 1$). (Each basipterygoid process is suspended from separate anterior and posterior struts.) *c*, Oblique lower right view of rear part of skull of giant petrel, *Macronectes giganteus*, quadrates and pterygoids removed ($\times 1.2$); *d*, parasagittal section through the right tympanic cavity of *Gavia* ($\times 1$). As the fenestra pseudorotunda is nearly perpendicular to the plane of the section it cannot be indicated. Abbreviations as in Romer³⁷, with the addition of bpt, basipterygoid process; bpt fac, basipterygoid facet; bt, basitemporal; co, cochlear prominence; cp, carotid pillar; fo, fenestra ovalis; fp, foramen perilymphaticum; fpr, fenestra pseudorotunda; ica, canal for internal carotid artery (course indicated by heavy line); ma, mastoid antrum; pitf, pituitary fossa; pocr, postcarotid recess; popr, paroccipital process; pqr, post-quadrates canal (posterior tympanic recess); prcr, precarotid recess; q, art, quadrate articulation; Rs, rhomboidal sinus; sbr, sub-basisphenoid recess; sc, canal for stapedia artery; Tc, tympanic cavity; tc, temporal canal (superior tympanic recess); tu, basioccipital tuber; vcm, middle cerebral vein.

the palatines articulate with the base of an ossified inter-orbital septum, but it is not difficult to derive this condition from that of *Sphenosuchus*, in which they extend medially above the pterygoids and probably met the cartilaginous interorbital septum, much as in *Stagonolepis*³.

Previous figures of the rear part of the skull of *Sphenosuchus*^{4,5,7} have been based on the left side in which, however, the paroccipital process has been bent upwards.

Preparation of the better preserved right side gives a more accurate impression of the build of the occiput and adjacent regions (Fig. 5). The bird-like construction of this part of the skull then emerges, although it was not at first recognized. Among the forms studied the closest resemblances are with the divers (Gaviiformes), the Procellariiformes, particularly the petrels, the penguins (Sphenisciformes), and the auks and gulls, particularly the razorbill, *Alca torda*. The first three of these groups, and sometimes the auks also, are placed as the most primitive of living carinate birds in taxonomic lists. There are great differences between *Sphenosuchus* and the birds because of the greater relative height of the occipital plate compared with that of the

shallow depressions, the outer one of which vees forward above the head of the quadrate; and the thin transverse crest with its paired dorsolateral culminations. The well-developed sagittal crest between large temporal fossae, and the orientation of the transverse crest in the vertical plane make for a particularly close resemblance to the Great Northern Diver (*Gavia immer*).

The generally accepted interpretation of the postorbital region of the bird skull is that it has been derived from a normal diapsid reptilian type, that is, with both an upper and lower temporal fenestra, by the breakdown of the bar between the two fenestrae and also of that separating the lower one from the orbit. The skull of *Sphenosuchus* seems to bear out this interpretation, and the upward and forward curvature of the upper temporal bar agrees with the relative positions of the relics of this bar in the bird skull. The assumption of some former movement at the postorbital bar provides an explanation for its loss during the perfection

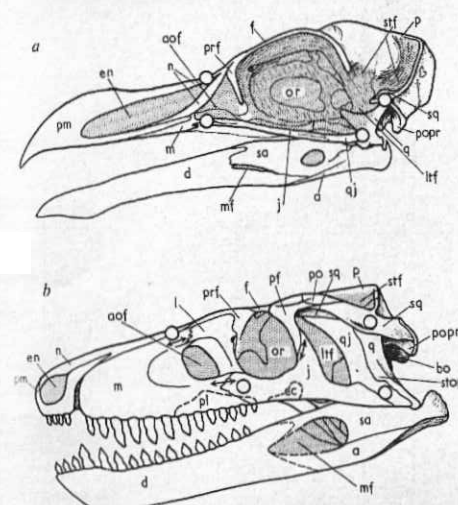


Fig. 2 Side views of skulls of *a*, Razorbill, *Alca torda* ($\times 1$); *b*, *Sphenosuchus acutus* ($\times 0.4$). O, Pivots or former pivots; ---, positions of palatine and ectopterygoid contacts within maxilla and jugal; stop, lateral stop on quadrate limiting backward movement; aof, antorbital fenestra; lf, lateral temporal fenestra; mf, mandibular fenestra; stf, supra-temporal fenestra.

of the kinetic apparatus, as its retention would only have been a hindrance to movement of the jugal. At some quite short antecedent stage in the ancestry of *Sphenosuchus* the upper part of the quadrate seems to have been remarkably free of the adjacent bones, as it is in birds. The prefrontal in the fossil sends a lateral process far down within the lachrymal. As the latter bone is essentially superficial to the prefrontal, and appears to have had a sliding contact with the maxillo-jugal bar, its presence in a kinetic skull would have become largely superfluous, so that it is not surprising that it has been lost from the skull of modern birds, leaving the lower end of the prefrontal ligamentously attached to the jugal and the lachrymal duct lying in a groove at the side of the prefrontal (Fig. 5c, f).

One of the most unexpected features of the skull of *Sphenosuchus* is that there seem to have been paired salt-excreting glands essentially like those of living sea-birds^{8,9}.

but relatively smaller, situated in shallow depressions on the upper surfaces of the frontals. The blood supply to these glands passed round the upper border of the orbit by four or five marginal grooves and foramina. The duct of the gland evidently entered the nasal chamber by means of a foramen situated, as in many birds, between frontal and prefrontal (Fig. 5c, f). Well developed salt glands were

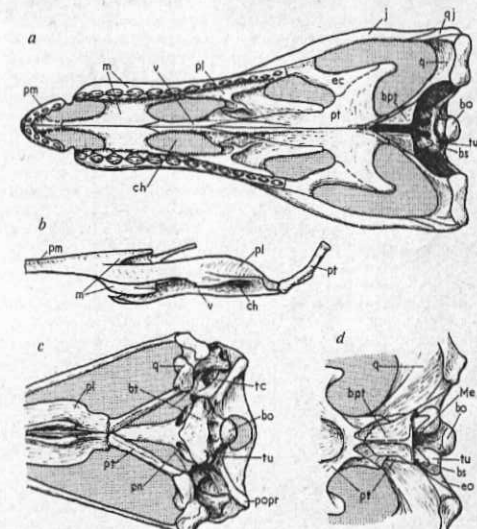


Fig. 3 *a*, Palatal view of skull of *Sphenosuchus* ($\times 0.46$); *b*, oblique lower view of left half of palate of Fulmar, *Fulmarus glacialis* ($\times 0.92$); *c*, lower view of rear part of skull of Wandering Albatross, *Diomedea exulans* ($\times 0.46$); *d*, same of the Lower Jurassic crocodile *Pelagosaurus typus* ($\times 0.55$), from BM (NH) No. 32599. ch, Choana; pn, pneumatic foramen communicating with precarotid recess; Me, median eustachian aperture, which opens directly above into a pair of sinuses within the basioccipital.

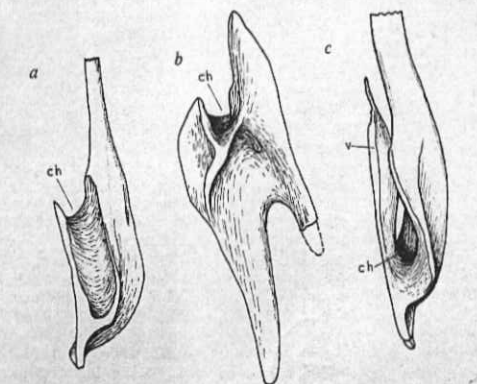


Fig. 4 Palatal views of left palatines of *a*, Razorbill, *Alca torda*, slightly oblique, anterior (upper) end incomplete ($\times 2$); *b*, *Sphenosuchus*, medial border (on left) incomplete, hidden by pterygoid ($\times 1.3$); *c*, *Fulmarus glacialis*, oblique, including also part of vomer ($\times 2$).

present in the Upper Cretaceous birds, *Ichthyornis* and *Hesperornis*⁹, but they have usually been regarded as having no more than adaptive significance for bird phylogeny; it may be, on the other hand, that their reduction or absence is the specialized condition.

Basipterygoid Processes

Perhaps the most significant feature, however, ranking close to the position of the quadrate articulation in importance, is the nature of the basipterygoid processes. These are very large structures, with almost flat medial surfaces only a few millimetres apart (Figs. 1b, 3a, 5a). They consist of delicate and incompletely ossified shells of bone, perhaps surrounding an inner cartilaginous core, and they were certainly at least partly pneumatized because they communicate freely above with the other air spaces in the skull. Both bird and crocodile skulls have a complex series of such air spaces which communicate with the middle ear cavity and the roof of the mouth, although they differ in detail. No serious attempt seems to have been made to determine the homologies of the various branches of the system between the two groups. This can now be done by the intermediary of *Sphenosuchus*, in which the skull is very extensively pneumatized (Fig. 1b); only two of the more

further back to join up with the lower surface of the rear end of the basisphenoid, leaving only a single aperture facing backwards, a state of affairs like that in the primitive Lower Jurassic crocodile *Pelagosaurus* (Fig. 3a, d) would have been attained. In the early growth stages of *Crocodylus cataphractus*, cartilaginous infrapolar processes from the basitrabecular regions grow back below the basal plate, and Müller¹¹ has shown that they ossify as the anterior part of the basisphenoid and thus form the anterior and ventral boundary to the median part of the eustachian system. Thus it seems that in this respect the embryonic development recapitulates phylogenetic history.

In well pneumatized bird skulls the internal carotid arteries generally run in bony tubes or grooves, which describe sigmoid curves along the sides of the cranium and pass upward in front to join just before entering the pituitary fossa. In their anterior course they are surrounded by an air space lying below the basisphenoid and above a triangular sheet of bone called the basi-temporal plate (Figs. 1c, 3c). In *Sphenosuchus* the basisphenoid, like that of birds, consists of thin sheets of bone penetrated by large pneumatic spaces. The internal carotids ran in thin-walled bony canals formed by the floor of a large air space (Fig. 1b, pocr) and turned upward in grooves on either side of a tapering pillar of bone to enter the base of the pituitary fossa. The similarity

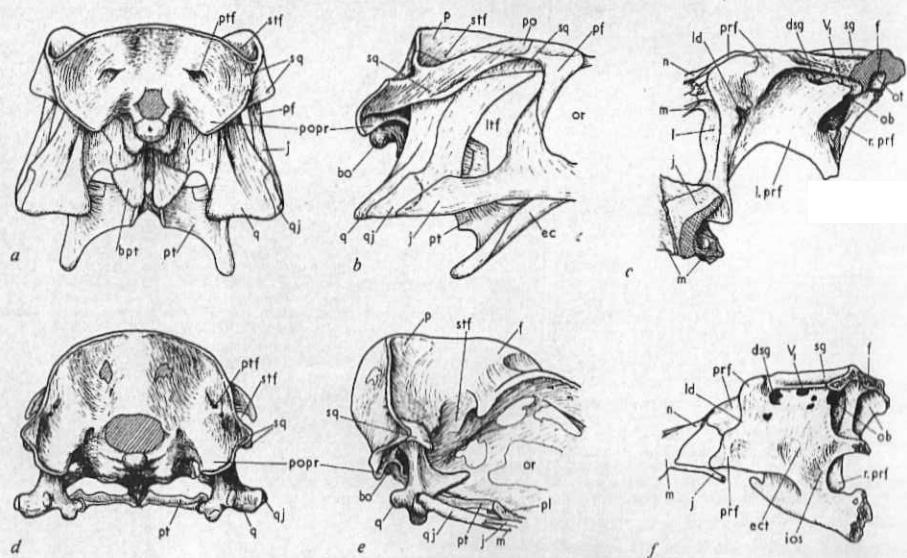


Fig. 5 a, Occipital view; b, right lateral view of postorbital part of skull, and c, posterolateral view of left prefrontal region of *Sphenosuchus*. Occipital sutures omitted in a, broken line in b indicates position of pivot within quadratojugal. d, e, Comparable views of skull of razorbill, *Alca torda*; f, posterolateral view of left prefrontal-ectethmoid region of *Fulmarus glacialis*. In e the posterodorsal process of the prefrontal has been displaced sideways by distortion; it originally lay below, but not touching, the flange at the side of the olfactory tract. a, b: $\times 0.6$; c, $\times 0.85$; d, e, $\times 1.4$; f, $\times 1.5$. dsq, Foramen for duct of salt gland; ect, ectethmoid; ios, interorbital septum; ld, position of lachrymal duct; ob, position of olfactory bulbs; ot, channel for olfactory tracts; pff, post-temporal fossa; sg, depression for salt gland; V₁, notch or foramen for ophthalmic branch of trigeminal nerve.

important conclusions can, however, be outlined here. There are good comparative anatomical reasons for thinking that the large hollow above and behind the basipterygoid processes (sbr in Fig. 1b) is equivalent to the median ventral portions of the eustachian (pneumatic) system of modern crocodiles. If the processes coalesced ventrally and grew

of this arrangement to that of the bird is obvious, although it would require illustrations of dissected skulls for a satisfactory comparison. A striking point of agreement in the early development of birds and crocodiles, and difference from other reptiles, lies in the formation and backward growth of infrapolar processes¹²; if it is assumed that the rear parts

of the basipterygoid processes grew backward in avian evolution in similar fashion to those of crocodiles, then it seems highly likely that they are represented (in a very much flattened form) by the paired basitemporals of the bird skull. The latter thus probably originated from replacement bones, as Müller¹¹ has shown for the crocodylian "basitemporals". It is rather curious that the evolution of the modern crocodylian skull was accompanied by strong antero-posterior compression of the basicranium, whereas in the case of birds the basicranium became flattened and the carotoids were spread apart, so that pocr and sbr of Fig. 1b became confluent between them. Nevertheless, these two widely divergent types can be derived from the *Sphenosuchus* pattern without too much difficulty.

The region of the inner ear is well preserved on both sides of the fossil, and it has been possible to remove the matrix completely from the vestibule and cochlear recess; on the left side a fracture has exposed a vertical section through the capsule. The positions of the sutures and foramina are thus as well known as in a modern reptile

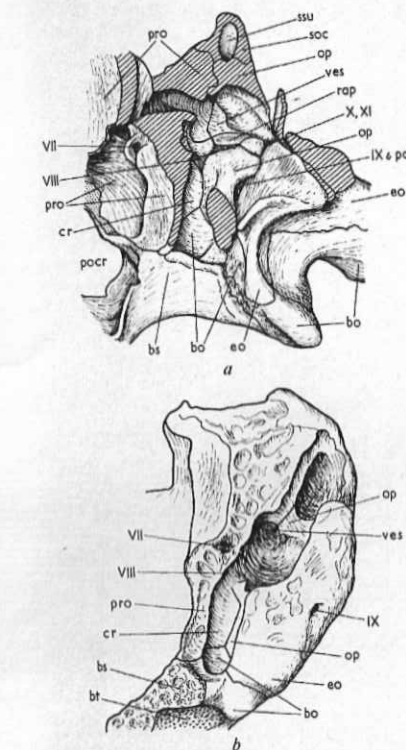


Fig. 6 Sutures in the cochlear recess. In each case the basisphenoid laps against the lagenar region, which is largely formed by the basioccipital. a, Natural parasagittal section through left inner ear region of *Sphenosuchus*. Slight disarticulation has occurred behind the cochlear nerve foramen. Broken bone cross-hatched ($\times 2.5$); b, dissection of rear part of cranium of young partridge (*Perdix perdix*), seen obliquely from below left and in front. A thin "skin" of basisphenoid and basitemporal has been left on the anterior and ventral surfaces of the basioccipital ($\times 7$); cr, cochlear recess; pd, perilymphatic duct; rap, groove for ramulus ampullae posterioris of cochlear nerve; ssu, sinus superior utriculi; ves, vestibule; VIII, cochlear branch of auditory nerve.

skull. The structures prove to be extremely similar, even in detail, to those in living crocodiles (Fig. 1b, d), in which, however, the tympanic cavity is almost completely enclosed by bone which surrounds the issuing nerves and the internal carotid artery. It is of particular interest that the cochlear recess is an elongated tubular structure. This housed the actual organ of hearing, indicating good ability in this respect. But comparison of the "simple crocodylian" structure of the *Sphenosuchus* ear with that of a young bird in which the sutures are still discernible, for example, a partridge (*Perdix perdix*), reveals an even closer resemblance in several respects than with the crocodile (Fig. 6). Thus the vestibule is in line with the long axis of the cochlear recess rather than lying behind it, and the basioccipital takes a greater share at the lower end in the cup housing the lagena. The elongated cochlear structures of birds and crocodiles, which resemble each other very closely and are more advanced than in other reptiles¹³, are usually assumed to be independently derived from thecodonts and to have been common to all archosaurs¹⁴. A similar structure cannot, however, be inferred for any thecodont skull so far described, and the shortness (in the vertical sense) in this group of that part of the prootic adjacent to the fenestra ovalis (Fig. 1a) strongly suggests that it did not occur¹⁵⁻¹⁷. The development of an elongated cochlear duct seems rather to be part of a general improvement in hearing structures which, because of the forward and inward movement of the quadrate head, also involved the formation of a spacious tympanic cavity protected behind by the paroccipital process, and of a definite external auditory meatus that is lacking in most reptiles. There is no reason to suppose that this group of associated changes occurred more than once in archosaurian history. According to Langston¹⁸, a somewhat elongated lagena (that is, cochlea) is a common dinosaurian feature, but the tubular cochlear recess and characteristic build of the otic capsule of crocodiles and birds does not seem to occur in dinosaurs.

Common Origin

The evidence from the nature of the quadrate articulation, the inner ear region, the homologies of the pneumatic spaces connected with the middle ear, the vestiges of kinetism, the palatal structure, the occiput and the peculiar basipterygoid processes of *Sphenosuchus* together suggest a common origin for birds and crocodiles. This is in agreement with embryological resemblances emphasized by Müller¹¹. The clear conclusion emerges, however, that many supposedly diagnostic crocodylian characters are consequences of the fixation of a former streptostylic-kinetic system. The most important of these have already been mentioned. Thus the indications are that the skull of *Sphenosuchus*, although technically crocodylian, was derived from a type with a primitive avian kinetic system and many other bird-like features. Although it occurred too late itself to be an actual ancestor of most crocodiles, *Sphenosuchus* nevertheless probably corresponds fairly closely to an early stage in the evolution of the group. The recently proposed⁴ classification of crocodiles now seems to have been oversimplified and it would seem more likely that, on the whole, cursorial forms preceded and gave rise to amphibious types—as Kermack¹⁹ suggested—probably because of competition from bipedal coelurosaurs (small agile dinosaurs which arose in the late Trias). The difference in position of the vestibule relative to the cochlea in modern crocodiles compared with that of *Sphenosuchus* is in keeping with a trend towards flattening of the skull, and there has been a significant shift in emphasis in the pneumatic spaces from a low to a high position, the latter giving greater stability to the head of an amphibious animal.

It thus seems logical to consider seriously the possibility that crocodiles as a whole may have descended, perhaps as

successive "waves", from an unknown stock of late Middle to Upper Triassic reptiles which eventually gave rise to birds, and which may for convenience be called "proavians". Although the postulate of a common origin for birds and crocodiles does not necessarily imply an arboreal origin for the latter, the high degree of pneumatization of the skull of *Sphenosuchus* and other Triassic crocodylomorphs, and the slender, hollow bones of the limbs and girdles, suggests that this is a distinct possibility. Examination of the anatomy of living and fossil crocodiles lends further support to this view.

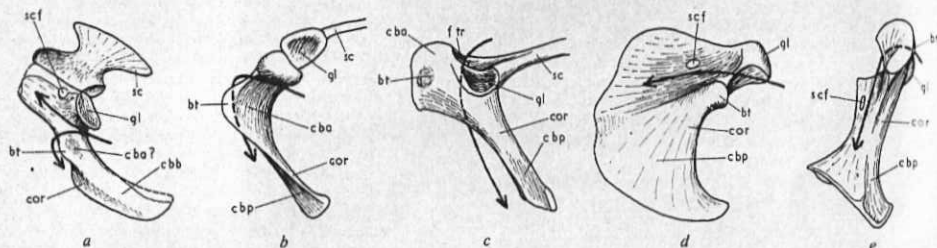


Fig. 7 The evolution of the bird coracoid. a, Ventrolateral view of left coracoid and scapula of *Sphenosuchus* (scapula foreshortened) ($\times 0.46$); b, d, lateral and anteroventrolateral views of left coracoid and part of scapula of *Archaeopteryx* (BM specimen) ($\times 1.84$); c, e, lateral and anteroventral views of left coracoid and part of scapula of sea eagle, *Haliaeetus albicilla* ($\times 0.46$). —, Generalized line of action of the supracoracoideus. bt, Biceps tubercle; cba, surface for coracobrachialis anterior; cbb, coracobrachialis brevis; cbp, coracobrachialis posterior; cor, coracoid; f tr, foramen triosseum; gl, glenoid; sc, scapula; scf, supracoracoideum foramen.

It has been suggested that the tendency to elongate the coracoid in early crocodylians, and the loss of the clavicle, were connected with cursorial galloping habits¹, and an analogy was in fact drawn with the flapping flight of birds, which also have elongated coracoids. It is, however, possible to see these changes, and particularly the formation of a biceps tubercle (Fig. 7a) in *Sphenosuchus* and its Triassic allies, as arboreal adaptations in the first instance, which led on to the unique avian condition of the shoulder-girdle, but which also proved preadaptive (but probably only during early stages) for cursorial activity in forms reverting to a ground life. The clavicle is still present in *Sphenosuchus*, but apparently had only a ligamentous connexion with the interclavicle—a very bird-like feature. In the typical bird shoulder-girdle (Fig. 7c, e) the supracoracoideus muscle passes as a tendon through the foramen triosseum between scapula, coracoid and clavicle, and, inserting near the head of the humerus, acts as the most efficient elevator of the wing. The evolution of this pulley system can be traced from *Sphenosuchus* through *Archaeopteryx*²⁰, with forward and upward migration of the tubercle until it eventually contacted the clavicle, and inward rotation of the originally anterior part of the coracoid and scapula. The advantage of this arrangement was apparently that it permitted elongation of the supracoracoideus and at the same time ensured that the latter exerted a forward pull in a constant direction. In earlier stages, however, the supracoracoideus could only have functioned as a protractor, presumably bringing the forelimb quickly forward through a wide arc in climbing and jumping, and later, gliding. In *Archaeopteryx* (Fig. 7b, d) the biceps tubercle is still well below the glenoid, there was no foramen triosseum, and hence the supracoracoideus could not have assisted directly in flapping flight. Furthermore, recent examination of the "sternum" of the specimen in the British Museum leads to the conclusion that this actually consists of parts of four cervical vertebrae. Thus, as well as lacking an efficient wing elevator, *Archaeopteryx* probably had only a rather narrow, cartilaginous sternum, as there is no reason to suppose that the coracoids were widely separated. These points

have an obvious bearing on the recent discussion concerning the flying ability of *Archaeopteryx*²¹⁻²⁴.

The forearm and hand of *Sphenosuchus* are unknown, but there is every reason to think, from the evidence of allied Triassic forms^{19,25,26}, that the radiale and ulnae were differentially elongated in the distinctive crocodylian manner (Fig. 8a). It is not generally recognised that functionally and anatomically, the bird and crocodylian elbow and wrist joints are surprisingly similar. Essentially, an oblique ridge on the humerus pushes the radius distally when the elbow is flexed, causing the radiale, ulnae and hand to rotate laterally

around the distal end of the ulna. This is also the basic mechanism for folding the bird wing (Fig. 8b). Its significance in crocodylians is not entirely clear, but it may have arisen originally as a grasping adaptation during climbing and jumping—in early life crocodylians are active climbers²⁷ giving an extra joint and enabling the hand to extend further round cylindrical objects such as branches and tree-trunks. In bird and crocodylian embryos also there is a striking similarity in the lateral deflexion of the wrist-hand axis from that of the forearm, and in the reduction of the two outer digits²⁸.

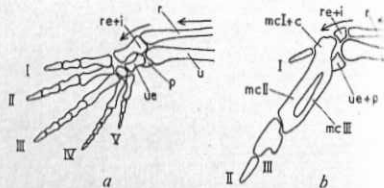


Fig. 8 Diagrams of the left wrist and hand in a, *Alligator*, and b, a bird from Gray²⁹. r, Radius; u, ulna; re, radiale; I, intermediate; ue, ulnae; p, pisiform; c, distal carpals; mc I-III, metacarpals I-III; I-V, digits I-V.

In both birds and ornithischian dinosaurs the pubis has rotated backward to lie alongside the ischium as a slender rod. According to Galton^{29,30}, this became possible when protraction of the hind limb was chiefly carried out by muscles originating from a long anterior process from the blade of the ilium, rather than from the pubis itself. Galton assumes, however, that the puboischiofemoralis internus 2 (in Romer's sense³¹) was a retractor of the femur, whereas it seems to me more likely that no muscle inserted on the summit of the greater trochanter and that pif2 was always a strong protractor in dinosaurs—a view which has been reached independently by A. Charig (personal communica-

tion). The only other comment that need be made here is that at least some Triassic crocodylians also had a well developed anterior iliac process³². The previously unexplained fact that, during the later part of the Trias, the crocodylian pubis became more slender and was gradually excluded from the acetabulum, now suggests some connexion with the proximal reduction and backward rotation of the bird pubis, which had already been accomplished in the earliest known bird, the Upper Jurassic *Archaeopteryx*. It is suggested that the crocodylian pubis became reduced in importance and "nearly turned back" during an arboreal stage, but was arrested because of a change in habits and was subsequently excluded from the acetabulum as a response to amphibious life. Apparently one crocodylomorph, namely the Upper Jurassic (possibly Upper Triassic) *Hallopus*⁴ (Fig. 9), did succeed in turning the pubis back—at any rate it is hard to see bone 24 of my diagram, considered but rejected as a pubis, in any other light, especially in view of the bird-like femur of this animal.

The hypothesis of an arboreal origin for crocodylians by repeated regressions from a primitive proavian stock also involves the derivation of the bird ankle-joint from the crocodylian type, as the latter was already well established in Triassic members of the group^{19,29-31}, and was evidently also present in *Sphenosuchus*. The essence of the change is believed to lie in the conversion of the crocodylian calcaneal heel, whose lever action would have been important in climbing and jumping, to the bird tibial cartilage as part of a "tendon-sling" tarsus that is more effective when landing on the hind limbs alone. The calcaneal heel and tibial cartilage have similar relationships to the gastro-

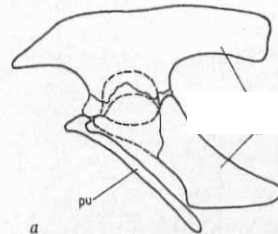


Fig. 9 New restoration of the pelvis of *Hallopus victor* (Marsh), in left lateral view ($\times 3/4$), pubis and ischium foreshortened, the pubis from a colour transparency. il, Ilium; is, ischium; pu, pubis.

nemius and peroneus longus³³ and each is functionally part of the foot, with which it rotates; in the crocodile the heel ossifies from a separate centre³⁴. During the evolution of the bird tarsus transverse compression seems to have caused the calcaneal heel to move medially, losing ossification, and its medially-facing sinus has apparently engulfed the flexor tendons which, in the bird, pass in canals through the tibial cartilage. Freed from its connexion with the heel, the body of the calcaneum would no longer be obliged to rotate with the foot and could transfer its allegiance to the crus, thus perfecting the mesotarsal joint. In the bird embryo the tarsus has a distinctly crocodylian appearance³⁵, with a dorsolateral process of the astragalus contacting the lower end of the fibula above the calcaneum. It is difficult to see why the anteriorly placed ascending process in the bird should develop in this lateral position if it is simply a newly evolved stabilizing structure. It is suggested that the crocodylian dorsolateral process (which lies partly behind the tibia) has migrated forward, because the forces tending to rotate the astragalus in quadrupedal locomotion are greatest

when the cruro-metatarsal angle is opening (during the propulsive phase), but in bipedal locomotion these forces are greatest when this angle is closing (during landing). The ascending process presumably takes up a position best suited to resist rotation. The tarsus of prosauropod dinosaurs illustrates an intermediate stage of this migration.

Other indications of arboreal adaptation in *Sphenosuchus* include the relatively long humerus, the marked inward and forward curvature of the lower half of the tibia, and reduction of the first metatarsal.

From the wealth of detailed evidence in the skull of *Sphenosuchus*, and from embryological and other resemblances between birds and crocodylians, it is difficult to avoid the conclusion that these two groups are much more closely related than has hitherto been conceded. As a result, it can no longer be assumed that anatomical structures which they have in common were also present in Triassic crocodylians, still less in dinosaurs or flying reptiles. Living crocodylians seem, to a surprising extent, to represent a "frozen" stage in the evolution of birds, and their Triassic ancestors seem to have been "drop outs" from a process of clandestine evolution which remains largely unknown to us.

I intend to give full acknowledgment to the many people who have helped me in this study in a detailed monograph on *Sphenosuchus* which is in preparation. At this time I would particularly thank Mr David Burleigh, of the Hancock Museum, Newcastle upon Tyne, for the loan of ornithological material.

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