Cranial anatomy and relationships of a new Triassic bird from Texas

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CONTENTS

SUMMARY

The oldest known fossil bird from the Late Triassic (about 225 million years ago) Dockum Formation of Texas, provides insights into the anatomy, evolution and phylogenetic relationships of early birds. In life, this adult bird was about the size of a pheasant (*Phasianus*) counting its long bony tail. Many characters of the skull show that the Texas species is more closely related to other birds than to any known group of archosaurs. The skull is lightly built, pneumatized, with an enormous orbit and expanded temporal region. The teeth are restricted to the tip of the jaws, the posterior teeth having been lost. The temporal region is modified from the diapsid condition, as in modern birds, where the orbit is confluent with the

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upper and lower temporal openings because of the breakdown of the temporal arcades. The relatively large brain size and the modification of the brain architecture in avian fashion show neurosensory specializations that may be associated with balance, coordination, flight, agility and high metabolic activity. The new species had binocular vision, which suggests that it was a visually oriented predator. Auditory acuity may be associated with vocal behaviour. The quadrate was streptostylic and the whole upper jaw was moved prokinetically as in modern birds.

Among current hypotheses for the relationships of birds among archosaurs, both theropod and crocodilian hypotheses have been supported by shared apomorphies. Some of the avian features in the crocodilian skull may have been acquired convergently because of homoplasy. Conversely, the highly akinetic skull and monimostylic quadrate along with primitive brain architecture in early crocodylomorphs negate its close phyletic relationships with birds. Within archosaurs, the theropods are closest to birds, but just what taxon is the sister group among theropods is uncertain at this time.

Numerical cladistic analysis of 30 cranial characters generated a hypothesis of the phylogenetic pattern of early avian evolution. By using theropods and sphenosuchids as comparative outgroups and root for the tree, the analysis confirms the monophyly of the class Aves. *Archaeopteryx* is the most primitive taxon and is sister group to all other birds. *Archaeopteryx*, *Avimimus* and the Texas bird are successively closer to the remaining avian taxa or Ornithurae. *Hesperornis*, *Ichthyornis* and *Gobipteryx* are the Cretaceous representatives of the Ornithurae. The Triassic bird extends the known avian record back at least 75 million years and documents an early stage in the evolution of modern birds.

The avian skull evolved in response to two functional requirements: efficient feeding mechanism, leading to the development of cranial kinesis, and neurosensory specializations leading to the enlargement of the braincase and orbit. Cranial kinesis, braincase inflation and otic specialization greatly modified the architecture of early avian skulls from the theropod condition.

Phylogenetic analysis suggests that theropods shared a common ancestry with birds, but it is indeterminate from the fossil record whether or not the immediate common ancestor itself was a theropod.

1. INTRODUCTION

Although living birds are one of the best known group of vertebrates, their origin, evolution, and early radiation are poorly documented in the fossil record. The rarity of fossil birds is generally attributed to the extreme fragility and generally small size of their bones. Most bird bones are thin and hollow, an adaptation that lightens the skeleton for flight. Such delicate bones are preserved only under the most favourable conditions. Another factor that militates against preservation of birds is the bias to the fossil record, which favours organisms that lived close to, and therefore tended to be trapped in, low-energy lacustrine and near-shore marine environments.

Fossil remains of Mesozoic birds are extremely scarce. Only three Mesozoic avian taxa, *Archaeopteryx* (Owen 1863), *Hesperornis* and *Ichthyornis* (Marsh 1880) have been extensively described on the basis of fairly complete skeletons. All three were discovered in the past century in non-clastic carbonate rocks that indicate lagoonal or near-shore marine deposits. Although our knowledge of Mesozoic terrestrial birds has improved over the past decade with the discovery of *Ambiortus* (Kurochkin 1985), *Gansus* (Hou & Liu 1984), and *Gobipteryx* (Elzanowski 1977, 1981) from Asia, *Enantiornis* (Walker 1981) from South America, *Nanantius* (Molnar 1986) from Australia and *Alexornis* (Brodkorb 1976) from North America, these fossil taxa are tantalizing in being too fragmentary to establish their affinities. A new bird specimen from the Early Cretaceous of Spain is represented by a nearly fully articulated postcranial skeleton, but it lacks the skull (Sanz *et al.* 1988). Similarly a diverse avifauna from the Cretaceous of New Jersey has been known for over a century (Marsh 1870; Olson & Parris 1987), but the material is represented by fragmentary postcranial elements. A new Early Cretaceous bird has been discovered in China with strut-like coracoid and reduced tail, but the skull is fragmentary (Rao & Sereno 1990). A loon-like diving bird has been reported from the Late Cretaceous of Antarctica (Chatterjee 1989). Thus what now appears to be the first two thirds of avian evolution is preserved only patchily in the fossil record, leaving large morphological and temporal gaps that are yet to be filled.

Archaeopteryx lithographica, from the Late Jurassic (150 Ma) Solnhofen Limestone of Bavaria, Germany has been generally considered as the oldest known bird. Its discovery in 1861, just two years after publication of Darwin's *Origin of species*, was immediately accepted as providing a link between two major classes of vertebrates: reptiles and birds. *Archaeopteryx* has remained the subject of lively scientific debate since its discovery. In spite of voluminous publications, there is little consensus about its status, ancestry, relationships, mode of life, and flight capabilities. Here I report the discovery of a new primitive bird from the Triassic of Texas which lived at least 75 Ma BP than *Archaeopteryx*. Although there must have been still earlier birds, this protobird from Texas has a dramatic significance of its own.

Two individuals, both of the same species of this protobird, were found in the summer of 1983, in the Late Triassic (225 Ma) Dockum Formation near Post, Garza County, in western Texas. A quarry there has produced unusual concentrations of rare tetrapods including the ictidosaur *Pachygenelus* (Chatterjee 1983), the fabrosaur *Technosaurus* (Chatterjee 1984), the rauisuchian *Postosuchus* (Chatterjee 1985), a brachyopid amphibian, a pterosaur, a sphenodontid, a squamate and possibly a mammal (Chatterjee 1986).

The protobird skeletons were exposed accidentally during removal of the overburden of the bone bed by a jackhammer (figure 1 *c*). Because most of the skeletons were concealed in matrix, the importance of this discovery was not fully appreciated at that time. Later, when the two specimens were prepared and compared for systematic study, they revealed the following interesting features.

1. The two skeletons represent a new taxon, showing a mosaic of theropod and avian characters.
2. The bones are thin with hollow shafts.
3. The animal is relatively small compared with any known theropods; the large individual would be about 60 cm long, comparable to the Solnhofen specimen of *Archaeopteryx* (Wellnhofer 1988), the small one would be about half the length of the larger, and corresponds to the size of the Eichstätt specimen (Wellnhofer 1974).
4. The skull is fundamentally bird-like and does not resemble the skull of any known archosaurs. The orbits are large, frontally placed, and appear to be confluent with the two temporal fenestrae. The brain is enlarged and has reached avian proportions, with neurosensory specializations associated with flight. Teeth are present only near the tips of the jaws. The quadrate, palate, and otic capsules are of a primitive avian type; the quadrate is streptostylic and the skull is prokinetic (Chatterjee 1987).
5. The postcranial skeleton does not have as many fused bones as modern birds.
6. The posterior cervicals are heterocoelous.
7. The morphology of the shoulder girdle and forelimb suggests that the animal was capable of aerial locomotion. The coracoid is elongate and strut-like, with a prominent acrocoracoid process indicating flapping capabilities. The furcula bears a large hypocleideum and the sternum is ossified.
8. Semilunate carpal is similar to that of juvenile bird with a single distal metacarpal facet.
9. The morphology of the pelvic girdle and hindlimb indicates that the animal had erect and bipedal gait. The ilium and ischium are fused distally with a large ischiadic fenestra, as in modern birds. The astragalus extends antero-dorsally as an ascending process, a feature first shown by Huxley (1870) to be unique to theropods and birds.

What is the affinity of this new Texas species? Was it a 'theropod-like bird' or 'bird-like theropod'? Without the presence of feather impressions, the status of the Texas species as a true bird deserves careful scrutiny. Since feathers are rarely preserved in the fossil record, osteological characters are used here to assess the affinity of the Texas species. Although avian features are clearly evident in the postcranial skeleton, discussion in this paper will be restricted to the cranial anatomy. The nature of temporal configuration provides a practical guide for distinguishing birds from theropods. A phylogenetic analysis of cranial characters supports a hypothesis that the Texas species had achieved a structural organization well beyond that of any theropods and is more closely related to birds. Conversely, it reveals some primitive features that give us a unique insight into an early stage of avian evolution. The structures of the Texas bird form a perfect example of mosaic evolution, retaining some theropod features but possessing others that are typically avian, as would be expected in an ancestral form.

The protobird from Texas pushes back avian origins to the Late Triassic when other major groups of vertebrates such as dinosaurs, crocodilians, pterosaurs, lissamphibians, squamates, turtles and mammals originated. The recognition of the Texas species as the 'Urvogel' or the earliest bird will require a radical modification of current views of the origin, evolution, and relationships of Mesozoic birds. It may close the temporal and structural gap between reptilian and avian classes.

In this paper, the new species is formally named and described, and its cranial anatomy is examined with emphasis on skull kineticism, evolution, and phylogenetic relationships. In a subsequent paper, the postcranial skeleton will be described with speculations on protobird's flight capabilities.

2. GEOLOGIC SETTING

In the arid and semi-arid regions of western Texas, the panoramic exposures of the Dockum Formation are among the most visible and beautiful parts of the landscape. The Dockum Formation extends as an almost continuously north-trending outcrop from an area north of San Angelo to the Canadian River Valley northwest of Amarillo (figure 1 *a*). It is a redbed formation of 70–700 m of continental clastics and is composed of mudstone, sandstone, and lenticular 'lime-pellet' rock (calcrete). The depositional setting of the Dockum Formation is generally recognized as a flood plain of low relief cut by meandering streams, in a hot; humid and seasonally arid environment with lush vegetation (Chatterjee 1985).

The Dockum Formation rests unconformably on the Late Permian Quartermaster Group and is capped by Cretaceous, Tertiary, or Quaternary sediments (figure 1 *b*). Currently the Dockum Formation is subdivided into three members: Tecovas, Trujillo, and Cooper in ascending order (Chatterjee 1986). It has yielded a variety of tetrapods in recent years including metoposaurs, brachyopids, rhynchosaurs, protorosaurs, trilophosaurs, squamates, parasuchids, aetosaurs, poposaurs, coelurosaurs, fabrosaurs, pterosaurs, ictidosaurs and now birds (Chatterjee 1985). Some taxa help to tie the Dockum Formation more precisely with the type Triassic sequence of central Europe. For example, the metoposaurs, aetosaurs, parasuchids and poposaurs are quite similar to those of German middle Keuper, indicating a Late Triassic (Carnian–early Norian) age.

The parasuchid genera offer further biozonation of the Dockum, as in the German Keuper. The lower unit, the Tecovas Member is characterized by *Parasuchus*, and the upper Cooper Member contains *Nicrosaurus*. The intervening Trujillo sandstone is usually barren. The Dockum Formation is therefore of great importance in the tempral sequencing of North American Late Triassic deposits. The bird fossils,

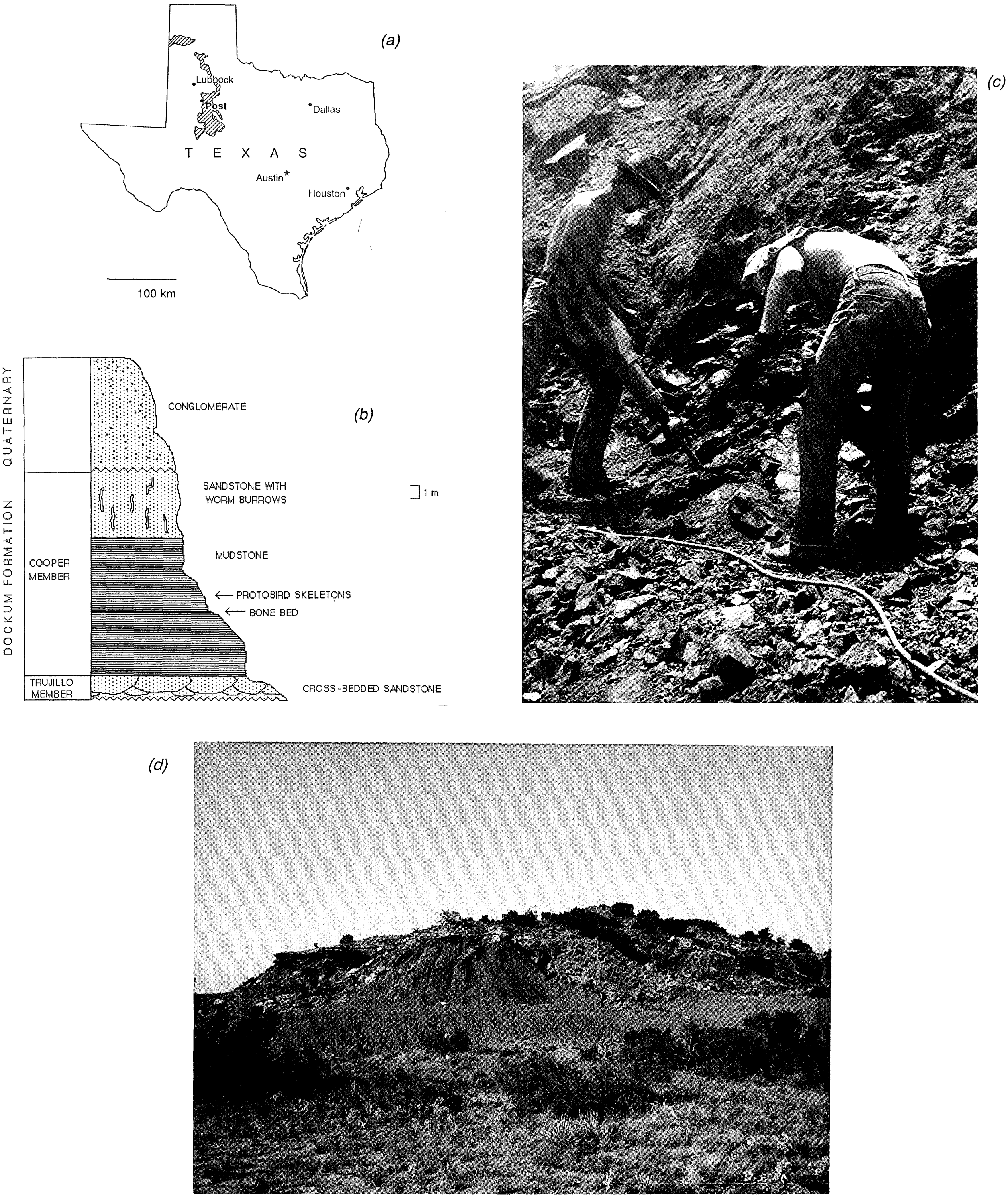


Figure 1. (*a*) Location map of the Post quarry in Garza County, West Texas; area of outcrop of the Dockum Formation, hatched; (*b*) geological section of the Dockum Formation at Post quarry showing two different levels of bone-bearing beds; (*c*) protobird skeletons were exposed while removing the overburden by a jackhammer; the blade of the jackhammer points to the approximate location of the two skeletons; left, Bryan J. Small, right, J. Bruce Moring; (*d*) Post quarry from a distance; the flat platform indicates the horizon of the primary bone bed; protobird skeletons were found about one metre above this bone bed.

discussed in this paper, were collected from the upper Cooper Member, of Early Norian age (225 Ma).

3. MATERIALS AND METHODS

Both bird skeletons were collected from the Post Quarry, lying side by side slightly above the bone bed, and were tightly encased in a block of mudstone. The small individual retained some degree of natural association. In the large specimen, the bones were disarticulated and jumbled together (figure 2). Surprisingly, the preservation of the delicate cranial elements is excellent in both specimens, but the long bones suffered damage along the hollow shafts, which

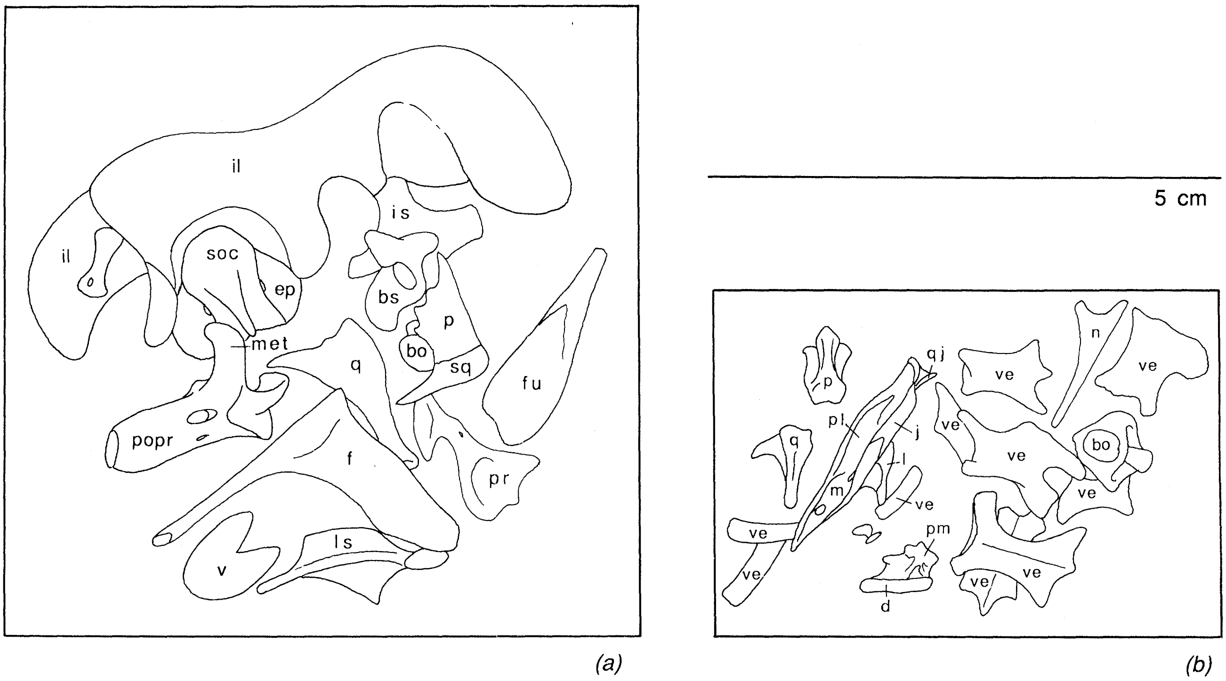


Fig. 2. Some skeletal elements of protobird as preserved in the matrix; the mudstone block was broken into several pieces, making it difficult to orient them in relation to each other; two of these smaller blocks are shown here containing important cranial elements; (*a*) disarticulated bones of a large individual (TTU P 9200); (*b*) disassociated bones of small individual (TTU P 9201); for abbreviations, see key to abbreviations.

are often missing. Other missing bones show some sort of *post mortem* disturbance. There is no sign of intermixing of other Dockum vertebrates with the bird bones, as they were recovered about a metre above the bone bed.

All the bones that are present in both large and small individuals arte listed below.

Large individual: partial skull (premaxilla, frontal, parietal, squamosal, lacrimal, quadrate, basioccipital, basisphenoid, alaparasphenoid, supraoccipital, epiotic, exoccipital, opisthotic, prootic, laterosphenoid, dentary, prearticular, articular, portion of angular and surangular) and partial postcranial (two vertebrae, portion of furcula, distal end of scapula, ilium, ischium, portion of pubis, femur) material.

Small individual: partial skull (maxilla, nasal, parietal, jugal, quadratojugal, vomer, palatine, pterygoid, quadrate, basioccipital, predentary, portion of dentary, prearticular, articular, portion of angular and surangular) and partial postcranial (fairly complete vertebrate column except for the sacrum, scapula, coracoid, humerus, radius, ulna, articulated carpals and metacarpals, phalanges, portion of tibia and fibula, astragalus, calcaneum, metatarsals, phalanges) material.

Removal of the fossil material from the matrix was done entirely under an 'Olympus' binocular microscope, fitted with a camera and a camera lucida, with which the progressive development was recorded from time to time. Clay matrix was softened by applying acetone, which penetrated well, and enhanced the contrast between bone and matrix. The softened matrix was easily removed by small dental picks.

Once the bones were exposed, a dilute solution of 'Glyptal 1202' cement in lacquer thinners was applied to increase the structural strength required for removal of fragile elements. Some bones were encased with a hard calcareous coating that was difficult to remove mechanically. After experimenting with various acids, dilute formic acid (1%) was found suitable. It acted quickly on the encrustation, and its action could be monitored under the microscope. The acid was applied directly to the encrustation by brush. With continued soaking, the encrustation was peeled off, exposing the fresh surface of the bone. After each acid treatment, the area was promptly washed with water.

After the bone layer was exposed, additional reinforcement became necessary to hold the fossil rigid enough for further preparation. This was done by making a rim around the matrix, of epoxy sculpting putty, 'Sculpall'. The Sculpall rim allowed safe handling of the block, and prevented it from collapsing into pieces. Hard matrix was easily removed with the Foredom flexible shaft power tool, which allowed access into difficult places. During the entire extraction process, the specimen was carefully monitored for damage. Whenever cracks were noticed a dilute solution of Glyptal was applied.

The removal of fragile elements presented special problems. It was a slow and painstaking process, often resulting in cracks and breaks in the bones. Once a bone was broken, it was joined immediately with 'Super Glue'. Major breaks and missing parts were repaired with Sculpall or Plaster of Paris. A thinned solution of 'Butvar B-76' (polyvinyl butyral) in acetone was applied to each prepared bone as a protective coating.

A few disarticulated bird bones were found on Collier's ranch, about 10 miles southeast of Crosbyton in Crosby County, Texas. Here, the Late Triassic bone

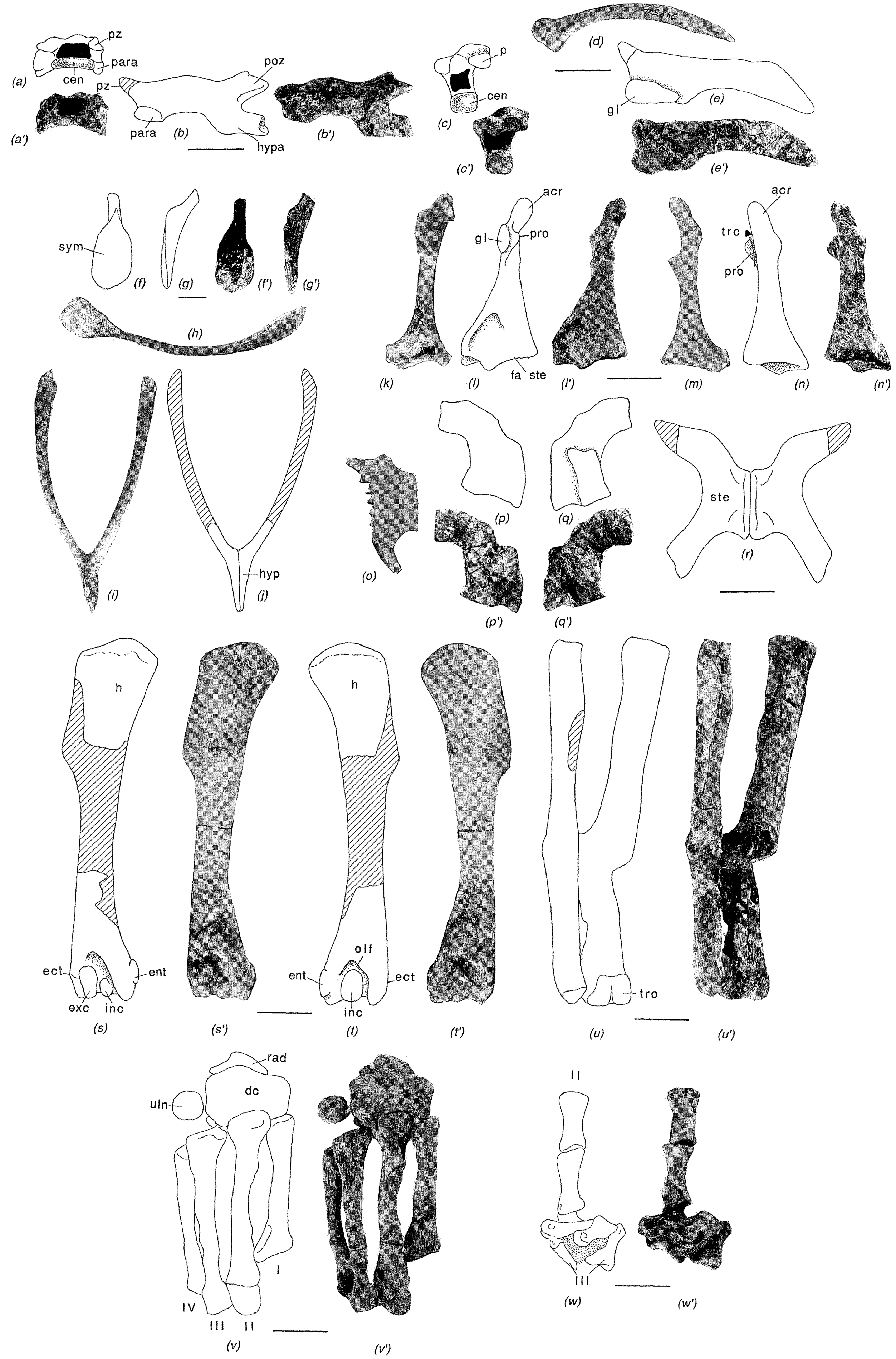


Figure 3. For description see opposite.

bed is a thin layer of 'lime-pellet' rock, interlayered with mudstone of the Lower Tecovas Member. The bones in this quarry are highly dispersed and show a diverse mixture of terrestrial, aquatic, and subaquatic assemblages. The preservation is excellent, and the specimens need little preparation. A beautiful humerus from this quarry shows all the avian hallmarks. So far, only vertebrae, coracoid, and limb elements of birds have been recovered from this site, and the affinity of this material will be discussed in a separate paper.

4. SYSTEMATIC PALAEONTOLOGY

Class Aves Linnaeus, 1758
Order Protoaviformes, new order
Family Protoavidae, new family
Genus *Protoavis*, new genus

Generic description. Same as for family and order (figures 3–7). Skull long and narrow with a sharply tapered snout and a relatively deep, expanded temporal region; elliptical external naris, bounded by premaxilla and nasal; maxilla reduced laterally with a large palatal component; antorbital fenestra single, large and triangular; orbit relatively enormous, circular, directed anteriorly to permit binocular vision; temporal region modified in avian fashion by loss of diapsid arch, postorbital bar, and squamosal-quadratojugal bar, resulting in confluence of supra- and infratemporal fenestrae and orbit; postorbital bone lost; postorbital process formed by frontal and laterosphenoid; squamosal reduced; zygomatic process in squamosal well developed; palate of palaeognathous type; vomers long and narrow, partly fused, meeting maxilla anteriorly and pterygoid posteriorly; palatine fused to pteryoid and not contacting parasphenoid rostrum; choana posteriorly placed, close to basipterygoid articulation; pterygoid highly reduced; ectopterygoid lost; quadrate streptostylic with development of a medial orbital process, ventral condylar articulation with pterygoid, and lateral cotylus for quadratojugal; prokinetic hinge present; skull highly encephalized; cerebellum and cerebrum contacted dorsally, displacing optic lobes ventrally; cerebellar protruberance reflected on external surface of supraoccipital; presence of epiotic on occiput; olfactory lobes reduced; vallecula present bordering Wulst; basioccipital horizontal; stapedial fossa contains three foramina as in birds: fenestra ovalis, fenestra pseudorotunda, and entrance to posterior tympanic recess; large metotic process added to exoccipital; vagus foramen diverted backward; parabasal notch present for the passage of internal carotid artery; all five tympanic diverticula present; both anterior and posterior tympanic recesses have developed contralateral communications; eustachian tube bony; anterior vertical canal highly enlarged, enclosed sagittally in an oval tube around a deep floccular recess; cochlear recess tubular and elongated; predentary bone possibly present; mandibular elements fused posteriorly and compressed laterally; tricondylar articulation between mandible and quadrate; teeth restricted to the tip of the jaws by loss of posterior teeth.

Posterior cervicals heterocoelous; cervical ribs fused in adult; coraco-scapular joint movable; scapula elongated and oriented posteriorly; coracoid strut-like with a prominent acrocoracoid process; furcula present with a large hypocleideum; sternum ossified; humerus with large deltopectoral crest; distal condyles modified in avian fashion with external condyle elongate proximo-distally, internal condyle rounded; carpus with a large semilunate carpal, showing single distal facet; small extensor process on McI; preacetabular ilium elongated to avian dimension; renal fossa present; ischium rotated parallel to ilium and fused to it distally; ischiadic fenestra present; ischia opened ventrally without symphysis; tibia with both internal and external cnemial crests; ankle joint mesotarsal; astragalus and calcaneum fused; ascending process of astragalus with foramen at base; metatarsals appressed together proximally; hallux distally articulated and reversed.

Type species: *Protoavis texensis*, new species.

Horizon: Cooper Member, upper Dockum Formation, early Norian, Late Triassic.

Derivation of name: The generic name refers to 'first bird'. The specific name is given in honour of the State of Texas.

Specific diagnosis: Same as for genus.

Holotype: TTU P 9200, partial skull material of a large individual (figure 6).

Paratype: TTU P 9201, partial skull and partial postcranial material of a small individual (figure 7).

Locality: (Lat. 33° 31′ 17″ N; Long. 101° 18′ 54″ W), 9 miles southeast of Post, R. C. Miller Ranch, Garza County, Texas.

Fig. 3. Postcranial elements of *Protoavis* showing vertebra, shoulder girdles and fore limbs; (*a*) and (*a*′) anterior view of a cervical vertebra of *Protoavis* showing heterocoelous centrum, small individual; (*b*) and (*b*′), same, lateral view; (*c*) and (*c*′), same, posterior view; (*d*) left scapula of Black vulture (*Coragyps*), dorsal view; (*e*) and (*e*′) same view of scapula of *Protoavis*, small individual; (*f*), (*f*′) and (*g*), (*g*′) medial and anterior views of left furcula of *Protoavis*; (*h*), (*i*) medial and anterior view of furcula of chicken; (*j*) anterior view of furcula of *Protoavis*, large individual; note development of large hypocleideum; (*k*) left coracoid of Black vulture, dorsal view; (*l*) and (*l*′), same view of coracoid of *Protoavis*, small individual; (*m*) left coracoid of Black vulture, ventral view; (*n*) and (*n*′) same view of coracoid or *Protoavis*, small individuals; note development of procoracoid and acrocoracoid processes and triosseal canal; (*o*) left sternum of juvenile ostrich (*Struthio*), ventral view; (*p*), (*p*′) and (*q*), (*q*′) ventral and dorsal views of left sternum of *Protoavis*, small individual; (*r*) restoration of sternum of *Protoavis* ventral view (*s*), (*s*′) and (*t*), (*t*′) palmar and anconal views of right humerus of *Protoavis*, small individual; (*u*) and (*u*′) anconal view of right radius and ulna of *Protoavis*, small individual; (*v*) and (*v*′) external view of right carpometacarpus of *Protoavis*, small individual; note development of large semilunate carpal (*dc*) and possible quill nodes on metacarpal III; (*w*) and (*w*′) left manus, digits II and III jumbled together, small individual; restored area hatched; scale bar 5 mm.

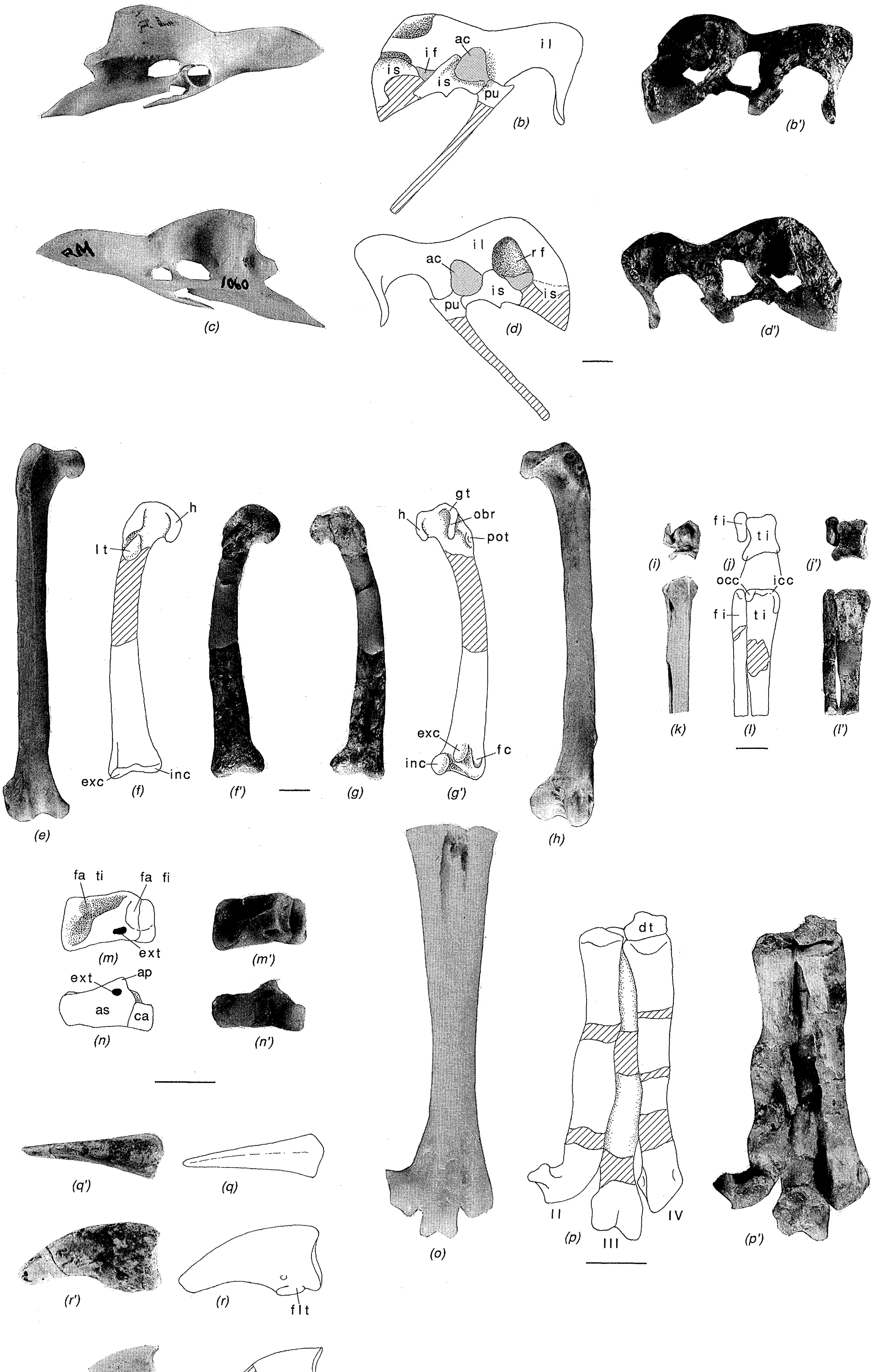


Figure 4. For description see opposite.

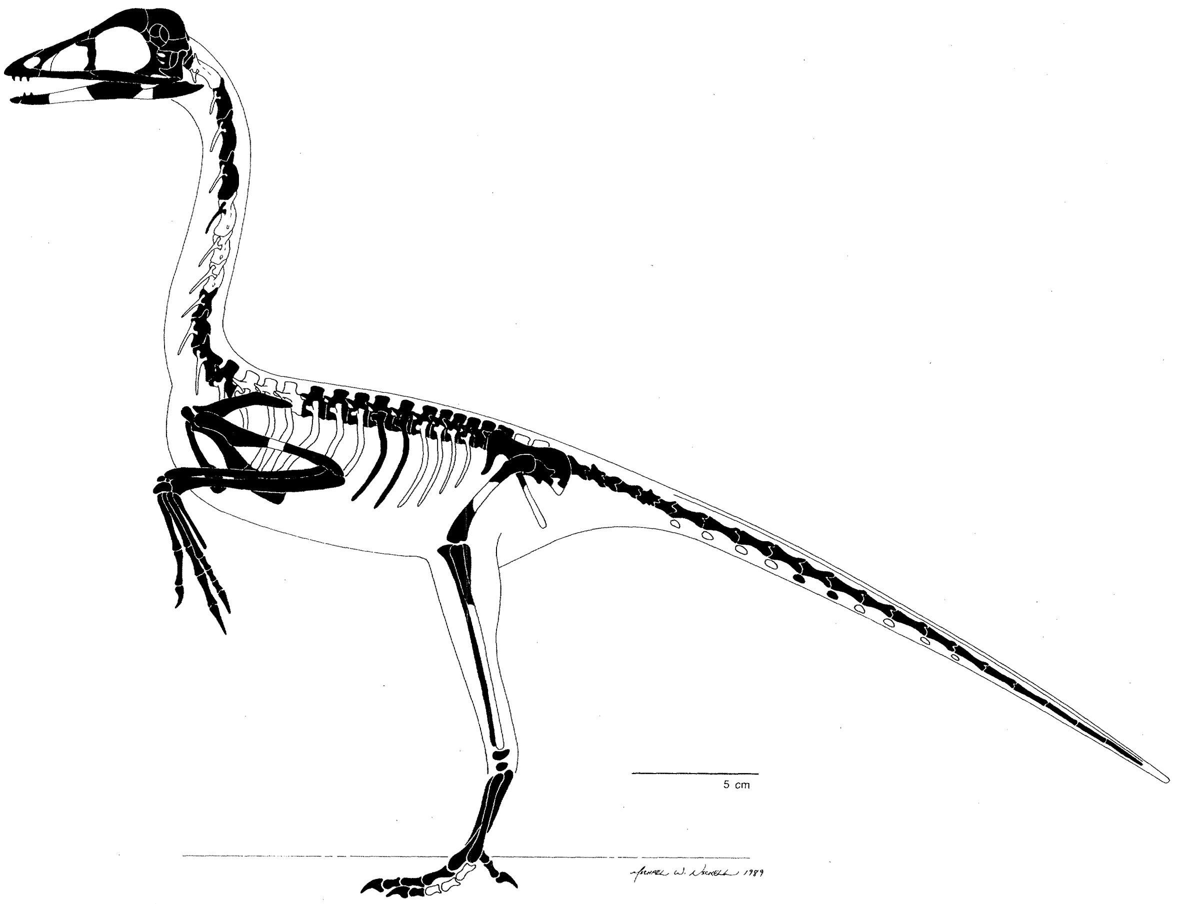


Figure 5. *Protoavis texensis*, n. sp; composite skeletal restoration representing the size and proportion of the large individual.

5. DESCRIPTION OF SKULL

The adult skulls of modern birds are so modified that they are difficult to compare with those of primitive avian groups. In neognaths, the skull bones are fused at an early age and their sutures usually cannot be discerned. It is, therefore, problematic to homologize the cranial elements of early Mesozoic birds with those of modern ones. In ratites, however, the fusion of the skull bones is delayed and the sutures remain open, which is a neotenous feature. Juvenile skulls of several species of modern birds were useful for comparison with *Protoavis*, in which the shape and relationships of each bone can easily be determined.

In the large specimen (9200) of *Protoavis*, the disarticulated skull bones of the roof and the braincase were loosely sutured (figure 2*a*). The lack of fusion, a primitive avian feature known in *Archaeopteryx*, *Hesperornis*, *Ichthyornis* (Martin 1983*a*), the *Lithornis*-cohort (Houde 1986), and in living ratites, is not the result of immaturity, as the surface area of the bones is smooth and non-porous as in adult birds. The palate and the lateral part of the skull, as preserved in the small specimen (9201), are found in articulation (figure 2*b*). The bones in both specimens are excellently preserved with little distortion. Individual elements are delicate and lightly built, apart from the braincase, in which the bones are more robust. They provide three-dimensional anatomical information and show the nature of the articulations between adjacent elements. The large skull would have been twice the size of the small one, as determined by the proportions of the common elements (quadrate, braincase). The morphological variation between the two specimens is

Figure 4. Postcranial elements of *Protoavis* showing pelvis and hind limbs. (*a*) Lateral view of right pelvis of pigeon (*Columba*); (*b*) and (*b′*) same view of pelvis of *Protoavis*, large individual; (*c*) medial view of right pelvis of pigeon; (*d*) and (*d′*) same view of pelvis of *Protoavis*, large individual; note ilium and ischium are fused in *Protoavis* to enclose ischiadic fenestra; also reneal fossa is well developed medially to accommodate kidney; (*e*) anterior view of right femur of Black-crowned Night heron (*Nycticorax*); (*f*) and (*f′*) same view of femur of *Protoavis*, large individual; (*g*) and (*g′*), (*h*) posterior view of right femur of *Protoavis*, large individual; posterior view of right femur of heron; (*i*) proximal view right tibia and fibula of heron; (*j*) and (*j′*) same view of tibia and fibula of *Protoavis*, small individual; note development of external cnemial crest on tibia; (*k*) anterior view of right tibia and fibula of heron; (*l*) and (*l′*) same view of tibia and fibula of *Protoavis*, small individual; (*m*), (*m′*) and (*n*), (*n′*) proximal and anterior views of fused astragalus-calcaneum of *Protoavis*, small individual; (*o*) external view of left metatarsal of pigeon; (*p*) and (*p′*) same view of metatarsals of *Protoavis*, small individual; (*q*), (*q′*) and (*r*), (*r′*) external and lateral views of claw of *Protoavis*, small individual; (*s*) and (*s′*) lateral view of claw, small individual; scale bar 5 mm.

Figure 6. *Protoavis texensis* n. sp. holotype (TTU P 9200), large individual.

small and may reflect allometry. As restored, the skull of the holotype is about 72 mm long, 39 mm wide, and 30 mm deep.

(*a*) *Dermal roofing bones* (*figures 8 and 9*)

The *premaxilla* bears three alveoli at the front (figure 8*a*, *b*). It is deeply emarginated posteriorly by the external naris. The nasal process extends backward to meet the inner surface of the nasal. The maxillary process is deeper and more robust. Posteriorly it has two distinct facets for the maxilla. Farther dorsally, another facet receives the descending process of the nasal. Thus the external naris is entirely bounded by the premaxilla and the nasal, and the maxilla is excluded from its boundary. Two premaxillae remain separate for most of their lengths; only the extreme anterior ends are conjoined. A large sinus is found behind the symphysis for housing the premaxillary diverticulum (figure 8*b*).

The *maxilla* is edentulous as in modern birds, and forms a sharp ventral edge that was probably covered in life by a horny rhamphotheca (figures 8*e*, 9*b*). It is reduced in lateral aspect, forming a rod-like structure that extends backward to overlap the jugal. The maxilla tapers anteriorly and forms the whole lower margin of the antorbital fenestra, which is single and triangular. It is likely that the antorbital fenestra housed a large air-filled diverticulum of the nasal cavity: the antorbital sinus, as in modern birds (Witmer 1990). Mesially each maxilla has a palatal process that joins the vomer and the palatine around the choana.

The *nasal* (figure 8*c*) is a long, narrow bone that forms the roof of the skull above the antorbital fenestra. Anteriorly it bifurcates to meet the premaxilla and to form the posterior border of the naris. Behind the naris it has a small ventral contact with the maxilla. Posteriorly it is a flat thin plate that loosely overlaps the frontal.

The *frontal* is an elegant, shell-like bone, the ventral surface of which is rounded and smooth over the brain cavity, and hollow and scooped over the orbit (figure 8*i*, *j*). Anteriorly the bone is narrow, pointed and flattened to insert under the nasal. It has a distinct orbital rim that extends laterally as a free orbital process in conjunction with the laterosphenoid. The suture between the frontal and the laterosphenoid is intimate and complex. The frontal receives the laterosphenoid postero-laterally in a descending orbital flange. The fronto-parietal suture is straight and squamous for the most part; however the orbital flange has a complex union with the parietal posteriorly.

The *parietal* forms an arched roof over the occiput with a parasagittal crest (figure 8*k*). The postero-lateral process is overlapped by the squamosal. Each parietal forms a transverse occipital crest which marks the posterior limit of the origin of M. adductor

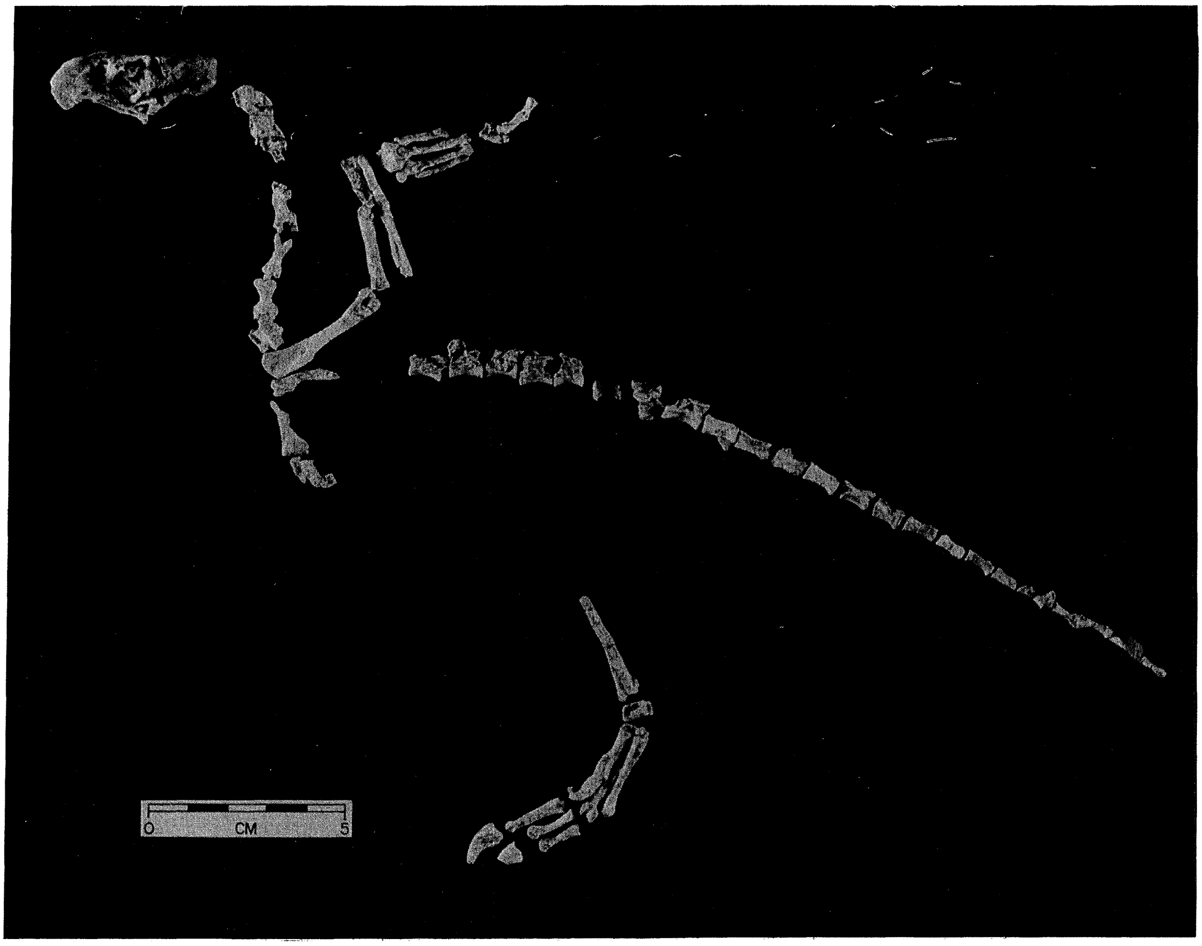


Figure 7. *Protoavis texensis* n. sp. paratype (TTU P 9201), small individual.

mandibulae externus. The crest extends laterally toward the squamosal, but weakens medially. Ventral to this crest, each parietal has a ventral occipital plate that covers the supraoccipital medially. On the sidewall of the braincase, the parietal contacts the laterosphenoid and epiotic.

The *lacrimal* (sometimes called 'prefrontal' in birds; Jollie (1957)) forms a vertical bar between the orbit and the antorbital fenestra (figures 8*d*, 9*b*). The dorsal bar supports the conjoined fronto-nasal plate. Ventrally it makes a sliding contact with the jugal bar. In many living birds, this joint becomes more mobile, and is ligamentously attached. The *prefrontal* and *postfrontal* are apparently absent in *Protoavis*.

The *jugal* is a rod-shaped bridge between the maxilla and the quadratojugal (figures 8*e*, 9*b*). In archosaurs, it is usually a three-pronged bone, from which an ascending process joins a ventral process of the postorbital to form a bar between the orbit and the infratemporal fenestra. In *Protoavis*, with the loss of the ascending process of the jugal, the orbit becomes confluent with the infratemporal fenestra. A small projection represents the base of the vanishing ascending process.

The *postorbital* bone is apparently absent in *Protoavis* as in modern birds. In some theropods this bone is loosely connected to the frontal and squamosal, and can be easily disarticulated. In theropods, even if this bone is lost after death, both frontal and squamosal show distinct facets for its articulation. In addition, the anterior process of the squamosal is bifurcated where it articulates with the postorbital (figure 8*f*, *g*). In *Protoavis*, neither the frontal nor the squamosal show any facets for the reception of the postorbital. Moreover, the anterior process of the squamosal is single. All these features indicate that the postorbital is absent and the temporal region is modified in avian fashion.

The *quadratojugal* is a simple horizontal bar extending posteriorly to meet the quadrate in a cotylus (figures 8*e*, 9*b*). Unlike the archosaurian condition, the ascending process of the quadratojugal in front of the quadrate is absent.

The *squamosal* is distinctively avian-like in form (figure 8*i*). It is reduced and lacks the descending process for the quadratojugal. Anteriorly it has a short zygomatic process that, as in modern birds, juts down over the quadrate head and covers the superior tympanic recess. The squamosal embraces the parietal medially. Ventrally it has a elliptical socket for the reception of the quadrate head (figure 10*a*). A large air space from the middle ear cavity lies postero-ventrally between the squamosal and the braincase (figure 21*h*).

(*b*) *Palatal complex* (*figures 10 and 11*)

The right side of the palate is preserved intact in the small individual (see figure 8*e*,*h*). It has been crushed from both lateral and posterior directions. Because of

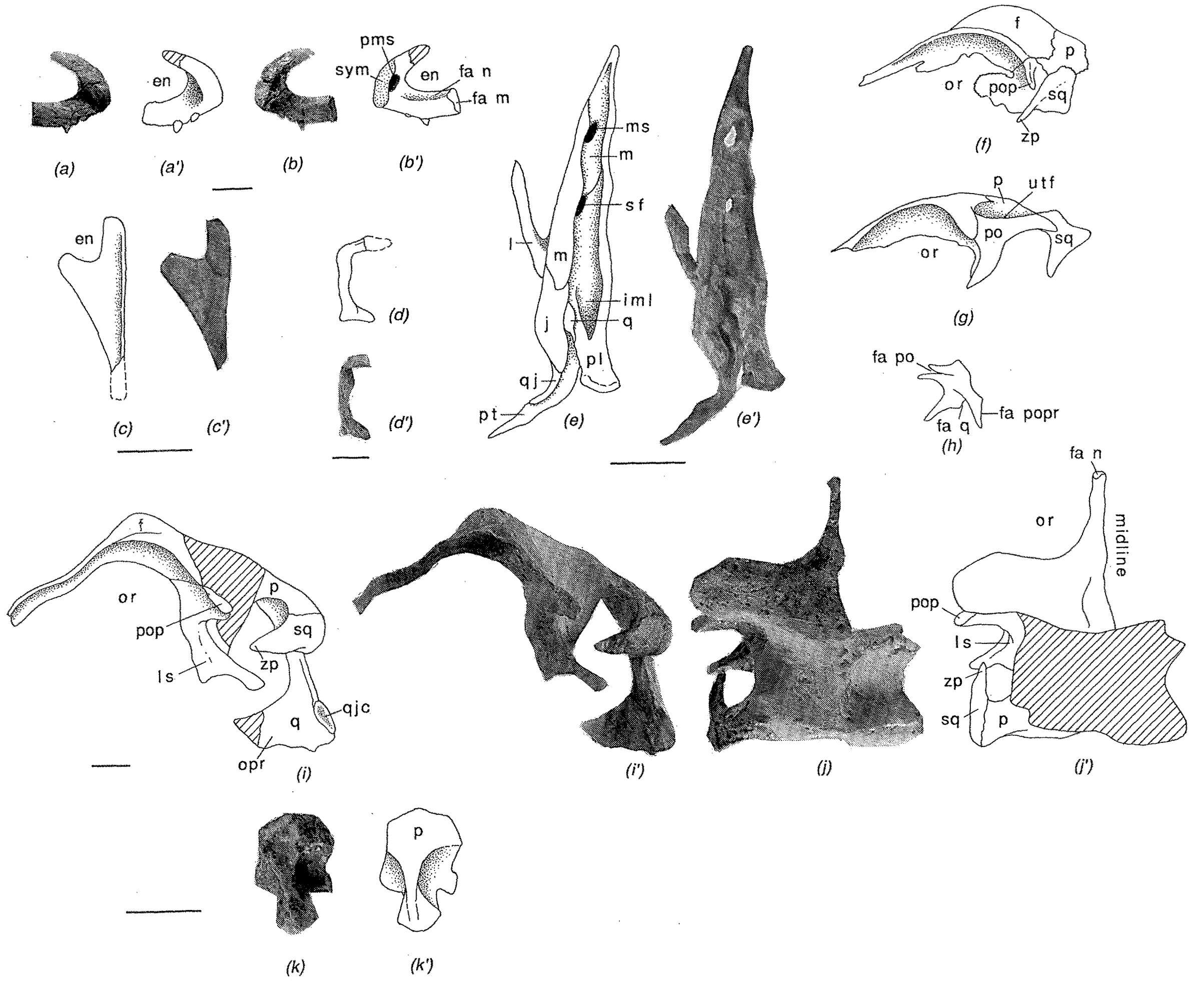


Figure 8. *Protoavis texensis* n. sp; dermal roofing bones; (*a*), (*a*′) and (*b*), (*b*′) lateral and medial views of right premaxilla, large individual; (*c*) and (*c*′) ventral view of right nasal, small individual; (*d*) and (*d*′) medial view of left lacrimal, large individual; (*e*) and (*e*′) lateral view of right side of skull and part of palate, small individual; (*f*) left lateral view of posterior-half of skull roof of juvenile *Rhea*; (*g*) the same view of *Troodon* showing the presence of upper temporal fenestra (modified from Currie (1985)); left lateral view of squamosal of *Deinonychus* (after Ostrom 1969); note in theropods squamosal is large, the postorbital process is bifurcated, and the descending process is robust to receive quadratojugal; (*i*) and (*i*′) left lateral view of posterior-half of skull roof of *Protoavis* of large individual showing avian-like temporal configuration with loss of prootic bone; orbit is confluent with upper and lower temporal fenestrae; the squamosal is highly reduced; both postorbital and zygomatic processes are developed; disarticulated bones assembled; (*j*) and (*j*′) dorsal view of skull roof of *Protoavis*, large individual; disarticulated bones assembled; (*k*) and (*k*′) dorsal view of parietal, small individual; scale bar 5 mm.

lateral compression, the jugal bar is plastered against the palatine. Posterior compression has dislodged the right quadrate into the choana and pushed the quadrate ramus of the pterygoid slightly upward. The left quadrate of each individual was found disarticulated, and each is in excellent condition (figure 10*b*–*e*).

The palate is narrow, flexible and lightly built. It is made of the same elements as found in reptiles, except that the ectopterygoid is absent. As a result, the palate has lost the lateral contact with the jugal bar in avian fashion. The choanae are placed posteriorly and are bounded by the palatines, pterygoids and vomers.

The *premaxillae* have short palatal processes. The *maxillae* contribute large palatal components, and show air sinuses in front, presumably housing the diverticulum from the olfactory capsule. Posteriorly the maxilla has a broadly overlapping and flexible contact with the palatine, and the suture is interrupted by the subpalatal fenestra (figure 8*e*).

The *vomers* are long, narrow elements, which are fused anteriorly, and inserted into the palatal processes of the maxilla (figure 10*h*). Posteriorly they become separate elements, each unites laterally with the palatine. The bone extends posteriorly to receive the pterygoid, and forms the anterior margin of the choanae.

The *palatine* is an elongate, subrectangular plate that has a distinctive 'intermuscular lamina' (McDowell 1978) for the M. pterygoideus internus, as in modern birds (figure 8*e*). The medial edge is more pronounced than the lateral one, and forms a vertical trough to border the rear end of the choana. The whole arrangement is very similar to that of the ratites and *Fulmarus*.

The *pterygoid* is relatively short as in modern birds

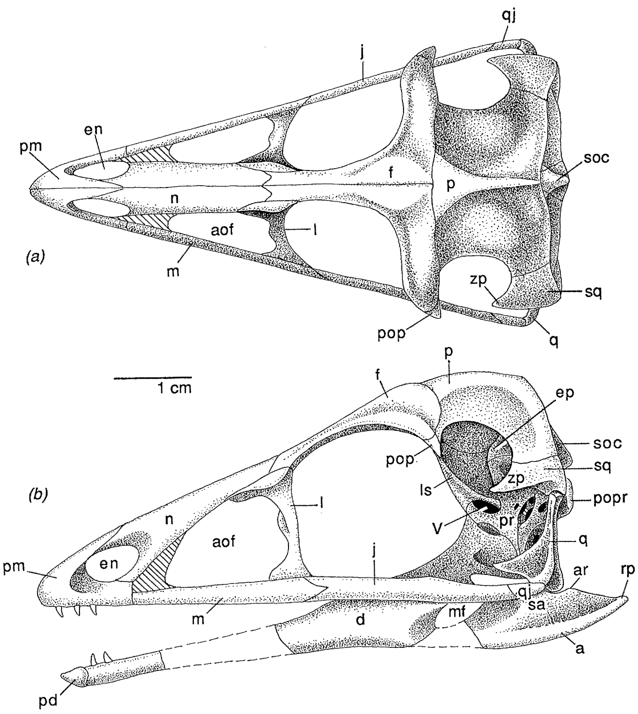


Figure 9. *Protoavis texensis* n. sp. (magn. ×1); composite restoration of skull; (*a*) dorsal view; (*b*) left lateral view.

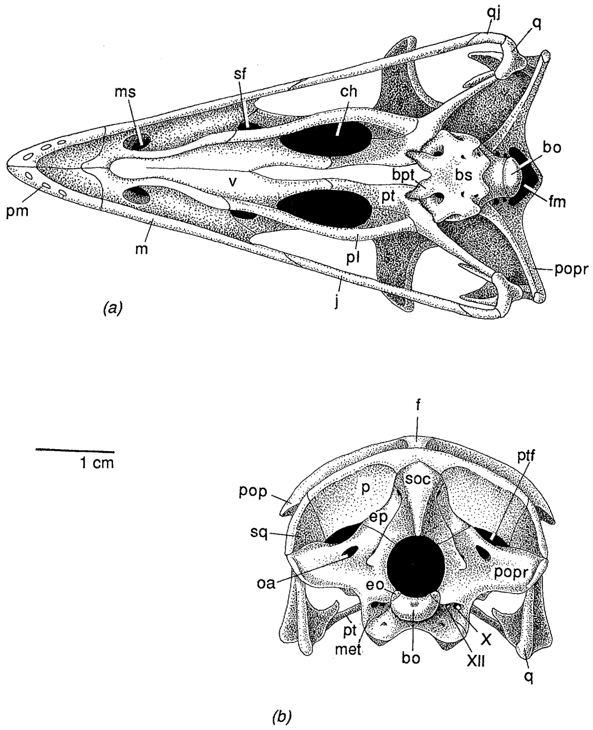


Figure 11. *Protoavis texensis*, n. sp. (magn. ×1) composite restoration of the skull; (*a*) palatal view; (*b*) occipital view.

(figures 8*e*, 11*a*). In theropods, the palatal ramus of the pterygoid is extensive and extends well past the orbits anteriorly; posteriorly it has a transverse flange that receives the ectopterygoid. In *Protoavis*, the palatal ramus is reduced and lacks the transverse flange for the ectopterygoid. Anteriorly it is forked around the choana, as in *Apteryx* (McDowell 1948) and *Gobipteryx* (Elzanowski 1976). The medial process receives the vomer and the lateral one contacts the palatine. In the ostriches, the pterygoid takes part in the formation of the choana, but fails to reach the vomer.

The quadrate ramus of the pterygoid is a thin and narrow bar, directed posteriorly to contact the distal end of the quadrate. Antero-laterally it shows a large socket for the reception of the basipterygoid process.

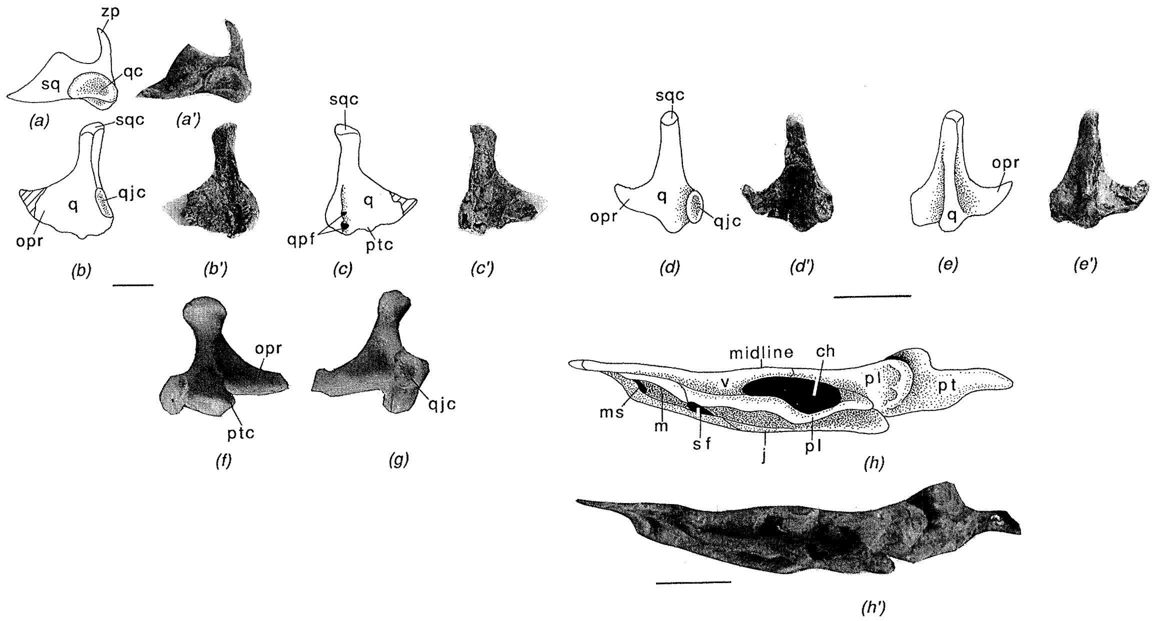


Figure 10. *Protoavis texensis* n. sp., palatal complex; (*a*) and (*a′*) ventral view of left squamosal showing quadrate cotyle and zygomatic process, large individual; (*b*) and (*b′*) lateral view of left quadrate of large individual showing cotyle for quadratojugal, orbital process and head; (*c*) and (*c′*) medial view of same showing pterygoid condyle and pneumatic foramina; (*d*) and (*d′*) lateral view of left quadrate of small individual; (*e*) and (*e′*) postero-medial view of same; (*f*) and (*g*) medial and lateral views of quadrate of penguin (*Pygoscelis*) for comparisons; (*h*) and (*h′*) palatal view of right palate of small individual; note choana has been shifted considerably backward with loss of ectopterygoid bone; scale bar 5 mm.

Both specimens of *Protoavis* lack *ectopterygoids*, which were primitively present in archosaurs. Furthermore, the outer margin of the quadrate ramus of the pterygoid is overlapped by the palatine, leaving no place for the ectopterygoid. Loss of the ectopterygoid seems to be a synapamorphy for birds.

The *quadrate* (figure 10*a–e*) shows many avian traits except for the head, which has a single dorsal knob pivoting at a ventral socket of the squamosal, while in modern birds, the quadrate head consists of outer and inner knobs, the latter articulating with the prootic. There is a prominent orbital process in medial aspect, directed anteriorly, for attachment of one of the temporalis muscles. This process is pointed forward as in birds of prey. ventral and medial to this process is a small condyle for the reception of the pterygoid. In addition, the ventral edge of the orbital process probably makes additional contact with the pterygoid, as in ratites.

Laterally the quadrate has an oval cotylus for articulation with the quadratojugal. Above this joint, the anterior border of the quadrate is free due to loss of the squamosal-quadratojugal bar. The mandibular articulation of the quadrate is tripartite. It is roughly triradiate in outline (figure 11*a*) as in many birds, with one part projecting backwards, well behind a straight line between the inner condyle and quadratojugal articulation.

(*c*) ***Braincase*** (***figures 12 and 13***)

The braincase is preserved in both specimens, which together furnish detailed information about its morphology and the architecture of the brain and inner ear. The isolated basioccipital is represented in the small individual. The braincase of the large individual is virtually complete except for the parasphenoid rostrum, and the hypophyseal fossa.

The morphology of the braincase is similar to that of *Rhea* and *Archaeopteryx*. It is broad, flat, pneumatized and inflated. The dorsal profile of the occiput is highly arched due to the configuration of the parietal. The post-temporal fenestra, bounded by the parietal above and paroccipital process below, is reduced to a small aperture; ventral to it lies the occipital foramen (figure 11*b*). The former aperture appears to penetrate the superior tympanic recess, the latter invades the posterior tympanic recess as in some birds (e.g. *Falco*; see, for example, Suschkin (1899)). Walker (1985) suggested that the post-temporal fenestra transmitted the ramus occipitalis of the stapedial artery, and that the ventral foramen carried a branch of it. The ramus occipitalis is enclosed within a bony tube in some birds (e.g., *Larus* and *Grus*) as it traverses the superior tympanic diverticulum.

In occipital view (figures 11*b* and 13*c*), the foramen magnum is large compared to the occipital condyle. The *basioccipital* contributes the major part of the occipital condyle, which is oval in outline and very small. The basal tubera are short, transversely oriented, and show depressions on the posterior face for the attachment of neck musculature (M. rectus capitis anterior).

The basioccipital of the small individual (figure 13*a*, *b*) is remarkably similar to that of juvenile birds. It has a flat and paper-thin cranial floor that shows twin elliptical concavities for the pons varolii. Lateral to each concavity, the occipital recess is visible where it formed the base of the recessus scalae tympani. Farther anteriorly, at the junction of the basisphenoid, lie a pair of lateral Eustachian foramina, each forms a distinct bony tube and runs along the ventral surface of the basipterygoid process. Ventrally the basioccipital shows a concave basal sinus.

The *basisphenoid–parasphenoid* is a composite bone formed by the fusion of the dermal parasphenoid to the ventral surface of the basisphenoid. The bone is extremely complicated because of the fact that it is permeated by various pneumatic spaces. Anterolaterally, the basisphenoid shows a pair of basipterygoid processes, which are reduced considerably, as in some other birds, with little ventral projection (figure 13*d*). In theropods, these processes are well-developed and project considerably ventrally below the level of the basal tubera, thus adding a great vertical depth to the braincase.

The avian parasphenoid is a complex bone. Jollie (1957) identified as many as seven centres of ossification. The portions of the parasphenoid that extend out from the dorsal margin of the sella are called alaparasphenoid (tympanic wings, see Erdmann (1940)). The *alaparasphenoid* region is beautifully preserved in *Protoavis* (figure 12*j*). It is an elongated and inflated area forming the lateral wall of the anterior tympanic recess. Anteriorly the alaparasphenoids converge towards each other, each terminating dorsally into a spherical dorsum sellae. The bone is interrupted by a large foramen for the internal carotid artery (carotid entrance foramen, see Saiff (1976)). Dorsal to each basipterygoid process, the exit of the palatine artery, a branch of the carotid artery, can be seen. Beneath the floor of the anterior tympanic recess and dorsal to the carotid foramen is the entrance to the Eustachian canal, which runs along the ventral surface of basipterygoid process and opens into the hind portion of the palate as a small slit. The whole arrangement of the carotid canal, anterior tympanic recess and the Eustachian tube is similar to that of modern birds. Posteriorly the basisphenoid tapers into a tubular process to overlap the basioccipital. Two pneumatic foramina are visible here (figure 12*j*).

The *supraoccipital-epiotic* (figures 12*b–d*; 13*c*; 22*d*) complex is intact and is distinctly avian in morphology. It is a large, elegant, six-sided, winged unit, angular above and crescentic below, and is deeply hollowed out posteriorly for the attachment of the M. rectus capitis posterior. The supraoccipital is a narrow, vertical plate with a median crest for attachment of the nuchal ligament. Ventrally it contributes a little to the margin of the foramen magnum. Its suture with the epiotic is grooved and perforated submarginally for the posterior branch of the middle cerebral (= external occipital) vein, which probably arched over the anterior semicircular canal. This sinus canal continues farther downward along the exoccipital-opisthotic contact. In most birds there is a small foramen (sometimes two) as

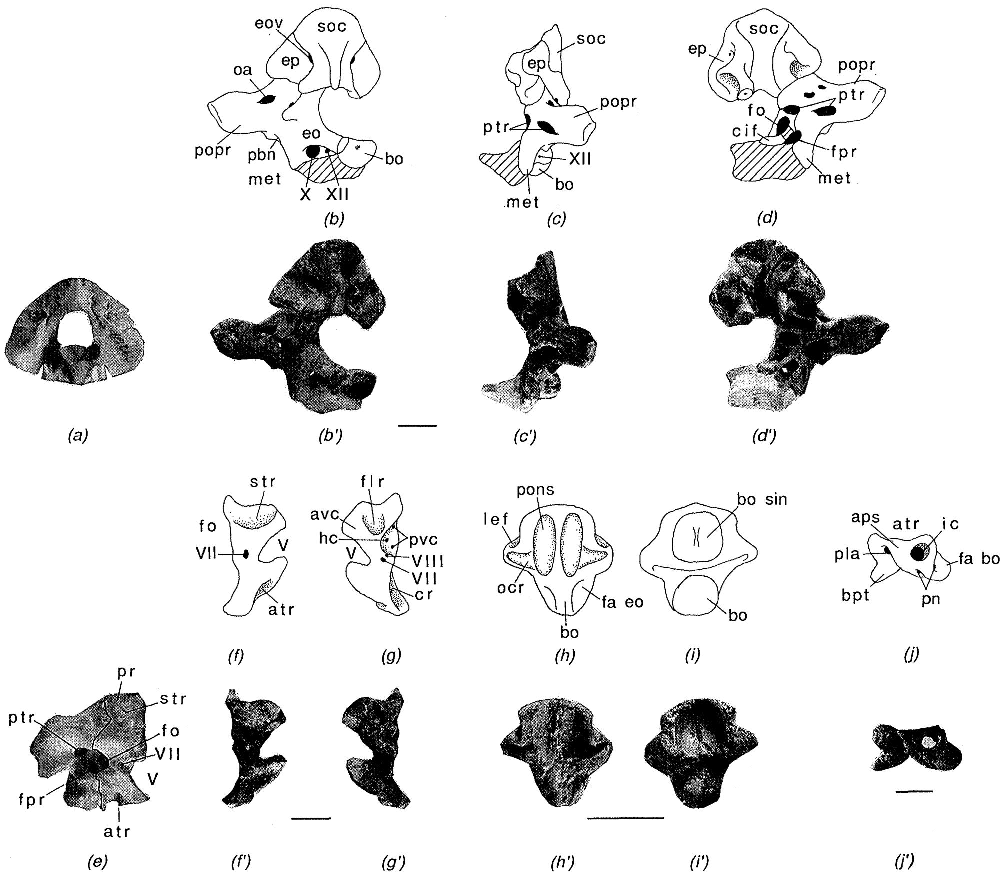


Figure 12. *Protoavis texensis*, n. sp., braincase; (*a*) posterior view of braincase of juvenile *Rhea* for comparisons; (*b*) and (*b'*) same view of braincase of *Protoavis*, large individual; disarticulated elements assembled; (*c*) and (*c'*) left lateral view of braincase, large individual; disarticulated elements assembled; (*d*) and (*d'*) anterior view of braincase, large individual; disarticulated elements assembled; (*e*) right lateral view of braincase of juvenile Mute swan (*Cygnus*) showing otic capsule region; (*f*), (*f'*) and (*g*), (*g'*) lateral and medial views of right prootic of *Protoavis*, large individual; (*h*), (*h'*) and (*i*), (*i'*) dorsal and ventral views of basioccipital, small individual; (*j*) and (*j'*) left lateral view of parabasisphenoid, large individual; scale bar 5 mm.

in *Protoavis*, on the sinus canal for the external occipital vein.

Jollie (1957) claimed that a separate ossification of an epiotic element is an apomorphy for birds; however, it is present in crocodilians at an early ontogenetic stage (de Beer 1937). In most birds the epiotic has no posterior exposure and is sheathed by the supraoccipital, but in some birds (e.g. *Turdis*, *Passer*, *Pygoscelis*), there is a posterior exposure. Both *Protoavis* and *Archaeopteryx* (Walker 1985) have an epiotic with posterior exposure. The epiotic plays an important role in the formation of the canaliular systems in birds. Medially each epiotic in *Protoavis* shows a sulcus for the posterior branch of the external occipital vein.

The *exoccipital-opisthotic* suture has been obscured by fusion. Laterally each paroccipital process, presumably formed by the opisthotic, extends horizontally and abuts against the squamosal. The quadrate head has moved somewhat forward to create a moderate tympanic cavity and a distinct external auditory meatus in front of the paroccipital process (figures 9*a* and 11*b*).

Each exoccipital contributes slightly to the occipital condyle, but they are separated from each other by a longitudinal furrow on the dorsal surface of the basioccipital (figure 13*c*). Usually the hypoglossal (XII) nerve exits via two foramina in each exoccipital. In our specimen, one foramen is preserved. Farther laterally is a foramen that may have transmitted the vagus (X) and spinal accessory (XI) nerves (figure 13*c*). Internally this foramen shows a deep fossa for the ganglia of X. The two exoccipitals curve around the foramen magnum and taper dorsally to meet the supraoccipital. Laterally each exoccipital extends down the basal tubera and forms the posteroventral margin of the tympanic cavity (figure 12).

In modern birds, the internal carotid artery passes through the bony tube of the carotid canal in the skull base above the Eustachian tube (Kesteven 1925). In *Protoavis*, the tubular parabasal canal is lacking. Instead, there is a parabasal notch, which opens ventrally, and is formed by a projection of the exoccipital to form an incipient carotid foramen (figure 11*c*). The internal carotid most likely entered the middle ear cavity from the neck through this notch.

The otic capsule of *Protoavis* is remarkably avian in that the stapedial recess contains three openings: the fenestra ovalis, the fenestra pseudorotunda, and the entrance to the posterior tympanic recess. A large metotic ossification has been added to the anteroventral surface of the exoccipital to form the floor and most of the posterior wall of the recessus scalae

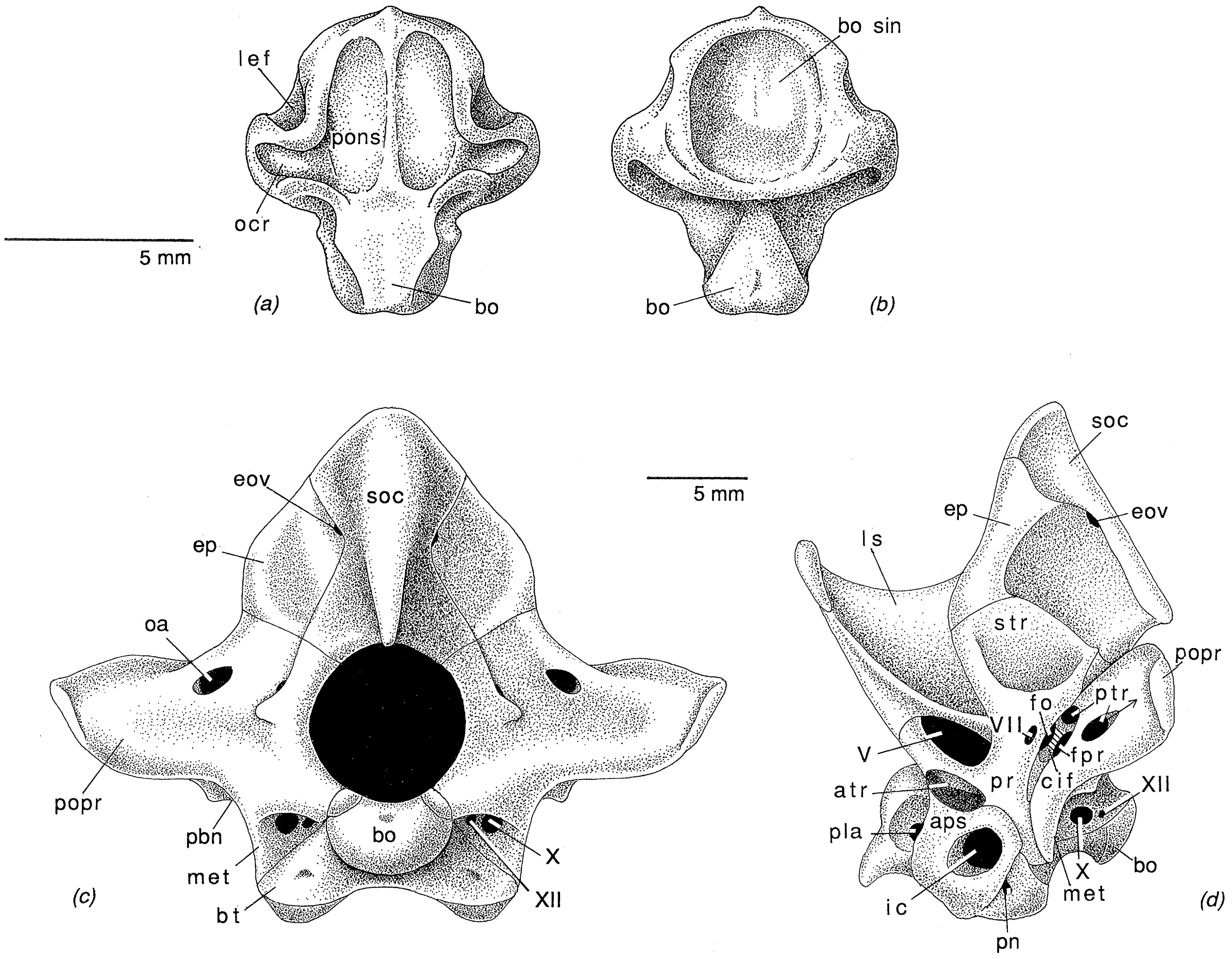


Figure 13. *Protoavis texensis*, n. sp., braincase; (*a*) and (*b*) dorsal and ventral views of the isolated basioccipital of small individual; (*c*) and (*d*) posterior and lateral views of the braincase, composite restoration.

tympani; the latter contained the large, laterally placed perilymphatic sac, leading to the formation of a fenestra pseudorotunda and a secondary tympanic membrane. As a result, the vagus foramen has been diverted backward behind or through the metotic.

A cartilaginous plate typically, in birds, becomes attached to the occipital arch, the outer edge of the basal plate and the auditory capsule. This plate, the *metotic* process (Sonies 1907; de Beer 1937) provides a floor for the recessus scalae tympanum, and forms the attachment for the secondary tympanic membrane. In *Protoavis*, the metotic ossification seems to be highly pneumatized (figure 12*c*, *d*). A thin bar of the opisthotic, the crista interfenestralis, separates the fenestra pseudorotunda from the fenestra ovalis. The prootic forms the anterior margin of the fenestra ovalis. The opisthotic is highly reduced, as in modern birds, and is exposed as a thin crista in the otic region (Jollie 1957). In crocodiles and some dinosaurs, wherever the vagus canal is diverted back at the occiput, a subcapsular process is presumably added to the exoccipital (Walker 1985). De Beer (1937) considered the avian metotic cartilage and crocodilian subcapsular process to be homologous, whereas Rieppel (1985) maintains that these two structures have independent origins. The metotic cartilage, he believes, is a neomorph condensation in birds, arising independently at a position opposite the centre of the metotic fissure and below the canalicular portion of the otic capsule.

The *prootic* is hour-glass-shaped, with expanded ends and a constricted shaft (figures 12*f*, *g*; 13*b* and 21*b*). It is remarkably similar to that of *Archaeopteryx* and modern birds in morphology (figure 21). Dorsally the bone contacts the epiotic by an extensive suture and covers the inner aspect of the labyrinth. A large lateral depression is found here indicating the anterior entrance of the superior tympanic recess. The shaft is pierced by the primary facialis foramen (VII) and forms the anterior margin of the fenestra ovalis. Anteriorly it is notched by the trigeminal foramen (V), which is enclosed dorsally by the laterosphenoid. Ventrally the bone shows a large fossa on its outer surface, the anterior tympanic recess.

The *laterosphenoid* (= orbitosphenoid, see Jollie (1957)) lies in the posterior wall of the orbit ventral to the orbital extension of the frontal (figures 8*i* and 13*d*). It is differentiated into two parts: a thin, broad ventral plate and a tapering, upward-curving lateral process. The ventral plate joins the prootic to enclose the trigeminal foramen. The lateral process underlies the parietal and projects outward and upward to form the postorbital process along with the frontal.

On the outer surface of the bone a ridge extends down from the lateral process. The inner surface of the laterosphenoid is differentiated into two concavities by a low ridge. The upper one indicates the cerebral fossa, the lower one the optic fossa. A shallow depression on the floor of the optic fossa lodged the Gasserian ganglion. The bone is perforated on its outer surface by the trigeminal foramen. The two laterosphenoids meet at the midline antero-ventrally but the contact is interrupted by a large notch for the optic (II) foramen.

(*d*) ***Lower jaw*** (***figures 14 and 15***)

The lower jaw is preserved in four fragments. The splenial and coronoid are not represented in the collection. The jaw is laterally compressed so that Meckel's canal is almost obliterated as in modern birds. The *dentaries* are elongate, blunt anteriorly, and are probably joined by a predentary bone as in *Hesperornis* and *Ichthyornis* (Martin 1987). A small *predentary* bone, very similar to that of *Hesperornis* was found close to the dentary (figure 14*a*). Anteriorly the dentary probably bears two teeth, but the posterior part of its ramus is toothless and forms a sharp dorsal edge, which was presumably covered by a horny rhamphotheca in life. At its posterior end, the dentary forks to form the anterior margin of the mandibular fenestra in archosaurian fashion. In birds, the mandibular fenestra is variable in development. An additional fenestra in the surangular may be present in some birds. Many birds, however, have lost one or both of these fenestrae completely.

The posterior segment of the jaw is preserved in two fragments, in which the prearticular, articular, angular and surangular are fused to each other, and their identities are obscured (figures 14*d–f* and 15). The mandibular cotylus is divided into lateral and mesial concavities, as in some birds, though simpler in form. The medial concavity is deep, and somewhat transversely oriented. The lateral one is a narrow band directed longitudinally and probably extends onto the surangular bone, curving upward to form the external process for the attachment of the postorbital ligament. As a result, the surangular forms a prominent dorsal process in front of the articular concavity, but descends farther forward. There is a prominent medial process, as in birds, supporting the medial cotylus of the quadrate. Behind this concavity lies a pneumatic foramen which suggests the passage of a siphonium to the internal cavity of the articular. Posteriorly there is a prominent retroarticular process for insertion the M. depressor mandibulae.

(*e*) ***Dentition***

Teeth are present at the anterior part of the jaws, but absent more posteriorly. There are three maxillary and two mandibular teeth, which are somewhat damaged. The teeth are simple, slightly compressed medio-laterally but the detailed structures are hard to determine on the specimens. A constriction at the base of the crown may be present (figure 14*g*, *h*). Replacement activity is shown by an empty socket and a newly erupted tooth. The teeth presumably replace each other from beneath and medially, as in archosaurs. One replacing tooth is found invading the pulp cavity of the predecessor from the lingual side; the root of the latter is absorbed at this point (figure 14*b*).

Modern birds are toothless. *Protoavis* had already become edentulous at the back part of the jaw.

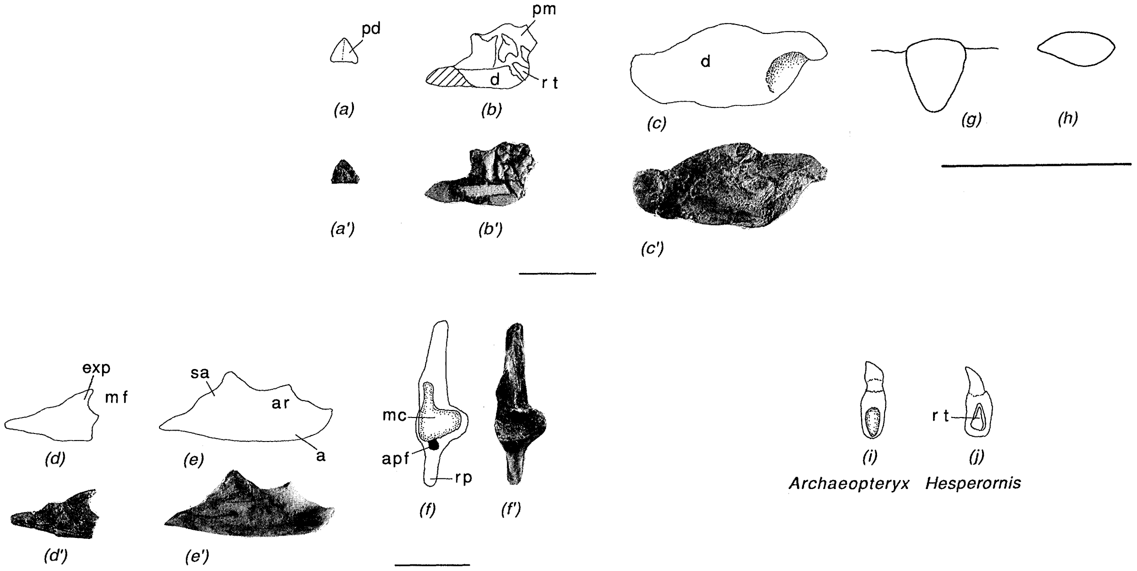


Figure 14. *Protoavis texensis*, n. sp., lower jaw and dentition; (*a*) and (*a′*) dorsal view of predentary, small individual; (*b*) and (*b′*) left medial view of conjoined premaxilla and dentary, showing replacing tooth, small individual; (*c*) and (*c′*) left lateral view of dentary, small individual; (*d*) and (*d′*) right lateral view of posterior part of lower jaw, showing external process and part of lateral mandibular fenestra, large individual; (*e*) and (*e′*) left lateral view of posterior part of jaw, small individual; (*f*) and (*f′*) the same, dorsal view showing mandibular cotyle; (*g*), (*h*) tooth morphology of *Protoavis*, third premaxillary tooth, lateral view, and second premaxillary tooth, cross-sectional view; (*i*) and (*j*), tooth morphology and resorption pit of Mesozoic bird; (*i*) after Martin (1985); (*j*) after Marsh (1880); scale bar 5 mm.

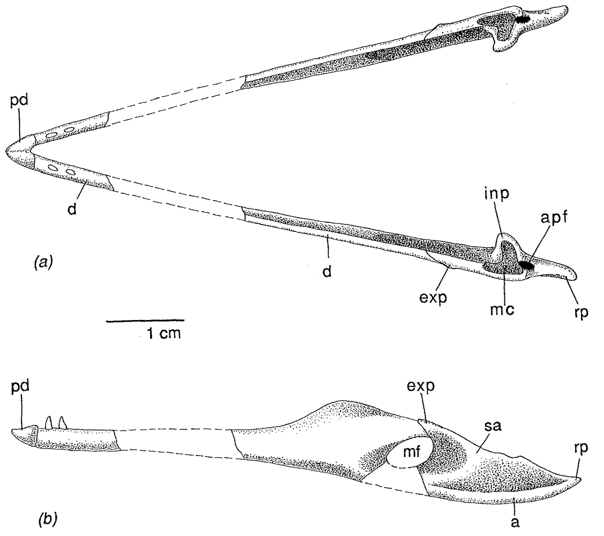


Figure 15. *Protoavis texensis* n. sp. (magn. × 1); composite restoration of the lower jaw; (*a*) dorsal view; (*b*) left lateral view.

Surprisingly many of the later Mesozoic birds retained many teeth. There are 13 teeth in the upper and 11 in the lower jaws of *Archaeopteryx*. *Hesperornis* possessed 14 teeth in the maxilla and 33 teeth in the dentary, but the premaxilla became toothless. In *Ichthyornis*, most of the upper jaw is missing, but the dentary may contain as many as 26 teeth (Martin & Stewart 1977). In all these post-Triassic toothed birds, the teeth resemble those of crocodilians in possessing highly expanded, barrel-shaped roots (figure 14*i*, *j*) (Martin 1983*a*). Teeth of this shape have been reported in theropod *Troodon* (Currie 1987). Teeth are absent in the terrestrial Cretaceous bird *Gobipteryx* (Elzanowski 1981).

6. NEUROSENSORY ORGANS

Marsh (1874, 1880), Edinger (1941, 1951), Jerison (1973), and Hopson (1979) made important contributions to the field of palaeoneurology, and traced the evolutionary sequence of brain, behaviour and intelligence of extinct vertebrates. Here, I attempt to reconstruct the brain and sensory organs of *Protoavis*, albeit indirectly, from various internal cranial indicators. The perception of the outside world appeared to be excellent in *Protoavis*. Its most fully developed senses were sight and hearing. It appears that the Late Triassic saw the beginning of a major trend toward the increase in relative brain size in early birds. Both the development of visual and hearing acuity may be recognized as correlated with that effect. Although this study is speculative, it may nevertheless, give some clue to recognize the possible selection pressures on early birds that led to a dramatic modification of the neurosensory organs from those of their reptilian progenitors.

(*a*) *The brain*

The brain of *Protoavis*, like that of modern birds, appears to have filled the braincase almost completely, so that the artificial endocast not only looks like a brain but also provides fairly accurate information about brain size and external morphology. The three-dimensional impressions of the brain are preserved inside of the cranial cavity which is defined by the frontal, parietal, supraoccipital, epiotic, prootic, laterosphenoid, basioccipital, basisphenoid and parasphenoid bones. The pituitary region is missing in both specimens.

Because the cranial elements are largely separated, preparation of piecemeal endocasts of the different regions of the brain was necessary. A composite model of the brain was restored by joining various portions of the endocasts to represent the size and proportion of that of the large individual. Several drawings of the internal views of the endocranial cavity were made to check the size and proportion of the endocast. From this endocast an attempt has been made to reconstruct the brain itself. The 'brain' portion of the endocast is delimited by the root of the hypoglossal nerve posteriorly, and the base of the olfactory tract anteriorly, as suggested by Jerison (1973).

The brain is relatively large and deep, forming an arc around the back of the enormous orbit. In the large individual with a length of 72 mm, width of 39 mm, and height of 30 mm, the brain occupies 35 mm of length, 18 mm of maximum width, and 22 mm of maximum height. The brain was much larger and better differentiated than that of reptiles. The difference is mainly because of the enlargement of the cerebral hemispheres and the cerebellum, which forced the optic lobes into a ventral position. Archosaurs show a generally primitive pattern of brain morphology with a narrow and elongated brain, a forebrain and medulla that are oriented approximately horizontally, and a pronounced midbrain flexure (Hopson 1977). However, in some Late Cretaceous theropods such as *Troodon* (Russell 1969) and *Dromiceiomimus* (Russell 1972), the brain was relatively larger than in the majority of theropods.

(i) *Brain morphology*

The endocast preserves many details of the external morphology of the brain of *Protoavis* (figure 16*a*–*e*). The olfactory bulbs are small, narrow, and closely appressed, suggesting a poor sense of smell. The olfactory bulbs are highly variable among modern birds, they are well developed in the Galli, Anseres, ratites, but extremely reduced in Psittaci, Passeres and Accipitres. The cerebral hemispheres are greatly enlarged, ovoid, and separated from each other by a deep median furrow. Anteriorly each cerebrum shows a low, ridge-like swelling, the sagittal eminence (Wulst). Running parallel to the sagittal eminence is a shallow groove, the vallecula, which corresponds well to that of archaic brain of the bee eater (*Merops*) (Portman & Stingelin 1961). The cerebrum extends backward to the posterior edge of the parietal. The upper surface of the laterosphenoid forms the ventro-lateral boundary of the cerebrum.

Another interesting feature that separates *Protoavis* from most reptiles is the ventro-lateral displacement of the optic lobes. The large optic fossa is preserved on the inner wall of the conjoined prootic-laterosphenoid, close to the endocranial floor. In dorsal view only the outer margin of the optic lobes are barely visible. Such impressive tectal development undoubtedly reflects the predominance of the visual system in the life of *Protoavis* (figure 16).

The optic lobes are displaced ventro-laterally because of enlargement of the cerebral hemispheres, as they are in modern birds, pterosaurs (Edinger 1941; Jerison 1973) and some theropods (Raath 1977; Russell 1969). As a result, the cerebellum made contact with the posterior border of the cerebrum in these vertebrates.

In *Protoavis*, the actual contact between the cerebrum and cerebellum is preserved in the small individual (figure 16*b*). The cerebellum is large, erect, with a dorsal swelling, presumably to mediate the neural coordination necessary for flight. The cerebellar fossa is shared between the parietal and the supraoccipital and has produced a corresponding protruberance on the occiput as in modern birds. Behind the cerebellum, the medulla is constricted and constitutes a relatively smaller portion of the brain than in reptiles.

The floccular lobe (auricle) is large and prominent on the posterolateral side of the cerebellum, somewhat bent backward and extending into a special, deep floccular recess. This feature shows that critical powers of maintenance of balance and sustained muscular control, which were centred in the cerebellum, were well developed. The flocculi are generally lacking or are minute in the quadrupedal archosaurs. In bipedal dinosaurs (e.g. theropods and ornithopods), pterosaurs and birds, however, an enlarged floccular lobe has been reported, suggesting refined neuromuscular coordination in response to specialized locomotion (Jerison 1973; Edinger 1941; Hopson 1979). Balance was more important to these animals than to quadrupedal forms.

On the floor of the braincase, a pair of elliptical pockets lodged the pons varolii of the medulla. The paired pons are separated from each other by a longitudinal furrow (figure 13*a*). The presence of pontine structures are reported in many recent birds (e.g. *Gallus*); they probably correspond with similar structures of mammals (Brodal *et al.* 1950). The pons connects the cerebrum with the cerebellum to supply information regarding muscular movements (Romer 1970).

Among reptiles, coelurosaur and pterosaur brains approach avian morphology and configuration, presumably as a consequence of similar neurosensory specializations associated with balance. Edinger (1941) reported a probable vallecula in the cerebrum of pterosaurs. However, Hopson (1979) denied its existence in pterosaurs, and concurred with Jerison (1973), that the pterosaur brains were not expanded to an avian level.

(ii) *Relative brain size*

Like other organs, the brain is large or small in different species, according to whether body size is large or small. Thus the relation between brain size and body size in various groups of vertebrates may provide clues to the degree of encephalization. Other correlates such as dexterity, sensory development, activity levels, intensity of metabolism, and intelligence are potentially associated with brain size.

It has long been known that the relationship of brain mass to body mass is not simply linear: brain mass increases more slowly than body mass from a small to large animal within a particular group. Snell (1891) first used an allometric equation relating brain mass (E) to body mass (P):

$$E = kP^{\alpha},$$

where k is the y intercept, which is usually termed as the index of cephalization and α is the coefficient of allometry.

Jerison (1973) plotted the brain mass against body mass for a large series of living vertebrates in log–log coordinates, and found two separate cluster of points, a lower one for the lower vertebrates (bony fish, amphibians, and reptiles), and an upper one for the higher vertebrates (birds and mammals). In both cases the data fall along a line with a slope of 0.66, expressed in the allometric equation as:

$$E = kP^{0.66}.$$

Jerison delimited the brain–body maps for the lower and higher vertebrates by enclosing cluster of points within minimum convex polygons, and indicated the slopes of these polygons (0.66) by plotting visually fitted lines. The y intercepts (k) of these lines are 0.07 for higher vertebrates and 0.007 for lower vertebrates, reflecting a tenfold increase in relative brain size in the shift from lower to higher vertebrates. The higher the value of k, the larger the brain at any given body size.

Jerison modified the index of cephalization and used a new estimate of the relative brain size of various groups of vertebrates. This he termed the encephalization quotient (EQ), which is the actual size of the brain divided by its expected size for an average living vertebrate. The expected size is determined by an equation, which states that the brain size equals two thirds the power of the body size multiplied by a constant (k) that represents the index of cephalization. For lower vertebrates, using living crocodilians as standard (*sensu* Hopson (1980)), Jerison estimates:

$$\text{brain mass} = 0.005\ (\text{body mass})^{0.66}.$$

In the case of higher vertebrates, by using living mammals as standard, he reports:

$$\text{brain mass} = 0.12\ (\text{body mass})^{0.66}.$$

Thus Jerison's encephalization quotient (EQ) for lower vertebrates, especially for the archosaurs will be:

$$\text{EQ} = (\text{brain mass})/[0.005\ (\text{body mass})^{0.66}],$$

whereas his encephalization quotient (EQ) for birds and mammals is:

$$\text{EQ} = (\text{brain mass})/[0.12\ (\text{body mass})^{0.66}].$$

To determine the EQs for extinct vertebrates one needs to estimate both the brain size and body size.

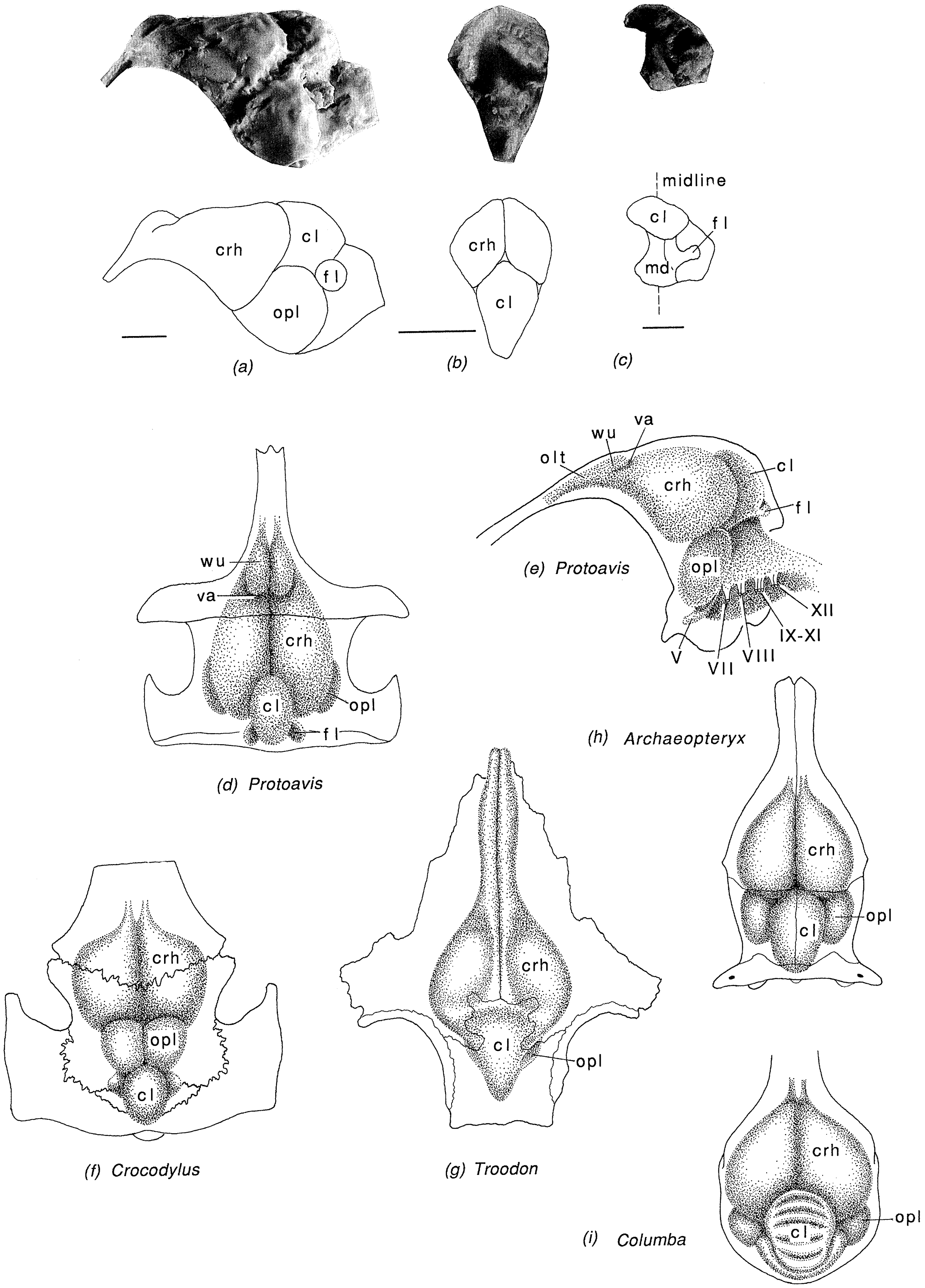


Figure 16. Restoration of brain of some archosaurs and birds from endocasts; (*a*) left lateral view of endocast of *Protoavis*, large individual, partly composite; (*b*) dorsal view of posterior part of endocast of *Protoavis*, showing confluence of cerebral hemispheres with cerebellum, small individuals; (*c*) dorsal view of posterior part of endocast of *Protoavis* showing the supraoccipital component of cerebellum and floccular lobe, large individual; (*d*) restoration of brain of *Protoavis*, dorsal view; (*e*) restoration of brain of *Protoavis*, lateral view; (*f*) dorsal view of brain of *Crocodylus* (after Bühler 1985); (*g*) dorsal view of brain of *Troodon* (modified from Russell 1969); (*h*) dorsal view of brain of *Archaeopteryx*, (after Bühler 1985); (*i*) dorsal view of brain of *Columba*; (after Bühler 1985).

(iii) *Estimating brain size*

The impression of the vallecula onto the inside of the braincase suggests that the brain of *Protoavis* appears to have filled the cranial cavity almost completely, so that the endocast is a good measure of the brain volume. There are two common methods of estimating brain size from the endocast: one by the water displacement method, using Archimedes' principle, the other by the graphic double integration method outlined by Jerison (1973). The endocast of *Protoavis* displaced about 3.5 ml of water, indicating an approximate brain weight of 3.5 g. In Jerison's numerical double integration method, the brain is modelled as an elliptical cylinder, where the height, major and minor axes of the cylinder can be calculated from the dorsal and lateral views of the brain. The length of the brain from the base of the olfactory tract to the point of exit of the hypoglossal (XII) nerve is the altitude of the cylinder. The average of the successive heights and widths at regular intervals in lateral and dorsal views represent the major and minor axes of the ellipse, respectively. The estimated brain mass of *Protoavis* from this graphical method becomes 3.32 g (figure 17). Although such an estimate must be treated with caution, it does suggest that *Protoavis* had relatively large brain size.

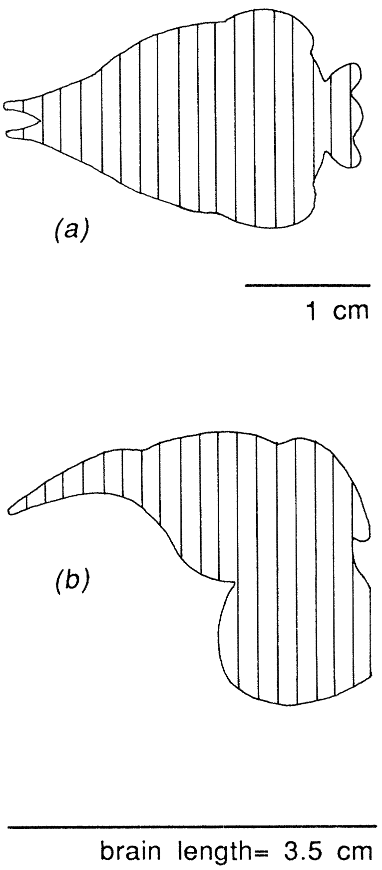


Figure 17. Graphic double integration to estimate the volume of the endocast of *Protoavis*. Mean lengths of solid lines drawn through the brain portion of the endocast are 1.1 cm and 1.1 cm for dorsal (*a*) and lateral (*b*) projections respectively. Volume estimate = (0.55) (0.65) (3.5) Π = 3.32 ml; weight estimate = 3.32 g.

(iv) *Estimating body size*

The adult individual of *Protoavis* is somewhat larger than the London *Archaeopteryx* specimen, but corresponds well with the holotype of *Compsognathus* in linear measurements (see table 1). Because of the uncertainties of the number of the caudal series, the head and body lengths (snout tip to cloaca) of these three animals are used to estimate the body size (table 2), by using Jerison's equation (1973). *Compsognathus* seems to be heavier than *Protoavis* in spite of having similar linear measurements. This is why a separate equation is used to estimate its body size. The heavier build of *Compsognathus* is reflected by the larger diameter of the hind limb. In all bipedal forms, the hind limbs are important from a mechanical point of view; they are used both for locomotion and body support. As a result, their diameter tends to be correlated with the average body size. Maloiy *et al.* (1979) and Yalden (1984) have used various allometric equations to estimate the body size of living and fossil birds from the hind limb diameters. By using these equations, the average estimated body mass is 300 g for the London specimen *Archaeopteryx*, 600 g for the large individual of *Protoavis*, 900 g for *Compsognathus*, and 47000 g for *Troodon*. By using modern analogues, the body size of *Protoavis* ranges from *Buteo* (558 g) to *Phasianus* (625 g).

(v) *Encephalization quotient*

In table 3, the encephalization quotients (EQs) of pterosaurs, theropods and early birds are presented using Jerison's equation (6), as discussed earlier. These data are also plotted in figure 18 superimposed on Jerison's minimum convex polygon for living reptiles and birds. The estimates of brain and body size of *Protoavis* give a relative brain size that falls entirely within the avian polygon and is a clear departure from the reptilian level. By contrast, pterosaurs were clearly reptilian.

Crile & Quiring (1940) tabulated brain and body masses of various living birds from which the corresponding EQs were calculated and presented in figure 19 for comparisons. The EQ of *Protoavis* falls within the lower third of the avian range. This shows that *Protoavis* was as highly encephalized as some living birds. Its brain lay well outside the range of theropods and pterosaurs.

(vi) *Significance of brain enlargement*

Jerison (1973) discussed the possible adaptive zone in which the brain enlargement of early birds might have occurred. He noticed that although both birds and pterosaurs exploited aerial niches that demanded enhanced equilibrium sense and motor coordination, the pterosaur brain was still reptilian in relative size, whereas birds were more encephalized. From this he argued that the aerial niche, per se, did not necessarily produce selection pressure toward avian brain enlargement. The degree of encephalization of two different aerial vertebrates may be related to the demands of particular ecological niches in which there were selective advantages for species further encephalized. The low EQs of pterosaurs may be correlated

Table 1. *Selected linear measurements (in mm) of Archaeopteryx, Protoavis and Composognathus*

	Archaeopteryx^{a}			*Protoavis*^{c}	*Compsognathus*^{b}
	(Eichstätt)	(Berlin)	(London)	(large)	(holotype)
1. skull length	39	52	?60	72	75
2. scapula length	25	42	46	70	38
3. coracoid length	—	—	?15	33	10
4. humerus length	41.5	63.5	75	70	39
5. radius length	35	54.4	65	72	24.7
6. McII length	17.8	28	34.4	34	13.9
7. ilium length	20	32	38	44	50
8. ischium length	14.5	20	25.5	20	40
9. pubis length	31.5	48	51.5	30	60
10. femur length	37	52.6	60.5	66	67
11. femur diameter	3.3	3.5	3.8	5	6
12. tibia length	50.5	68.5	80.5	82	87.7
13. tibia diameter	2.5	3	3.5	4.5	5.5
14. Mt II length	28.5	34.5	40.7	42	48.8
15. precaudal length	114.5	179	194.5	268	277
16. caudal length	142.5	172	210	260	348
17. total vertebral column length	257	351	404.5	528	703
18. head and body length (skull + precaudal)	153.3	231	254.5	350	355
19. estimated total length	296	403	464.5	600	778

[a] *Archaeopteryx* data from Wellnhofer (1974); [b] *Compsognathus* data from Ostrom (1978) and measurements from the cast. [c] In *Protoavis*, various linear measurements are estimated and extrapolated to represent the size of the large individual.

with their adaption to cliff dwelling against an open expanse of water. These reptiles still lived in an almost two-dimensional world. Contrary to this, the early birds probably inhabited woodland niches, most nearly like those of living tree-dwelling primates, in a three-dimensional world. In woodland, the confusingly mottled background of leaves, branches and other foliage provides a strong selection pressure for enlargement of the brain as a processing centre for visual information, integrated with auditory acuity. The sense of smell and associated brain centres, on the other hand, would decrease, because odours would be quickly dispersed high among the trees (Bock 1969). Jerison thus reasoned that the evolution of enhanced vision and hearing in woodland niches is the key factor in the encephalization of tree-dwelling early birds. The mode of life of *Protoavis* fits into the woodland scenario, as envisioned by Jerison, in which the vision and hearing became increasingly important in response to a three-dimensional world, which would lead to an increase in brain size. The social structures of early birds required the development of a more efficient system of communication to avoid interactions with the emerging dinosaurs. This might have caused a tremendous selective pressure for increased brain size.

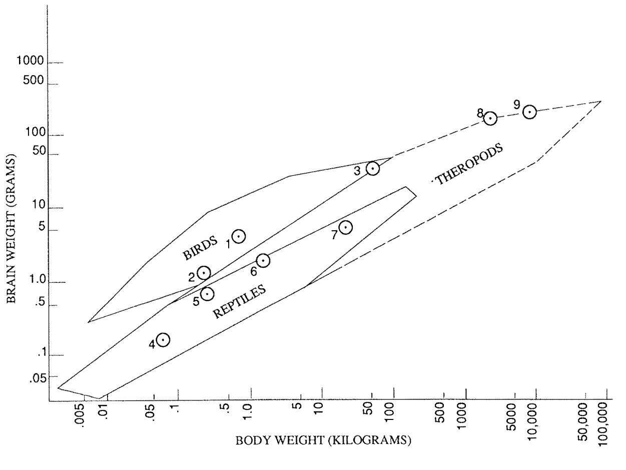


Figure 18. Brain/body size relations in some theropods pterosaurs and birds. 1, *Protoavis*; 2, *Archaeopteryx*; 3, *Troodon*; 4, *Pterodactylus*; 5, *Rhamphorhynchus*; 6, *Scaphognathus*; 7, *Pteranodon*; 8, *Allosaurus*; 9, *Tyrannosaurus*. Modified from Jerison (1973) and Hopson (1980).

Hopson (1977, 1980) suggested that there might be a possible correlation between the EQ and the degree of endothermic metabolism. He argued that the EQs of certain coelurosaurs (such as *Troodon*) and *Archaeopteryx* fall within the range of living endotherms, indicating that they were metabolically as active as living birds and mammals. With EQ = 0.41, *Protoavis* lies within the range of living birds, and was probably endothermic also.

(*b*) *The eye*

The orbits are so large and deep that the right and left cavities nearly touch each other in the median plane as in modern birds. The enormous size of the orbit in *Protoavis* clearly indicates a large eyeball, about 20 mm diameter, which would provide larger and sharper images. Like most living birds, it must have been a visual animal. The control systems for visual activity in the brain centres, such as the optic lobes, cerebellum, and forebrain that were involved in processing visual information appear to have been well developed in *Protoavis*. Flying animals demand high

Table 2. *Estimates of the body mass of Protoavis and other vertebrates*

extrapolation based on...	birds		theropods		allometric equation	
	Archaeopteryx (London)	*Protoavis* (large)	*Compsognathus*	*Troodon*		
1. head and body length (snout to cloaca)	(25 cm)	(35 cm)	(36 cm)			
body mass (g)	312	612	648		$P = 0.5\ L^2$	(1)
			1091		$P = 0.021\ L^{3.03}$	(2)
2. diameter of femur	(3.8 mm)	(5 mm)	(6 mm)	(96 mm)		
body mass (g)	306	568	972	47000	$D = 6.4\ W^{0.44}$	(3)
3. diameter of tibia	(3.5 mm)	(4.5 mm)	(5.5 mm)			
body mass (g)	281	553	952		$D = 5.6\ W^{0.37}$	(4)
4. average estimated body mass (g)	300	600	900	47000		

Equations (1) and (2) (after Jerison 1973), where P = body mass in grams, L = length in cm; equations (3) and (4) (after Maloiy *et al.* 1979), where W = mass (kg), M = mass (g), and D = diameter of bone (mm).

resolving power for better perception of movements and for the avoidance of collisions.

Walls (1963) has discussed the correlation between food habits (predator and prey species) and the position of the eyes in the avian skulls. In predatory birds (such as *Buteo*, *Tyto*, *falco*), the orbits are frontally placed, giving them excellent binocular vision. In the prey species, on the other hand, the orbits are laterally placed, allowing the widest field of view to keep watch for impending dangers. In *Protoavis*, the orbits are directed more towards the front, as in birds of prey, with a prominent posterior vertical wall extending considerably laterally to support the large eye. Because the visual field of a single eye is constant at about 170° in vertebrates (Walls, 1963), the estimated binocular overlap of *Protoavis* would be close to 60°. Wide binocular vision indicates that *Protoavis* may have been a visually oriented predator (figure 20) because it would offer the possibility of some distance judgement to locate food more accurately.

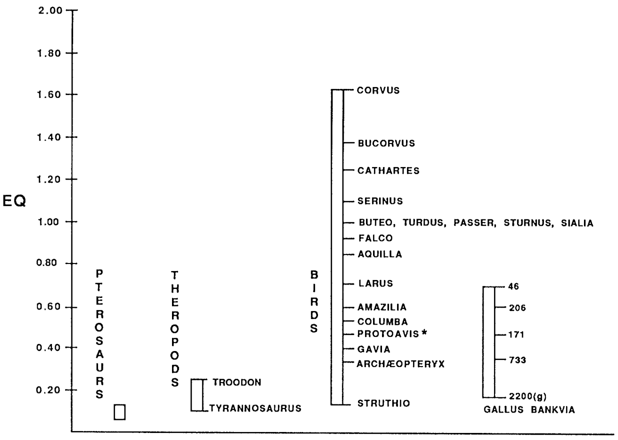


Figure 19. Encephalization Quotients (EQs) for pterosaurs, theropods and birds calculated, using the average mammal equation of Jerison (1973), where

$$EQ = \frac{\text{brain weight}}{0.12\ (\text{body weight})^{0.66}}$$

EQs for pterosaurs were calculated from Jerison (1973), for theropods from Hopson (1980), and for recent birds from Crile & Quiring (1940). Note the *Buteo*, *Turdus*, *Passer*, *Sturnus* and *Sialia* lie at 1.00, whereas crow is at the apex. *Archaeopteryx* and *Protoavis* lie at the lower range of EQ, whereas ratites lie at the bottom. The right-hand bar shows that body weight is inversely correlated with EQs. A large individual (2200 g) of a leghorn fowl shows a smaller EQ than that of the small individual (46 g).

(*c*) *The ear*

Hearing is, after vision, the second most important sense in birds. The avian ear is divided into three parts: the outer, middle and inner ears. The outer is merely an open tube that carries airborne sound to the eardrum at its base. The middle ear is essentially a cavity in which the stapes picks up sound vibrations of the eardrum and transmits them through the fenestra ovalis and into the fluids of the cochlea of the inner ear. The inner ear contains the sensory receptors for both hearing and balance.

In *Protoavis* the outer ear would be located in a space between the quadrate head and the paroccipital process. The middle ear was a large cavity taking up much of the posterolateral region of the skull. The stapes is not preserved, but the fenestra ovalis and the fenestra pseudorotunda are located in the lateral wall of the otic capsule in the similar topographic positions as in modern birds. In addition, several pneumatic cavities are present in this area. The inner ear region consists of a delicate, interconnected bony labyrinth. In the following discussion, the function of the pneumatic cavities and inner ear structures will be investigated to assess the levels and qualities of hearing and balance in *Protoavis*.

(i) *Pneumatization in the middle ear cavity*

An additional feature shared by *Protoavis* and modern birds (as well as a few archosaurs) is a system of pneumatic spaces in the bones surrounding the middle ear. In modern birds, the diverticula of the tympanic cavity are differentiated into five components that invade the sides and floor of the braincase, the sides and roof of the skull, the otic capsule, quadrate and articular (de Beer 1937; Bremer 1940; Witmer

Table 3. *Estimates of the encephalization quotient (EQ) of Pterosaurs, Theropods and Early birds*

	Pterosaurs[b]				Theropod	Early birds	
	Pteranodon	*Pterodactylus*	*Scaphognathus*	*Rhamphorhynchus*	*Troodon*	*Archaeopteryx* (London)	*Protoavis* (large)
body mass (g)	20000	60	1500	310	47000	300	600
brain mass (g)	4.8	0.14	1.7	0.70	37	1.76	3.32
EQ[a]	0.06	0.08	0.11	0.13	0.25	0.34	0.41

[a] $\mathrm{EQ} = \dfrac{\text{brain mass}}{0.12\ (\text{body mass})^{0.66}}$. (After Jerison 1973.)

[b] Pterosaurs data from Jerison (1973); brain mass estimates of *Archaeopteryx* and *Troodon* from Hopson (1977). Hopson (1980) estimated the 'corrected' EQ of *Allosaurus* as 0.146 and of *Tyrannosaurus* as 0.1 after removing the effect of large body size.

1990). The tympanic air system communicates with the external environment via the median openings of the Eustachian tube in the roof of the mouth. The function of tympanic pneumaticity is poorly understood. It may produce some resonance effects, and is often correlated with enhanced hearing. Tympanic pneumaticity is well-developed in *Protoavis*, and there is osteological evidence indicating the presence of all five major diverticula in topographic positions similar to modern birds (figure 21).

(ii) *Anterior tympanic recess (ATR)*

The ATR is an antero-medially directed conical air space, lying between the medial side of the alaparasphenoid and lateral side of the prootic and basisphenoid. On the prootic ventral to the facial foramen is a large fossa containing two pneumatic foramina. Because the prootics approach each other along the midline, the tympanic fossae of two sides converge anteromedially. This indicates that the contralateral communication of the anterior tympanic recess was probably developed in *Protoavis*. This feature is attributed to mechanisms of sound localization in birds (Rosowski & Saunders 1980). An anterior tympanic recess on the prootic is perhaps recognized in *Archaeopteryx* (Whetstone 1983; Walker 1985); but contralateral communication is difficult to ascertain because of imperfect preservation.

The alaparasphenoid of *Protoavis* is highly inflated as in modern birds, enclosing the ATR medially. The lateral wall contains a large entrance for the carotid canal. Behind this entrance pneumatic foramina are visible. The medial wall enclosed the Eustachian tube within the tympanic recess.

(iii) *Superior tympanic recess (STR)*

The entrance and size of the STR in relation to the quadrate capitula are variable in modern birds and have been used as significant taxonomic characters (Lowe 1926). The STR may occur anterior, posterior, or on both sides of the quadrate capitula in modern birds. In neognaths, the STR has either a large pneumatic anterior entrance (e.g. gannet, fulmar, albatross), or a relatively large posterior entrance (e.g. duck, fowl, kestrel), but not both. Both seem to be present in the ratites (Saiff 1981), as well as in *Protoavis*.

The anterior entrance of the STR is represented by a large lateral depression on the prootic at the dorsal region in front of the quadrate head in *Protoavis* (figures 13*d* and 21*f*). This depression is bounded by the osseous labyrinths of the inner ear, and is very similar to a depression that occurs in the prootic of many juvenile birds, *Archaeopteryx* (Whetstone 1983; Walker 1985), *Hesperornis* and perhaps *Enaliornis* (Witmer 1990). A large jaw muscle (M. pseudotemporalis superficialis) originates from this recess in some birds (Saiff 1974). Currie (1985) questioned whether the prootic depression in *Archaeopteryx* is pneumatic or muscular. However, Witmer (1990) maintained that this depression is pneumatic in nature as it communicated with the occipital foramen.

The posterior entrance of the STR is highly elaborate in *Protoavis*, in which a large lateral air space is enclosed between the skull roof and the braincase. Each squamosal shows a large pneumatic recess on its postero-medial surface (figure 21*h*). Unlike modern birds, the supraoccipital in *Protoavis* does not contact edge to edge with the parietal, but is inserted at its undersurface, leaving a large air space between the two bones. Both parietal and supraoccipital show some degree of trabeculation. In contrast to *Archaeopteryx*, the squamosal of *Protoavis* appears to roof the STR as in ornithurine birds. The post-temporal fossa communicates with the posterior entrance of the STR through which the ramus occipitalis of the stapedial artery would traverse the air space. The situation is very similar to the condition in modern birds (Midtgard 1984). However in neognaths, the superior tympanic diverticulum contributes to the formation of the 'double-headed' quadrate. This is not so in *Protoavis*, Mesozoic birds and ratites.

(iv) *Posterior tympanic recess (PTR)*

In *Protoavis* the main entrance of the PTR is located within the stapedial fossa as in modern birds, and it lies posterodorsal to the fenestrae ovalis and pseudorotunda (figures 13*d*, 21*b*). This recess extends laterally as a large chamber within the paroccipital process, sending one diverticulum to the opisthotic to communicate with the STR. The lateral entrance to the PTR is well developed at the antero-medial surface of the opisthotic. A third diverticulum probably passed through the metotic process, since the latter is highly inflated. The occipital foramen communicates with

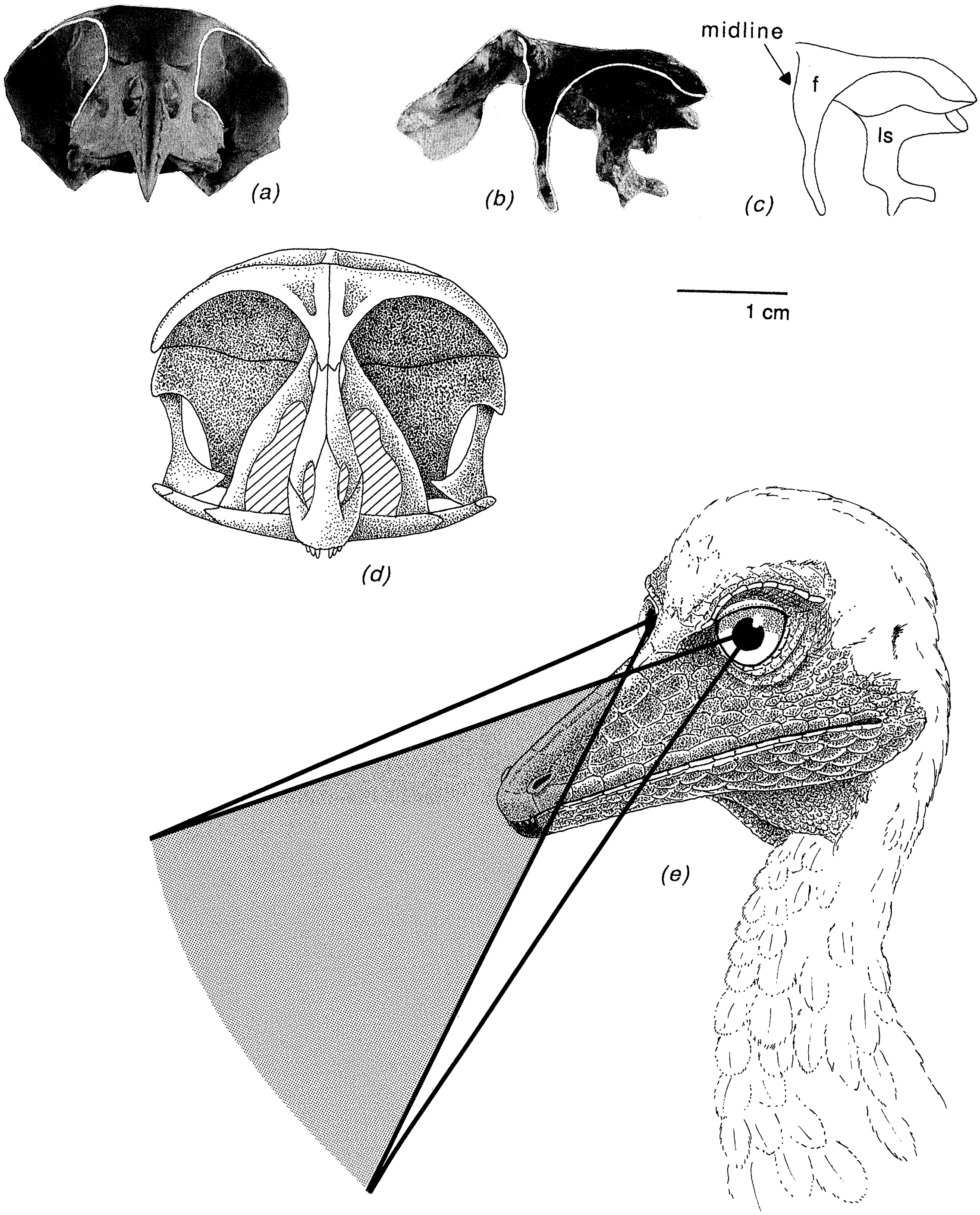


Figure 20. Estimate of the binocular vision of *Protoavis*; (*a*) anterior view of skull of red-tailed hawk (*Buteo*) showing frontal positions of orbit; (*b*) and (*c*) same view of *Protoavis*; (*d*) restoration of skull of *Protoavis*, anterior view; disarticulated elements assembled; (*e*) life restoration of head; with both eyes facing forward, *Protoavis* shows strong adaptations of stereoscopic vision as in birds of prey.

PTR as in some modern birds (e.g. *Diomeda*, *Morus*). Two dorsal branches of the occipital foramen lead into the STR. Medially the contralateral PTR closely approach one another. It seems likely that contralateral connections were established in the PTR via the air cells in the epiotic and supraoccipial, as in modern birds.

(v) *Quadrate sinus*

The quadrate diverticulum shows a great degree of morphological variation among modern birds. In most of the diving birds this diverticulum is absent and the adult quadrate bone is apneumatic (Witmer 1990). In other birds, the diverticulum enters the quadrate bone near the base of the orbital process. In *Protoavis* a pneumatic foramen is located in a similar topographic position to the orbital process. There is an additional foramen a little more dorsally on the shaft (figure 21*f*).

(vi) *Articular sinus*

The articular diverticulum (or siphonium) is a posteroventral outgrowth of the middle ear sac that invades the lower jaw at the base of the medial process

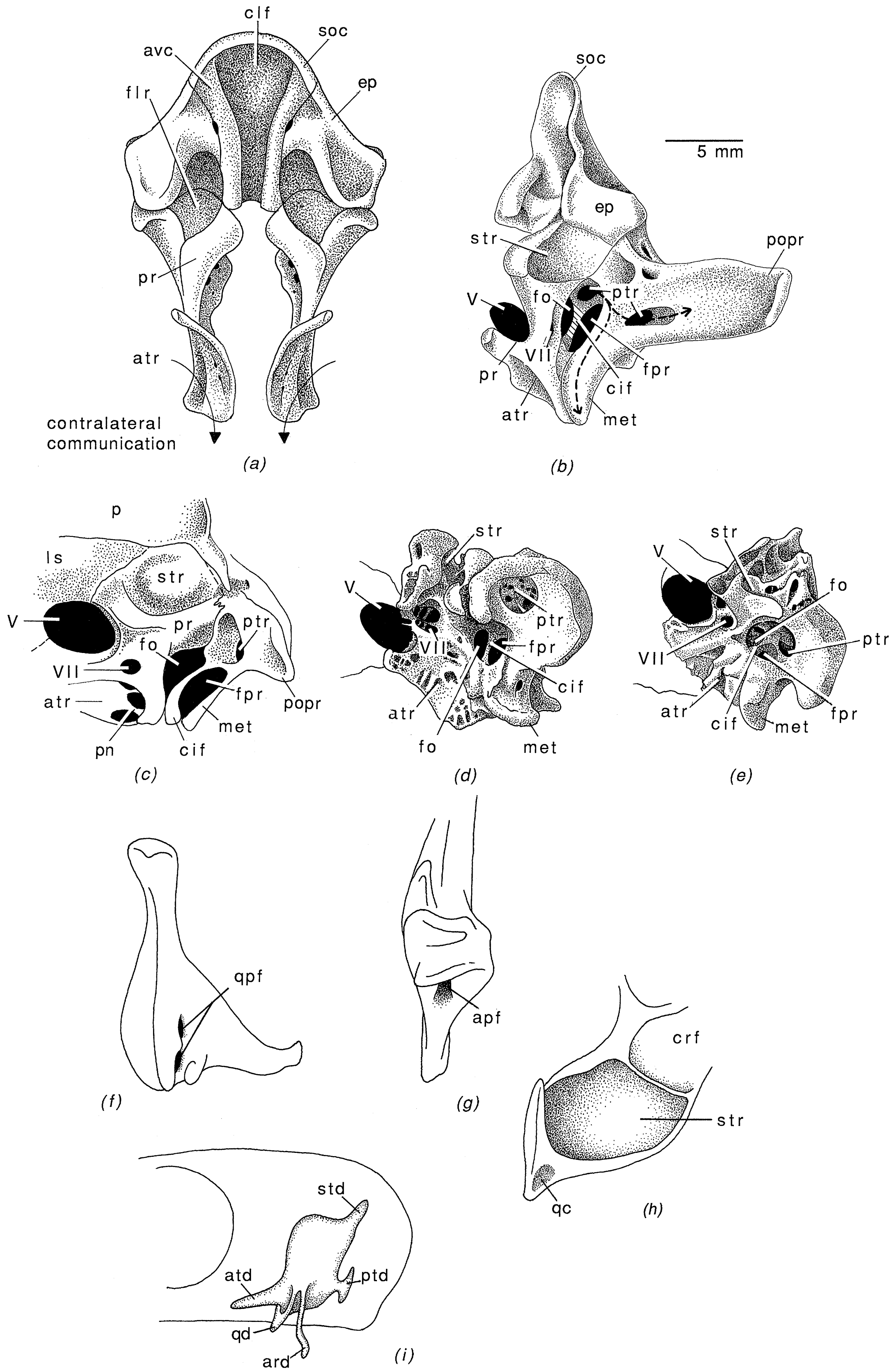


Figure 21. For description see opposite.

in modern birds. In *Protoavis* a similar pneumatic foramen is found in the articular, which encloses a large chamber (figure 21*g*).

(vii) *Significance of tympanic pneumaticity*

There is currently a great deal of interest concerning the significance of the tympanic pneumaticity in connection with the origin of birds (Whetstone & Martin 1979; Walker 1972, 1985; Currie 1985). Unfortunately, the taxonomic distribution of tympanic pneumaticity is not well known among archosaurs. Modern crocodiles exhibit some of these tymapnic diverticula but lack the PTR; the STR is present as a cavity but is not pneumatized (Parker 1883; Walker 1972). Some pneumatic features, taken in isolation can be found in individual members of theropods and rauisuchians. The LTR (lateral tympanic recess), behind the ATR, has been reported from ornithomimids (Osmolska *et al.* 1972), *Syntarsus* (Raath 1985), *Postosuchus*, *Allosaurus*, *Tyrannosaurus* and troodontids (see Barsbold 1983; Currie 1985), the PTR in troodontids (Currie 1985, 1987), *Itemirus* (Kurzanov 1976), *Postosuchus*, *Syntarsus* (Raath 1985) and *Tyrannosaurus* (Molnar 1985); and pneumatic quadrates and articulars are known in troodontids (P. J. Currie, personal communication) tyrannosaurs (Molnar 1985) as well as in *Postosuchus* (figure 28). However, the STR has so far not been recognized in theropods and therefore may be an avian character. However, if these recesses are defined in terms of the bones which surround them in the modern forms (crocodiles and birds) as the criterion of homology, this definition would probably eliminate some theropod comparisons.

It has long been known that the air chambers of the skull are well developed in birds that hear well. Functionally, the development of the tympanic diverticula represents an enlargement of the air cushion medial to the tympanic membrane which produces a dampening effect for better detection of low frequency (1–5 kHz) sound (Whetstone & Martin 1979).

In addition to enhanced audition, contralateral communication of the ATR may help in localization of sound through an 'interaural pathway' which provides directional information (Rosowski & Saunders 1980); Lewis & Coles 1980; Witmer 1990). It seems likely that *Protoavis* evolved an 'interaural pathway' to localize sounds, which would be advantageous in a three-dimensional tangle of tree branches.

Inner ear. Birds have always been credited with acute and discriminating hearing ability. It is the inner ear that is the sensory receptor for both equilibrium and sound. Basically the inner ear of a bird is comparable to that of other vertebrates, but it has some pertinent peculiarities. It is structurally more complex than that of reptiles, for instance, in its large size and greater differentiation of the canalicular systems and cochlear process (Ibragimova 1958). In reptiles, the bony labyrinth is primarily contained within the prootic, and opisthotic supraoccipital elements. In birds (and crocodiles), the epiotic additionally participates in the formation of the bony labyrinth. The canals themselves are angular in most reptiles, whereas in birds they are always rounded. In birds, the vestibular cavity is small, whereas in reptiles, the vestibule is by far the largest part of the labyrinth. Further, in most reptiles the canals surround the vestibule while in birds, they lie entirely away from it. In most reptiles the cochlea is very small, whereas in birds it is drawn out in the form of a tube (Gray 1908).

In archosaurs, two vertical semicircular canals, the anterior and posterior, arise at their proximal ends by the common crus from the upper surface of the utriculus. In birds, the crus lies further ventrally at the mid-height of the inner ear, so that the dorsal loops of the two vertical canals are physically separated from each other. The anterior vertical semicircular canal is usually the longest in birds, has the largest ampulla, and typically lies in the sagittal plane; threequarters of the canal is enclosed in the epiotic. As a result, the epiotic in birds exhibits a characteristic C-shaped bony tube on its mesial aspect around the floccular recess for enclosing the anterior vertical canal. In bipedal dinosaurs, floccular recesses are present but lack the enlarged C-shaped bony tube around them.

The general structure of this region of *Protoavis* is identical with that in modern birds. On the inner surface of the otic capsule, a large floccular recess is hollowed out, and around it the various parts of the inner ear are arranged (figure 22*a*). The flocculi, which are functionally connected with the vestibulum of the ear, are generally lacking or are minute in the cerebellum of quadrupedal reptiles. The epiotic of *Protoavis* shows a C-shaped bony tube for the anterior vertical semicircular canal, which arches over the entrance to the floccular recess. The front limb of the anterior canal continues ventrally into the prootic and seems to expand into an ampulla of the distal end. Below this ampulla lies a small vestibular cavity for housing the utriculus as in modern birds. The sacculus lies postero-ventral to it. Below and behind the vestibule, a large concavity, the internal auditory meatus, shows foramina for the facial (VII) nerve and anterior and posterior rami of the acoustic (VIII). A short vertical tube extends from the upper surface of the utricular cavity toward the posterior limb of the

Figure 21. Otic capsule and tympanic recesses; (*a*) *Protoavis*, anterior view of braincase showing ATR; ATR from two sides converge anteriorly indicating development of contralateral communication; (*b*) *Protoavis*, antero-lateral view of braincase showing ATR, STR and PTR; (*c*) *Archaeopteryx*, left lateral view of braincase, London specimen (after Walker 1985); (*d*) *Rhea*, left lateral view of braincase, juvenile; (*e*) *Cygnus* (Mute swan), left lateral view of the braincase, juvenile; (*f*) *Protoavis*, postero-medial view of quadrate showing quadrate pneumaticity; (*g*) *Protoavis*, dorsal view of articular showing articular pneumaticity; (*h*) *Protoavis*, ventral view of right squamosal showing the STR; (*i*) tympanic diverticula of a typical neognath (after Witmer 1990); in *Protoavis*, the otic capsule is extremely avian and all five tympanic recesses appear to be present as in modern birds.

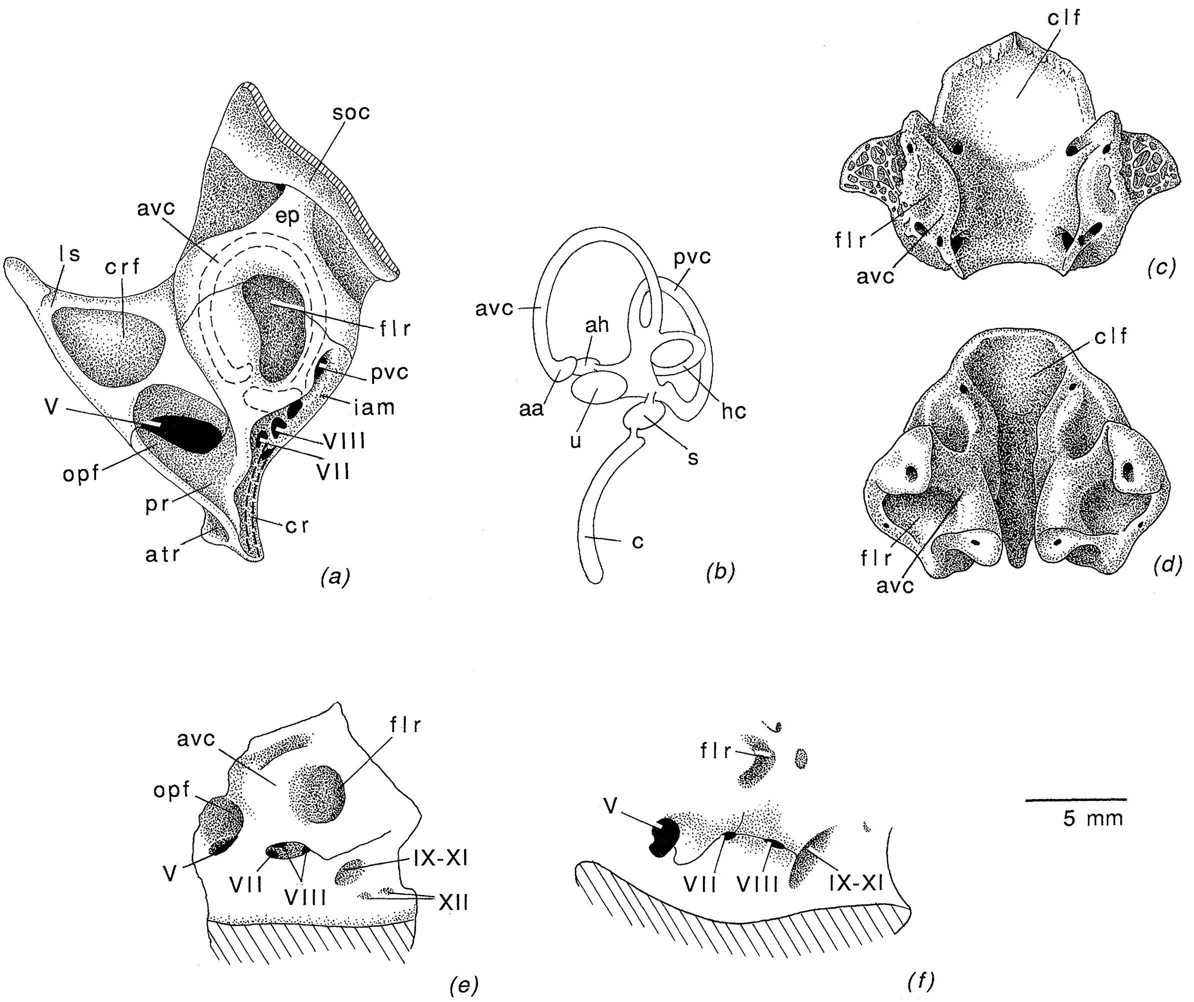


Figure 22. Inner ear. (*a*) *Protoavis*, internal view of the right side of part of the braincase showing floccular recess, and C-shaped bony tube for anterior vertical semicircular canal; (*b*) restoration of inner ear of *Protoavis*; (*c*) Rhea, ventral view of supraoccipital–epiotic complex showing osseous labyrinth; (*d*) *Protoavis*, ventral view of supraoccipital–epiotic complex showing osseous labyrinth; (*e*) *Hesperornis*, internal view of the right side of braincase showing floccular recess and anterior semicircular canal (after Edinger 1951); (*f*) *Dromaeosaurus*, internal view of the right side of the braincase showing floccular recess (after Colbert & Russell 1960).

anterior canal. This tube enclosed the crus commune from which both anterior and posterior vertical canals arise at their proximal ends (figure 22*b*).

Three large canals are visible on the posterior surface of the prootic, on the opisthotic suture; the upper and lower middle ones indicate the exit of the posterior vertical canal, the middle one that of the horizontal canal (figures 12*g* and 22*a*). The posterior canal is mainly enclosed in the opisthotic. It is oriented in a transverse plane below and behind the anterior vertical canal. On the outer surface of the prootic, ventral to the STR, the horizontal canal forms a segment of a circle with the concavity turned outwards.

Gray (1908) recognized two types of anterior vertical semicircular canals in birds, upright and drooping. The former type occurs in *Buteo*, *Goura*, and *Turdus*, in which the long axis of the canal is almost vertical. The latter type is found in *Rhea*, *Columba*, *Gallus*, *Rhynchotus*, *Anas*, *Nycticorax* and *Licmetis*, in which the long axis lies in an oblique posterodorsal plane. In *Protoavis*, the anterior canal is in an upright position.

It is generally believed that the labyrinth of good fliers has thin and large semicircular canals with pronounced ampullary ends (e.g. pigeons, owls, thrushes, peregrines, ravens and eagles) whereas in poor fliers, the canals are short and thick, with poorly marked ampullae (e.g. hens) (Hadžiselimović & Savković 1964). The canals of *Protoavis* appear to fall between these two extremes, suggesting that the animal was capable of powered flight to a certain degree.

Reception of auditory sensation is confined in reptiles to the papilla basilaris of the lagena, which is a short, ventral outgrowth of the sacculus. In birds (and crocodiles) the lagena is elongated to form a bony tubular cochlea. Correlatively, the perilymphatic duct, which remains closely applied to its base, expands in a double loop, and is eventually exposed as a secondary tympanic membrane through the fenestra pseudorotunda through which the vibrations would be dissipated. A somewhat elongated cochlea is known in some dinosaurs, but a tubular cochlear recess like that of birds and crocodiles does not seem to occur in these groups (Walker 1972).

In *Protoavis*, avian auditory refinement is clearly developed. Behind the fenestra ovalis lies the fenestra pseudorotunda in avian fashion through which the foramen perilymphaticum is visible internally as in modern birds. Anteroventral to the fenestra ovalis, the lower part of the prootic encloses a highly elongated, tubular cochlear recess. Posteriorly the recess is bounded by the opisthotic. The outer surface of the prootic shows a typical cochlear prominence. The cochlea must have been as long as the anterior vertical canal. The elongated cochlea suggests enhanced auditory reception in *Protoavis*, resulting in improved discrimination of sound frequency. The ability for three-dimensional orientation and associated features, as suggested by the contralateral communications of the ATR and a well-developed inner ear, would be more likely to evolve in arboreal forms in woodlands that have a confusingly variegated background than in species that live on the ground. Localization of environmental sounds in space must have been accomplished by *Protoavis*.

In modern amphibians (frogs), reptiles (crocodiles, geckos) and birds, a well-developed inner ear is associated with vocal behaviour. There is a good match between hearing and vocalization in species. The maximum audible frequency of a species tends to be correlated with average range of its vocal frequencies. It is likely that *Protoavis* was vocal and presumably could hear its own voice for communication. Refined hearing might have played an important role in such activities as communication, alerting others of impending dangers, mating, the care of young, and the maintenance of social behaviour.

7. CRANIAL KINESIS AND QUADRATE MOVEMENT

(*a*) *Terminology*

The skulls of many groups of vertebrates have specific areas of possible movement. Such movement is called *cranial kinesis* (Versluys 1910). Among extant reptiles, the skulls of most lizards and snakes are kinetic, whereas those of turtles, crocodilians and sphenodontids are akinetic. All modern birds have kinetic skulls (Bock 1964).

In modern lizards, two different kinds of movements are recognized, depending on the location of the joints (Frazzetta 1962). A *metakinetic* joint lies between the parietals and the braincase whereas a *mesokinetic* joint which lies between the frontals and the parietals.

All modern birds are able to move the upper jaw, or part of it, with respect to the braincase. The upward and downward motions of the upper jaw are usually referred to as *elevation* (= protraction) and *depression* (= retraction), respectively. Force to raise and lower the upper jaw is provided mainly by M. protractor quadrati et pterygoidea, attached to the palatines, pterygoids and quadrates. Unlike the lizard condition, the kinetic areas in birds are not true joints, but flexible bending zones, and are always located anterior to the orbits. Two main types of avian kinesis are recognized relative to the position of the dorsal line of flexure (Hofer 1949; Bock 1964; Bühler 1981; Zusi 1984). In a *prokinetic* hinge, bending occurs at a single transverse axis across the rear ends of nasals and premaxillae, so that the entire upper jaw moves as a unit. In a *rhynchokinetic* hinge, bending of the dorsal bar (premaxilla and medial portion of nasal) occurs at one axis, and that of the lateral portion of the nasal at another. Rhynchokinesis requires at least one or more flexible hinge in the upper jaw (figure 23). Different forms of rhynchokinesis are characterized by the location, number and extent of the hinges in the dorsal bars. Vertebrates possessing two kinetic joints are termed *amphikinetic*.

In addition to skull kinesis, modern squamates and birds exhibit *streptostyly*, which refers to the ability of the quadrate to swing antero-posteriorly under the skull roof relative to the braincase (Stannius 1856). If the quadrate is fixed, it is called *monimostylic*. In some vertebrates, limited movements of the quadrate are possible other than streptostyly. New terms are introduced here to identify these movements. If quadrate movement is restricted to the posterior direction relative to the resting position of the quadrate, this is termed *opisthostyly*. If the quadrate moves in a transverse direction, it is termed *parastyly*.

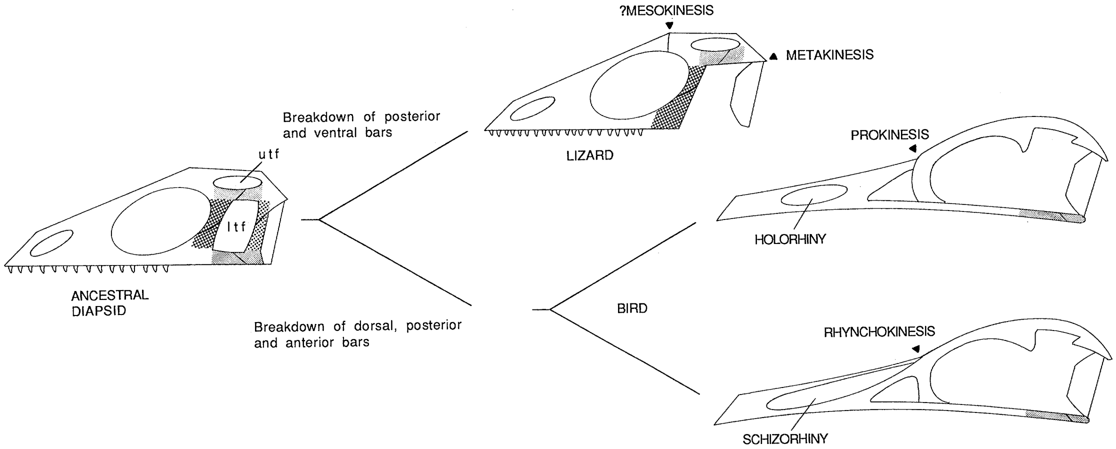


Figure 23. Modification of the diapsid temporal region in response to streptostyly. In diapsid, the lower temporal fenestra is framed by four bony bars. Lizards achieved streptostyly by the breakdown of the posterior and ventral arcades of the lower temporal fenestra. Birds acquired streptostyly by the loss of anterior, dorsal, and posterior arcades. The locations of metakinesis, mesokinesis, prokinesis and rhynchokinesis on the skull roof are shown by solid pointer.

Parastylic movements are common in a variety of squamates, theropods, and birds to increase throat diameter.

Avian cranial kinesis is powered by the propalinal movement of the quadrate. In considering the evolution of birds from archosaurian diapsids, the origin of the streptostylic condition is an important functional theme. The analysis of cranial kinesis has taxonomic applications of several kinds and is important in establishing the systematic positions of *Archaeopteryx* and *Protoavis* within the class Aves.

(*b*) ***Streptostylic quadrate***

Although some archosaurs may have possessed either parastylic or opisthostylic quadrates, it appears that a non-streptostylic quadrate occurs universally in this group. Some blocking structures prevent streptostyly in archosaurs. For example, the quadrate is bound to the quadratojugal by a long immovable suture, and to the palate by a deep overlap of the pterygoid. Furthermore, the posterior arch of the lower temporal opening, the squamosal–quadratojugal bar, acts as a bony stop in front of the quadrate, thereby preventing streptostyly (figure 24).

Streptostyly cannot be achieved without modifications to the diapsid framework, especially the ventral bar. In all archosaurs the diapsid arch is intact (figure 24*a*). The lower temporal opening is framed by four bony bars: the anterior bar is formed by the postorbital and jugal bones, the dorsal by the postorbital and squamosal bones, the posterior by the squamosal and quadratojugal bones, and the ventral by the jugal and quadratojugal bones. Lizards and birds have both adopted different styles to eliminate some of these bony bars, the former by the breakdown of the ventral and posterior ones, the latter by the loss of the anterior, dorsal and posterior bars (figure 23). As a result, the upper part of the quadrate becomes free from the adjacent bones and forms the posterior margin of the lower temporal opening. This is accompanied by a reduction in width of the quadrate ramus of the pterygoid, which now articulates movably and more ventrally with the quadrate. The dorsal head of the quadrate fits into a shallow socket on the undersurface of the squamosal, which thus forms a fulcrum about which the quadrate can swing. In birds, the jugal bar and the pterygoid are joined to the foot of the quadrate by 'pin joints' which allow rotation even though the lower temporal arcade remains intact. In lizards, the quadrate mobility is enhanced by the breakdown of the lower temporal arcade, and the development of the sliding joint between the quadrate and the pterygoid. The function of streptostyly seems to be different in the two groups, being concerned with the upper jaw movements in birds, and mainly with movements of the lower jaw in lizards (Robinson 1967).

The quadrate of *Protoavis* had achieved an avian mode of streptostyly (figure 24*b*). Increase in mobility

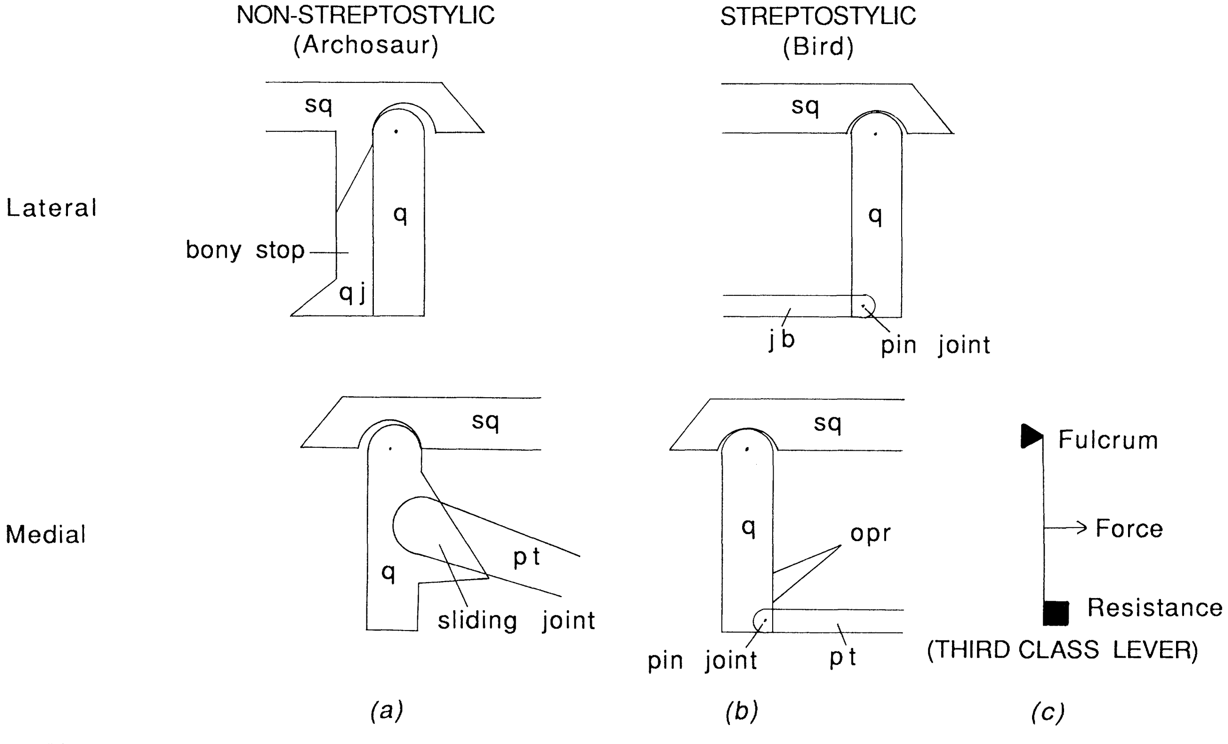


Figure 24. Functional interpretation of non-streptostylic (archosaurs) versus streptostylic (birds) quadrate; diagrammatic representation of the left quadrate to show its nature of articulations with adjacent elements (*a*) in archosaurs, the squamosal-quadratojugal bar acts as a bony stop to prevent the forward movement of the quadrate. Moveover, the pterygoid overlaps the quadrate more dorsally close to the fulcrum (squamosal-quadrate joint). (*b*) In birds, the bony stop in front of the quadrate is eliminated, so that quadrate can move freely antero-posteriorly. The pterygoid-quadrate articulation forms a pin joint at the ventral surface of the orbital process; the orbital process becomes free for the insertion of the M. protractor pterygoidea et quadrati; (*c*) diagrammatic medial view to show that the quadrate articulation of bird forms a third class lever system.

is associated with the loss of three bars from the lower temporal region, namely the anterior, dorsal and posterior ones as in modern birds. Both the quadratojugal and the quadrate ramus of the pterygoid have minimized their contacts with the quadrate to enhance the mobility. These articulations form 'pin joints' as in modern birds, and are restricted to the foot of the quadrate. Development of the orbital process in *Protoavis* serves as an effective lever arm for the M. protractor pterygoidei et quadrati, which pulled the quadrate forward. The spherical head of the quadrate fits into a concavity of the squamosal to form a diathroidal ball and socket joint so that the quadrate can swing freely in any direction.

Functionally, the quadrate of *Protoavis* operated as a class III lever as in modern birds, with the force applied at a point between the fulcrum (squamosal-quadrate joint) and the resistance (quadrate-quadratojugal and quadrate-pterygoid joints). The ventral shift of the resistance points from the archosaurian condition have increased the length of the resistance arm, a condition that favours speed at the expense of the force (figure 24*c*).

(*c*) *Upper jaw mobility*

The avian skull is divided into four functional kinetic units that are linked together, and which function together to elevate and depress the upper jaws (Bock 1964; Bühler 1981). These kinetic units are: (i) the upper jaw (or portion of it); (ii) the palate (including the jugal bar and the quadrate); (iii) the braincase (including parietal, frontal and squamosal); and (iv) the lower jaw. The upper jaw mobility is executed by a streptostylic quadrate, jugal bar, palatoquadrate bridge, and a set of muscles.

In the avian structural system streptostyly in strict sense cannot occur without some kind of cranial kinesis. The presence of metakinesis or mesokinesis seems remote in the *Protoavis* skull. Moreover, metakinesis is independent of streptostyly. The strong overlap of the parietal on the occiput and the butt joint of the laterosphenoid with the skull roof negate any possible movement at the metakinetic joint. Similarly, the complex interlocking articulation of the orbital flange of the frontal with the parietal on one hand and with the laterosphenoid on the other prohibits any movement at the mesokinetic joint. It appears that the posterior part of the skull roof (including frontal, parietal, lacrimal and squamosal bones) is incorporated in the braincase as a rigid stationary unit. The development of a large avian brain and an enormous eye in *Protoavis* clearly suggests that the region of bending would have to lie anterior to the eye if cranial kinesis were to be preserved.

Rhynchokinesis in *Protoavis* is almost certainly ruled out by the complete ring of bone formed by the premaxillae and nasals around the external naris. On the other hand, prokinetic movement might have been possible if the nasals were capable of being moved on the frontals. In fact, the fronto-nasal joint is extremely narrow transversely and the posterior region of the nasal sits in a shallow trough of the frontal, suggesting the existence of prokinesis. In modern prokinetic birds, the upper jaw is kinetically connected to the rest of the skull by three types of bending zones (Bühler 1981): one dorsally in the craniofacial hinge, a pair laterally in the jugal bars, and a pair ventrally in the palatal bars (figure 25*d*, *h*). The bending zone is usually recognized by an extreme flattening of the bone or the development of a multilayered, sandwich-like structure. In rare cases, the craniofacial hinge is a true articulation (Zusi 1984).

In *Protoavis*, the craniofacial hinge is a narrow, squamous joint between the nasal and frontal bones. This is the only link between the dorsal bar of the upper jaw and the cranium. The lacrimal of each side acts a fulcrum for the dorso-ventral rotation of the nasal along this hinge. In modern prokinetic birds this hinge is far more complex, and both the premaxillae and the nasals are fused to the cranium by a flexible lamina at the posterior ends. Bending occurs in a flattened region of the premaxillae and nasal dorsal to the anterior end of the mesethmoid. In *Protoavis*, both the interorbital and nasal septa are unossified, which would favour cranio-facial bending.

In *Protoavis*, the lateral bending zone is developed within the maxilla–jugal bar at the ventral margin of the antorbital fenestrae. Here the bone is thinner and is flattened dorso-ventrally to allow flexion. The loss of maxillary teeth may have enabled the flattening and lightening of the lateral bar of the upper jaw. The actual lateral bending zone may be restricted to the maxilla–jugal contact, which forms a multilayered sandwich-like structure, allowing flexibility. The lateral hinge is aligned medially with the palatal bending zone, which is formed along the squamous joint of the palatine and maxilla. The palatal hinge would run across the vomer medially, but the bone is so narrow and thin at this region that it would not restrict bending.

In modern birds, the bending zones evolved in relation to the intimate fusion of the cranial elements. In *Protoavis*, the dorsal and palatal bending zones are connected by articulations rather than bending zones. This is somewhat similar to the condition of modern psittaciforms, where there is a separate upper jaw bone, a separate jugal bar, and a separate palatine bone (Bühler 1981). These movable articulations allow extreme mobility of the upper jaw.

Another prokinetic feature in the skull of *Protoavis* is the modification of the upper jaw into a rigid unit. The premaxilla and nasal are tightly united to enclose a holorhinal naris, a condition that makes deformation within the upper jaw impossible (Hofer 1955). The upper jaw is kinetically connected with the rest of the skull by various links and hinges. The maxilla, jugal and quadratojugal are reduced to a rod-like structure to form the typical avian 'jugal bar'. The lacrimal is functionally part of the cranium. A sliding contact is established between the lacrimal and the jugal bar. More posteriorly, all the interfering struts between the skull roof and the jugal bar are eliminated with the development of streptostyly. Free mobility of the jugal bar is essential in avian kinesis. It links the premaxilla and the quadrate by movable articulations.

Similarly, the pterygoid-palatine bar has become mobile with the loss of ectopterygoid and epipterygoid, and the development of a flexible joint between the pterygoid and the quadrate. The basipterygoid articulation is loose, which increases the range of movement of the pterygoid-palatine bar. Anteriorly the maxilla-palatine joint serves as a hinge between this bar and the upper jaw. Thus the jugal bar and the pterygoid-palatine bar are modified into a pair of 'push-rod' systems so that the force from the quadrate can be transmitted effectively to the beak.

(*d*) *Kinetic mechanism*

Frazzetta (1962) investigated mesokinesis (fronto-parietal joint) of the lizard skull from a mechanical point of view, and regarded it as a mechanism consisting of links and joints. The muzzle, posterior part of the skull roof, quadrate and pterygoid form a quadratic (four-bar) crank chain having parallel axes. The mechanism is such that if one link is fixed and another moved, the movements of the other two can be predicted. Such a mechanism is termed 'mobility 1' (Alexander 1983). By analogy, when the posterior part of the skull roof is held stationary, and the ventral end of the quadrate is pushed forward, the pterygoid moves forward, and the muzzle unit is presumed to move dorsally at the mesokinetic joint. This motion is the result of a force directed anteriorly along the pterygoid bone by the Mm. levator and protractor pterygoideii. The jaw adductors and pterygoideus muscles are the main retractors when the muzzle is lowered.

A similar quadratic crank mechanism has been suggested for birds (Alexander 1983; Bühler *et al.* 1988). The kinetic mechanism of *Protoavis* can be analysed in the same fashion. Cardboard models with links and joints were built to simulate the main movements of the kinetic mechanism (figure 25). The rigid upper jaw is connected to the stationary braincase unit at the craniofacial hinge dorsally, with the jugal bar laterally, and with the palatine bar ventrally. The quadrate, which forms another link, is hinged to the braincase at its head, and is flexibly attached to the jugal bar and the pterygoid-palatine bar on either side of its foot. Because the jugal bar and the pterygopalatine bar share similar mechanical functions, a link between the quadrate and the upper jaw, they are considered functionally as a single unit to simplify the model. Thus the upper jaw, the jugal bar, the quadrate, and the braincase form a four-bar crank chain. If the braincase is held stationary, and the quadrate is swung forward, this movement is imparted to the jugal bar, which in turn pushes the upper jaw forward. Since the upper jaw is flexibly attached to the braincase at the craniofacial hinge, the forward push of the jugal bar pushes the upper jaw dorsally.

In the lizard skull, the quadrate is bound to the pterygoid by a ligament that allows the forward movement of the quadrate that is independent of the pterygoid. This articulation is not a 'pin joint' as claimed by Frazzetta (1962), but a sliding joint. Laterally the quadrate lacks bony connection with the jugal. This arrangement enhances streptostyly but minimizes the mobility of the mechanism. A loop of four links with a sliding joint at the pushing end fails to produce any movement at the other end (figure 25*c*). As the quadrate is swung forward it slides past the pterygoid. Motion of the quadrate is not imparted to the pterygoid bone, and thus fails to reach the muzzle unit. Likewise, the firm articulation between pterygoid and ectopterygoid prevent any potential kinesis. This analysis raises a serious question about the mesokinesis of lizards. Various recent experiments gathered from cinematography and strain gauge measurements failed to detect any movement across the mesokinetic joint in lizard skulls during feeding, which indicates that the fronto-parietal suture may not have any kinetic function (Throckmorton 1976; Smith & Hylander 1985). Similarly, mesokinesis attributed to various theropods (Madsen 1976; Colbert & Russell 1969) is difficult to explain because the parietal is intimately sutured with the frontal, and the quadrate is non-streptostylic in those taxa.

Mesokinesis has been suggested for some early fossil birds, such as *Archaeopteryx* (Bock 1964), *Hesperornis* (Martin 1983*b*), and the *Lithornis*-cohort (Houde & Olson 1981), where the fronto-parietal suture is a transverse squamous type and may indicate some potential movement. However, the braincase is intimately fused with the frontal and parietal, a condition that precludes any such movement at this joint. Bühler *et al.* (1988) suggest that the suture between the frontals and parietals in those birds may be a growing zone with no kinetic function.

(*e*) *Jaw coupling*

In most birds, the upper and lower jaws are coupled in such a fashion that there is a mechanical linkage between the elevation of the upper jaw and the depression of the lower jaw (Bock 1964). Typically, such coupling is effected by the postorbital ligament, when loaded by muscle action. This ligament extends from the ventral tip of the postorbital process to the external process of the mandible anterior to the quadrate's articulation in such a way that it restricts the depression of the mandible. The mandible pivots downward anterior to the postorbital ligament and upward posterior to it upon contraction of the depressor mandibulae. This not only opens the mandible but pushes the quadrate forward, raising the upper jaw (Zusi 1967). Because both osteological attachments of the postorbital ligament are present in *Protoavis*, the development of jaw coupling is a distinct possibility in this early bird. Alexander (1983) suggested that the postorbital ligament would add another rigid link, hinged to the braincase and lower jaw. The whole skull is then converted to a mechanism of six links and seven joints (figure 25*i*). The postorbital ligament and coupled kinesis make it easier for the bird to keep its mandible in a closed position without the expenditure of muscular energy.

(*f*) *Stops and guides*

In birds, protraction and retraction of the upper jaw

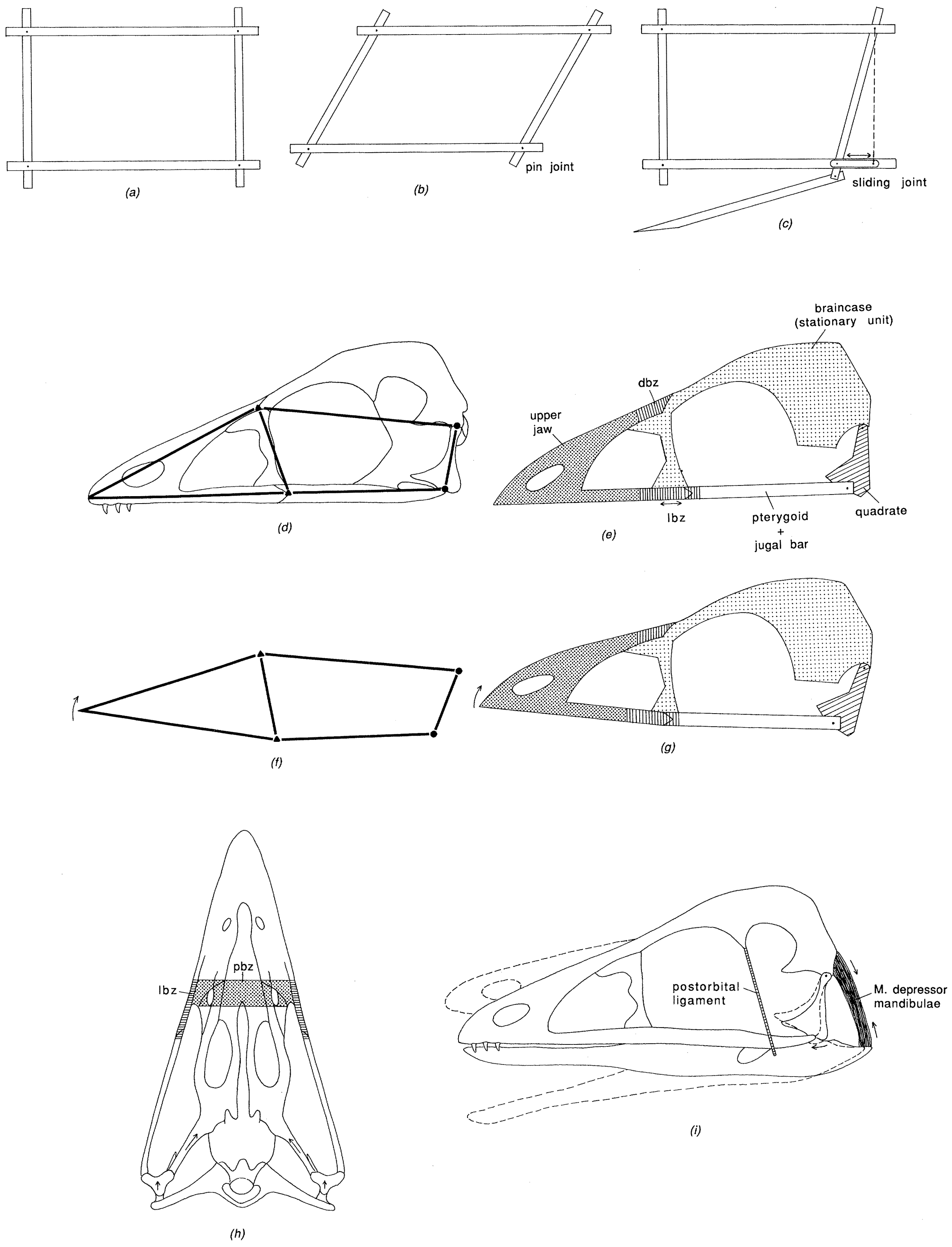


Figure 25. Functional interpretation of prokinesis in the skull of *Protoavis*, based on the quadratic crank model of Frazetta (1962) and Alexander (1983); (*a*) a four-link crank chain joined by hinges; (*b*) if one link is fixed and another moved, the movements of other links can be predicted. This is a simple mechanism of mobility 1; (*c*) in lizard, the quadrate-pterygoid articulation forms a sliding joint that gives the mechanism negative mobility; it is possible that the forward movement of the quadrate would fail to raise the muzzle unit; however, the quadrate becomes highly mobile in lizards to facilitate lower jaw movement; (*d*) *Protoavis* skull at rest, showing the locations of dorsal (DBZ) and lateral (LBZ) bending zones, as well as four hinges; (*e*) the same, diagrammatic, to show different kinetic units; (*f*) application of quadratic crank model; quadrate moved forward, resulting in elevation of the upper jaw; (*g*) the same, in kinetic units, to show the elevation of the upper jaw; (*h*) palatal view of the *Protoavis* skull at rest, showing the palatal bending zone (PBZ); (*i*) the elevation of the upper jaw and the depression of the lower jaw in *Protoavis* might be coupled by the postorbital ligament.

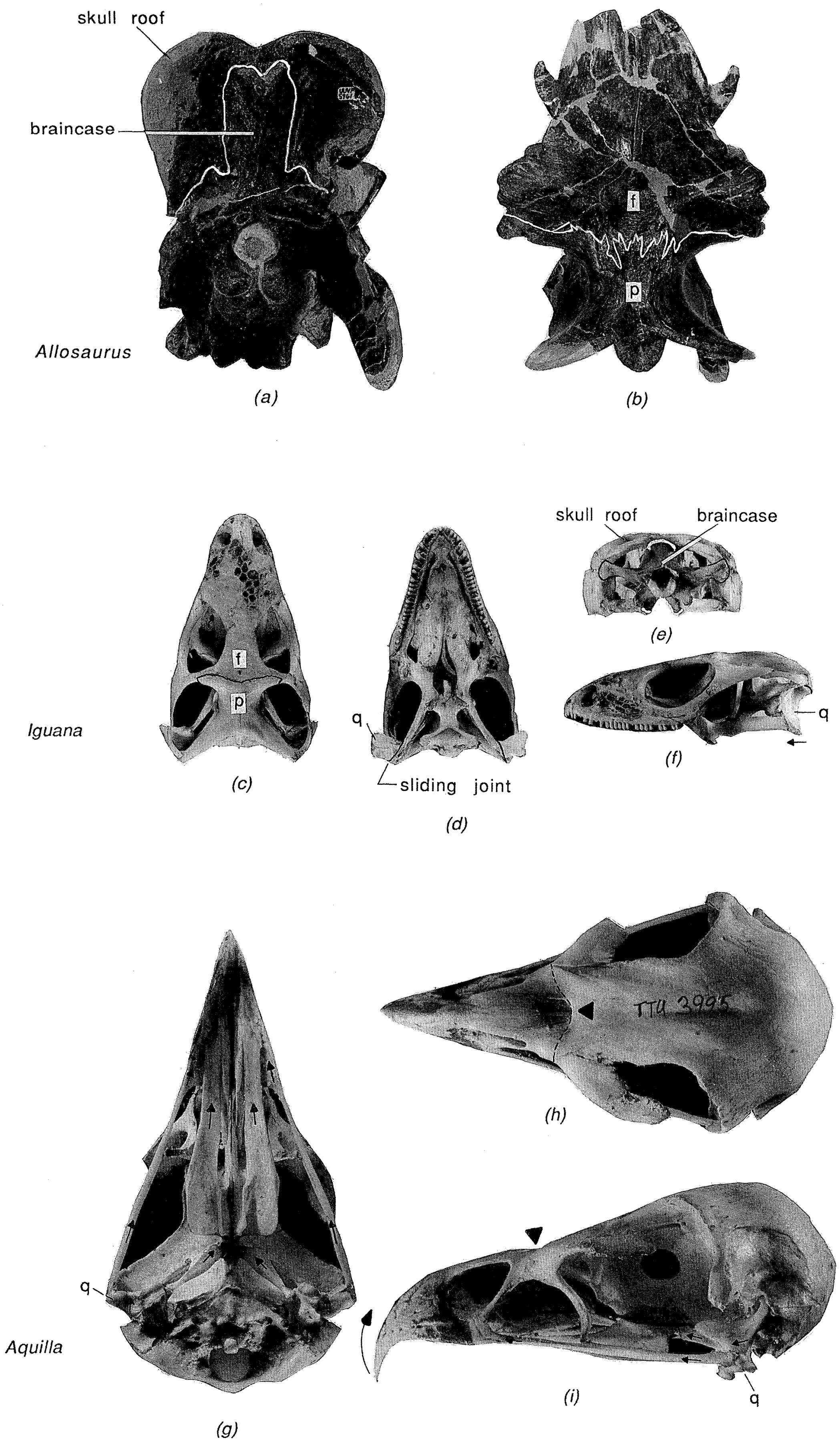


Figure 26. For description see opposite.

are limited by several devices, or 'stops'. Fisher (1955) recognized some of these stops while studying the kinetics of avian skulls. Protraction is limited mostly by soft parts (mainly ligaments) of the head. In some birds (e.g. crows), however, the orbital process abutting against the orbital wall acts as a bony stop to protraction. The bony structures that stop retraction are more widespread. That might be expected as retraction is the position of rest. In *Protoavis*, the basipterygoid process would restrict the posterior movement of the pterygoid from the normal retracted position. The nature of bony overlaps between the palatine and the maxilla along the palatal bending zone would only allow an upward swing of the upper jaw, but inhibit a downward swing from its resting position. The sliding groove and ridge joint between the lacrimal and jugal bar may act as a guide for the antero-posterior movement of the latter.

8. THE RELATIONSHIPS OF *PROTOAVIS*

The origin of birds has been a subject of great controversy for more than a century. Systematists have claimed for many years that birds are closely related to reptiles through a long line of extinct forms. Archosaurs are generally considered as the closest relative to birds because of their antorbital fenestra and diapsid temporal configuration. However, the precise relationship of birds among different lineages of archosaurs remain largely speculative. A cladistic analysis (Hennig 1966; Eldredge & Cracraft 1980; Wiley 1981) is undertaken here to determine which archosaur is most closely related to *Protoavis* and to evaluate internal relationships within the Mesozoic birds.

The cladistic method is based on a single component in phylogeny, the branching of lineages. It assumes that taxa derived from more recent common ancestry will share a greater number of inherited, derived similarities. The most important step in cladistic analysis is the attempt to partition similarity into ancestral (plesiomorph) and derived (apomorph) characters at each hierarchial level, and cluster taxa on the basis of shared derived characters (synapomorphies). Groups sharing the same synapomorphies are erected by using the comparative technique of outgroup analysis (Farris 1982; Maddison *et al.* 1984). The monophyly of the ingroup of taxa is tested by the parsimonious distribution of postulated synapomorphies.

Mayr (1981) pointed out that one of the major differences between cladistics and evolutionary taxonomists is the treatment of autapomorphous characters that were acquired by and are restricted to a clade after it branched off from its sister group. Cladists combine two groups into a single taxon on the basis of synapomorphies; they automatically give sister groups the same rank. Evolutionary taxonomists, on the other hand, rank groups by considering the relative weight of their autapomorphies. Autapomorphous characters measure the degree of evolutionary divergence between two related taxa. For instance, cladists combine theropods and birds into a single taxon Theropoda on the basis of presumed synapomorphies (Gauthier 1986). However, evolutionary taxonomists separate birds from theropods on the basis of suite of autapomorphies in connection with their shift to aerial living. Charig (1982) also recommended a similar approach for phylogenetic analysis and classification, combining the best components of both cladistic and evolutionary systematics.

In the following discussion I have adopted this integrated method, as outlined by Mayr (1981) and Charig (1982), giving equal importance to both autapomorphies and synapomorphies; the former are diagnostic characters unique to a taxon of a given rank, the latter are unique to a pair of taxa ('sister-groups').

There is a semantic question regarding the composition of archosaurs and theropods. On cladistic grounds, birds should be included in a same clade with theropods and archosaurs (Gauthier 1986). Yet, ornithologists always regard birds as an independent vertebrate class (Welty 1982). There is no consensus of deciding which view is advisable. To maintain the stability in taxonomy and to avoid confusion, a new name (?*Theravis*) should be given while combining well-established taxa such as theropods and aves. For discussion and comparison, I have used the three taxa 'Archosauria' (= non-avian archosaurs), 'Theropoda' (non-avian theropods) and 'Aves' in traditional sense (Ostrom 1976; Carroll 1988).

(*a*) *Comparisons of Protoavis with archosaurs; external relationships*

Protoavis achieved a level of avian structural organization well beyond that of any archosaurs, and acquired a large suite of avian characters. On the other hand, it shares a number of primitive features with the potential outgroups. Various cranial characters are compared here among related archosaur taxa to ascertain the plesiomorphic and apomorphic features of *Protoavis*.

Among archosaurs, four different taxa have been advanced as the principal candidates as the closest

Figure 26. Skull kinesis in some diapsids and birds; (*a*) occipital view of skull of *Allosaurus*; the braincase is intimately fused to the skull roof prohibiting metakinesis; (*b*) dorsal view of skull of *Allosaurus*, frontal and parietal are tightly sutured prohibitng mesokinesis; (*c*) dorsal view of skull of *Iguana*; traditionally mesokinesis or fronto-parietal mobility has been suggested for lizards; (*d*) palatal view of same showing a sliding joint between quadrate and pterygoid; the forward movement of quadrate would fail to transmit force through the pterygoid bar to the muzzle unit in most lizard skulls; this arrangement of quadrate-pterygoid articulation questions the validity of mesokinesis in most lizards; (*e*) occipital view of *Iguana* showing flexible articulations of braincase with skull roof and palate, indicating presence of metakinesis; (*d*) same, lateral view; with loss of lower and posterior temporal arcades, the quadrate of lizard is highly streptostylic; (*g*), (*h*) and (*i*) ventral, dorsal and lateral views of skull of Golden eagle (*Aquilla*) showing prokinesis and streptostyly; pointer indicates craniofacial hinge.

relatives of *Archaeopteryx* and the rest of the birds. These are: (i) ornithischians; (ii) ornithosuchians (= pseudosuchians); (iii) crocodylomorphs, and (iv) theropod dinosaurs. These relationships are re-examined and evaluated here in the context of *Protoavis*.

(i) *Ornithischian relationship*

Galton (1970) suggested that ornithischians such as ornithopods may be a sister group of birds, as both taxa presumably share a unique synapomorphy, the opisthopubic pelvis. His hypothesis has attracted little support. Because the pubic reversion occurred independently in several theropods (Ostrom 1976, 1985; Barsbold 1979), and probably in the crocodylomorph *Hallopus* (Walker 1977), this character cannot be taken as a reliable indicator of relationship. Later Galton rejected his own hypothesis and supported a theropod relationship (Bakker & Galton 1974).

Ornithopods share a unique feature with *Protoavis*, *Ichthyornis* and *Hesperornis* in the possession of a predentary bone (figure 27*e*). However, other autapomorphies in the ornithischian skull, as listed below, negate any close relationships between early ornithopods (such as fabrosaurs) and *Protoavis*:

(i) heterodont teeth;

(ii) cheek teeth leaf-shaped, adapted for plant eating;

(iii) presence of a supraorbital bone;

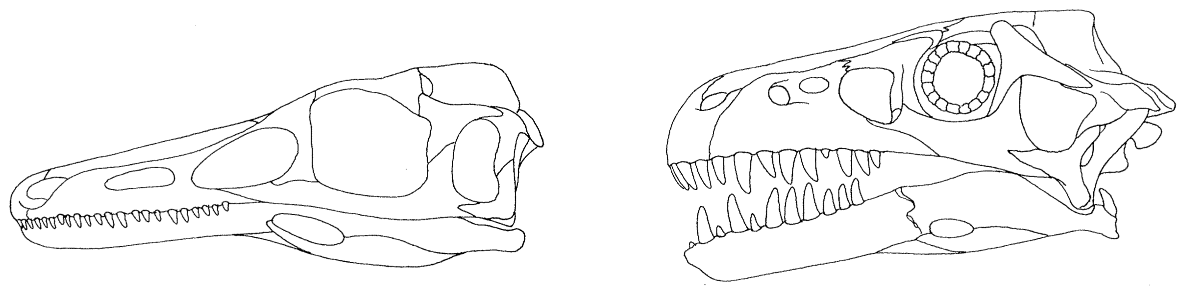
(iv) antorbital fenestra small, partially occluded by maxilla;

(v) quadratojugal relatively massive.

In addition, ornithopods lack tympanic recesses and otic specializations characteristic of early birds, indicating early divergence between these two groups.

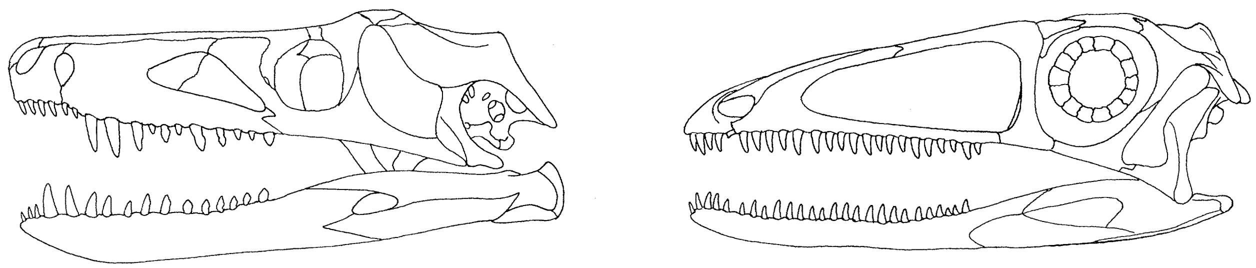
(ii) *Crocodilian relationship*

Walker (1972, 1974, 1977) proposed that birds are more closely related to crocodiles than to other groups of archosaurs. He derived his hypothesis from the morphology of *Sphenosuchus*, a primitive crocodylo-



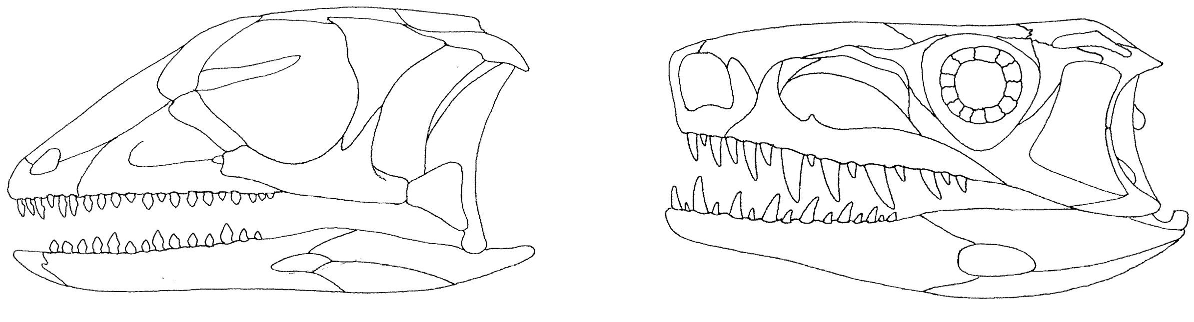
(a) Troodon

(b) Dromaeosaurus



(c) Dibothrosuchus

(d) Syntarsus



(e) Lesothosauras

(f) Euparkeria

Figure 27. Skulls of different groups of archosaurs for comparison, left lateral view; (*a*) (after Russell 1969); (*b*) (after Colbert & Russell 1969); (*d*) (after Raath 1977); (*e*) (after Thulborn 1970); (*f*) (after Ewer 1965).

morph from the Triassic–Jurassic boundary that possessed many avian features. Walker's hypothesis was endorsed by Whetstone & Martin (1979, 1981), and Martin (1983*a*, *b*, 1985) who argued that birds and crocodilians share several synapomorphies in otic structures and tooth morphology, not found in other groups of archosaurs. A list of characters proposed to support a crocodilian relationship of birds can be found in the works of Walker (1972) and Martin (1983*b*). The most important of these characters are:

(i) forward position of quadrate head, articulating with squamosal and prootic;
(ii) a kinetic skull with streptostylic quadrate;
(iii) loss of descending process of squamosal;
(iv) presence of tympanic recesses;
(v) presence of bony eustachian tubes;
(vi) presence of fenestra pseudorotunda;
(vii) presence of elongated, tubular cochlear recess;
(viii) similar dental morphology.

The most important of these, according to Walker, is the forward movement of the quadrate head, leading to a prootic contact in both groups, as well as the development of kineticism. Later, Walker (1985) realized that the quadrate head of *Archaeopteryx* is of normal archosaurian pattern. It is single-headed, contacting only the squamosal, not the prootic. Hence the condition in *Sphenosuchus* appears to be specialized. The prootic-quadrate articulation appears to have arisen independently in crocodiles and in later birds. Walker thus doubted his own hypothesis of crocodilian relationship, and concluded that the skull of *Sphenosuchus*, at least in the adult, was akinetic and monimostylic. It seems that some of the similarities between crocodilians and birds are apparently the result of parallel evolution. Some of the otic similarities (characters 4, 5, 6) are now found to occur variably in some groups of theropods (figure 28*d*) (Currie 1985; Molnar 1985), which has considerably weakened the hypothesis of crocodilian relationships.

To assess the relationship between sphenosuchid and *Protoavis*, I have examined the skull of *Dibothrosuchus*, a beautifully preserved sphenosuchid from the Early Jurassic of China, which was reported briefly by Wu (1986). The skull of *Dibothrosuchus*, as in other crocodylomorphs, was built for strength and rigidity (figure 27*c*). Coupled with massive fusion between braincase and pterygoid is the immovable incorporation of the quadrates into an otic, occipital and dermal roofing unit. The quadrate probably exhibits the most autapomorphic features (figure 29*e*–*g*). The dorsal head is differentiated into three processes directed anteriorly, posteriorly, and medially. The anterior and medial processes form the postero-lateral wall of the supratemporal fenestrae. The medial process is firmly sutured to the braincase, while the anterior and posterior processes fuse with the squamosal, making the quadrate entirely monimostylic. Although the descending process of the squamosal is reduced, this loss of strength is compensated by the enlargement of the ascending process of the quadratojugal, which forms the entire posterior border of the lower temporal fenestra to form an effective blocking device in front of the quadrate. Also the backward growth of the pterygoids over the lateral part of the braincase, and the fusion of the braincase, palate and the quadrate prevent any potential kinesis. The skull roofing bones are strongly sutured, prohibiting any dorsal bending. The monimostylic quadrate and akinentic nature of the skull of *Dibothrosuchus* make it difficult to accept that the similarities of the otic capsule and the tympanic recesses with *Protoavis* were the result of an immediate common ancestry.

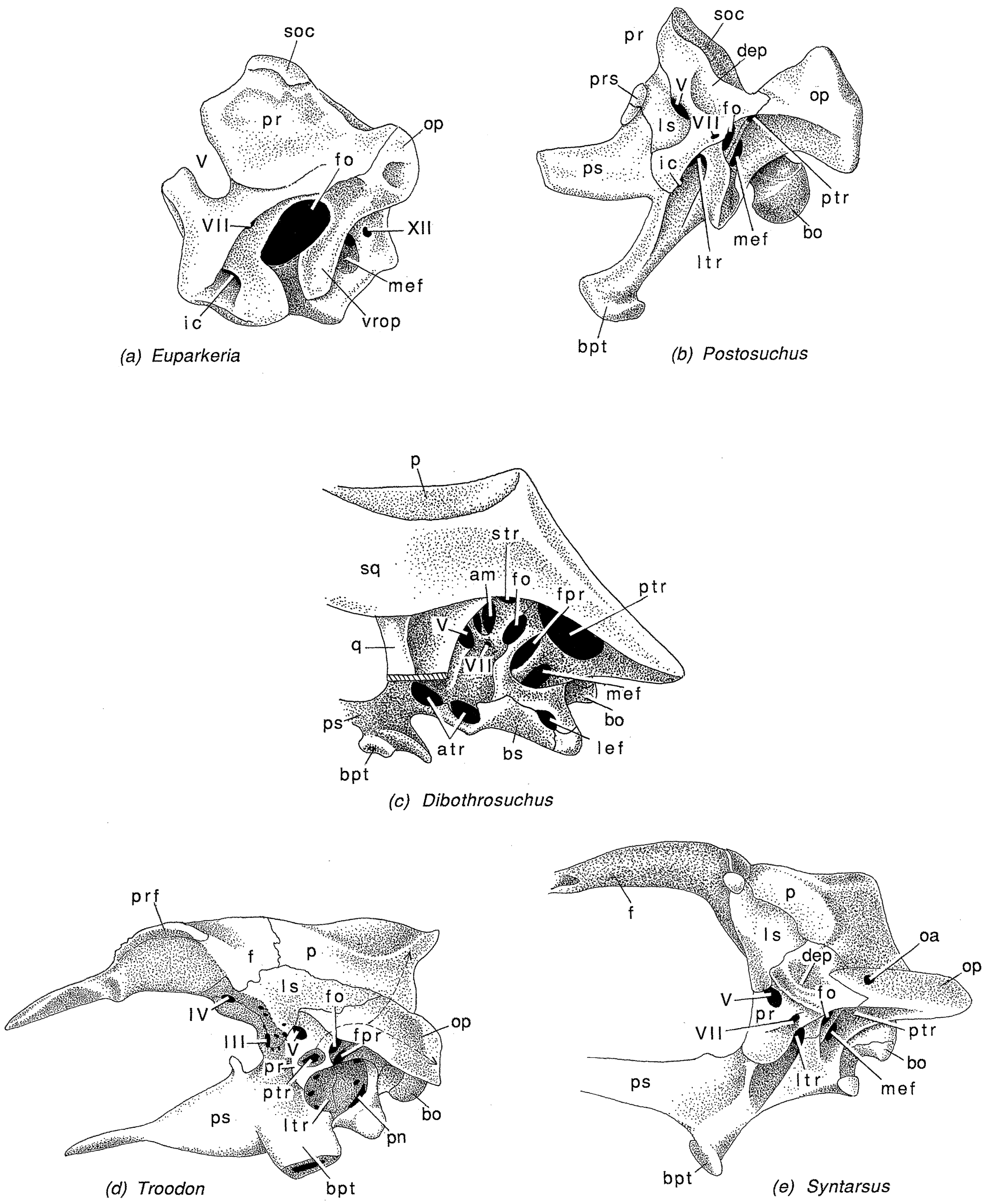
The suite of autapomorphies unique to *Dibothrosuchus* is further evidence for dismissing its close affinity with *Protoavis*. The autapomorphous characters in *Dibothrosuchus*, listed below, vastly outnumber the avian similarities:

(i) distinctive tooth notch in the upper jaw;
(ii) presence of incisive foramen;
(iii) quadrate with three heads instead of one;
(iv) fusion of quadrate with braincase, squamosal and pterygoid;
(v) postero-lateral wall of upper temporal fenestrae formed by quadrate:
(vi) fusion of pterygoid with braincase, squamosal and pterygoid;
(vii) entire posterior border of the lower temporal fenestra formed by quadratojugal;
(viii) strong overhang of squamosal at the side of quadrate and along the upper edge of lower temporal fenestra;
(ix) prefrontals with large ventral flanges meet each other along the interorbital septum to floor the olfactory bulb;
(x) STR is present as a canal, tunnelling through the posterior wall of the upper temporal fenesta.

All these autapomorphies coupled with the akinetic nature of the skull and primitive configuration of brain (figure 16*f*), provide the most serious argument against the crocodilian hypothesis. On the other hand, if sphenosuchids did not form a clade with *Protoavis*, how can we explain the otic resemblances between these two groups? Convergent evolution is a distinct possibility. Pneumatization patterns are similar in *Protoavis* and sphenosuchids, but not identical, and probably tend to follow 'pockets of weakness' in the skull so that they assume similar positions. The otic specializations in both groups indicate enhanced auditory capabilities, which perhaps evolved in parallel fashion associated with vocalization, and may reflect homoplasy rather than common ancestry.

(iii) *Ornithosuchian* (= pseudosuchian) *relationship*

In 1913, Broom described from the Early Triassic *Cynognathus* Zone of South Africa a small, carnivorous, bipedal archosaur, *Euparkeria capensis*, which he believed was a common ancestor to both birds and dinosaurs. Later, Heilmann (1926) endorsed *Euparkria* as the key to avian ancestry. Although Heilmann considered seriously the possibility of theropods as a potential ancestor of *Archaeopteryx*, he discounted this relationship on the grounds that theropods lacked clavicles (now known to be false), whereas birds possess them in the form of a furcula. His acceptance of *Euparkeria* as the putative avian ancestor is more by default than by direct demonstration. He derived



(a) *Euparkeria*

(b) *Postosuchus*

(c) *Dibothrosuchus*

(d) *Troodon*

(e) *Syntarsus*

Figure 28. Braincase of archosaurs, left lateral view; (*a*) (modified from Cruickshank (1972) and Evans (1986)); (*b*) (modified from Chatterjee 1985); (*d*) (modified from Currie 1985); arrow indicates the course of PTR; (*e*) (after Raath 1985).

Archaeopteryx from the 'pseudosuchians' only because they were bipedal, and because they had primitive character states that would not bar them from giving rise to *Archaeopteryx* (Tarsitano & Hecht 1980). The term 'pseudosuchia' means different things to different people and needs clarification. The suborder Pseudosuchia has been resurrected to include those taxa that are characterized by a 'crocodile-normal' ankle joint (e.g. Parasuchia, Aetosauria and Rauisuchia). On the other hand, the Suborder Ornithosuchia accommodate those taxa that are distinguished by a 'crocodile-reverse' ankle joint (e.g. Euparkeriidae and Ornithosuchidae) (Chatterjee 1982). Thus Heilmann's 'pseudosuchian origin' has the same meaning as 'ornithosuchian origin' in current usage.

Euparkeria possesses several plesiomorphic features in the skull (figures 27*f*, 28*a*) unknown in both theropods and *Protoavis*, and thus cannot be considered as the

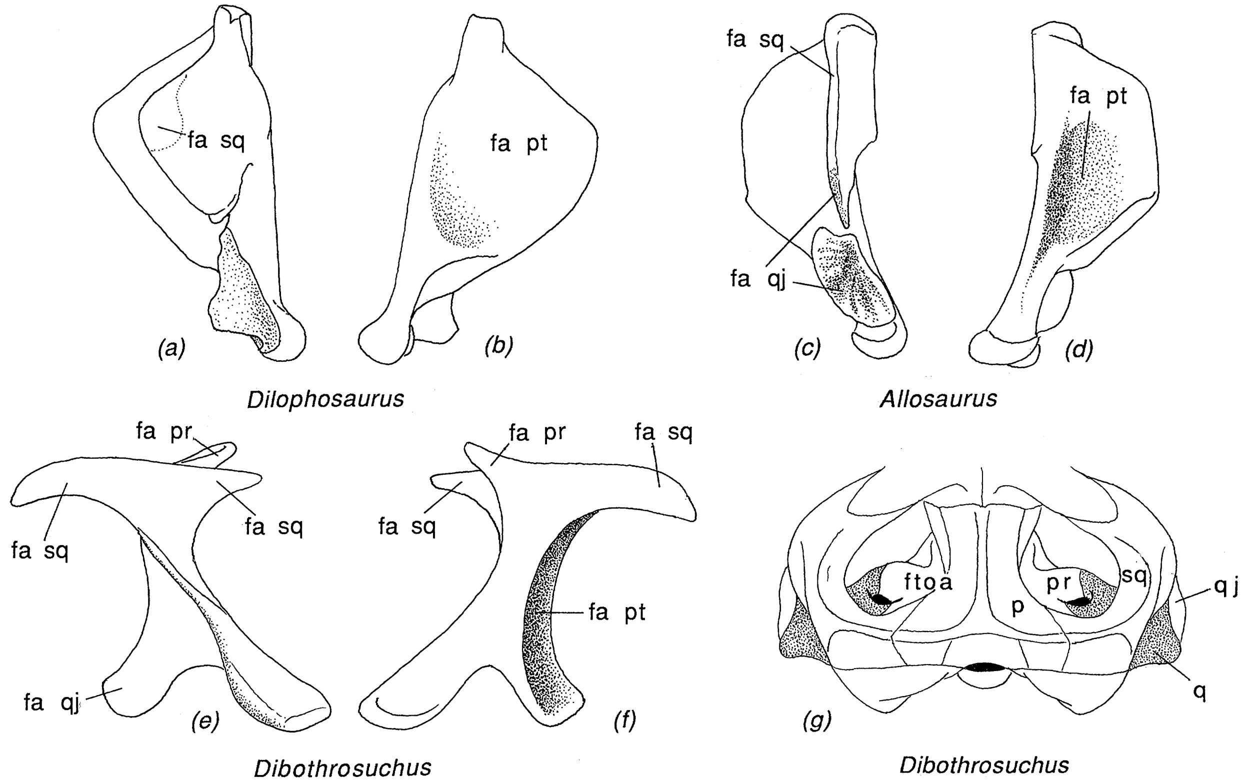


Figure 29. Quadrates of archosaurs; (*a*) and (*b*), lateral and medial views of quadrate of *Dilophosaurus* (after Welles 1984); (*c*) and (*d*), same views of *Allosaurus*; (*e*) and (*f*), same views of *Dibothrosuchus*; (*g*); dorsal view of the posterior part of the skull of *Dibothrosuchus*, showing the relationship of quadrate (stippled) with adjacent bones; the quadrate is highly specialized and monimostylic in *Dibothrosuchus*.

immediate outgroup. The primitive features of *Euparkeria* include:

(i) presence of palatal teeth;
(ii) choana terminal in position;
(iii) presence of interparietal;
(iv) unossified laterosphenoid;
(v) presence of postfrontal;
(vi) ventral ramus of opisthotic large.

A new version of ornithosuchian relationships has been suggested by Tarsitano & Hecht (1980). They believe that *Archaeopteryx* evolved at a point between the *Lagosuchus* and *Euparkeria* levels of organization. *Lagosuchus*, known from the Middle Triassic of Argentina, has been suggested to be ancestral to saurichians (Bonaparte 1975) or dinosaurs (Bakker & Galton 1974). Its implication to the ancestry of birds is attractive. Ostrom (1976) acknowledges that among all ornithosuchians, only *Lagosuchus* evolved a significant suite of postcranial characters that suggests a close relationship to *Archaeopteryx*. Unfortunately, the skull of *Lagosuchus* is too poorly known to make any meaningful comparison with *Protoavis* for phylogenetic analysis.

(iv) *Theropod relationship*

Ostrom (1973, 1975, 1976, 1985) provided the first detailed evidence for a closer relationship between small advanced theropods (such as *Ornitholestes*, *Deinonychus* and *Velociraptor*) and *Archaeopteryx*, mainly on the basis of postcranial similarities because he lacked reliable information on the skull of *Archaeopteryx*. He documented an impressive array of postcranial synapomorphies between small theropods and *Archaeopteryx* and concluded that '*Archaeopteryx* is directly descendent from a small unknown *Ornitholestes*-like coelurosaurian dinosaur' (Ostrom 1976, p. 173). Thus he implied both 'sister-group' as well as 'ancestor-descendent' relationships between small theropods and *Archaeopteryx*.

Although the theropod hypothesis is widely accepted, it remains uncertain at this stage which taxa of theropods are phyletically closest to birds (Cracraft 1986). Gauthier (1986) provided the first detailed phylogenetic hypothesis of theropods and recognized three clades, Ceratosauria, Carnosauria and Coelurosauria, which are successively closer to birds. Gauthier has redefined Coelurosauria to include highly derived theropods such as Ornithomimidae, Dromaeosauridae and Troodontidae, as well as birds. Raath (1977, 1985), on the other hand, maintained that ceratosaurs are closer to birds than to other groups of theropods. Here, I use both coelurosaurs and ceratosaurs as comparative outgroups to assess their relationship to *Protoavis*.

Theropods share the following synapomorphies with *Protoavis*: highly encephalized skull; cerebellum contacts cerebrum dorsally, displacing optic lobes ventrolaterally; vertical, T-shaped lacrimal with dorsal exposure on the skull roof.

Deinonychosaurs (Troodontidae + Dromaeosauridae), the highly advanced Cretaceous theropods, are often considered as a sister group of *Archaeopteryx* and birds (Ostrom 1976; Gauthier & Padian 1985; Gauthier

1986). Within deinonychosaurs, *Troodon* is placed closer to birds (Currie 1985, 1987).

Because *Troodon* is believed to have shared a common ancestry with birds, it is necessary to compare its cranial features in detail with those of *Protoavis*. The skull and braincase of *Troodon* are relatively well known (Russell 1969; Barsbold 1974; Currie 1985, 1987). In addition, a beautifully prepared braincase of *Troodon* (TMP 86.36.467), currently under study by Dr P. J. Currie, reveals many interesting features.

The general architecture of the skull of *Troodon* is very similar to that of *Protoavis* (figure 27*a*). The teeth are compressed sidewise, and the jaws lack interdental plates. The orbits are enormous, frontally placed with a large component of binocular vision. The braincase is highly inflated with an estimated EQ approaching that of living birds. The occiput is plate-like, but interrupted by a series of foramina for external occipital arteries and veins. The vagus foramen has been diverted backward with the development of a subcapsular process, supporting the fenestra pseudorotunda. The presence of elaborate tympanic recesses with contralateral communications suggest that *Troodon* has a much greater sensitivity to airborne sound than other theropods (figure 28*d*). In their sensory acuity, degree of cerebral integration, agility, and possible habitats, *Troodon* is comparable to some of the living ratites (Russell & Seguin 1982).

Troodon shares the following similarities with *Protoavis*:

(i) presence of PTR;
(ii) presence of fenestra pseudorotunda;
(iii) presence of eustachian canal;
(iv) large frontally placed orbits;
(v) highly encephalized skull;
(vi) absence of interdental plates;
(vii) a constriction at the base of the tooth crown.

However, all of these observed similarities cannot be considered decisive, unique characters, as some of them (characters 1–3) are also present in sphenosuchids and other theropods. Characters 4 and 5 occur in dromaeosaurids (Sues 1978), whereas characters 4–6 appear to be present in ornithomimids (Russell 1972) and character 7 is present in crocodilians. The presence of these similarities in different lineages of archosaurs greatly diminishes their utility for establishing phylogenetic relationships between *Troodon* and *Protoavis*.

On the other hand, *Troodon* has acquired a suite of autapomorphies which may indicate evolutionary divergence from *Protoavis*:

(i) Presence of 'lateral tympanic recess' (LTR): Barsbold (1974) and Currie (1985) described a prominent lateral depression on each side of the braincase behind the prootic, which has developed contralateral communication. The two ears might have communicated via this channel. The LTR (= basisphenoid recess of Osborn (1912)) appears to be related to periotic sinuses. It is present in different archosaurs such as *Postosuchus*, *Syntarsus* (Raath 1985), ornithomimids, *Allosaurus* and *Tyrannosaurus*. It is a non-avian trait. In birds, the ATR is located farther forward, anterior to the prootic, and is covered laterally by the alaparasphenoid. The LTR and ATR may be analogous structures, both probably linked to localizing sound in space (Witmer 1988).

(ii) Forward position of the PTR: in birds, the PTR occurs postero-dorsal to the fenestra ovalis within the opisthotic; in *Troodon* it occurs anterior to the fenestra ovalis within the prootic. The location corresponds well with 'antrum mastoideum' of *Dibothrosuchus* (figure 28*c*, *d*). However, the PTR has pneumatized the whole paroccipital process and supraoccipital, with the development of a contralateral communication.

(iii) Highly pneumatized basioccipital: in *Troodon* and related coelurosaurs, the basioccipital is fenestrated by intricate lateral and dorsal sinuses. Such elaborate pneumaticities are lacking in *Protoavis* and birds.

(iv) Large parasphenoid capsule: the presence of a bulbous parasphenoid capsule is characteristic of troodontids and ornithomimids. This feature appears to be highly specialized from the avian condition.

(v) Enlarged hollow, basipterygoid processes: in the avian lineage, the basipterygoid processes are reduced or lost.

(vi) Reduced prootic: the prootic appears to be highly reduced in *Troodon*. In *Protoavis* and juvenile birds, this element is tall and hour-glass shaped;

(vii) Presence of prefrontal foramen: a unique feature in the skull of *Troodon* is the presence of a small foramen near the junction of prefrontal and frontal.

There are some plesiomorphic features in the skull that indicate that *Troodon* was far off from achieving avian streptostyly. This is somewhat surprising because initial stages of streptostyly are encountered in some early lineages of ceratosaurs:

(1) robust squamosal–quadratojugal bar: this robust blocking device would prohibit streptostyly in *Troodon*. In *Euparkeria*, *Syntarsus* and *Dilophosaurus*, there is a tendency to reduce this bar;

(2) quadrate-paroccipital articulation; the quadrate head fits primarily in a facet of the paroccipital process in *Troodon*. In *Syntarsus*, *Dilophosaurus* and *Allosaurus*, the quadrate head has moved forward, and is received mainly by the squamosal. The forward placement of the quadrate head is an important avian trend.

It thus appears from this discussion that the alleged similarities between *Troodon* and birds are not unique, and are more likely to represent parallel evolution rather than common ancestry. One of the difficulties of equating anatomic features of *Troodon* with those of *Protoavis* is that they are separated by more than 160 Ma. No troodontid is known from the pre-Cretaceous sediments. Obviously the Cretaceous *Troodon* is far removed, both structurally and temporally, from the Triassic *Protoavis*. One can argue that many of the autapomorphies of *Troodon* might have been developed independently after splitting from the common ancestry. Future discovery of early troodontids may settle this question.

Dromaeosaurids are considered by some workers as the closest relative to birds (Paul 1984; Gauthier 1986). I could not find any significant feature in the skull of *Dromaeosaurus* to substantiate this claim. The braincase is simple, unspecialized and lacks any pneumaticities. The quadrate is immovably fixed to the pterygoid and squamosal. The palate is primitive and lacks the maxillary false palate. *Dromaesaurus*, however, shares three derived features with *Protoavis*: (i) the presence of a pair of pontine recesses on the floor of the braincase; (ii) the vagus foramen has been diverted backward with development of a subcapsular process, (iii) the floccular recess is well developed, surrounded by a semicircular bony tube. However, these features are not unique, but known in some other theropods.

Raath (1977, 1985) proposed an alternative hypothesis, that *Archaeopteryx* is more closely related to Ceratosauria (*sensu* Gauthier 1986) such as *Syntarsus* than to later deinonychosaurs (figure 27*d* and 28*c*). He identified the following avian features in *Syntarsus*:

(i) presence of PTR;
(ii) presence of LTR;
(iii) presence of occipital foramen on paroccipital process;
(iv) presence of a dorso-lateral depression on prootic.

However, none of the features are unique avian characters, as they are also reported in a variety of archosaurs. Characters 1–4 are present in *Allosaurus* and characters 1, 2 and 4 are present in *Postosuchus*.

The otic capsule appears to be primitive in *Syntarsus*. The metotic foramen occurs behind the fenestra ovalis. The subcapsular process and fenestra pseudorotunda are apparently absent. The basipterygoid processes are highly enlarged contrary to the avian condition.

Syntarsus shows the following autapomorphous features:

(i) diastema between premaxilla and maxilla;
(ii) absence of posttemporal fenestra;
(iii) squamosal lies medial to quadrate's lateral wing;
(iv) parietal reduced.

However, as discussed earlier, *Syntarsus* shows two interesting trends which may be precursors to the origin of avian streptostyly. These are the loss of the squamosal–quadratojugal joint, and the presence of a separate squamosal socket for the quadrate head. Because *Syntarsus* is known from the Triassic–Jurassic boundary, its temporal gap with *Protoavis* is minimal. Thus *Syntarsus* is closer to *Protoavis* from a kinetic and temporal point of view, whereas *Troodon* is closer to *Protoavis* on the basis of overall cranial shape and neurosensory specializations. This suggests that many of the presumed avian lineages were independently evolved in different lineages of theropods. It is difficult to ascertain at this stage which theropod is closer to *Protoavis*. Instead of a particular taxon, both deinonychosaurs and ceratosaurs will be considered as outgroups of *Protoavis* to infer its relationships with other Mesozoic birds.

(*b*) *Avian features in the skull of Protoavis*

It appears from the comparative analysis of cranial characters that *Protoavis* exhibits the following avian apomorphies, not found in any archosaurs. Both theropods and crocodilians are used as outgroups for assessment of plesiomorphic characters:

(i) absence of prefrontal;
(ii) absence of postorbital bone, so that two temporal fenestrae are confluent;
(iii) squamosal with a single, forwardly directing zygomatic process;
(iv) loss of ascending process of jugal so that orbit is confluent with lower temporal fenestra;
(v) posterior shift of choana close to basipterygoid articulation;
(vi) absence of ectopterygoid bone;
(vii) pterygoid highly reduced and forms the posterior margin of choana;
(viii) absence of ascending process of quadratojugal;
(ix) presence of lateral cotylus for quadratojugal;
(x) orbital process of quadrate is free and well developed;
(xi) ventral condylar articulation of quadrate with pterygoid;
(xii) dorsal process of maxilla is reduced;
(xiii) fronto-nasal hinge narrow and possibly flexible;
(xiv) possible presence of lateral bending zone at jugal bar;
(xv) possible presence of palatal bending zone between maxilla and palatine;
(xvi) cerebellar fossa extended to supraoccipital with external protuberance;
(xvii) reduced olfactory lobes;
(xviii) ATR covered laterally by laterosphenoid;
(xix) enlarged semi-elliptical bony tube for anterior vertical semicircular canal;
(xx) enlarged supraoccipital–epiotic complex in occiput, separated by a sinus canal;
(xxi) quadrate articulates with mandibles by means of three condyles;
(xxii) posterior mandibular elements fused and compressed laterally thus reducing Meckelian canal;
(xxiii) presence of lateral process in surangular for attachment of posterior ligament.

It appears from the above list that *Protoavis* had acquired an array of synapomorphies with birds and should be ranked at a different categorical level from the theropods or crocodilians. The acquisition of such a large suite of avian characters may be related to its shift to aerial adaptation. The major structural changes from archosaurs to birds took place in temporal configuration, palato-quadrate morphology, specializations in the braincase and otic structures, and in the mandible. This analysis suggests that *Protoavis* is taxonomically separated from all archosaurs and should be included in the class Aves.

(*c*) *Comparisons of Protoavis with Mesozoic birds: internal relationships*

The major deficiency in our knowledge of the history of birds is their inadequate Mesozoic record, which is tantalizing but not informative. Certainly, birds had a worldwide distribution during this period, but an adequate fossil record becomes available only from the

Tertiary upwards. Few Mesozoic birds are known with well-preserved cranial material, which limits the character analysis. The taxa lacking cranial information are excluded from the present phylogenetic analysis, but are considered later in conjunction with the study of postcranial material. There are just four taxa of Mesozoic birds known with skull material adequate enough to allow comparison with *Protoavis*. These are *Archaeopteryx*, Hesperornithiformes, *Ichthyornis*, and *Gobipteryx*. In addition, *Avimimus* is included as a potential member of Mesozoic birds. A brief review of these avian taxa is given below with highlights on cranial morphology.

(i) *Archaeopteryx*

Until recently, our knowledge of the evolution and relationships of early birds has been based entirely upon the Late Jurassic *Archaeopteryx* thought to be the oldest and most primitive known bird. Primarily because of the presence of flight feathers, the avian relationships of *Archaeopteryx* have seldom been questioned in the past. Even so, opinion has been divided regarding the phylogenetic placement and evolutionary significance of *Archaeopteryx*. Ostrom (1976) concludes that the skeleton of *Archaeopteryx* is virtually identical to that of coelurosaurs with the exception of the furcula and unique ischial morphology. He maintains that 'the question of origin of birds can be equated with the question of the origin of *Archaeopteryx*'. On the other hand, many workers (Martin 1983*a*, 1985, 1987; Thulborn 1984; Charig 1985) are more cautious about the phylogenetic significance of *Archaeopteryx*. They argue that *Archaeopteryx* is not an ancestral bird and is far off the main line of avian evolution. There are some who consider *Archaeopteryx* a feathered dinosaur (Lowe 1935, 1944; Paul 1984; Thulborn 1984; Kurzanov 1985). Others state that birds are a member of theropod dinosaurs (Gauthier & Padian 1985; Bakker 1986; Gauthier 1986). The status of *Archaeopteryx* on the basis of available cranial information is less certain and further study is necessary to affirm or deny its avian nature in a definitive manner. Moreover, it will be necessary to provide an osteological definition of Aves on the basis of cranial morphology and to decide whether or not *Archaeopteryx* is to be included in the class.

Archaeopteryx is represented by six skeletons from the Late Jurassic Solnhofen Limestone (Lower Tithonian) of Germany. Cranial elements are known from the Eichstätt, Berlin, London and Solnhofen specimens, of which the Eichstätt is by far the best. Wellnhofer (1974) provided the first skull restoration of the Eichstätt specimen, which also forms the basis for later restorations. The skull is crushed sidewise in such a fashion that the dermal roofing bones and the jugal bar were pushed toward each other, thus obscuring the details of temporal configuration. The palatal configuration is virtually unknown, although Wellnhofer identified the ectopterygoid as a separate element. The quadrate is visible in lateral aspect and may hold an important key in assessing the affinity of this animal. The skull is poorly preserved in the Berlin specimen (Heilmann 1926), but general features such as the sizes and shapes of the skull, orbit, antorbital fenestra and external naris are apparent in this specimen. The Berlin specimen provides one crucial taxonomic feature: there is a large, triangular, postorbital bone, bordering the relatively enormous circular orbit. This shows that the upper temporal arch was still intact and the two temporal openings were not confluent. The London specimen, having undergone additional preparation recently, provides valuable information about the braincase and the quadrate (Whetstone 1983; Walker 1985) and indicates that the skull was encephalized in avian fashion (Jerison 1973; Hopson 1980; Bühler 1985). The skull of the Solnhofen specimen (Wellnhofer 1988) consists primarily of the snout region and awaits further description.

To understand its systematic position, the quadrate morphology and temporal configuration of *Archaeopteryx*, which has been a major source of confusion for many years, needs to be resolved. Walker (1985) provided for the first time a description of the quadrate morphology of *Archaeopteryx* and documented that it is more archosaur-like than has previously been suspected. He identified the 'undetermined bone' (de Beer 1954) on the slab posterior to the London skull as a right quadrate. He observed that the lower articular surface is missing, but the dorsal articular head is intact and single. He identified both the pterygoid and lateral wings of the quadrate, but found some discrepancies in relative size with those of the Eichstätt specimen. In the Eichstätt specimen, the quadrate is visible in articulation from the right side. It has an extensive medial wing that received an overlapping quadrate wing of the pterygoid more dorsally than in archosaurian fashion. As a result, there is no development of an orbital process. The lateral wing is also visible in the Eichstätt specimen as a narrow flange. The quadrate head appears to be single, and fits into the undersurface of the squamosal.

I have examined the isolated quadrate of the London specimen and concur with Walker's interpretation. However, I believe that the quadrate in question belongs to the left side, as the right quadrate is found attached to the skull, where the two distal condyles for mandibular articulation can be seen (figure 30). Once the isolated quadrate of the London specimen is identified as the left element, it compares closely with that of the Eichastätt specimen, in which the medial wing is more extensive than the lateral one. The quadrate is extremely theropod-like. Its overall similarity with that of *Allosaurus* is striking (figures 30*a–d*, *g*, *h*). The lateral wing has an articular surface for the reception of the descending process of the squamosal as in other theropods. The dorsal head is single, with a prominent spherical knob for articulation with the squamosal. The pterygoid wing is extensive and built in archosaur fashion. The ventral mandibular condyles are bipartite. The quadrate of *Archaeopteryx* does not show any feature that may be suggestive of its avian identity.

Contrary to this interpretation, Haubitz *et al.* (1988) claimed that the quadrate of the Eichstätt specimen is double-headed as in modern neognaths. Their interpretation is based on computed tomography (CT)

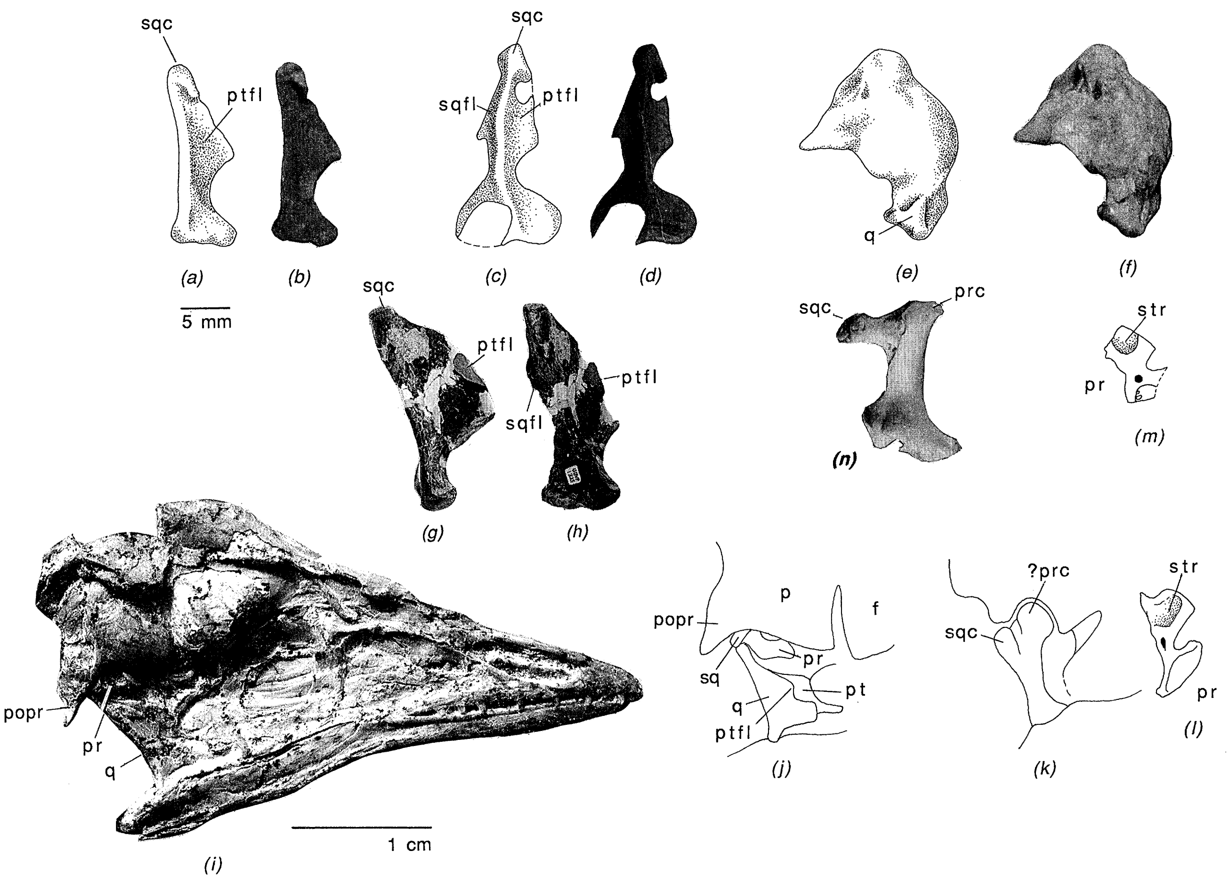


Figure 30. Nature of *Archaeopteryx* quadrate; (*a*) and (*b*) posterior view of left quadrate of London specimen showing a large pterygoid flange and a single-headed quadrate (squamosal capitulum of quadrate); (*c*) and (*d*) the same, postero-medial view, showing squamosal and pterygoid flanges; (*e*) and (*f*) part of occiput of London specimen, showing the right quadrate in place; (*g*) and (*h*) posterior and postero-medial views of left quadrate of *Allosaurus*; note the quadrate of *Archaeopteryx* is very similar to that of theropod; (*i*) right lateral view of the skull of Eichstätt specimen; (*j*) the same, showing the nature of articulation of quadrate with adjacent bones; note prootic bone occurs in front of the quadrate head; (*k*) interpretation of the 'double-headed' *Archaeopteryx* quadrate with the help of computed tomography X-ray image in an oblique plane of 32 to the plane of the skull (after Haubitz *et al.* 1988); however, the quadrate appears to be composite; the putative prootic capitulum is interpreted here as a part of prootic; (*l*) right prootic of *Protoavis* showing similar configuration of putative 'prootic capitulum'. (*m*) Right prootic of *Archaeopteryx*, London specimen (reversed from left side) for comparison; note prootic lacks otic facet for prootic capitulum; (*n*) posterior view of right quadrate of *Buteo*, showing double-headed quadrate; note squamosal capitulum is stouter than prootic capitulum; in (*k*), the reverse is the case.

X-ray image of the Eichstätt specimen, taken at an angle of 32° to the plane of the skull (figure 30*k*).

There are several inconsistencies in this new interpretation, which I believe, are inadmissible. First, their reconstructed quadrate appears to be a composite, and may contain more than one bone, as can be seen in the negative of the CT image. Second, the 'prootic capitulum' they claim to have found looks unusually large, bigger than the squamosal capitulum. Usually in modern neognaths, the reverse is true. Third, the quadrate head of the London specimen, which permits a three-dimensional view, is single, intact, and fails to show any feature that might have indicated the postmortem loss of the 'prootic capitulum'. Fourth, the prootic of the London specimen is virtually complete and there is no sign of a socket on the prootic for the reception of the 'prootic capitulum'. Fifth, the rest of the quadrate is so primitive and archosaur-like that it is difficult to believe that only the head evolved in neognath fashion. In fact, none of the Mesozoic birds show any bifurcation of the head (figure 33).

It seems likely that their putative 'prootic capitulum' is a part of the prootic. This becomes apparent if one examines critically the Eichstätt skull, especially the region of quadrate articulation. Here the head of the quadrate is in contact with a piece of bone that is identified as a squamosal (Walker 1985). In front of it, there is a large crescentic bone, the upper-half of the prootic, which contains the STR at the centre, as in the London specimen. When the plane of the reconstructed image was rotated at a 32° angle, the antero-dorsal part of the prootic would lie in front of the quadrate head and would be superimposed on the quadrate in a CT image. The putative articulation of the 'prootic capitulum' with the braincase probably reflects the corresponding articulation between prootic and epiotic. This can be demonstrated by rotating the prootic–epiotic complex of the *Protoavis* specimen at a similar angle (figure 30*l*). I conclude, therefore, that the quadrate of *Archaeopteryx* is single-headed, and theropod-like in construction, as noted by Walker (1985).

What was the nature of the temporal configuration of *Archaeopteryx?* This is another crucial taxonomic feature used to assess its avian relationship. Unfortunately the temporal region is imperfectly preserved in both the Berlin and Eichstätt specimens, and this character is entirely missing in the London one. Heilmann (1926) restored the Berlin skull as a typical archosaur-like diapsid, although the actual specimen does not permit such detailed and precise reconstruction. Both Wellnhofer (1974) and Ostrom (1976) were uncertain about the evidence of either temporal fenestrae. Thulborn & Hamley (1985) reconstructed the Eichstätt skull as a typical diapsid. Martin (1985) and Bühler (1985), on the other hand, favoured an avian-like temporal configuration, where the orbit and the two temporal fenestrae are confluent. However, this interpretation is difficult to reconcile, because the postorbital bone is known in both the Berlin and Eichstätt specimens, implying that the upper arch was still intact. However, the Eichstätt specimen exhibits a critical feature on the underlying slab (Wellnhofer 1974, Figure 5*c*). Two sides of the specimen are superimposed in figure 31*c* to get a composite picture of the preserved part of the Eichstätt specimen. It becomes clear that the jugal is typically avian and has lost the ascending process, so that the orbit communicates with the lower temporal fenestra. The apparent contact between the jugal bar and the postorbital bone is due to dorso-ventral crushing so that the posterior part of the skull roof and the jugal bar moved toward each other. The dorsal displacement of the jugal bar is also evident at the quadratojugal suture. The jugal has a forked posterior end for the reception of the quadratojugal; the former has been pushed upward relative to the latter. The quadratojugal appears to be in place. If this interpretation is correct, the temporal configuration of *Archaeopteryx* is transitional between the diapsid and avian conditions. A similar temporal configuration is seen in the Late Cretaceous *Avimimus* (Kurzanov 1985). In *Avimimus* both the postorbital-jugal bar and the squamosal-quadratojugal bar appear to have been eliminated so that the orbit is confluent with the lower temporal opening. In this respect the genus is more advanced than *Archaeopteryx*. On the other hand, the upper temporal arch is still intact with the retention of the postorbital bone. The confluence of the orbit with the lower temporal fenestra is a derived feature shared by *Archaeopteryx* and *Avimimus*.

Archaeopteryx appears to have retained the squamosal-quadratojugal bar in front of the quadrate, which would prohibit the forward movement of the quadrate. The quadratojugal is L-shaped, as in many theropods, with a prominent ascending process that reaches the mid-height of the quadrate. The extent of the squamosal is uncertain in *Archaeopteryx*. Whetstone (1983) and Martin (1985) believe that the squamosal is highly reduced or lost in *Archaeopteryx*, which may be an autapomorphous feature. Walker (1985), on the other hand, maintains that much of the bone is missing on the lateral side of the Eichstätt specimen except for a small fragment that is still attached to the quadrate head. The extent of the squamosal can be seen in the counterslab on the Eichstätt specimen (figure 31*a*). It may have the usual tetraradiate shape seen in theropods with an anterior process that would join the postorbital. Although the squamosal is missing in the London specimen, the lateral flange of the quadrate indicates that the squamosal may have a descending process. The ectopterygoid is retained to prohibit antero-posterior palatal movement. All these features collectively suggest that streptostyly was not achieved in *Archaeopteryx*. However, opisthostyly appears to be functional in *Archaeopteryx* as the quadratojugal-jugal contact is a loose joint, and the quadrate has a spherical head.

Other important landmarks preserved in the skull of *Archaeopteryx* are characteristics of the external naris, antorbital fenestra and orbit. The former is relatively large and elliptical, and is bound by the premaxilla, nasal and maxilla as in many theropods. In *Protoavis* and other birds, the premaxilla contacts the nasal and excludes the maxilla from the external naris. The large, triangular antorbital fenestra of *Archaeopteryx* is extensive and there are two additional anterior openings. Similar triple antorbital fenestrae are known in many coelurosaurs, but not in any birds. Its posterior border is formed by a T-shaped lacrimal, which may have a loose connection with the jugal bar. The orbit is relatively enormous, circular and contains sclerotic rings.

Whetstone (1983) and Walker (1985) gave somewhat different interpretations of the braincase and otic structure of the London specimen. I concur with Walker's analysis. The otic capsule, though primitive, is of basic avian type. The prootic is similar to that of *Protoavis*, constricted at the shaft, but expanded at the two ends. The bone is notched anteriorly and posteriorly by the trigeminal foramen and the fenestra ovalis respectively. Dorsally there is a prominent STR which may not be covered by the squamosal. The ATR appears to be partially represented at the ventrolateral surface of the prootic. The PTR is dorsal to the opisthotic threshold and continues to the paroccipital process. The shaft of the prootic is pierced by the facialis foramen. Both the fenestra ovalis and fenestra pseudorotunda appear to be larger than the normal avian condition, indicating that the cochlear recess may not be very elongate. The fenestra pseudorotunda is bordered posteriorly by the metotic ossification. In the occiput, the metotic process is represented as a large flange. Here the foramina for the nerves X and XII are visible. A sinus canal appears to separate the epiotic from the supraoccipital as in *Protoavis*. The posttemporal fenestra is reduced to a small aperture, as in *Protoavis*, accompanied by a ventral foramen, for the passage of the external occipital artery.

The lower jaw is shallow and probably lacks the external mandibular fenestra. It has a conspicuous downward bend behind the tooth, as in some theropods and birds. The teeth are conical with expanded roots that are separated from the crowns by a distinct constriction. The tooth row terminates below the

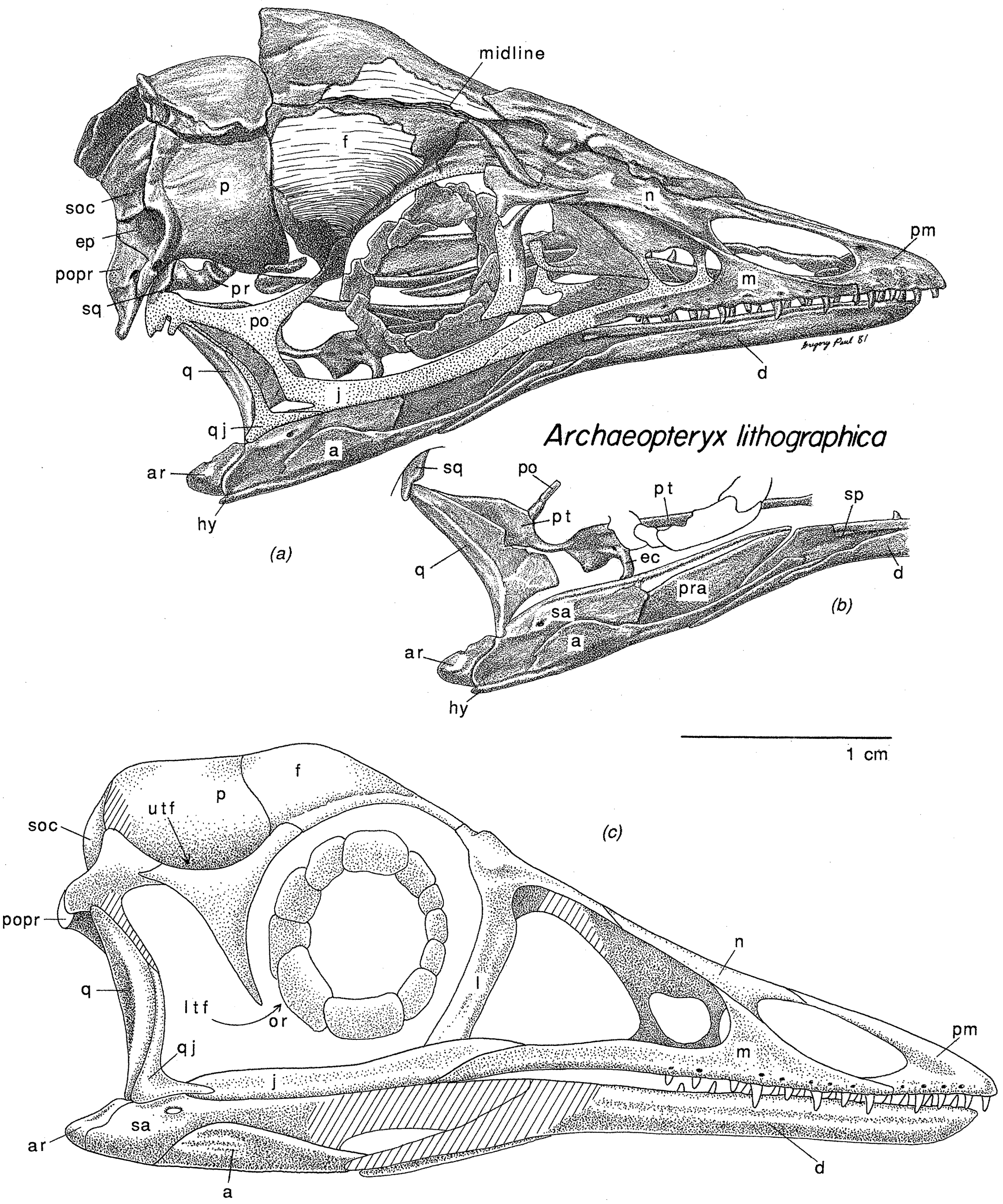


Figure 31. *Archaeopteryx lithographica*, Eichstätt skull; (*a*) right lateral view of the skull as preserved; stippled area is reconstructed from the counter slab; the skull was evidently crushed dorsoventrally so that the postorbital bone is pushed to the jugal bar; the presence of postorbital bone indicates that the upper arch was intact; (*b*) detailed structure of the quadrate region; (*c*) restoration and interpretation of the skull; when the postorbital is restored in normal position, the lower temporal opening appears to be confluent with the orbit as in *Avimimus*; (*a*) and (*b*), modified from Wellnhofer (1974), redrawn by Gregory S. Paul.

midpoint of the antorbital fenestra, a condition shared by many deinonychosaurs. In ceratosaurs, the tooth row continues farther backward. This may indicate that the loss of teeth might have occurred from back to front in this clade.

(ii) *Hesperornithiformes*

The order Hesperornithiformes consists of medium to large flightless birds that show evidence of great diversity and cosmopolitan distribution during the Cretaceous. At present there are four described genera of Hesperornithiformes: *Enaliornis*, *Baptornis*, *Parahesperornis*, and *Hesperornis*. Of these, *Enaliornis* is the oldest known genus, recovered from the Early Cretaceous Greensand of Cambridge, England. Seeley (1876) described several isolated elements of different individuals, but much of the material is badly abraded. Although *Enaliornis* resembles the loon level of adaptation for foot-propelled diving, its affinity has been debated for a long time. Martin (1983*a*) allocated this genus to Hesperornithiformes on the basis of several characters in skull (including the loose fronto-parietal joint), tibiotarsus (broad triangular cnemial cres), and tarsometarsus (external anterior ridge and enlarged outer trochlea). Witmer (1990) reinterpreted the braincase of *Enaliornis* as 'extremely avian', and recognized all three tympanic recesses (ATR, STR and PTR); the ATR shows evidence of contralateral communication.

The cranial anatomy of *Baptornis* is poorly known. Marsh (1880) described this genus from the Late Cretaceous Niobrara Chalk of Kansas. Martin & Tate (1976) discussed a few isolated cranial elements (e.g., premaxilla, frontal, partial quadrate and posterior part of the jaw), but the postcranial material is well represented. *Baptornis* was a less specialized diving bird than the contemporaneous *Hesperornis*, though they were closely related to each other.

A nearly complete skeleton of a hesperornithid bird, now housed at the University of Kansas (KUVP 2287), was described by Williston (1898) as *Hesperornis gracilis*, an identification that was later corroborated by Gingerich (1976). Martin (1984), however, pointed out that this specimen is sufficiently different from *Hesperornis* and erected a new taxon, *Parahesperornis alexi*. Although the skull of *Parahesperornis* closely resembles that of *Hesperornis*, taxonomic distinctions can be seen in the lacrimal, quadrate, fronto-parietal suture and the braincase. The dentition and palate appear to correspond well with those of *Hesperornis*. The premaxilla is edentulous, and the maxilla and dentary bear teeth set in sockets. Witmer (1990) identified all three tympanic recesses (STR, ATR and PTR) in *Parahesperonis*. In addition, he noticed an articular sinus in this genus, which is absent in *Hesperornis*.

Hesperornis is by far the best known and most widely distributed taxon of the Cretaceous foot-propelled birds, recorded from the Late Cretaceous marine sediments of Kansas, Alaska, Manitoba, the Northwest Territories, South Dakota, Montana, Wyoming and Alberta (Olson 1985). There has been one report of an occurrence of *Hesperornis* in non-marine rocks of Alberta (Fox 1974). Our knowledge of the cranial anatomy of *Hesperornis* is based entirely on three specimens housed at the Yale Peabody Museum (Marsh 1880; Gingerich 1976), the Smithsonian Institution (Lucas 1903) and the University of Kansas (Witmer & Martin 1987).

The skull is about 26 cm long with an elongate, overhanging beak that was presumably covered by a horny sheath (figure 32*d*). The external naris is set fairly posteriorly. Teeth are retained in the maxilla and the dentary, but are absent in the premaxilla. The temporal configuration is like that of modern birds, where the orbit is confluent with two temporal fenestrae. The postorbital and ectopterygoid bones are absent. The braincase is inflated and intimately fused with the skull roof. The quadrate is modern-looking. The dorsal head is single but articulates with both squamosal and prootic as in ratites. The orbital process is well developed. Gingerich (1973) suggested that the skull of *Hesperornis* is streptostylic and shows a unique intracranial mobility, which he called 'maxillokinesis'. A distinct groove is situated obliquely on the dorsolateral surface of the maxilla is for articulation with processes of the premaxilla and nasal. This groove may be associated with the fore-and-aft movements of the maxilla relative to the rest of the skull. Bühler *et al.* (1988) disputed this maxillokinesis hypothesis. Instead, they suggested that the skull is prokinetic and streptostylic. The two halves of the dentary are separate, but possibly connected to a small predentary bone (Martin 1987).

Gingerich (1976) concluded that the palate of *Hesperornis* is primitive, theropod-like, and of a palaeognathous type (figures 33*d*, *e* and 38*g*). Witmer & Martin (1987) concurred that the palate retained many plesiomorphic features common to archosaurs. However, they denied 'palaeognathy' for *Hesperornis*. Instead, they believed that the palate is highly specialized. They recognized several autapomorphous features unknown in other birds. These are: (i) reverse peg and socket joint between pterygoid and basipterygoid; (ii) short, very complex pterygoid; (iii) complex, long and unfused vomers that do not articulate with the pterygoids.

(iii) *Ichthyornis*

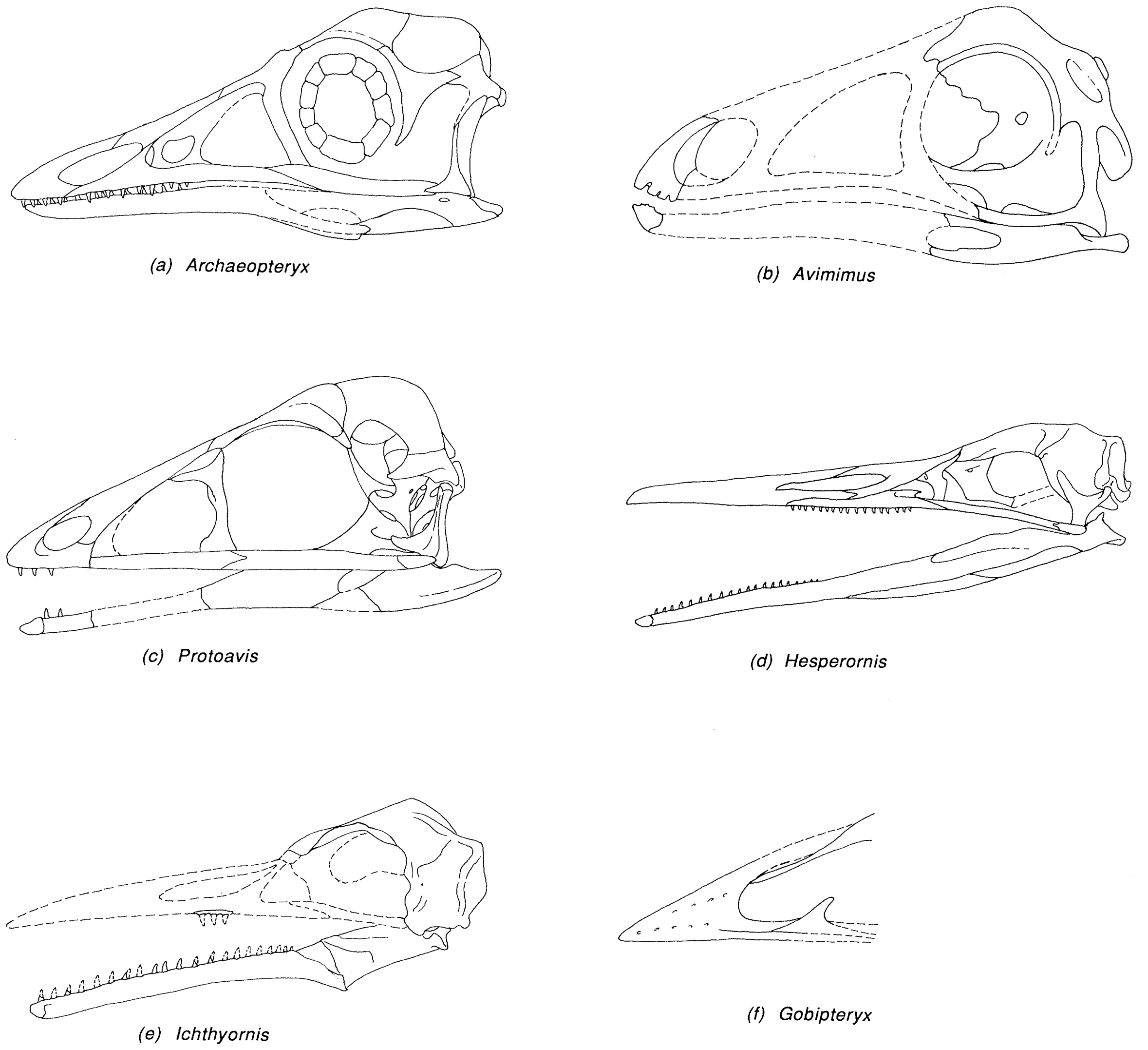
Marsh (1880) described a volant toothed bird from the Late Cretaceous Niobrara Chalk of Kansas as *Ichthyornis*, which superficially resembles gulls and terns. It is the sole genus of the order Ichthyornithiformes and is restricted to the Late Cretaceous marine deposits of North America. Currently it is known from Kansas, Texas, Alabama, New Mexico, Manitoba and Alberta (Olson 1985).

The cranial information of *Ichthyornis* is solely based on two skulls, housed at the Yale Peabody Museum. The skulls are badly crushed and mounted on exhibit, thus preventing detailed study. Several isolated jaws are known (Gingerich 1972; Martin & Stewart 1977). The bill and the maxilla are virtually unknown, but the posterior part of the skull, quadrate and tooth-bearing mandible are well represented. The quadrate and temporal configuration are similar to those of modern birds, and the braincase appears to be inflated (figures 32*e* and 33*a–c*). The teeth are probably absent in the premaxilla, but present in the maxilla and the dentary. The teeth are similar to those of *Hesperornis*; they are set in a groove in young individuals but are fully socketed in the adult. There are as many as 26 teeth in the mandible. The lower jaw has a well-developed intramandibular joint as in *Hesperornis*. The dentary is blunt anteriorly and bears a prominent facet for articulation with a predentary bone (Martin 1987).

Witmer (1990) recognized both articular and quadrate sinuses in *Ichthyornis*. However, the nature of the tympanic recesses are difficult to assess until the skulls at the Yale Peabody Museum are accessible for detailed study.

(iv) *Gobipteryx*

Elzanowski (1974, 1976, 1977) described this terrestrial bird from the Late Cretaceous Barun Goyot



(a) *Archaeopteryx* (b) *Avimimus* (c) *Protoavis* (d) *Hesperornis* (e) *Ichthyornis* (f) *Gobipteryx*

Figure 32. Skulls of Mesozoic birds; (*b*) (modified from Kurzanov, 1987); (*d*) and (*e*) (after Marsh, 1880) (*f*) *Gobipteryx* (after Elzanowski 1977).

Formation of the Gobi Desert, Mongolia. Later (1981), he reported the discovery of some embryonic skeletons from the same formation that probably belong to *Gobipteryx*. The cranial material is crushed and distorted, and is difficult to interpret. The adult skull is about 45 mm long. The external naris has been shifted backward with the development of a beak. The palate shows many features of palaeognathy (figures 32*f*, 39*d*). The choana is set posteriorly and the pterygoid articulates with the vomer to form a median bar. Behind the choana there is a large palatine recess. The ectopterygoid appears to be absent. Elzanowski (1977) claims that the quadrate is avian-like in the development of an orbital process and pterygoid condyle, but archosaur-like in having bicondylar mandibular articulation. However, others (Martin 1983*a*; Olson 1985) believe that the quadrate of *Gobipteryx* is primitive and is distinctly similar to that of *Archaeopteryx*. Unfortunately this important bone is not properly figured by Elzanowski. The temporal configuration is unknown. There is a bony mandibular symphysis. Unlike all other known Mesozoic birds, *Gobipteryx* is entirely edentulous.

(v) *Avimimus*

Kurzanov (1983, 1985, 1987) described *Avimimus* from the Late Cretaceous Negmet Formation of Mongolia, and documented a suite of avian characters not present in *Archaeopteryx*. Thulborn (1984) suggested that *Avimimus* is more closely related to modern birds than *Archaeopteryx*.

The skull of *Avimimus* is incompletely preserved (figure 34). It is about 85 mm long, 43 mm wide, and 45 mm high. The orbits are frontally placed with stereoscopic vision. Teeth are present at the front of the premaxilla, but not at the tip of the dentary. The upper temporal arch is intact, but the orbit and the lower temporal opening are confluent with the development of a typical avian jugal bar. The squamosal–quadratojugal bar is absent. The quadrate is archosaur-like with two distal condyles. It is immovably fused with the pterygoid, squamosal and jugal. The ectopterygoid is also present, indicating that streptostyly was not achieved. The skull appears to be highly encephalized. Critical information on the tympanic recess of the braincase is lacking. The foramen magnum is considerably larger than the

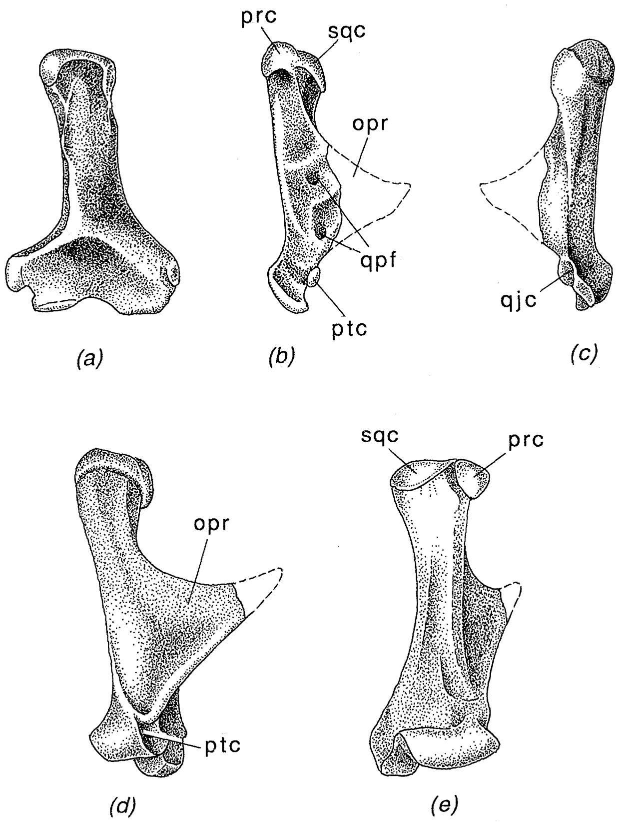


Figure 33. Quadrates of Late Cretaceous birds; (*a*), (*b*) and (*c*); anterior, medial and lateral views of left quadrate of *Ichthyornis*; (*d*) and (*e*) medial and posterior views of left quadrate of *Hesperornis* (after Marsh 1880).

occipital condyle. The condyle is reduced, crescentic and somewhat ventrally placed. The paroccipital processes project downward and outward. The supraoccipital has a strong medial crest. The basioccipital contains a basal sinus as in *Protoavis*. The basipterygoid processes are reduced.

(*d*) *Phylogenetic relationships of Mesozoic birds*

This section enumerates primitive and derived character states to establish polarity for the placement of Mesozoic birds within the proposed phylogenetic scheme. Although material is too fragmentary to assess character-states of many genera, these genera are included to emphasize the diversity and complexity of early birds. Moreover, the results are congruent with the highly corroborated trees of Martin (1983*a*, 1987) and Cracraft (1986, 1988).

(i) *Character analysis*

Using the outgroup comparison method of Farris (1982) and Maddison *et al.* (1984), binary states for 30 cranial characters were coded: (0) primitive condition; (1) derived condition; (?) missing or uncertain characters. Character states were assigned to all ingroup taxa with cranial information (table 4). Both sphenosuchids and coelurosaurs were considered as successive outgroups for assessment of ancestral characters to minimize homoplasies and character conflicts. In this study, a series of morphoclines for characters in the skull were set up. The primary characters used

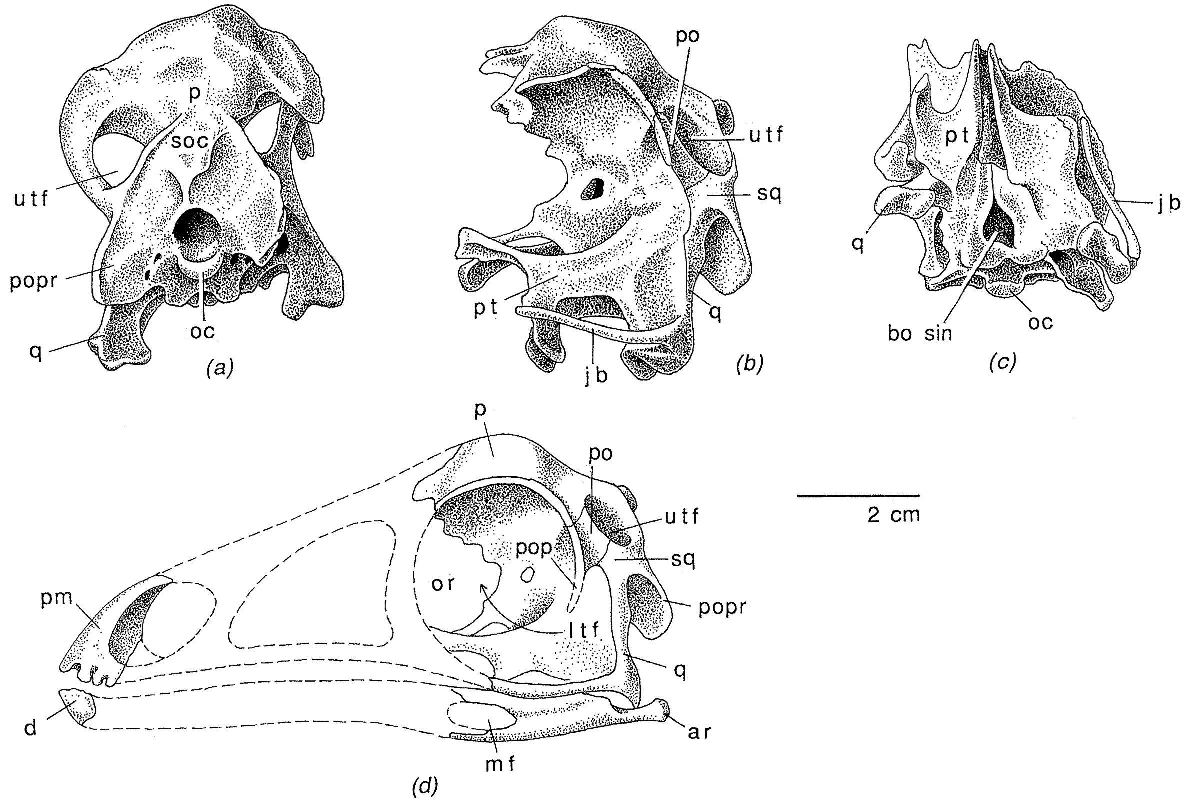


Figure 34. *Avimimus porentosus*; (*a*), (*b*) and (*c*) occipital, lateral and ventral views of the skull; note the upper arch is intact, but the lower temporal opening appears to be confluent with the orbit with the development of a typical avian jugal bar (after Kurzanov 1987); (*d*) restoration of the skull in left lateral view.

Table 4. *Matrix for character-states of taxa included in this study*

(Character-state codes: 0, primitive; 1, derived; ?, missing or uncertain)

	characters and character states																													
taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Gobipteryx	?	?	?	?	1	1	1	1	0	1	0	1	?	1	1	1	1	1	1	1	0	0	1	1	?	0	0	0	1	1
Ichthyornis	?	1	1	?	1	1	1	1	0	1	0	1	?	1	1	1	1	?	?	?	1	0	?	1	?	0	0	1	0	0
Hesperornis	1	1	1	?	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	0
Protoavis	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Avimimus	?	1	?	?	1	1	1	1	0	1	1	0	?	0	0	0	0	?	0	0	0	0	?	0	0	0	0	0	0	0
Archaeopteryx	1	1	1	1	1	1	1	1	1	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Theropods	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sphenosuchids	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

involve the degree of temporal modification along with development of preorbital kinesis and neurosensory specializations (table 4).

1. Metotic structure: (0) small, (1) large. The presence of metotic structure is an avian feature. The subcapsular process is developed to some extent in outgroups.

2. Olfactory lobes: (0) large, (1) small. The olfactory lobes are highly reduced in all birds.

3. Cerebellar fossa extended to supraoccipital: (0) no, (1) yes. This fossa is confined to the parietal in outgroups, but extended to the supraoccipital in all birds with an external protuberance.

4. Sinus canal between epiotic and supraoccipital on occiput: (0) absent, (1) present. This canal is absent in outgroups. The canal is visible in *Archaeotpteryx*, *Protoavis* and many juvenile birds.

5. Prefrontal bone: (0) present, (1) absent. The prefrontal is present in outgroups, (though considerably reduced in advanced theropods), but absent in all birds.

6. Braincase: (basioccipital–basisphenoid–parasphenoid complex): (0) vertical, (1) horizontal. The braincase is deep and vertical in outgroups, but horizontal and plate-like in birds.

7. External naris: (0) terminal, (1) shifted backward. The naris is forwardly placed in outgroups, but has shifted progressively backward in birds. The choana has also shifted backward in correlation with the external naris.

8. Diapsid temporal configuration: (0) unmodified, (1) partially modified. The diapsid condition is retained in all outgroups, but is partly modified in *Archaeopteryx* and *Avimimus*, where the orbit becomes confluent with the lower temporal fenestra.

9. Tooth row: (0) long, (1) reduced preantorbital. In *Archaeopteryx*, tooth rows terminate in front of the antorbital fenestra. In all outgroups, they continue far behind. This feature may be an apomorphy for *Archaeopteryx*.

10. Quadratojugal, ascending process: (0) present, (1) absent. This process is present in outgroups and *Archaeopteryx*, but lost in *Avimimus* and other birds, so that the quadrate becomes the posterior margin of lower temporal fenestra.

11. Dentition present in premaxilla but lost at front of dentary: (0) absent, (1) present. This may be an apomorphy for *Avimimus*.

12. Temporal configuration: (0) partly modified, (1) fully modified. The postorbital bone is present in outgroups, *Archaeopteryx* and *Avimimus*, but is lost in *Protoavis* and other ornithurine birds, so that two temporal fenestrae become confluent with the orbit.

13. Alaparasphenoid covers ATR: (0) no, (1) yes. This feature is absent in all outgroups, but present in *Protoavis* and other birds. Unknown in *Archaeopteryx* and *Avimimus*.

14. Squamosal, zygomatic process: (0) absent, (1) present. This process is absent in all outgroups, *Archaeopteryx* and *Avimimus*, but present in *Protoavis* and other birds.

15. Quadrate, lateral cotylus for quadratojugal: (0) absent, (1) present. The quadratojugal is sutured to quadrate in outgroups, *Archaeopteryx* and *Avimimus*, but forms a peg and socket joint in *Protoavis* and other birds.

16. Quadrate, orbital process: (0) absent, (1) present. This process is absent in outgroups, *Archaeopteryx* and *Avimimus*, but present in *Protoavis* and other birds.

17. Quadrate, ventral condylar articulation with pterygoid: (0) absent, (1) present. The pterygoid is sutured dorsally to the quadrate in outgroups, *Archaeopteryx* and *Avimimus*, but articulates ventrally in *Protoavis* and other birds.

18. Maxilla, dorsal process: (0) large, (1) small. The dorsal process of maxilla is large in outgroups and *Archaeopteryx* to contact nasal, but is reduced in *Protoavis* and other birds.

19. Preorbital kinesis: (0) absent, (1) present. This feature is absent in outgroups and *Archaeopteryx*, but is present in *Protoavis* and other birds.

20. Ectopterygoid bone: (0) absent, (1) present. This bone is present in outgroups *Archaeopteryx* and *Avimimus*, but lost in *Protoavis* and other birds.

21. Quadrate, articulation with mandible: (0) by two condyles, (1) by three condyles. The condyle is bipartite in outgroups, *Archaeopteryx* and *Avimimus*, but in *Protoavis* and other birds, this is tripartite. The posterior condyle may be reduced secondarily (as in *Gobipteryx* and some modern birds).

22. Dentition, teeth restricted to the tips of the

premaxilla and dentary: (0) absent, (1) present. This is an apomorphic feature for *Protoavis*.

23. Nasals meet broadly (virtually along their entire length) in mid-line: (0) present, (1) absent. The nasals are broadly in contact in outgroups, *Archaeopteryx* and *Protoavis*, but are separated anteriorly by the intervening premaxillae in later birds.

24. Nasal process of premaxilla extends posteriorly to level of lacrimals: (0) absent, (1) present. The nasal process of premaxilla does not extend to the level of the lacrimal in outgroups, *Archaeopteryx* and *Protoavis*, but does so in later birds.

25. Mesethmoid, ossified: (0) absent, (1) present. This is absent in outgroups, *Archaeopteryx* and *Protoavis*, but present in *Hesperornis* and other birds.

26. Reverse peg and socket joint between pterygoid and basipterygoid: (0) absent, (1) present. This may be an autapomorphic feature for *Hesperornis*, where a process of the pterygoid fits into a facet of the basipterygoid.

27. Combination of short, complex pterygoid with narrow, elongate palatine: (0) absent, (1) present. This peculiar pterygoid-palatine morphology is unique in *Hesperornis*.

28. Quadrate, pterygoid condyle: (0) small, (1) large. In *Ichthyornis*, the pterygoid condyle is highly pronounced.

29. Edentulous jaws: (0) absent, (1) present. *Gobipteryx* is the only Mesozoic bird known to possess this character.

30. Bony mandibular symphysis: (0) absent, (1) present. *Gobipteryx* is the only Mesozoic bird known to possess this character.

(ii) *Results: phylogenetic pattern of Mesozoic birds*

Character-state data for 30 cranial characters were subjected to cladistic analysis. Undirected trees were generated with Phylogenetic Analysis Using Parsimony (PAUP) program (version 2.4.1) of Swofford (1985). Most parsimonious trees were generated using Branch-and-Bound option which guarantees to find the shortest tree. By using the core taxa, a single most parsimonious tree was found at 31 steps with a consistency index of 0.968. This tree contains an unresolved trichotomy of the three Cretaceous genera (*Gobipteryx*, *Hesperornis* and *Ichthyornis*) (figure 35). The relationships of each lineage are therefore highly corroborated. The tentative nature of this analysis must be stressed because of the imperfect cranial information of Mesozoic birds. This is the first attempt to define the major clades of Mesozoic birds by use of branching diagram and postulated cranial synapomorphies.

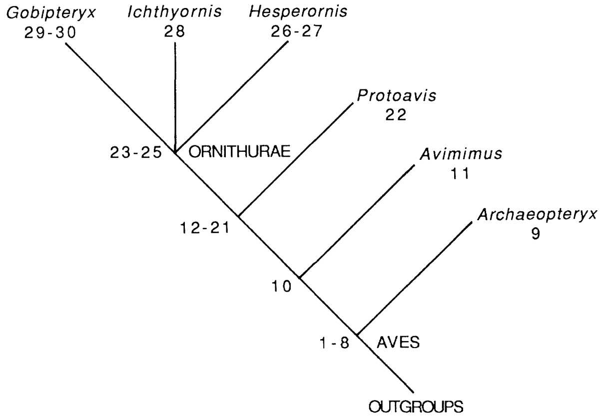


Figure 35. Cladogram showing the phylogenetic relationships of Mesozoic birds. Most parsimonious phylogenetic hypothesis of the core ingroup taxa using theropods and sphenosuchids as the root of the tree (31 steps, consistency index = 0.968). Character numbers refer to those discussed in the text.

Phylogenetic analysis indicates that the taxon Aves is a monophyletic group; *Archaeopteryx* is the most primitive member of this clade. *Archaeopteryx*, *Avimimus* and *Protoavis* are successively closer to the Cretaceous genera such as *Gobipteryx*, *Ichthyornis* and *Hesperornis*. The phylogenetic relationships of Mesozoic birds, on the basis of shared derived features, are translated into a classification in the following section.

(*e*) *Classification of Mesozoic birds*

The cladogram is converted into a phylogenetic tree on the basis of stratigraphic sequence of taxa (figure 36). Because no ancestral taxon is specified, the tree is consistent with the cladogram (Eldredge & Cracraft 1980). Moreoever the fossil record of Mesozoic birds is poor, so the cladogram produces the best approximation to the correct tree (Fortey & Jefferies 1982). On the other hand, the phylogenetic tree not only depicts the interrelationships of core taxa, but also indicates the probable historical time of origin of synapomophies. Thus the tree incorporates an important component of evolution. This classification is a written version of the phylogenetic hypothesis presented here and is based on cranial characters only. Each Mesozoic avian genus has been assigned to a corresponding higher level taxon or order, but none of the Mesozoic fossils that is included in this analysis can be referred to modern orders.

Class Aves Linnaeus, 1758
Temporal range: Late Triassic to Recent
Included taxa: *Archaeopteryx*, *Avimimus*, *Protoavis* plus all other birds.

Synapormorphies of Aves

The class Aves is postulated to be monophyletic because its members share the following eight derived characters: (1) metotic structure present; (2) olfactory lobes small and reduced; (3) cerebellar fossa extended to supraoccipital with external protuberance; (4) presence of sinus canal between epiotic and supraoccipital; (5) prefrontal bone absent; (6) braincase horizontal; (7) external naris located posteriorly; (8) partly modified disapsid temporal configuration where the orbit is confluent with the lower temporal fenestra.

Order Archaeopterygiformes
Genus *Archaeopteryx* von Meyer, 1861
Type species *Archaeopteryx lithographica* von Meyer, 1861

Apomorphous character of Archaeopteryx

(9) Teeth present in premaxilla, maxilla and dentary; tooth rows terminate in front of antorbital fenestra.

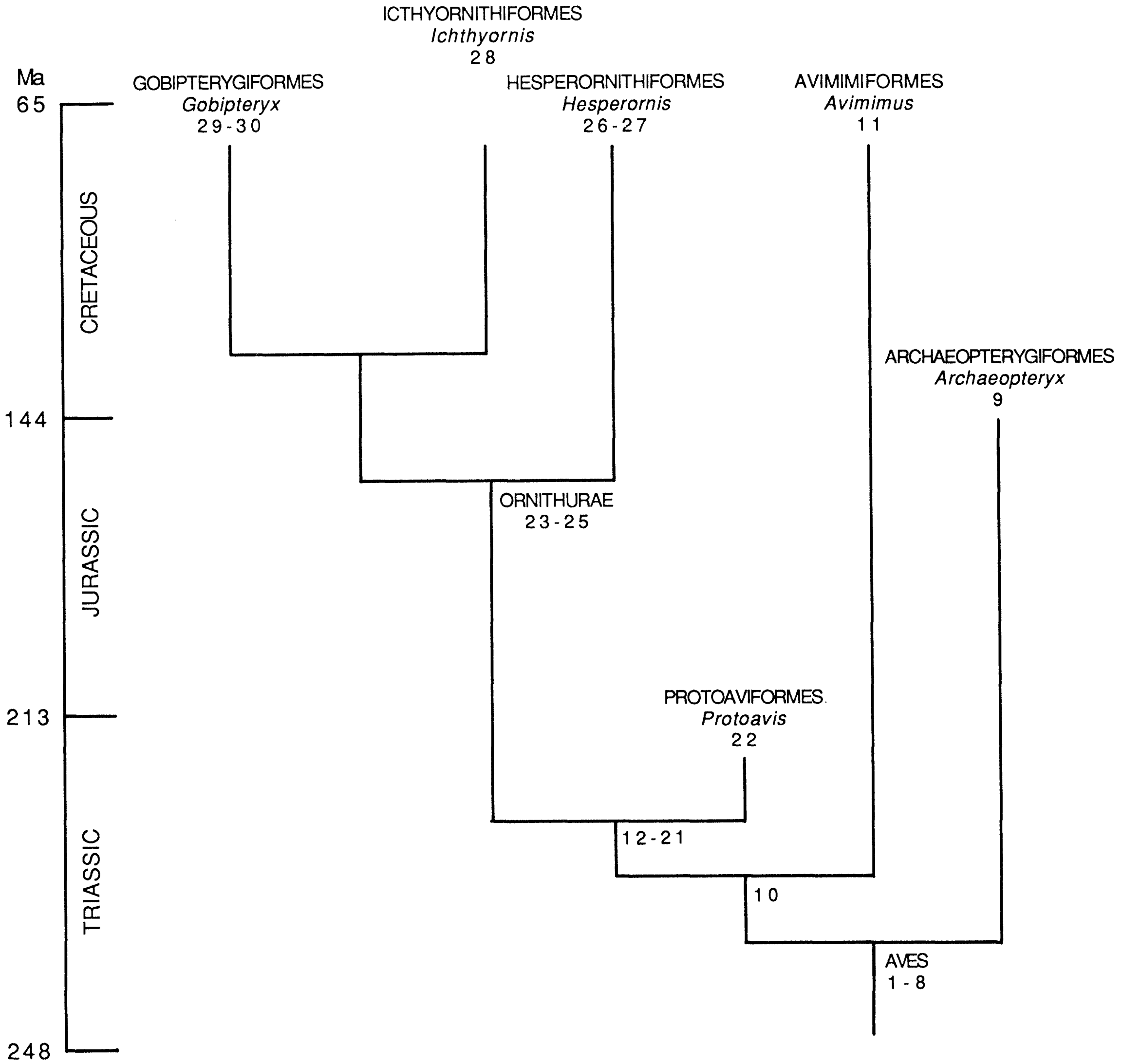


Figure 36. Phylogenetic tree showing the interrelationships of Mesozoic birds, derived from the cladogram of figure 33.

Order Avimimiformes

Genus *Avimimus* Kurzanov, 1981

Type species *Avimimus portentosus* Kurzanov, 1981

Apomorphous characters of Avimimus

(10) Ascending process of quadratojugal is lost as in other birds, so that the quadrate forms the posterior margin of the lower temporal fenestra; however, unlike any other birds, the quadrate is fused to the squamosal; (11) teeth present in premaxilla, but absent in maxilla and dentary.

Order Protoaviformes, new order

Genus *Protoavis*, new genus

Type species *Protoavis texensis*, new species

Protoavis is the sister-group of all other birds less *Archaeopteryx* and *Avimimus*; this latter taxon is termed the Ornithurae. *Protoavis* shares the following derived characters with the Ornithurae: (12) Diapsid temporal configuration 'fully modified' so that orbit is confluent with two temporal fenestrae; (13) alaparasphenoid covers ATR; (14) presence of zygomatic process on squamosal; (15) quadrate with lateral cotylus for quadratojugal; (16) quadrate with free orbital process; (17) ventral condylar articulation of quadrate with pterygoid; (18) dorsal process of maxilla reduced, resulting in loss of extensive sutural connection with nasal; (19) presence of preorbital kinesis; (20) ectopterygoid bone absent; (21) quadrate articulates with mandible by means of three condyles.

Apomorphous feature of Protoavis

(22) Teeth restricted to the tips of the jaws; maxilla edentulous.

Subclass Ornithurae Haeckel, 1886

Temporal range: Early Cretaceous to Recent.

Included taxa: Hesporornithiformes, *Icthyornis*, *Gobipteryx* and other birds.

Synapomorphies of the Ornithurae

The Ornithurae are considered to form a monophyletic group on the basis of the following four synapomorphies: (23) nasals do not meet broadly but are separated anteriorly by the intervening premaxillae; (24) the nasal process of premaxilla extends posteriorly to the level of lacrimals; (25) presence of ossified mesethmoid.

Order Hesperornithiformes
Genus *Hesperornis*, Marsh 1872
Type species *Hesperornis regalis* Marsh, 1872

Apomorphous features of Hesperornis

(26) Reverse peg and socket joint between pterygoid and basipterygoid; (27) short broad pterygoid with narrow, elongated palatine.

Order Ichthyornithiformes
Genus *Ichthyornis*, Marsh 1872
Type species *Ichthyornis dispar* Marsh, 1872

Apomorphous feature of Ichthyornis

(28) Pterygoid condyle of quadrate highly pronounced.

Order Gobipterygiformes
Genus *Gobipteryx*, Elzanowski 1974
Type species *Gobipteryx minuta* Elzanowski, 1974

Apomorphous features of Gobipteryx

(29) Edentulous jaws; (30) bony mandibular symphysis.

9. EVOLUTION OF THE AVIAN SKULL

Birds were subject to selection pressures to decrease the size and weight of the skull for flight. Within the constraint of this economic framework, the avian skull evolved in response to two functional requirements: (i) efficient feeding mechanisms associated with endothermy and high metabolic activity, and (ii) neurosensory specializations associated with coordination, balance, flight and intelligence.

Endothermy has many advantages in that the organism is constantly operating at high activity and is independent of external sources of heat. But it also has serious disadvantages: endotherms need an order of magnitude more food than ectotherms, to supply the fuel that is burned physiologically to maintain a constantly high body temperature. This requirement of high intake of food has resulted in a series of modifications in the avian skull; (i) formation of a beak with loss of teeth, and (ii) ability to produce a wider gape by means of cranial kinesis. The most conspicuous osteological changes in the avian skull were the modifications of circumnarial, temporal and palatal regions associated with kineticism. Other modifications were related to the expanding brain and large orbit.

(a) Changes in the temporal region and the origin of streptostyly

The avian skull is highly modified from the reptilian diapsid condition. Most of the bars behind the orbit and between the two fenestrae have disappeared so that the two fenestrae are confluent with each other and also with the orbit (Goodrich 1958). Moreover, the squamosal–quadratojugal bar in front of the quadrate is eliminated. The quadrate, so freed, becomes streptostylic, and is capable of moving the upper jaw relative to the braincase.

Although avian kinesis was known to 18th century anatomists and has been analysed in terms of muscles, ligaments and adaptive modifications, the origin of streptostyly and preorbital kinesis in birds from the archosaurian condition has never been addressed properly. This is partly because of limited and inadequate skull material of early birds. Preorbital kinesis is the most important and basic feature of avian skull evolution and streptostyly is the prerequisite for it. The quadrate plays a central role in all movements of both the upper and lower jaw in birds. It is not clear from available fossil evidence when and how streptostyly evolved during the archosaur-bird transition. This problem is best approached by examining the temporal region of archosaurs and early birds from a functional point of view, and considering the possible changes that have occurred during this transition.

In all archosaurs the diapsid arch remains intact. Streptostyly cannot be achieved without modifications of the diapsid framework. Some blocking structures prevent streptostyly in archosaurs. Ewer (1965) suggested that the skull of *Euparkeria* is basically akinetic except for a limited back-and-forth movement of the quadrate in opisthostylic fashion. The head of the quadrate fits into a cup formed by the squamosal and opisthotic, indicating a kinetic joint. On the other hand, the squamosal–quadratojugal bar forms a bony stop in front of the quadrate that prevents streptostyly. The quadrate is firmly sutured to the quadratojugal as in most archosaurs, so that the two bones must move as a unit, if any mobility is permitted at the quadrate head. The quadratojugal–jugal articulation shows some flexibility. It is a loose lap joint which could allow some sliding movement in antero-posterior direction. Similarly, a slight sliding movement between the pterygoid and quadrate is a distinct possibility. Within these osteological constraints, the only possible movement is the posterior swing of the combined quadrate–quadratojugal bones from the normal resting position during contraction of M. depressor mandibulae. The anterior face of the paroccipital process would limit the posterior movement of the quadrate beyond the vertical attitude. Even a relatively small opisthostylic movement could be functionally significant during feeding. It would permit the backward movement of the lower jaw relative to the skull during the bite, which would assist in slicing and shifting the flesh back towards the throat ready for swallowing. Cruickshank (1972) attributed opisthostyly to *Proterosuchus*. A potential movement seems to exist between the squamosal and the conjoined quadrate–quadratojugal bones (figure 37).

In erythrosuchids, the quadrate is closely tied to neighbouring elements without any mobility and is entirely monimostylic. The squamosal–quadratojugal bar forms a stout pillar in front of the quadrate, and

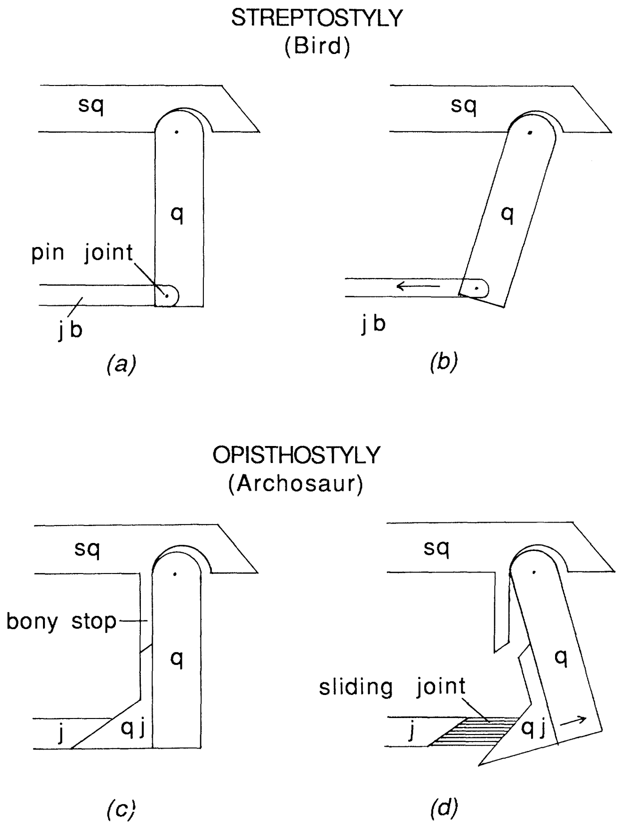


Figure 37. Opisthostyly versus streptostyly; opisthostyly appears to be present in some archosaurs (e.g., ornithosuchians and theropods), where the combined quadratojugal and quadrate could move posteriorly during contraction of M. depressor mandibulae (*c*) and (*d*); the descending process of squamosal acts as a bony stop to prevent streptostyly in these groups; in birds, on the other hand, with elimination of squamosals-quadratojugal bar, and acquisition of mobile joint between quadrate and quadratojugal, the quadrate can move forward.

may serve to strengthen this blocking device. The squamosal forms a pair of butt joints with the quadrate–quadratojugal, prohibiting opisthostyly. Similarly the jugal overlaps the quadratojugal laterally, as a clamping device that prevents any parastylic movement. A monimostylic quadrate seems to be prevalent in Late Triassic pseudosuchians such as parasuchids, rauisuchids, poposaurids and most stagonolepidids. Here the quadrate head is fused to the squamosal, and the massive quadratogugal is strongly sutured to the quadrate.

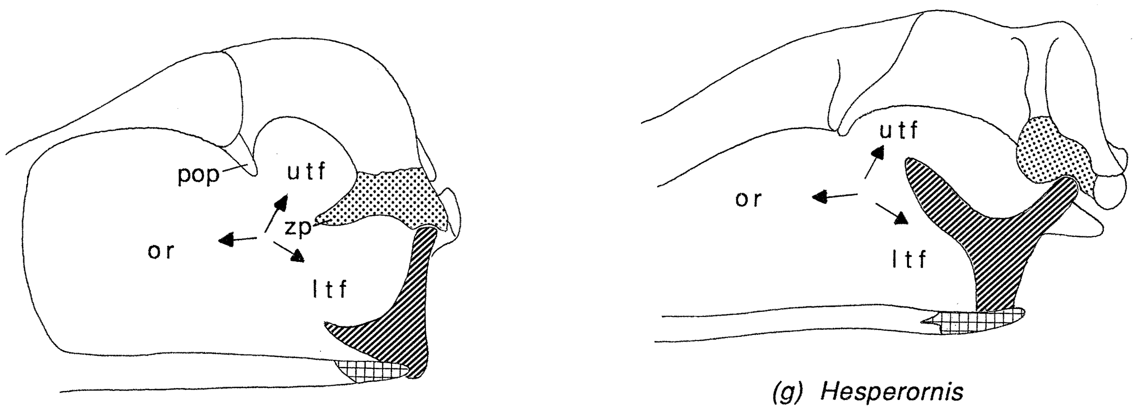
Crocodilians have been entirely akinetic and monimostylic from the beginning. Walker (1972) initially suggested a possible prokinetic mode for *Sphenosuchus*, but later he (1985) modified his views and suggested that the sphenosuchid skull is akinetic and monimostylic. Walker's later assessment is corroborated by the *Dibothrosuchus* skull.

It appears that there are two different styles of archosaur radiation in the Early Triassic on the basis of quadrate mobility: euparkeriid and proterosuchid radiation with opisthostyly, and erythrosuchid radiation with monimostyly. The opisthostylic condition that involved limited fore-and-aft movement of the quadrate could be the precursor to streptostyly. Streptostyly is directly related to upper jaw movements, whereas opisthostyly is related to lower jaw movements. It is within this opisthostylic lineage that one should search for the ancestry of birds.

Opisthostyly seems to be continued in the theropod lineage throughout the Mesozoic. In these groups, a wide gap is formed between the quadrate head and the paroccipital process, a gap that would increase the range of opisthostylic movement from the primitive condition represented by *Euparkeria*. In *Euparkeria* the squamosal–quadratojugal bar is already diminished to a slender bar, whereas in primitive ceratosaurid (e.g. *Syntarsus*, *Dilophosaurus*), the ascending process of the squamosal is reduced so that its contact with the quadratojugal is lost. Once this blocking device is completely eliminated, as in *Protoavis*, the quadrate is in a position to develop streptostyly.

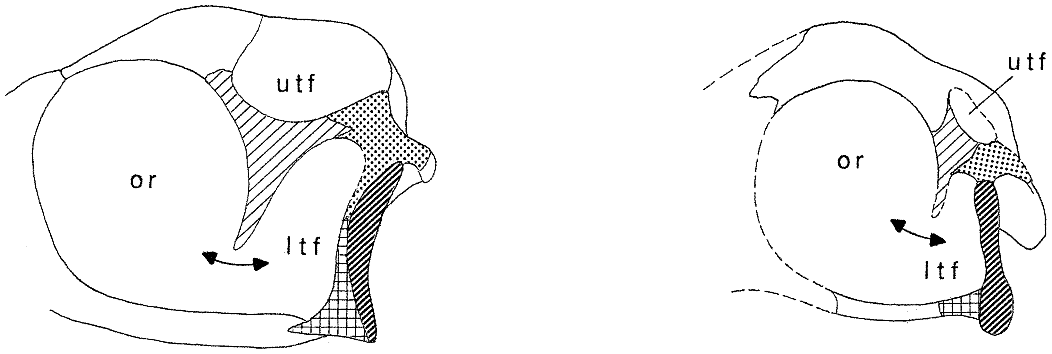
An intermediate condition of the temporal configuration is seen in *Archaeopteryx*, where the ascending process of the jugal is reduced so that the orbit is confluent with the lower temporal opening. This is the first stage toward the avian condition. The second stage would be the breakdown of the squamosal–quadratojugal bar which would permit the release of the quadrate and the inception of streptostyly. This configuration of the temporal region is represented by *Avimimus*. Kurzanov (1985) speculates that the postorbital ligament already evolved in *Avimimus* for 'jaw coupling' as is evident from a distinct postorbital process. The third stage would be the disappearance of the postorbital bone, so that the two temporal fenestrae become confluent and communicate with the orbit. This stage of temporal configuration is achieved by *Protoavis* (figure 38).

From the basic *Protoavis* design, many variations of the temporal region can be seen in recent birds. Two landmarks are usually present in this region: the postorbital process, formed by the frontal and the laterosphenoid, and the zygomatic process of the squamosal. These two processes form the lateral boundary of a single, large and incomplete temporal fossa that represents the combined upper and lower temporal openings of the dispasic condition. In some birds (e.g. swans, parrots), the postorbital process extends forward toward the lacrimal, so that the orbit is surrounded by the bone, and is separated from the temporal fossa (Bellairs & Jenkin 1960). In the paleognaths, the laterosphenoid prohibits the squamosal from contacting the frontal and the zygomatic process is directed laterally. In some neognaths, on the other hand, the squamosal contacts the frontal, and the zygomatic process is directed anteriorly (Lowe 1935). In *Protoavis*, the zygomatic process is directed anteriorly as in neognaths, but the squamosal fails to contact not only the frontal but also the laterosphenoid. In this respect it is more primitive than both palaeognaths and neognaths. In some recent birds (e.g. parrots, fowls), the zygomatic process is well-developed and makes contact with the postorbital process to form a secondary supratemporal fenestra. Because the hole is not present in juvenile forms, it is certainly a recent specialization, and is not a relic of the diapsid condition (Heilmann 1926).



(f) Protoavis

(g) Hesperornis

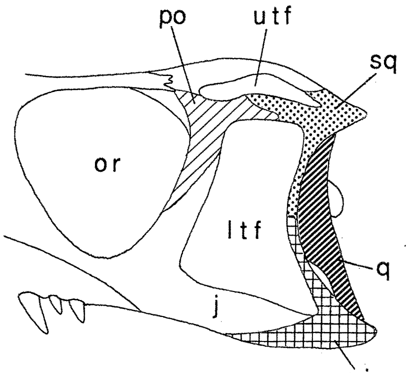


(d) Archaeopteryx

(e) Avimimus

(b) Syntarsus

(c) Dilophosaurus



(a) Euparkeria

Figure 38. Evolution of the avian temporal region; in archosaurs (*a*), (*b*) and (*c*), temporal arches are intact; the squamosal-quadratojugal bar is reduced in *Euparkeria* (Ewer 1965), in *Syntarsus* (Raath 1977) and *Dilophosaurus* (Welles 1984), squamosal lost contact with quadratojugal; a partial modification of temporal configuration can be seen in *Archaeopteryx* and *Avimimus* (Kurzanov 1987); in *Archaeopteryx*, the ascending process of jugal appears to be lost, so that orbit becomes confluent with lower temporal fenestra; in *Avimimus*, the squamosal-quadratojugal bar is further eliminated; in *Protoavis* and other birds, with the loss of postorbital bone, orbit becomes confluent with upper temporal fenestra; the confluence of orbit with both temporal fenestrae is regarded as an important character of *Protoavis* and the Ornithurae.

(*b*) *Modification of quadrate articulation*

One of the evolutionary novelties in the avian skull is the forward movement of the quadrate head from the reptilian condition, accompanied by modification of the quadrate articulation with the adjacent bones. The 'proquadrate condition' (*sensu* A. D. Walker, personal communication) of birds has been attained through a series of intermediate stages and can be traced along different lineages:

(i) *Stage 1*

The quadrate head is single, received jointly by the squamosal and paroccipital process (opisthotic); e.g., pseudosuchians, theropods and probably *Archaeopteryx* (Walker 1985).

(ii) *Stage 2*

The quadrate head had moved considerably forward and fits into a socket of the squamosal; it no longer articulates with the paroccipital process; instead, a space is created between the quadrate head and the paroccipital process for the external auditory meatus. The proquadrate condition has been achieved because of forward movement of the squamosal as a whole compared with its position in reptiles (Walker 1985). The squamosal covers the superior tympanic recess (STR); e.g. *Protoavis*.

(iii) *Stage 3*

The quadrate head, though single, is elongated transversely. With the expansion of the braincase, the prootic apparently is forced laterally until it establishes an additional contact for the quadrate head. The quadrate head shows bipartite articulations: laterally with the squamosal and medially with the prootic; e.g., *Hesperornis*, *Ichthyornis*, ratites and some neognaths. In ratite birds, the opisthotic and prootic receive the medial head of the quadrate, but in neognaths, there is no opisthotic component.

(iv) *Stage 4*

The dorsal end of the quadrate is bifurcated into antero-dorsal and postero-medial heads for articulation with the squamosal and prootic respectively. The separation of the two heads is due to the penetration of the superior tympanic diverticulum from the middle ear cavity (Jollie 1957), e.g., many neognaths.

A single quadrate head in *Protoavis* is homologous with the anterodorsal head (= squamosal capitulum) of neognaths, but the postero-medial head (= prootic capitulum) is a derived feature of ornithurine birds.

What is the functional significance of the additional quadrate-prootic articulation in later birds? In *Protoavis*, with the development of a typical ball and socket joint between the quadrate head and the squamosal, the quadrate is capable of moving in any direction to a certain extent; both streptostylic and parastylic movements are posible. In later birds, the bipartite articulations of the quadrate with the squamosal and the prootic form a simple hinge joint. This allows considerable movement of the quadrate in an antero-posterior direction, but restricts transverse movement. The parastylic movement is further limited in later ornithurine birds with the development of a bony mandibular symphysis. However, some birds are capable of lateral spreading movement with acquisition of intramandibular joints to enlarge the gular passage (Bühler 1981).

I have not used the 'proquadrate condition' of birds as a synapomorphy because of character conflicts. The quadrate head has moved forward independently in the crocodilians, and acquired its prootic contact, although in a different fashion (Walker 1985). In this group, the quadrate head bypassed the stapedial or temporal artery so that it became enclosed in a canal medial to the true head (squamosal capitulum). In birds, on the other hand, the proquadrate condition has been attained by expansion of the braincase and forward movement of the squamosal.

(*c*) *Modification of circumnarial bones*

In primitive archosaurs (e.g., *Euparkeria*), the external naris is terminal and is bounded by the premaxilla and nasal. This condition is somewhat modified in *Protoavis* and other birds with the progressive shift of the external naris. The ascending process of the premaxilla behind the naris (maxillary process) is suppressed, and the descending process of the nasal is enlarged. In *Archaeopteryx* and many theropods, the maxilla enters into the border of the external naris. This feature may be an autapomorphy. In later birds with further backward shift of the external naris, the nasal process of the premaxilla becomes enlarged and extends posteriorly, separating most of the nasal from the midline. The nasals become small peripheral bones bordering the antorbital fenestra and the external naris. The mesethmoid is ossified and exposed between the nasals. This arrangement allows a craniofacial bending zone between the upper jaw and the braincase, and is developed in ornithurine birds.

(*d*) *Evolution of the avian palate*

It is widely believed that the avian palate can be derived from the basic archosaurian pattern (Huxley 1868; Osborn 1912; Heilmann 1926; Gingerich 1976), but limited knowledge of the palatal structure of early birds makes this hypothesis little more than an interesting possibility. Witmer & Martin (1987) listed the following plesiomorphic palatal characters shared by advanced archosaurs and palaeognaths: (i) contact of the pterygoid and vomer; (ii) pterygoids and vomers exclude the palatines from the mid-line; (iii) palatines contact the maxillae but not premaxillae; (iv) vomers contact premaxillae; (v) palatal bones meet in by immovable sutures; (vi) presence of basipterygoid process.

It appears that the primitive palatal characters originally present in archosaurs persist for the most part in the palaeognathous palate, but the structural arrangement became considerably modified because of backward migration of the choanae, and development of palatal kinesis.

(i) *Backward migration of the choana*

In Early Triassic archosaurs such as *Euparkeria*, the choana lies at the front of the palate, but in the later archosarus (e.g. *Ornithosuchus*, *Postosuchus*, *Coelophysis*, *Dibothrosuchus*, *Allosaurus*, *Tyrannosaurus*, *Gallimimus*, *Oviraptor*, etc.) the choana has shifted backward so that the palatal processes of the maxilla form a false palate anterior to it (figure 39).

Within Mesozoic birds the choanae continue to shift posteriorly, as exemplified by *Protoavis*. As a result, the prechoanal region (palatal processes of the premaxillae and maxillae) expands considerably at the expense of the postchoanal region. Because the vomers form a median bar between the choanae, and maintain a connection with the pterygoids in archosaurs, the posterior shift of the choana creates an elongated vomer and suppressed pterygoid in the palaeognaths. The anterior process of the pterygoid is reduced. The palatine retreats laterally and becomes the sidewall of the choana. The backward migration of the choana brings it into proximity with the glottis, thus conferring some advantage in terms of respiratory efficiency, especially during feeding (McDowell 1948). This may aid in ingesting large amounts of food quickly in response to high metabolic activity.

(ii) *Palatal kinesis*

In archosaurs, cranial kinesis, if present, is restricted to the metakinetic joint where the basipterygoid process articulates with the pterygoid, but the quadrate is always non-streptostylic (Versluys 1910; Barsbold 1983). In birds, with the development of a streptostylic quadrate, the dorsal flexion zone is shifted in front of the orbit, allowing either prokinesis or rhynchokinesis. Because avian cranial kinesis is powered by the quadrate, from which the force is transmitted to the beak partly through the jugal bar and partly through the palatopterygoid bridge, a great deal of modification can be seen in these regions. In the palate, the ectopterygoid is lost, so that the force from the quadrate can be transmitted through the palate to the beak without much lateral obstruction. Also, the pterygoquadrate articulation has shifted ventrally from the archosaur condition with the development of an orbital process; the quadrate ramus of the pterygoid becomes narrow and articulates ventral to the orbital process.

Functionally the entire structure of the palaeognathous palate is of strength and rigidity as the individual bones are joined by immovable sutures. All extant palaeognaths are primarily rhynchokinetic, in which the region of cranio-facial bending is placed far more anteriorly than in neognaths (Bock 1963; Zusi 1984). Movements of the lower end of the quadrates are transmitted very efficiently to the beak because of the parallel alignments of the vomer and pterygopalatine bars.

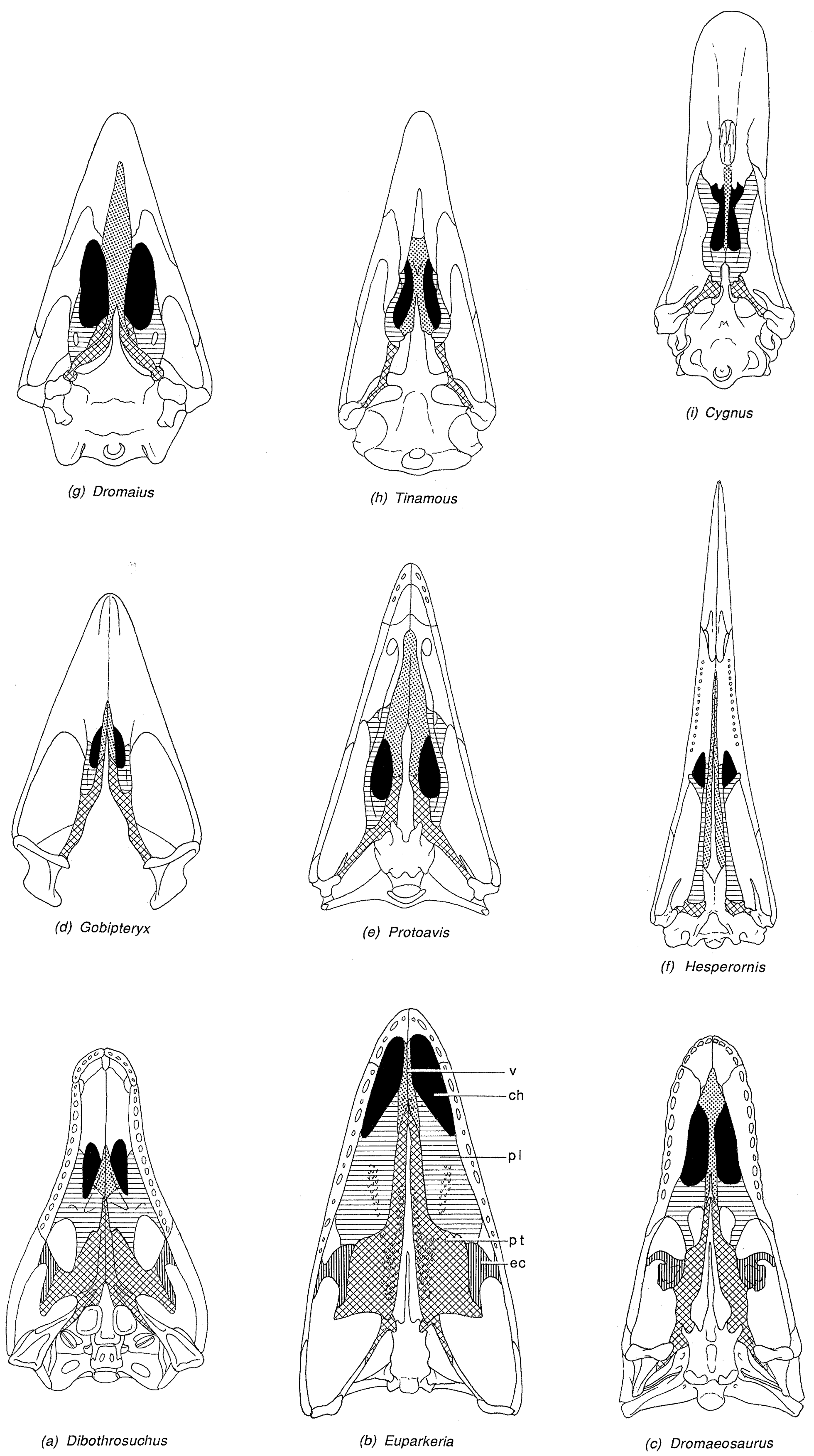
Balouet (1982) considered virtually all other features of the neognathous palate to be consequences of pterygoid segmentation. The embryonic pterygoid in many neognaths splits into two portions: the anterior part becomes detached and fuses with the palatine; the posterior one remains free and forms the adult pterygoid. Thus a movable intrapterygoid joint is established between anterior and posterior segments of an initially single bone, but appears to lie between the pterygoid and palatine in the adult (Pycraft 1901; de Beer 1956). In the adult, the palatine is enlarged as it incorporates the anterior part of the pterygoid, and approaches its contralateral fellow to form a median bar behind the choana. Anteriorly it passes below a shelf from the maxilla to reach the premaxilla. The adult pterygoid, with the loss of its anterior portion, appears to be separated from the vomer. The parasphenoid rostrum takes the role of the vanishing vomer and serves as a median support to brace the pterygoids and palatine. As a result, the basipterygoid articulation becomes superfluous in many birds and the processes are reduced or lost. Adult pterygoids are represented by a pair of stout bars that diverge from the parasphenoid rostrum to meet the condyles of the quadrate.

The centrally placed choanae and movable pterygoid-palatine joint make the neognathous palate light and flexible. Medially, the connection between the quadrate and upper jaw is effected the palatine-pterygoid bar. Each pterygoid bar converges on the parasphenoid rostrum and makes almost a right angle with its antimere. As a result, the force transmitted by the quadrate to the pterygoid is partially lost as a medially directed component; only the anteriorly directed component is transmitted by the palatine in a direct line to the premaxilla (Bock 1964). Functionally this arrangement provides a less efficient mechanism to transmit force from the quadrate to the beak than the palaeognathous condition.

(*e*) *Evolution of the avian cranial kinesis*

Bock (1964) developed an elaborate hypothetical stage of avian cranial kinesis from metakinesis via streptostyly and mesokinesis. Metakinesis may be a plesiomorphic feature for Early Triassic archosaurs. Cruickshank (1972) maintains that both *Euparkeria* and *Proterosuchus* had a metakinetic skull. This suggestion is supported by the fact that contacts of the braincase with the rest of the skull at the paroccipital process/squamosal junction, interparietal/supraoccipital junction, and the basipterygoid/pterygoid junction are movable, as indicated by the postmortem disassociation of intact braincases from skulls in several specimens. Furthermore, the lack of ossification of the laterosphenoid in both genera clearly shows that additional reinforcement of the skull roof with the braincase has not been established. Metakinesis seems to be present in erythrosuchids and all primitive archosaurs (Charig 1976). However, it tends to disappear in theropods with the development of a large laterosphenoid that forms a complex butt joint with the skull roof. In addition, the parietal develops a ventral flange that articulates intimately with the supraoccipital, prohibiting any movement.

Mesokinesis has been suggested for some theropods, such as *Allosaurus* (Madsen 1976) and *Dromaeosaurus* (Colbert & Russell 1969), which requires kinetic mobility at the fronto-parietal joint. However, the



(g) Dromaius

(h) Tinamous

(i) Cygnus

(d) Gobipteryx

(e) Protoavis

(f) Hesperornis

(a) Dibothrosuchus

(b) Euparkeria

(c) Dromaeosaurus

Figure 39. Evolution of the avian palate; (*a*), (*b*) and (*c*) palates of archosaurs; (*d*), (*e*) and (*f*) palates of Mesozoic birds; (*g*), (*h*), and (*i*) palates of recent birds; (*b*) *Euparkeria* (after Ewer 1965; Gow 1970); (*c*) *Dromaeosaurus* (after Colbert & Russell 1969); (*d*) *Gobipteryx* (after Elzanowski 1977); (*f*) *Hesperornis* (after Gingerich 1976; Witmer & Martin 1987). The important palatal modifications from archosaurs to early birds include loss of ectopterygoid, posterior migration of choana, the reduction of pterygoid; pterygoid segmentation is a novelty for neognaths (*i*).

tight suturing in these animals of the fronto-parietal joint precludes any such movement (figure 26). Furthermore, it is difficult to imagine how mesokinesis can function without the development of streptostyly. The theropod skull may have opisthostyly or parastyly, but never developed streptostyly. With the enlargement of the brain and orbit concomitant with the development of streptostyly and the reduction of the olfactory tract, the logical place for the development of a kinetic hinge in early birds, as documented by *Protoavis*, would be anterior to the orbits (Bock 1964).

Mesokinesis has also been proposed for *Archaeopteryx* (Bock 1964; Ostrom 1976), but rejected by others (Whetstone 1983; Bühler 1985) because of the firm suturing of the frontal to the parietal. Moreover, the presence of a squamosal-quadratojugal bar in *Archaeopteryx* would prevent streptostyly.

Bühler *et al.* (1988) recognized prokinesis in *Hesperornis* and *Parahesperornis*, and concurred with Bock (1964) that prokinesis is the primitive form of avian cranial kinesis from which rhynchokinesis was evolved. *Protoavis* supports the contention that prokinesis was an ancestral condition. Thus the hypothetical stages for the evolution of avian cranial kinesis from the primitive archosaur condition is as follows: metakinesis → opisthostyly → postorbital ligament → (streptostyly + prokinesis) → rhynchokinesis.

(*f*) *Evolution of the avian braincase*

The avian braincase exhibits remarkable modification from the archosaurian condition. The increase in the relative size of the brain of birds compared with most archosaurs has led to the development of a large neurocranium which becomes a swollen structure completely surrounded by bone. The expanded brain and large orbit crowded the cheek region. Much of the brain expansion is sheathed by new extensions of old roofing bones: frontals, parietals and squamosals. The basisphenoid complex has become a horizontal plate and the basipterygoid processes are reduced or lost. At the same time there is extensive pneumatization in the middle ear region, and this results in a complicated system of cavities that are ventilated from the nasopharynx. Important modifications in the avian braincase and the associated structures are discussed below.

(i) *Brain architecture* (figure 16)

In most archosaurs, the cerebrum, optic lobe and cerebellum are serially arranged. In early birds, as revealed from the endocast of *Protoavis*, the cerebrum is highly enlarged with the development of a typical avian Wulst, demarcated by a shallow vallecula. The olfactory lobe, on the other hand, is appreciably reduced from the archosaur condition. The small size of the olfactory lobe corresponds to the poorly developed sense of smell. This deficiency is compensated by enhancement of other two sense organs, sight and hearing. The orbit becomes enormous. The brain and eyes in birds lie in close proximity, separated only by a thin sheet of bone, the orbital flange.

The enlargement of the cerebral hemisphere led to its contact with the cerebellum dorsally, thus displacing the optic lobes ventrally and laterally. On the floor of the braincase, each optic lobe is housed in a special optic fossa. The relative ventral shift of the optic lobes from the archosaurian condition is correlated with the lower position of the trigeminal foramen near the floor of the braincase. The cerebellum has also become enlarged and has migrated farther backward, and the parietal and supraoccipital.

Both pterosaurs and some small theropods (e.g. *Troodon*) exhibit 'avian' shape of brain, indicating a similar level of coordination, balance, agility, intelligence and metabolic activity. However, the encephalization quotient (EQ) in these groups is somewhat lower than that of *Protoavis* (figure 18). Contrary to this situation, the architecture of the crocodilian brain is of primitive reptilian grade, with very low EQ value.

(ii) *Otic capsule* (figures 21 and 28)

In Early Triassic archosaurs (e.g. *Euparkeria*), the structure of the otic capsule is primitive, and consists of two bones, prootic and opisthotic. Laterally, two large foramina can be seen in the otic region. The anterior one is the fenestra ovalis which received the footplate of the stapes, and the posterior one is the metotic foramen. They are separated from each other by a robust bar of opisthotic. The metotic foramen is the embryonic fissure between the ear capsule and the occipital structures, and provided an exit for the ninth to eleventh cranial nerves and possibly the internal jugular vein. It may also have held an extension of the perilymphatic system of the inner ear as a release mechanism for the inner ear. In later pseudosuchians (e.g. *Postosuchus*) and early theropods (e.g. *Syntarsus*), the opisthotic bar is reduced to a bony septum: the crista interfenestralis, lying between the fenestra ovalis and metotic foramen. In sphenosuchids (e.g. *Dibothrosuchus*) and advanced coelurosaurs (e.g. *Troodon*, *Dromaeosaurus*), a subcapsular process is added to the otic capsule, as in modern crocodilians, to shift the perilymphatic duct to a new aperture, the fenestra pseudorotunda immediately behind the fenestra ovalis (de Beer 1937). The subcapsular process ossifies along the anterolateral and ventral part of the exoccipital, just above the hypoglossal foramen (XII), and projects below the otic capsule, thus enclosing the anteriormost portion of the metotic foramen, leading to the formation of the fenestra pseudorotunda. As a result, the vagus foramen in this group has been diverted backward behind the subscapular process (Walker 1985). Similar arrangement of the otic foramina can be seen in *Protoavis*, *Archaeopteryx* and other birds, where a new ossification, the metotic cartilage arises independently at a position opposite the centre of metotic fissure and below the canalicular portion of the otic capsule, which is eventually fused to the exoccipital (Saiff 1981). The metotic cartilage provides a floor for the recessus scale tympani and forms part of the attachment area for the tympanic membrane. The opisthotic is further reduced in birds, and becomes largely internal to form a slender bar. There is a growing consensus that the metotic cartilage and the subcapsular process are not homologous, the former is a separate ossification subsequently fused to the base of the exoccipital, the latter is a process of the exoccipital (Rieppel 1985). The development of the metotic process may be a new avian feature.

The prootic bone in *Protoavis*, *Archaeopteryx* and all other birds is a large, hour-glass shaped structure, notched anteriorly by the trigeminal foramen and posteriorly by the fenestra ovalis. A similar configuration of the prootic can be seen in *Euparkeria*. However, in advanced theropods (i.e. *Troodon*), the prootic is highly reduced and specialized. This may indicate that the prootic conformation in the avian lineage could be an ancient feature.

(iii) *Tympanic recess in the middle ear cavity* (figures 21 and 28)

Although tympanic recesses are well developed in early birds, the evolution and phylogenetic significance of these cavities are still poorly understood. The posterior tympanic recess (PTR) appears to be widespread among archosaurs, occurring in pseudosuchians (e.g., *Postosuchus*), theropods (e.g. *Syntarsus*, *Troodon*, tyrannosaurs), and early crocodylomorphs, but absent in modern crocodilians. The PTR is elaborate in *Protoavis* with two openings on the anterior surface of the opisthotic. The anterior tympanic recess (ATR) is restricted to crocodiles and birds. In other archosaurs (e.g. *Postosuchus*, *Syntarsus*, *Troodon*, *Allosaurus* and *Tyrannosaurus*), a lateral tympanic recess (LTR) occurs instead of ATR. The ATR and LTR may not be homologous, the former lies anterior to the prootic, the latter posterior to it. In *Protoavis*, the ATR is shared between the prootic and alaparasphenoid and has a contralateral communication. In sphenosuchids, on the other hand, it is not covered by any bone laterally. The superior tympanic recess (STR) is also known in sphenosuchids and early birds, but not in any theropods. In *Protoavis*, both anterior and posterior entrances of STR are present on the prootic's dorsolateral and the squamosal's ventral surface. In sphenosuchids, the STR is represented by a deep cavity that communicates with the temporal canal.

It is difficult to ascertain the sequential development of these three tympanic recesses; they are however fully developed in *Protoavis* in the same position as in modern birds, indicating that these features were developed at an early stage in avian evolution. Pneumatization of the middle ear may be associated with a refined hearing system and may indicate a certain amount of convergence between archosaurs and birds.

(iv) *Occiput* (figure 40)

The occiput in primitive archosaurs (e.g., *Euparkeria*) is characterized by a large post-temporal fenestra, bounded above by the squamosal-parietal bar, and below by the paroccipital process. It probably transmitted the occipital or cervical artery. In sphenosuchids and theropods, the post-temporal fenestra is reduced or lost, indicating a specialized condition. Contrary to this situation, this fenestra is moderately developed in *Protoavis* and *Archaeopteryx* and with a ventral foramen, transmitted the occipital artery (Walker 1985).

The occiput of *Protoavis* and *Archaeopteryx* are similar in build. In both cases, the parietal-supraoccipital articulation is primitive and archosaur-like, where a large ventral parietal flange overlaps the posterodorsal edge of the supraoccipital complex (figure 40). In later birds, the supraoccipital has an edge to edge contact with the parietal without any overlapping. In both *Protoavis* and *Archaeopteryx*, a sinus canal separates the supraoccipital from the epiotic, and the canal is interrupted by a foramen of the external occipital vein. The topographic relationships of the bones, foramen and sinus canal of the occiput are similar to those of juvenile penguins and other birds. The posterior exposure of epiotic in the occiput appears to be an avian apomorphy. A separate epiotic is not known to occur in reptiles (Jollie 1957). In young crocodiles, there may be a small epiotic internally that fuses with the supraoccipital in the adult (de Beer 1937).

Another interesting feature may be the method of enclosing the internal carotid artery in the occiput. In archosaurs, each carotid artery enters the middle ear region from the neck through the cranioquadrate passage. In *Protoavis*, as in some recent birds, there is a parabasal notch that indicates the course of the internal carotid artery. In other birds (e.g. *Gallus*), there is a carotid formen, completely enclosed within the exoccipital for the passage of the internal carotid.

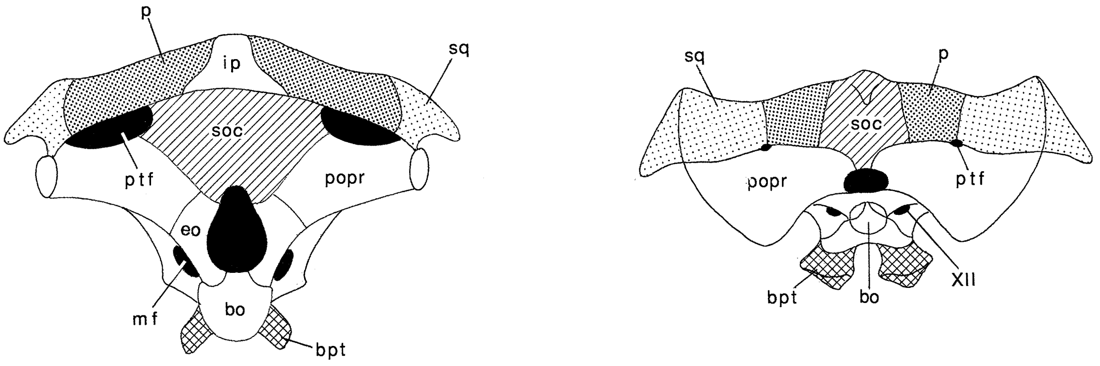
10. THE ORIGIN AND EARLY RADIATION OF BIRDS

The evolution of birds is a complex story that is slowly unfolding. Many avian features appear to have originated in parallel among various lineages of archosaurs, different elements developing at different rates since the beginning of the Triassic and continuing throughout the Mesozoic. The complex type of evolution displayed by the early evolution of birds strongly resembles that found in cynodont–mammalian evolution. Indeed, it was probably a common evolutionary pattern in the origination of higher taxa.

Because *Archaeopteryx* had held the central position of avian evolution, it was generally believed that there was a sequential relationship between the time of origin of theropods (developing first), and birds (appearing later) (Ostrom 1976). The discovery of *Protoavis* clearly indicates that theropods and birds were contemporaneous groups, both having appeared during the latter half of the Triassic. *Protoavis* pushes avian origin back by 75 Ma and requires a reinterpretation of the fossil record concerned with the early radiation of birds.

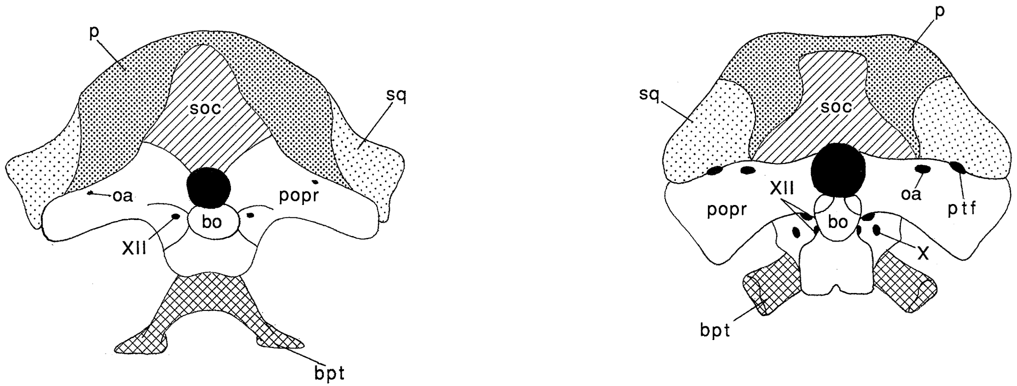
The discovery of *Protoavis* makes it the oldest member of the class Aves. At its first appearance, *Protoavis* was a highly specialized and derived bird. The pattern of bird evolution thus conforms to a very common macrovolutionary style among vertebrates: a major set of morphological changes appears suddenly at the time of initiation of a new clade, followed by a long period of stasis and minor refinement, a pattern indicative of punctuated evolution (Eldredge & Gould 1972).

There seems to be a conflict between antiquity and morphological primitiveness in the early radiation of



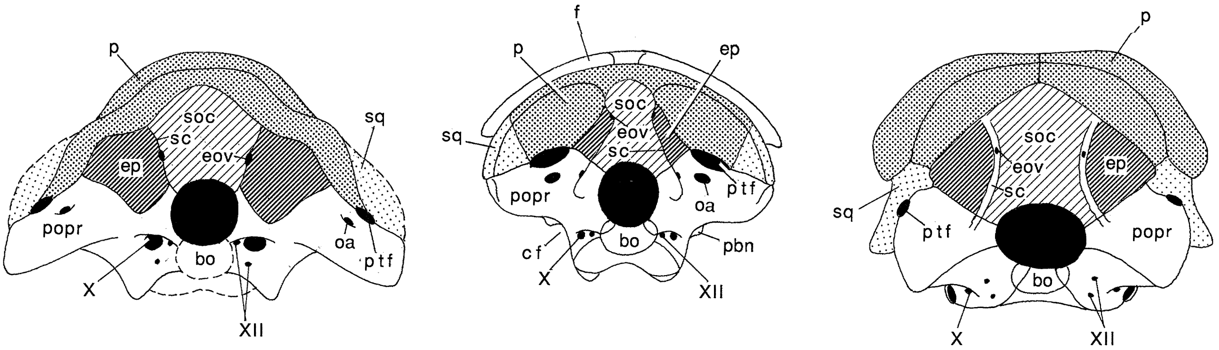
(a) Euparkeria

(b) Dibothrosuchus



(c) Syntarsus

(d) Troodon



(e) Archaeopteryx

(f) Protoavis

(g) Pygoscelis

Figure 40. Occiputs of archosaurs (*a*), (*d*) and birds (*e*), (*g*); in archosaurs, the parabasisphenoid is vertical with the development of large basipterygoid processes; there is no epiotic component in occiput. In birds, on the other hand the parabasisphenoid is horizontal where the basipterygoid processes are reduced or lost; there is a sinus canal which separates epiotic from supraoccipital in many birds; the foramen magnum is enlarged relative to occipital condyle; there may be a distinct bony passage for the internal carotid artery in occiput; (*a*) after Ewer 1965 (*c*) after Raath 1985; (*d*) modified from Currie (1985).

birds. *Archaeopteryx* is clearly more primitive in morphology, but it appeared much later than did *Protoavis*. Primitiveness and apparent ancientness are not correlated in every case in fossil records, especially when the avian record is so fragmentary. This apparent contradiction indicates that *Archaeopteryx* and *Protoavis* lie in two separate lineages, and is probably linked to the unequal survivorship of the sister taxon in the fossil record (Eldredge & Cracraft 1980). In other words, something resembling *Archaeopteryx* may have originated as early as the Middle or even Early Triassic.

Archaeopteryx appears to be a late example of the ancestral type, a 'living fossil' in the Late Jurassic avian world (Martin 1987). It did not give rise to modern birds but instead is on a distinct side line (Olson 1985). *Protoavis* is the sister-group of all other avian taxa, or Ornithurae. It seems to be not far removed from the line of their direct ancestry. The Ornithurae became highly diversified in the Cretaceous period, with cosmopolitan distribution, and includes several extinct genera such as *Hesperornis*, *Ichthyornis* and *Gobipteryx*. The Mesozoic diversification was followed by an explosive radiation of modern forms in the Early Tertiary (Olson 1985).

Although *Protoavis* is currently the oldest known bird, the question remains as to what preceded

Protoavis? What was the archosaur taxon from which it descended? The presence of *Protoavis* in Late Triassic sediments certainly suggests that the origins of birds are to be sought at some considerably earlier date. The phylogenetic results, along with the stratigraphic record of fossil taxa, indicate that the ancestral bird may have evolved some time in the Middle or Early Triassic.

Attempts to determine which of the known archosaurs is closest to the ancestry of birds have often been confused with a search for the 'sister-group' of birds. Cladism does not distinguish sister-species from ancestors and refuses to accept that ancestral species can be recognized. However, both kinds of relationships, sister-group and ancestral, are real; they do both exist in nature (Ridley 1986).

Phylogenetic analysis suggests that theropods shared a common ancestry with birds. Was the common ancestor itself a theropod, as claimed by Ostrom (1976), or an ornithosuchian? Unfortunately transitional fossils linking theropods and *Protoavis* at proper stratigraphic levels are yet to be discovered, which makes it difficult to identify the putative ancestry of *Protoavis*. No theropods of proper geological age (pre-Carnian) are known that possessed all the features required of an immediate ancestor of *Protoavis*. Thus the idea that birds are descended from small theropods, though highly attractive, is yet to be supported by fossil evidence.

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KEY TO ABBREVIATIONS USED IN FIGURES

Skull

a	angular
aa	ampulla for anterior vertical canal
ah	ampulla for horizontal canal
aof	antorbital fenestra
am	antrum mastoideum
apf	articular pneumatic foramen
aps	alaparasphoneoid
ar	articular
ard	articular diverticulum
atd	anterior tympanic diverticulum
atr	anterior tympanic recess
avc	anterior vertical canal
bo	basioccipital
bo sin	basioccipital sinus
bpt	basipterygoid process
bs	basisphenoid
bt	basal tubera
c	cochlear duct
cf	carotid foramen
ch	choana
cl	cerebellum
clf	cerebellar fossa
cif	crista interfenestralis
cr	cochlear recess
crh	cerebral hemisphere
crf	cerebral fossa
d	dentary
dbz	dorsal bending zone
dep	depression
ec	ectoptergoid
en	external naris
eo	exoccipital
eov	foramen for external occipital vein
ep	epiotic
exp	external process
f	frontal
fa bo	facet for basioccipital
fa eo	facet for exoccipital
fa m	facet for maxilla
fa n	facet for nasal
fa po	facet for postorbital
fa popr	facet for paroccipital process
fa pr	facet for prootic
fa pt	facet for pterygoid
fa q	facet for quadrate
fa qj	facet for quadratojugal
fa sq	facet for squamosal
fl	floccular lobe
flr	floccular recess
fm	margin of foramen magnum
fpr	fenestra pseudorotunda
ftoa	foramen for temporo-orbital artery
hc	horizontal canal
hy	hyoid
iam	internal auditory meatus
ic	foramen of internal carotid
iml	intermuscular lamina
inp	internal process
ip	interparietal
j	jugal
jb	jugal bar
l	lacrimal
lbz	lateral bending zone
lef	lateral eustachian foramen
ls	laterosphoneoid
ltf	lateral temporal fenestra
ltr	lateral tympanic recess
m	maxilla
mc	mandibular cotylus
md	medulla
mef	metotic fenestra
met	metotic process
mf	mandibular fenestra
ms	maxillary sinus
n	nasal
oa	foramen for occipital artery
oc	occipital condyle
ocr	occipital recess
olt	olfactory tract
op	opisthotic
opf	optic fossa
opl	optic lobe
opr	orbital process
or	orbit
p	parietal
pbn	parabasal notch
pbz	palatal bending zone
pd	predentary
pl	palatine
pla	palatine artery foramen
pm	premaxilla
pms	premaxillary sinus
pn	pneumatic foramen
po	postorbital
pons	recess for pons Varolii
pop	postorbital process
popr	paroccipital process
pr	prootic
prc	prootic capitulum of quadrate
prf	prefrontal
prs	presphenoid
ps	paraphenoid
pt	pterygoid
ptc	pterygoid condyle
ptd	posterior tympanic diverticulum
ptf	postemporal fenestra
ptfl	pterygoid flange
ptr	posterior tympanic recess
pvc	posterior vertical canal
q	quadrate

qc	cotyle for quadrate
qd	quadrate diverticulum
qj	quadratojugal
qjc	cotyle for quadratojugal
qpf	quadrate pneumatic foramen
rp	retroarticular process
rt	replacing tooth
s	sacculus
sa	surangular
sc	sinus canal
sf	subpalatal fenestra
sq	squamosal
sqc	squamosal capitulum of quadrate
sqfl	squamosal flange
std	superior tympanic diverticulum
str	superior tympanic recess
sym	symphysis
u	utriculus
utf	upper temporal fenestra
v	vomer
va	vallecula
vrop	ventral ramus of opisthotic
wu	wulst
zp	zygomatic process

foramina for cranial nerves in Roman numerals

Postcranial skeleton

acr	acrocoracoid
ac	acetabulum
ap	ascending process
as	astragalus
ca	calcaneum
cen	centrum
dc	distal carpal
dt	distal tarsal
ect	ectepicondyle
ent	entepicondyle
exc	external condyle
ext	extensor canal
fa fi	facet for fibula
fa ste	facet for sternum
fa ti	facet for tibia
fc	fibular condyle
fg	fibular groove
flt	flexor tubercle
fu	furcula
gl	glenoid facet
gt	greater trochanter
h	head
hyp	hypocleidum
hypa	hypapophysis
icc	inner cnemial crest
if	ischiadic foramen
il	ilium
inc	internal condyle
is	ischium
lt	lesser trochanter
obr	obturator ridge
occ	outer cnemial crest
olf	olecranon fossa
papa	parapophysis
pot	posterior trochanter
poz	postzygapophysis
pro	procoracoid
pu	pubis
pz	postzygapophysis
ra	radius
rf	renal fossa
ste	sternum
sym	symphysis
ti	tibia
trc	triosseal canal
tro	trochlea
ul	ulna
uln	ulnare
ve	vertebra

The digits are in Roman numerals.

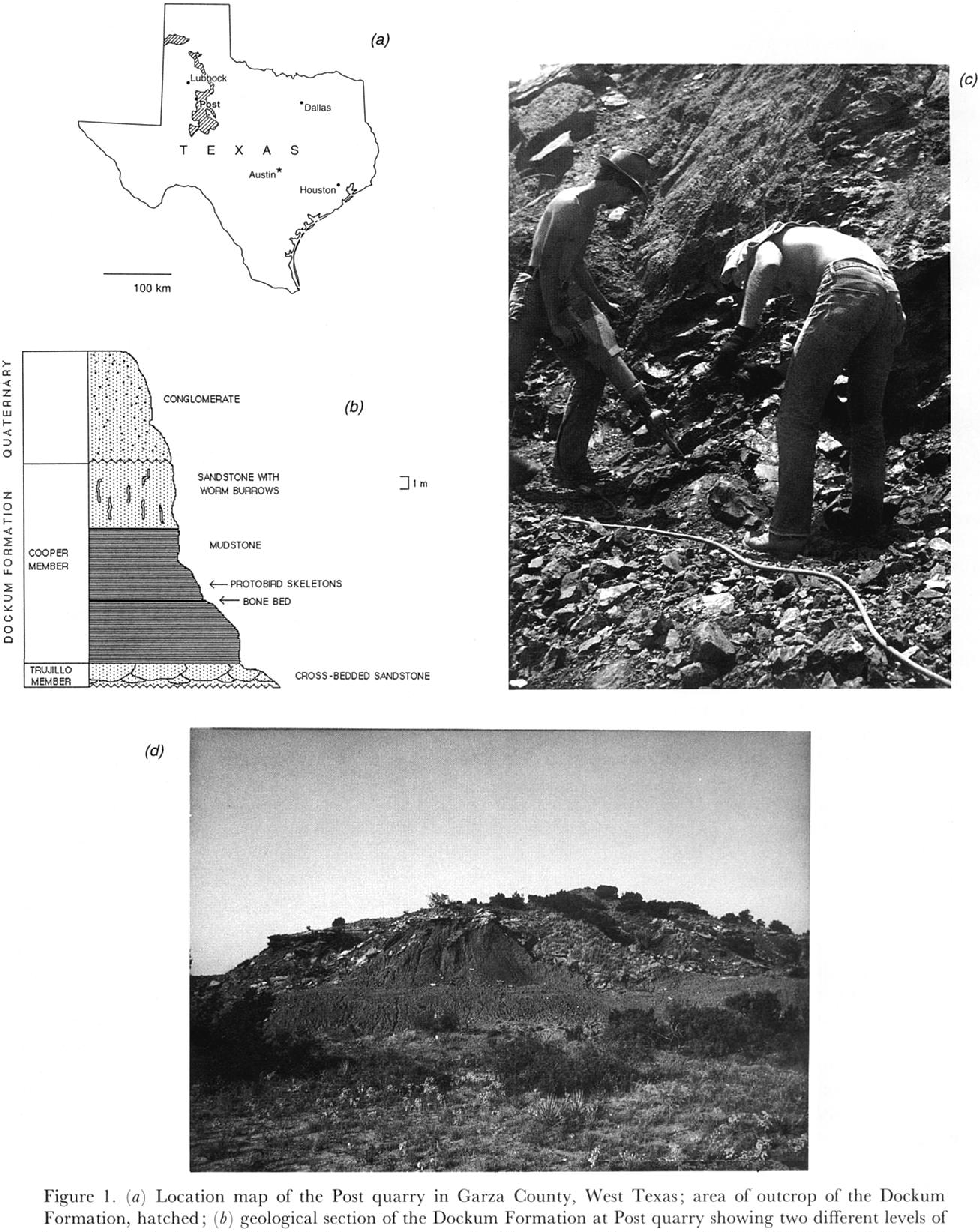

Figure 1. (*a*) Location map of the Post quarry in Garza County, West Texas; area of outcrop of the Dockum Formation, hatched; (*b*) geological section of the Dockum Formation at Post quarry showing two different levels of bone-bearing beds; (*c*) protobird skeletons were exposed while removing the overburden by a jackhammer; the blade of the jackhammer points to the approximate location of the two skeletons; left, Bryan J. Small, right, J. Bruce Moring; (*d*) Post quarry from a distance; the flat platform indicates the horizon of the primary bone bed; protobird skeletons were found about one metre above this bone bed.

Figure 3. For description see opposite.

Figure 4. For description see opposite.

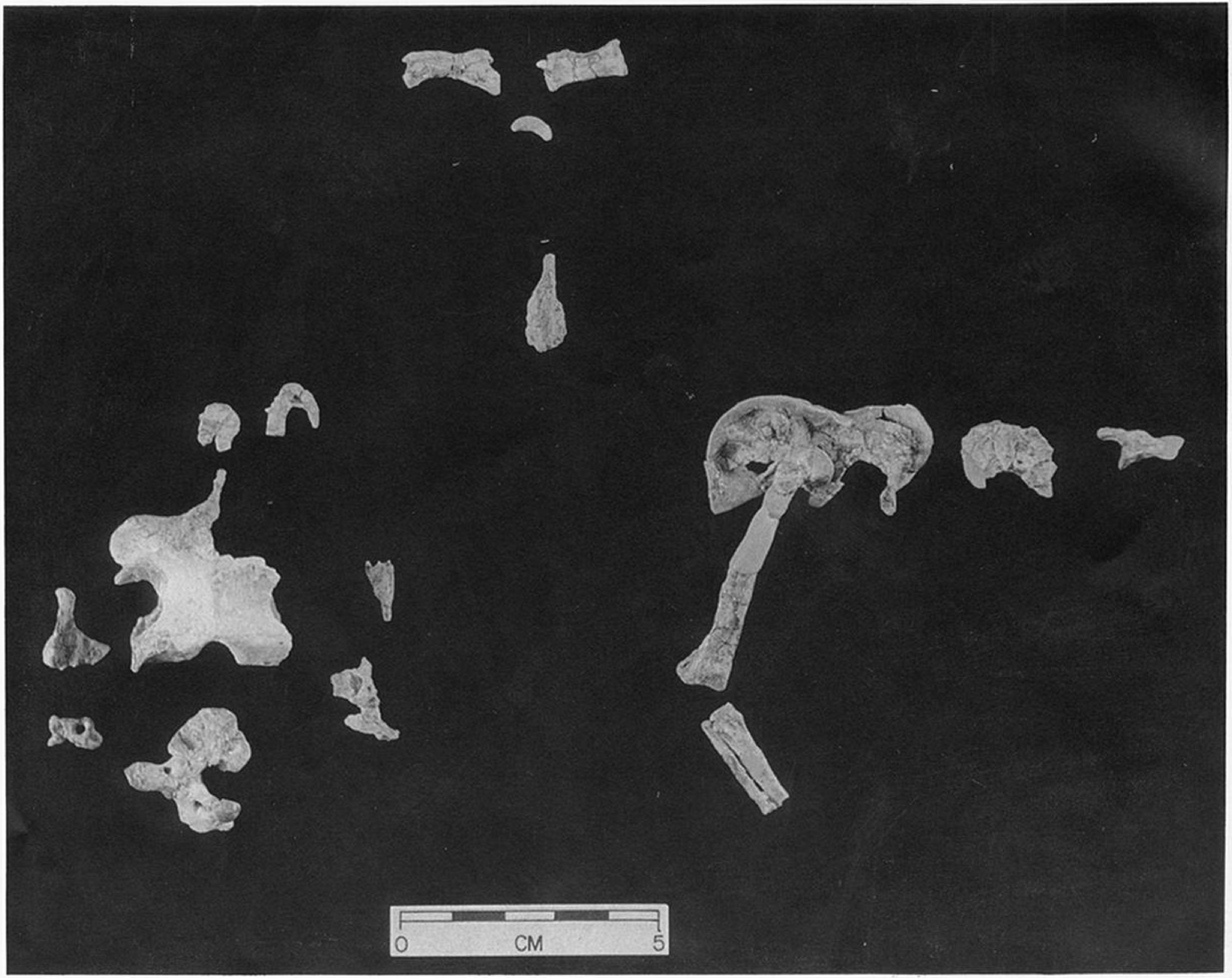

Figure 6. *Protoavis texensis* n. sp. holotype (TTU P 9200), large individual.

Figure 7. *Protoavis texensis* n. sp. paratype (TTU P 9201), small individual.

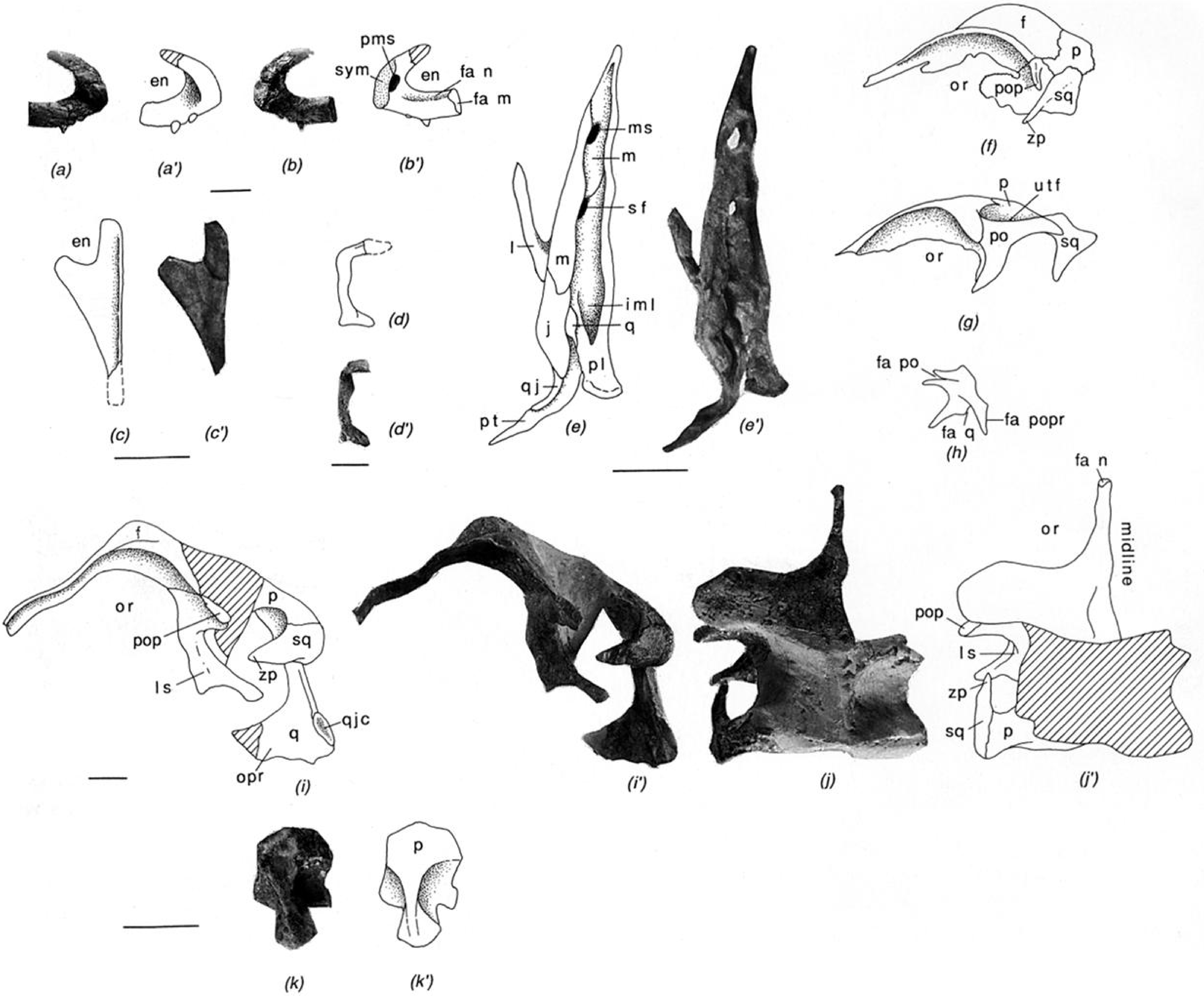

Figure 8. *Protoavis texensis* n. sp; dermal roofing bones; (*a*), (*a′*) and (*b*), (*b′*) lateral and medial views of right premaxilla, large individual; (*c*) and (*c′*) ventral view of right nasal, small individual; (*d*) and (*d′*) medial view of left lacrimal, large individual; (*e*) and (*e′*) lateral view of right side of skull and part of palate, small individual; (*f*) left lateral view of posterior-half of skull roof of juvenile *Rhea*; (*g*) the same view of *Troodon* showing the presence of upper temporal fenestra (modified from Currie (1985)); left lateral view of squamosal of *Deinonychus* (after Ostrom 1969); note in theropods squamosal is large, the postorbital process is bifurcated, and the descending process is robust to receive quadratojugal; (*i*) and (*i′*) left lateral view of posterior-half of skull roof of *Protoavis* of large individual showing avian-like temporal configuration with loss of prootic bone; orbit is confluent with upper and lower temporal fenestrae; the squamosal is highly reduced; both postorbital and zygomatic processes are developed; disarticulated bones assembled; (*j*) and (*j′*) dorsal view of skull roof of *Protoavis*, large individual; disarticulated bones assembled; (*k*) and (*k′*) dorsal view of parietal, small individual; scale bar 5 mm.

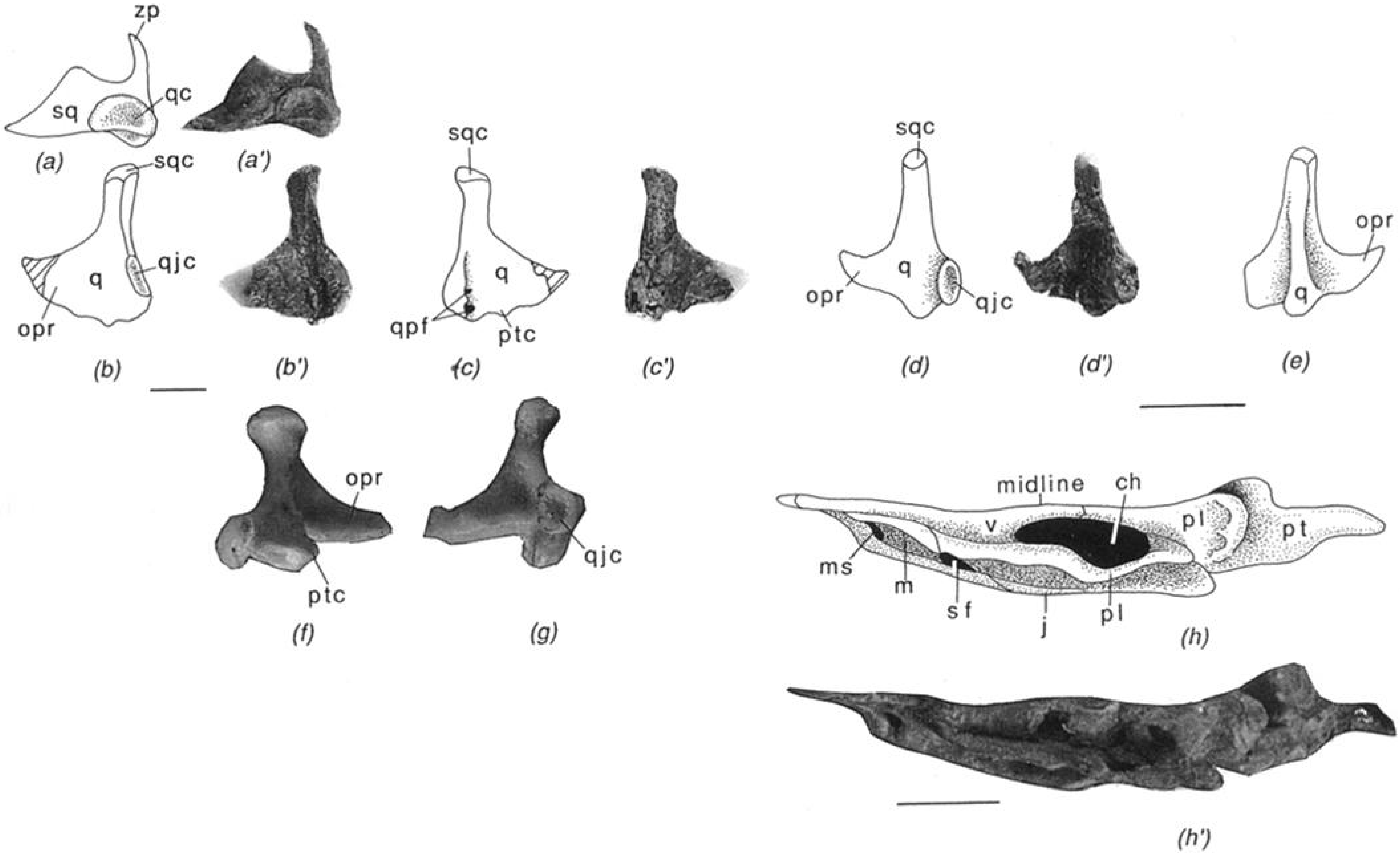

Figure 10. *Protoavis texensis* n. sp., palatal complex; (*a*) and (*a′*) ventral view of left squamosal showing quadrate cotyle and zygomatic process, large individual; (*b*) and (*b′*) lateral view of left quadrate of large individual showing cotyle for quadratojugal, orbital process and head; (*c*) and (*c′*) medial view of same showing pterygoid condyle and pneumatic foramina; (*d*) and (*d′*) lateral view of left quadrate of small individual; (*e*) and (*e′*) postero-medial view of same; (*f*) and (*g*) medial and lateral views of quadrate of penguin (*Pygoscelis*) for comparisons; (*h*) and (*h′*) palatal view of right palate of small individual; note choana has been shifted considerably backward with loss of ectopterygoid bone; scale bar 5 mm.

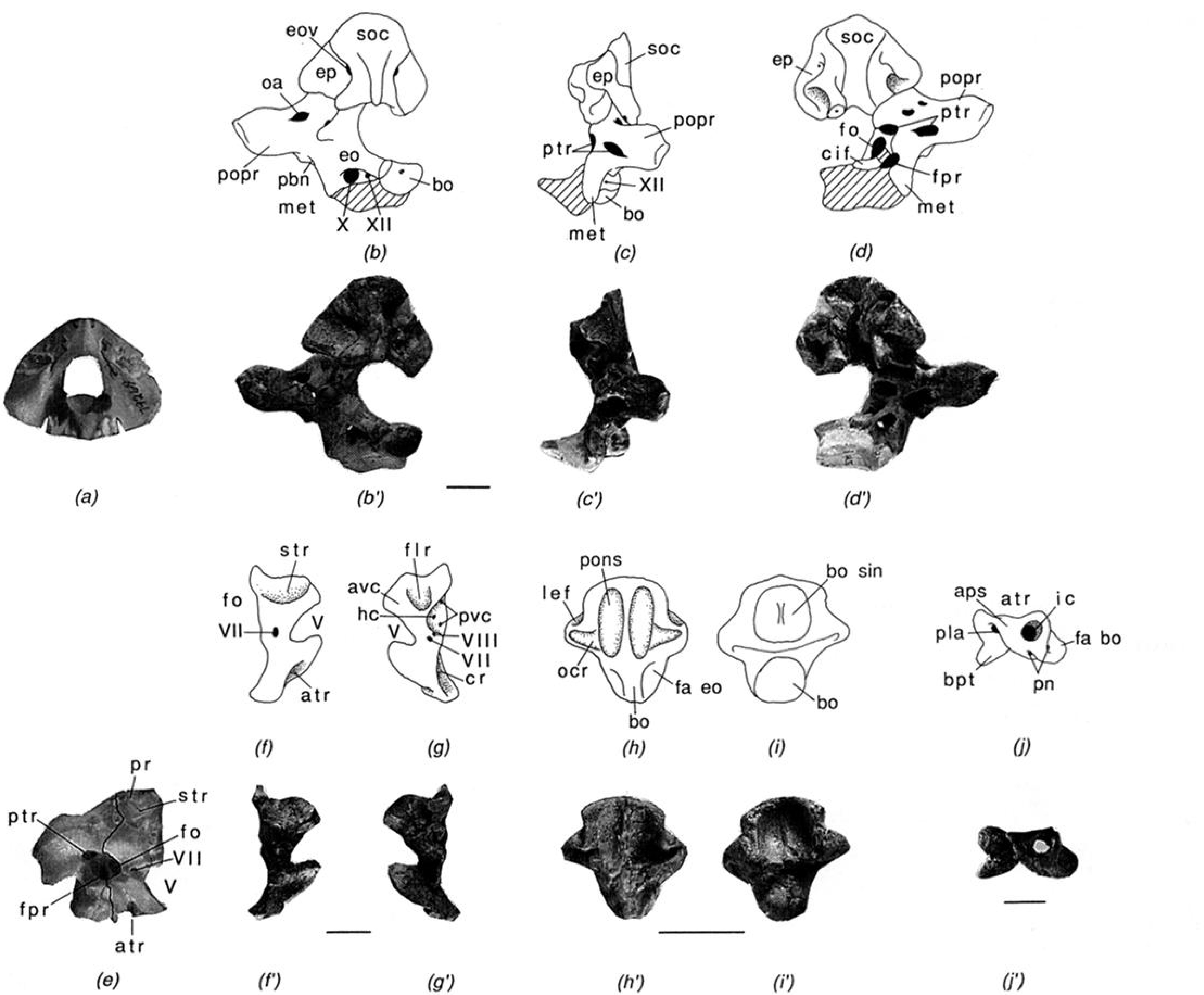

Figure 12. *Protoavis texensis*, n. sp., braincase; (*a*) posterior view of braincase of juvenile *Rhea* for comparisons; (*b*) and (*b′*) same view of braincase of *Protoavis*, large individual; disarticulated elements assembled; (*c*) and (*c′*) left lateral view of braincase, large individual; disarticulated elements assembled; (*d*) and (*d′*) anterior view of braincase, large individual; disarticulated elements assembled; (*e*) right lateral view of braincase of juvenile Mute swan (*Cygnus*) showing otic capsule region; (*f*), (*f′*) and (*g*), (*g′*) lateral and medial views of right prootic of *Protoavis*, large individual; (*h*), (*h′*) and (*i*), (*i′*) dorsal and ventral views of basioccipital, small individual; (*j*) and (*j′*) left lateral view of parabasisphenoid, large individual; scale bar 5 mm.

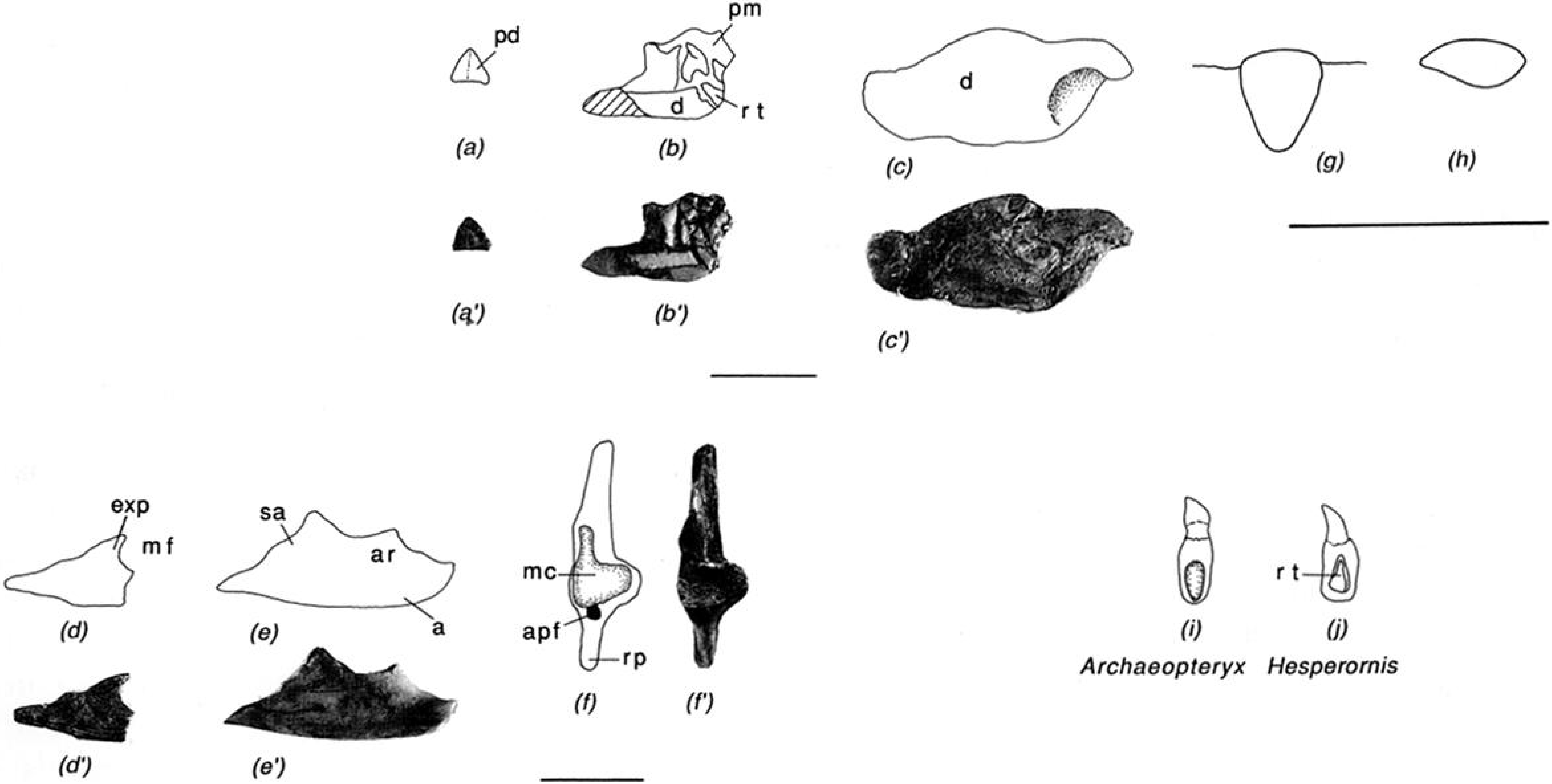

Figure 14. *Protoavis texensis*, n. sp., lower jaw and dentition; (*a*) and (*a*′) dorsal view of predentary, small individual; (*b*) and (*b*′) left medial view of conjoined premaxilla and dentary, showing replacing tooth, small individual; (*c*) and (*c*′) left lateral view of dentary, small individual; (*d*) and (*d*′) right lateral view of posterior part of lower jaw, showing external process and part of lateral mandibular fenestra, large individual; (*e*) and (*e*′) left lateral view of posterior part of jaw, small individual; (*f*) and (*f*′) the same, dorsal view showing mandibular cotyle; (*g*), (*h*) tooth morphology of *Protoavis*, third premaxillary tooth, lateral view, and second premaxillary tooth, cross-sectional view; (*i*) and (*j*), tooth morphology and resorption pit of Mesozoic bird; (*i*) after Martin (1985); (*j*) after Marsh (1880); scale bar 5 mm.

Figure 16. Restoration of brain of some archosaurs and birds from endocasts; (*a*) left lateral view of endocast of *Protoavis*, large individual, partly composite; (*b*) dorsal view of posterior part of endocast of *Protoavis*, showing confluence of cerebral hemispheres with cerebellum, small individuals; (*c*) dorsal view of posterior part of endocast of *Protoavis* showing the supraoccipital component of cerebellum and floccular lobe, large individual; (*d*) restoration of brain of *Protoavis*, dorsal view; (*e*) restoration of brain of *Protoavis*, lateral view; (*f*) dorsal view of brain of *Crocodylus* (after Bühler 1985); (*g*) dorsal view of brain of *Troodon* (modified from Russell 1969); (*h*) dorsal view of brain of *Archaeopteryx*, (after Bühler 1985); (*i*) dorsal view of brain of *Columba*; (after Bühler 1985).

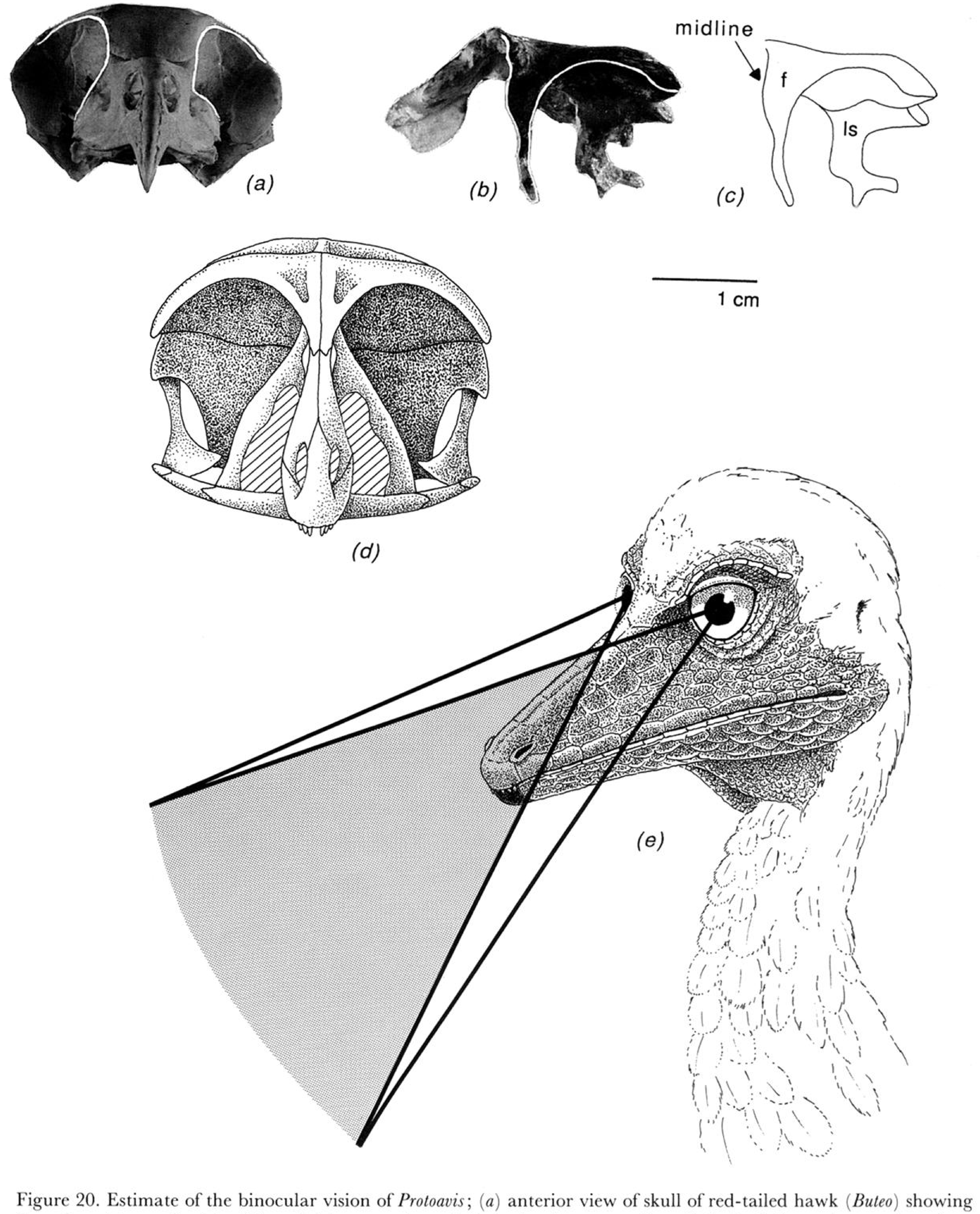

Figure 20. Estimate of the binocular vision of *Protoavis*; (*a*) anterior view of skull of red-tailed hawk (*Buteo*) showing frontal positions of orbit; (*b*) and (*c*) same view of *Protoavis*; (*d*) restoration of skull of *Protoavis*, anterior view; disarticulated elements assembled; (*e*) life restoration of head; with both eyes facing forward, *Protoavis* shows strong adaptations of stereoscopic vision as in birds of prey.

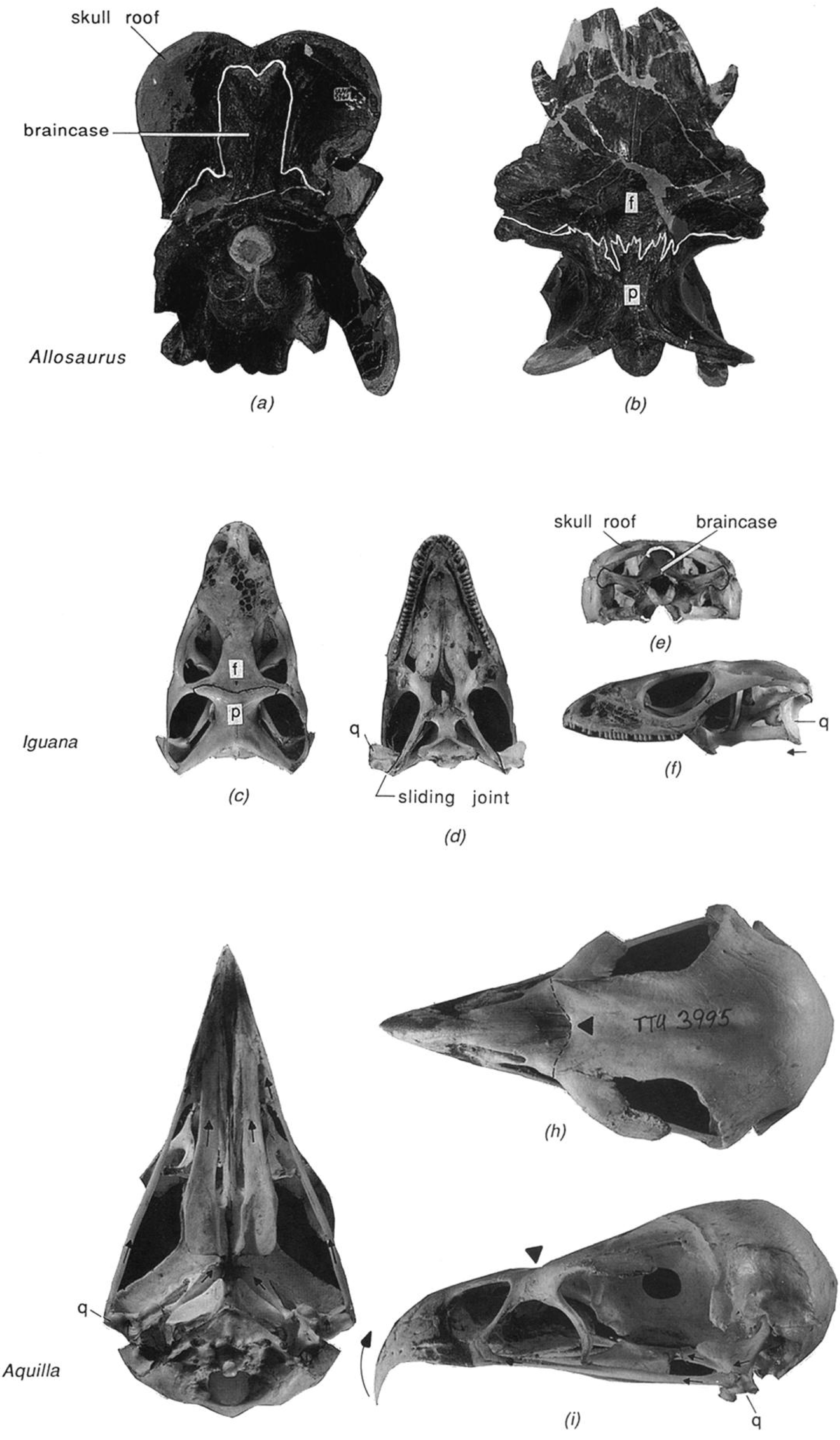

Figure 26. For description see opposite.

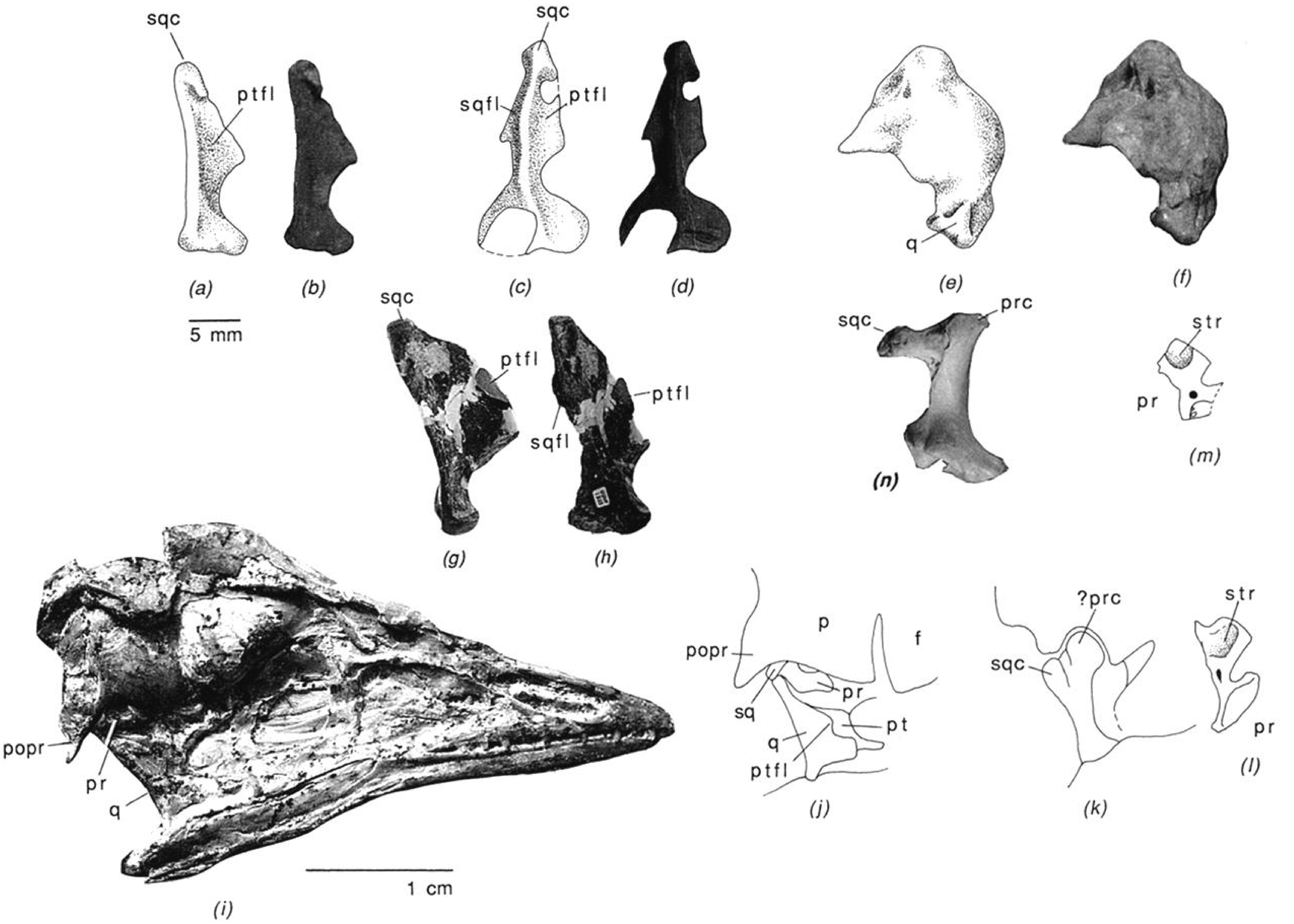

Figure 30. Nature of *Archaeopteryx* quadrate; (*a*) and (*b*) posterior view of left quadrate of London specimen showing a large pterygoid flange and a single-headed quadrate (squamosal capitulum of quadrate); (*c*) and (*d*) the same, postero-medial view, showing squamosal and pterygoid flanges; (*e*) and (*f*) part of occiput of London specimen, showing the right quadrate in place; (*g*) and (*h*) posterior and postero-medial views of left quadrate of *Allosaurus*; note the quadrate of *Archaeopteryx* is very similar to that of theropod; (*i*) right lateral view of the skull of Eichstätt specimen; (*j*) the same, showing the nature of articulation of quadrate with adjacent bones; note prootic bone occurs in front of the quadrate head; (*k*) interpretation of the 'double-headed' *Archaeopteryx* quadrate with the help of computed tomography X-ray image in an oblique plane of 32 to the plane of the skull (after Haubitz *et al.* 1988); however, the quadrate appears to be composite; the putative prootic capitulum is interpreted here as a part of prootic; (*l*) right prootic of *Protoavis* showing similar configuration of putative 'prootic capitulum'. (*m*) Right prootic of *Archaeopteryx*, London specimen (reversed from left side) for comparison; note prootic lacks otic facet for prootic capitulum; (*n*) posterior view of right quadrate of *Buteo*, showing double-headed quadrate; note squamosal capitulum is stouter than prootic capitulum; in (*k*), the reverse is the case.