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SKULL OF *ARCHAEORNITHOIDES* FROM THE UPPER CRETACEOUS OF MONGOLIA

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ABSTRACT. The skull fragment of *Archaeornithoides* comes from a juvenile individual and consists of maxillae, dentaries, and crushed palate bones. The total length of the skull is estimated as 5 cm. As in the theropods, the palatine is tetraradiate and, as in some of them, has a medial embayment for the subsidiary palatal fenestra. As in the Troodontidae, *Baryonyx*, and *Spinosaurus*, the interdental plates are absent, and the interdental septa are separated from the lingual wall of the dentary by a paradental groove. Also reminiscent of *Baryonyx* are the details of premaxilla-maxilla articulation and the presence of a median ridge in the rostral part of the palate. As in *Archaeopteryx*, the maxillary teeth are widely spaced, pointed, and smooth, without serrations, carinae, and constrictions. As in the Mesozoic and paleognathous birds, the palatal shelf of the maxilla is expanded and as in *Hesperornis* it supports two, rostral and caudal, pneumatic sinuses. These avian features suggest that *Archaeornithoides* is the closest known theropod relative of birds. Its consistent similarities to *Baryonyx*, *Spinosaurus*, and the troodontids narrow down the ancestry of birds to the theropods that possess the paradental groove and lack interdental plates.

INTRODUCTION

The skull ZPAL MgD-II/29, the holotype of *Archaeornithoides deinosauriscus* (Elzanowski and Wellnhofer, 1992), was found in 1965 by the Polish-Mongolian Paleontological Expedition in the locality Bayn Dzak (formerly Shabarakh Usu), Mongolia, in the fluviatile sandstones of the Djadokhta Formation, which is of Late Cretaceous, late Santonian, or middle Campanian age (Gradzinski, Kielan-Jaworowska, and Maryanska, 1977). The nature of these sediments precludes preservation of any non-mineralized parts such as feathers, which is noteworthy in view of the avian similarities and probable close relationships of *Archaeornithoides* to birds. The Djadokhta Formation yielded abundant lizards, protoceratopsids, and mammals; less than ten specimens each of turtles, crocodiles, and ankylosaurs; single speciments of *Oviraptor*, *Saurornithoides*, and *Velociraptor;* and rare, scattered teeth of carnosaurs, sauropods, and hadrosaurs (Osmólska, 1980).

ZPAL MgD-II/29 was first mentioned as the smallest known specimen of a theropod (Elzanowski, 1983, p. 87), a distinction already then shared with the juvenile dentary (UCM41666) of *Troodon* (Carpenter, 1982, fig. 2b, c, e). The holotype skull of *Lisboasaurus estesi*, a species recently identified as a maniraptoran theropod (Milner and Evans,

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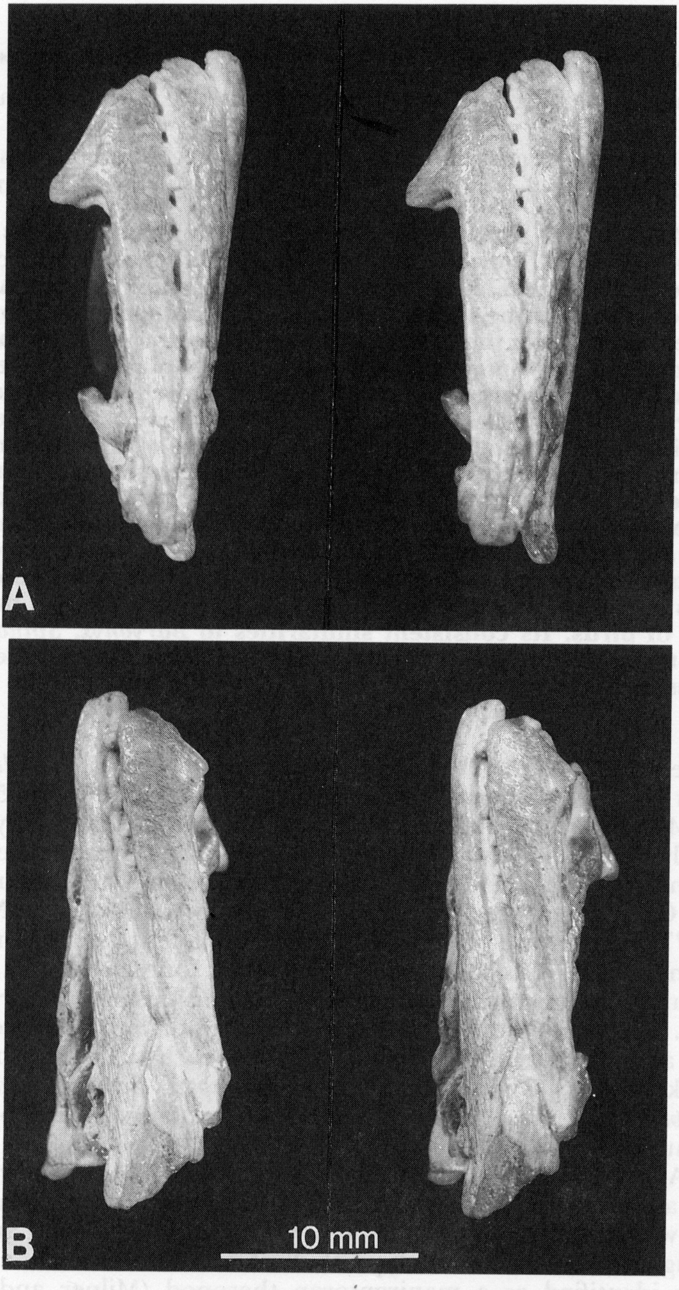

Fig. 1. *Archaeornithoides deinosauriscus,* stereophotographs of the skull fragment in right (A) and left (B) lateral views. For interpretation see Figure 2.

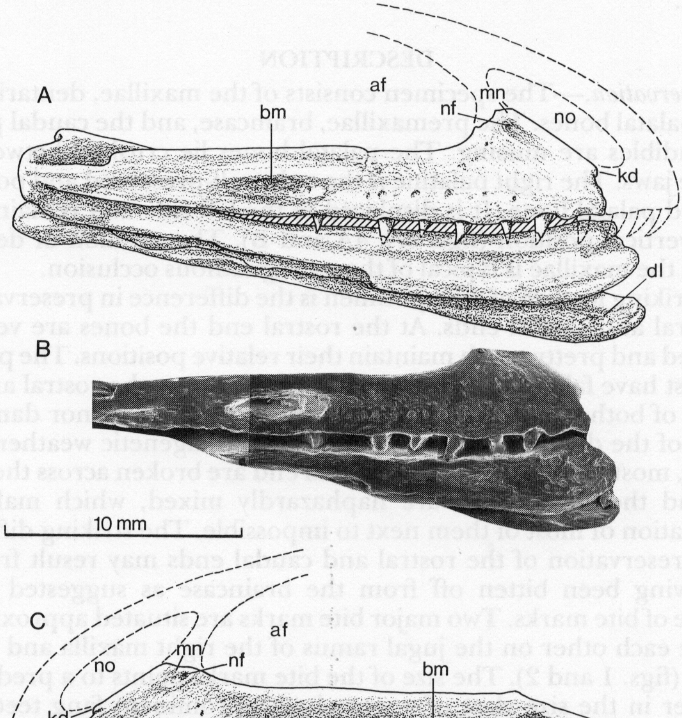

Fig. 2. *Archaeornithoides deinosauriscus,* skull fragment in right (A,B) and left (C,D) lateral views. (B) and (D) are SEM photographs. Abbreviations: af, antorbital fenestra; bm, bite mark; dl, left dentary; dr, right dentary; kd, dorsal knob of the maxilla; l, ledge; mn, nasal process of the maxilla; nf, nutrient foramen; no, nasal opening; tm, marks of premaxillary teeth.

1991), is even smaller than ZPAL MgD-II/29, though the difference is minimal.

DESCRIPTION

Preservation.—The specimen consists of the maxillae, dentaries, and rostral palatal bones. The premaxillae, braincase, and the caudal parts of the mandibles are missing. The palatal bones lie crushed between the opposite jaws. The right palatine is the only well-preserved and positively identified palatal bone. It is displaced to the left side and remains in an almost vertical position (figs. 3A, 4A and B). The position of dentaries between the maxillae is typical of the anisognathous occlusion.

A striking feature of this specimen is the difference in preservation of the rostral and caudal ends. At the rostral end the bones are very well preserved and pretty much maintain their relative positions. The premaxillae must have fallen out prior to the burial because the rostral articular surfaces of both maxillae are essentially intact (fig. 5). Minor damage to the tips of the dentaries is attributable to postdiagenetic weathering. In contrast, most of the bones at the caudal end are broken across their long axes, and their fragments are haphazardly mixed, which makes the identification of most of them next to impossible. The striking difference in the preservation of the rostral and caudal ends may result from the jaws having been bitten off from the braincase as suggested by the presence of bite marks. Two major bite marks are situated approximately opposite each other on the jugal ramus of the right maxilla and the left dentary (figs. 1 and 2). The size of the bite marks points to a predator or scavenger in the size class of a weasel with prominent fang teeth. The likely candidates are the deltatheridiid mammals, well represented in the Bayn Dzak assemblage (Osmolska, 1980).

Palatine.—The palatine is tetraradiate (figs. 3 and 4). The rostromedial, vomeral (choanal) process is stout and shows a medial articular facet for the vomer or pterygoid. The caudomedial, pterygoid process, which certainly extended to the body of the pterygoid bone, is slender and narrow. The medial outline of the bone, between the vomeral process rostrally and the pterygoid process caudally, is concave, indicating the presence of the subsidiary palatal fenestra. The rostrolateral maxillary process seems to be broken off at the rostral end. The caudolateral jugal process, visible only in the ventral view (figs. 3B and 4A), takes the form of a flattened buttress, which certainly abutted against the maxilla and/or the jugal. The dorsal surface, including its lateral part, seems to be flat. Fragments of the left palatine may be present between the right palatine and the left maxilla (fig. 4B).

Maxilla.—The maxillae are almost complete except for the ends of the nasal processes and the walls of the maxillary sinuses, both of which were certainly thin, fragile, and strongly protruding dorsally. The maxilla has a slender appearance which is primarily due to a long antorbital fenestra, which extends three fourths of the bone length, as well as to the caudal tapering of the jugal (subfenestral) ramus (figs. 1 and 2). The lateral surface bears a distinct row of foramina for branches of the maxillary nerve and a major pit with a nutrient foramen at the base of the nasal process. The maxilla overhangs the tooth crowns labially, which is very distinct on the left side. On the right side the teeth are appressed against the overhang, apparently due to the pressure from the underlying mandible that bent them off their vertical position sideward. The medial alveolar wall of the maxilla is not exposed.

At least eight and at most eleven teeth at various eruption stages were present in each maxilla (figs. 1 and 2). The first right maxillary tooth is missing. The mesial (rostral) six teeth are of similar size and regularly spaced, about 1 mm from one another. The remaining, distal (caudal) teeth are distinctly smaller and irregularly spaced, the seventh and the eighth being close to one another. The seventh tooth is 1.5 mm and 2.2 mm behind the sixth tooth in the left and right maxilla, respectively. The eighth tooth follows closely, only 0.5 mm behind on the right, and 0.3 mm behind on the left side. The most distal, positively identifiable cross section of a tooth is that of the eighth tooth, on each side some 13 mm from the rostral end of the maxilla. However, the tooth row may have extended for 3 more mm caudally and included 2 to 3 more teeth, as suggested by what appears to be traces of alveoli with the remains of barely erupted teeth.

The maxillary teeth are all smooth, without any trace of surface ornamentation, such as fluting or serrations, and without carinae. In lateral view the teeth are broadest at the base and pointed at the end, with the possible exception of the first tooth (preserved on the left side only), which seems to be almost peg-like. The third left and fourth right teeth represent the other extreme in being sharply pointed. The crowns are almost straight, some show barely noticeable caudal deflection, which is most pronounced in the fourth right tooth. Although the cross section cannot be determined accurately in any of the possible lateral views, it seems to be fairly variable along the tooth row. The first (left) tooth is nearly round. The next three teeth, second through fourth, and the fifth left, are moderately compressed labiolingually. The fifth right and both sixth teeth have the labial face strongly convex, which suggests a rounded or D-shaped cross section. There is a distinct asymmetry in the development of the last two well-identifiable caudal teeth: on the left side, the two cross sections are perfectly circular, whereas on the right side the seventh tooth seems to be laterally compressed, and the eighth tooth was definitely so as revealed by its cross section with sharp rostral and caudal edges.

A notch in the rostral margin of the maxilla (figs. 1 and 2) marks the subnarial foramen. The premaxillary articulation (fig. 5) is complex and reveals an intricate interdigitation. A rostral projection of the lateral maxillary wall slopes medially into a fossa, which seems to be perforated by the supraalveolar canal. Medial to this fossa, there are two knobs that line up dorsoventrally. Medial to these knobs, a large articular fossa passes smoothly onto the dorsal surface of the maxilla at the base of its

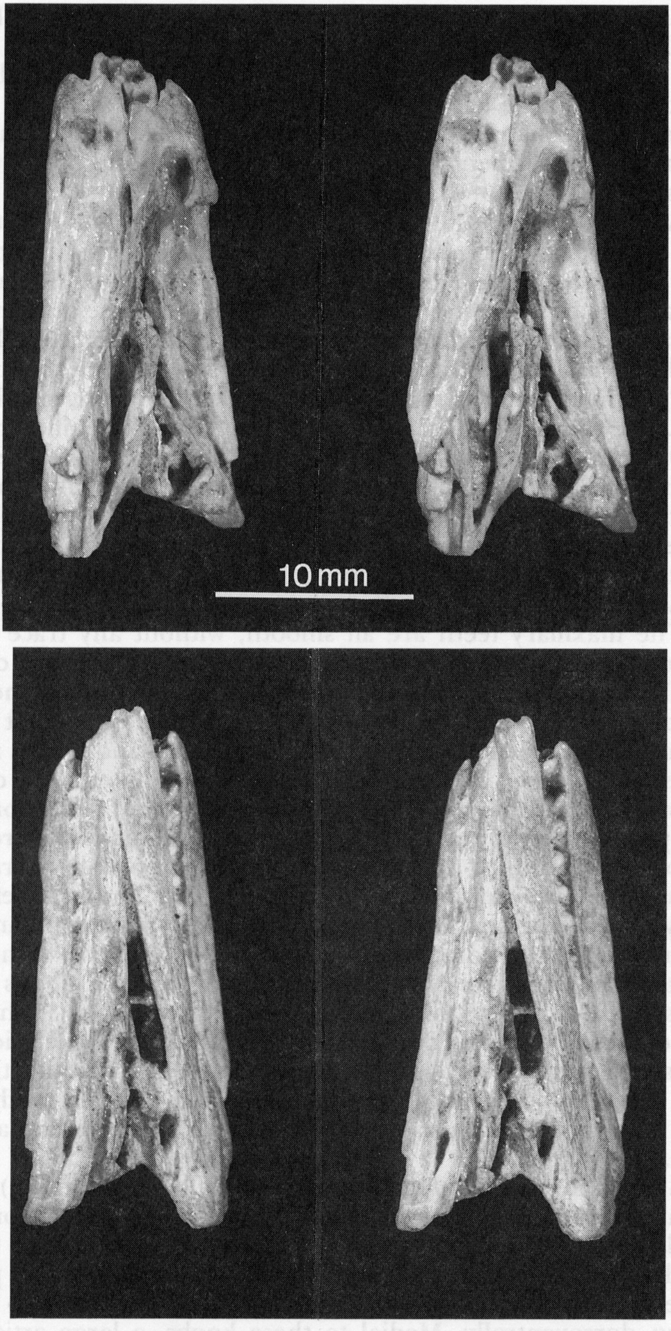

Fig. 3. *Archaeornithoides deinosauriscus,* stereophotographs of the skull fragment in dorsal (A) and ventral (B) views. For interpretation see figure 4.

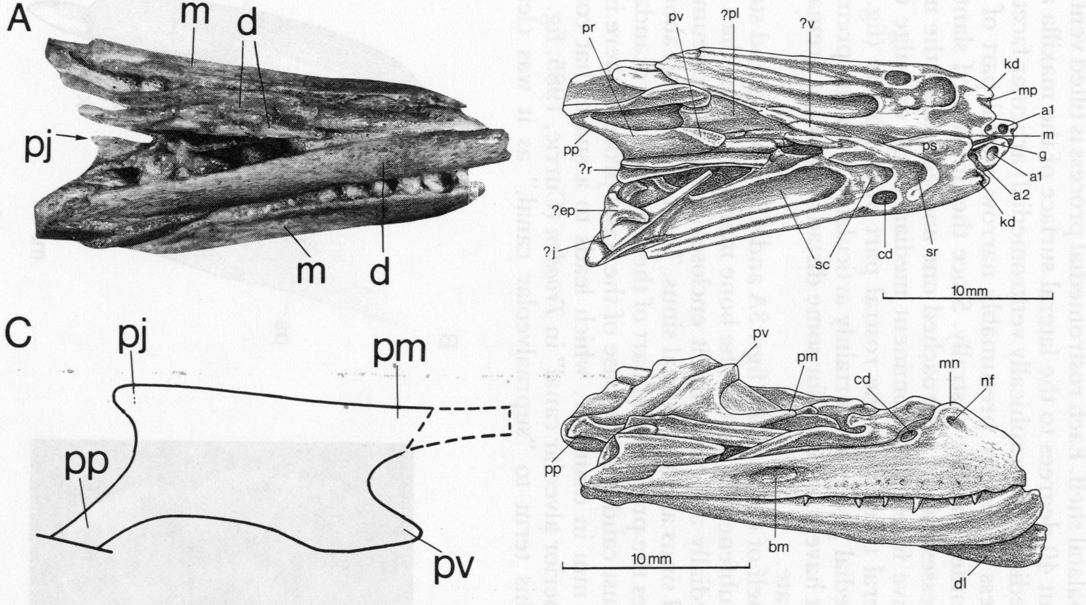

Fig. 4. *Archaeornithoides deinosauriscus,* skull fragment in ventral (A), dorsal (B), and dorsolateral (D) views. Except for the right palatine (pj, arrow), which is displaced to the left side of the specimen, the bone fragments visible between the dentaries in the ventral view could not be identified (see Preservation). (C) is an outline drawing of the right palatine. Abbreviations: a1, a2, dentary alveoli; cd, dorsal opening to the supraalveolar canal; d, dentary; dl, left dentary; ep, ectopterygoid; g, paradental groove; j, jugal; kd, dorsal knob of the maxilla; m, maxilla; mn, nasal process of the maxilla; mp, premaxillary fossa in the maxilla; nf, nutrient foramen; pj, jugal processes of the palatine; pl, left palatine; pm, maxillary processes of the palatine; pp, pterygoid processes of the palatine; pr, right palatine; ps, palatal shelf of the maxilla;pv, vomeral processes of the palatine; r, parasphenoid rostrum; sc, caudal sinus of the maxilla; sr, rostral sinus of the maxilla; v, vomer.

nasal process. This fossa flattens out and disappears altogether over a short distance, suggesting only a short overlap by the premaxilla which probably did not contact the nasal behind the nasal opening. Medial to the articular fossa is the rostromedial process which constitutes the rostral end of the palatal shelf. Each rostromedial process is tilted ventrad at an angle of about 40 degrees to the lateral surface of the maxilla and bears a distinct, medial (topographically ventromedial) articular facet for the opposite process or for the presumably narrow rostral part of the vomer, if this extended that far rostrally. Since the downward slanting rostromedial processes met or approached one another along the midline, they must have formed a prominent median ridge or bulge that separated two lateral troughs in the rostral part of the palate (fig. 5). Since the rostromedial processes certainly articulated with the premaxilla, the ridge must have continued for some distance onto the premaxillary part of the palate.

The palatal shelf of the maxilla (figs. 3A and 4B) is broad and stout, which makes the subfenestral part of the bone markedly wider than it is high (table 1). Medially and ventrally it encloses two major pneumatic sinuses, the rostral sinus and the caudal sinus. The rostral sinus, about 2 mm wide, excavates the prefenestral part of the maxilla. Laterocaudal to the rostral sinus, just caudal to the base of the nasal process, there is an opening, about 1 mm in diameter, which leads to a space that corresponds to the "superior alveolar canal" in *Troodon* (Currie, 1985, fig. 2B, C). We correct this term to "supraalveolar canal," as it was clearly

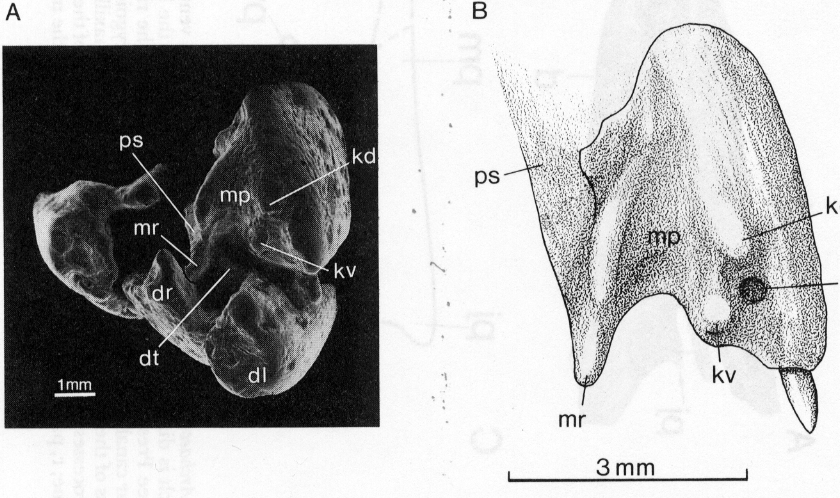

Fig. 5. *Archaeornithoides deinosauriscus,* SEM photograph of the entire skull fragment (A) and a drawing of the maxilla (B) in rostral view. Abbreviations: cr, rostral exit of the supraalveolar canal; dl, left dentary; dr, right dentary; dt, third dentary tooth; kd, dorsal knob of the maxilla; kv, ventral knob of the maxilla; mp, premaxillary fossa in the maxilla; mr, rostromedial process of the maxilla; ps, palatal shelf of the maxilla.

TABLE 1

Measurements of the skull and teeth of Archaeornithoides deinosauriscus *(in mm)*

Total length estimate		50
Maxilla		
length		24.5 (?+)
width, rostral		3.0
mid-length		4.0
height, mid-length		3.0
Mandible		
length		27.0 +
rostral depth (lingually)		2.8
Maxillary teeth		
fore-aft basal length (FABL)		
1st left	0.53	—
2nd left and right	0.50	0.66
3rd left and right	0.60	0.58
4th left and right	0.78	0.70
5th left and right	0.66	0.58
6th left and right	0.70	0.78
7th left and right	0.35	0.50
8th left and right	0.38	0.24

intended to describe the position of this space relative to the alveoli rather than to distinguish it from a nonexistent, inferior counterpart.

The entire dorsal surface of the palatal shelf, caudal to the rostral sinus, is strongly concave and circumscribed by the bony footings of the walls, presumably partly membraneous, that enclosed the caudal maxillary sinus. The footing of the medial wall is strongest rostrally and slightly convex toward the midline. The footing of the lateral wall starts abruptly some 10 mm caudal to the rostral end of the bone (that is 4 mm caudal to the rostral margin of the antorbital fenestra), is strongest, that is, thickest and highest, at the mid-length of the antorbital fenestra, which may possibly indicate a bony pillar in a fully ossified skull, and gradually decreases caudalwards. The lateral wall of the caudal sinus and the dorsal rim of the jugal ramus run parallel to each other and enclose a distinct groove in between.

There is a distinct asymmetry in the form of sinuses, in particular in their rostrocaudal extension, in the two maxillaries. On the right side the rostral and caudal sinuses are contiguous. On the left side, the rostral sinus extends farther caudally than it does on the right side and remains broadly separated from the caudal sinus. This asymmetry affects the opening to the supraalveolar canal as well. Pneumatic structures of the upper jaw are known to be strongly asymmetric in crocodiles (Wegner, 1958).

Dentary.—Both dentaries are almost completely preserved except for slight damage to the rostral tip of the left dentary and heavy damage to the caudal half of the right dentary (see Preservation). Despite its broken tip, the left dentary projects more rostrally than the right one does, which implies some longitudinal dislocation of at least one of the mandibular rami. Even with the allowance for this dislocation, the short rostral projection of the dentaries permits only a compact premaxilla, no longer than 4 mm, unless it projected far beyond the mandibles.

A salient feature of the lateral surface of the dentary is a distinct ledge approximately coextensive with the row of six major maxillary teeth and vanishes both rostrally and caudally. The ledge bears several irregular pits, most likely tooth marks, on its dorsal surface. In the rostral continuation of the ledge on the left dentary there are three distinct, narrowly, and evenly spaced pits, which may represent the tooth marks of the premaxillary teeth. No such pits are visible on the right dentary, however. The lateral outline of the dentary cannot be exactly determined because the alveolar margin is covered by the maxilla.

At the tip of the right dentary there is a bony, tooth-like dorsal projection rostromedial to the first distinct alveolus. Lateral to this projection, there may have been a minute rostralmost alveolus (of less than 0.5 mm in diameter), which cannot be identified with any confidence and has not been included in our count of alveoli. The tip of the left dentary is broken off across the first distinct alveolus, which we assume to be the first alveolus. The interdental septa (fig. 4B) are continuous with the labial wall of the dentary and descend toward the lingual wall which, as preserved in the left dentary, is somewhat lower than the labial wall but still higher than, and thus projecting over, the lingual ends of the septa. The lingual wall is gone in the right dentary. Each septum is separated from the lingual wall by a shallow paradental groove (fig. 4B), which ends in the first alveolus. Due to the confluence with the paradental groove, the alveoli seem to be rostrocaudally (mesiodistally) compressed. There is no trace of interdental plates. A mandibular tooth, the only one visible, remains in the third alveolus of the left dentary (fig. 5A). Its crown is perfectly conical, definitely not compressed labiolingually, and smooth without any trace of sculpture. Other dentary teeth are probably preserved behind the maxilla.

The average fore-and-aft diameter of three alveoli exposed at the rostral ends of both dentaries is about 0.8 mm, which indicates no essential size difference between the maxillary and dentary teeth (table 1). The average fore-and-aft width of the four interdental septa is 0.5 mm, which is about half the average distance between the maxillary teeth. This suggests either a dense terminal rosette of teeth, which is present in a number of theropods, or a difference in the spacing of maxillary and dentary teeth, or both as in *Baryonyx walkeri* (Charig and Milner, 1990). Consistent with the presence of a terminal rosette of long, caudally recurved premaxillary teeth are the three aforementioned putative tooth marks on the left dentary.

Other bones.—A small fragment just caudal to the preserved contact between the two maxillae may represent the vomers (figs. 3A and 4B). A trough-shaped, apparently median element, preserved to the right of the palatine (figs. 3A and 4B), is tentatively identified as a parasphenoid rostrum by reason of its similarity to this element in *Dromaeosaurus*

(Colbert and Russell, 1969, fig. 5). Another possible interpretation is of it being a vomer which in birds forms a dorsally open trough that slides on the parasphenoid/mesethmoid complex.

Dorsally overlying the caudal end of the right maxilla is a bony rod which probably represents the rostral moiety of the right jugal (figs. 3A, 4B). Medially appressed on this rod is a small triradiate element that may possibly represent the ectopterygoid as suggested by its position, size, and, most important, its shape comparable to the ectopterygoid in *Syntarsus* (Colbert, 1989, fig. 43B).

Size and individual age.—The estimate of the total length of the skull as 5 cm (table 1) is based on a remarkably constant length ratio of the upper jaw, as measured up to the caudal end of the maxilla, to the total skull length, which safely falls between 0.5 and 0.6 in *Archaeopteryx, Saurornithoides,* and *Velociraptor,* despite considerable differences in the internal proportions of their maxillae.

The skull is from a juvenile individual as revealed by the unfinished surface of the bones and the aforementioned presence of barely erupted back teeth. The bones, including the maxillae, dentaries, and the palatine are covered by tiny, 0.03 to 0.08 mm wide, possibly erosionally enlarged primary canals (fig. 6) in the freshly deposited primary vascular bone of the fibrolamellar type which is characteristic of mammals, birds, and most dinosaurs (Reid, 1987). Indeed, such a regular, canaliculate sculpture occurs on the bones of juvenile birds but not crocodiles and other recent reptiles (personal observation). We discovered it at one spot on the maxilla of *Compsognathus longipes,* which is represented by the juvenile specimen B.S.P. AS I 563. As is typical of the primary vascular bone of periosteal origin, the primary canals run predominantly parallel or

Fig. 6. *Archaeornithoides deinosauriscus,* close-up of the rostral ends of the right maxillary and dentary showing the unfinished surface of the bones, covered with primary vascular canals.

subparallel to the long axes of bones (Enlow, 1969), in this case those of the dentary, the jugal ramus of the maxilla, and its nasal process. There are irregular vortexes in the arrangement of canals around the rostral end of the antorbital fenestra, where the jugal ramus and nasal process meet at angles.

A possible juvenile character is the great relative length of the antorbital fenestra which amounts to 75 percent of the total bone length. The corresponding figures are 59 percent for *Archaeopteryx* (Wellnhofer, 1974; fig. 5) and 68 percent for *Saurornithoides* (Osmólska and Barsbold, 1990; fig. 11.1A) which appears to have the longest antorbital fenestra among known theropods. The fenestration of the upper jaw, including the maxilla, is known to be more extensive in the juvenile as compared to grown up varanids (Mertens, 1942, p. 147).

DISCUSSION AND COMPARISONS

The tetraradiate palatine with the embayment for the subsidiary palatal fenestra and slender pterygoid process is similar to that in *Dromaeosaurus* (Colbert and Russell, 1969) but does not show any indication of the lateral fossa on the dorsal side, which has been figured in *Velociraptor* (Osmólska, 1985, fig. 4). The subsidiary fenestra is also present in the Ornithomimidae (Barsbold and Osmolska, 1990, fig. 8.1.D), the palatine of which seems to be highly transformed. Gauthier (1986) used the presence of a subsidiary palatal fenestra as one of the two cranial synapomorphies to define a "coelurosaurian" clade composed of the ornithomimids, an unresolved polytomy including the oviraptorids, and six other non-carnosaur taxa, the "Deinonychosauria" including the dromaeosaurids and troodontids, and birds. The fenestra is now known to be absent in the oviraptorids (Barsbold, Maryanska, and Osmólska, 1990, fig. 10.1.D), and the palatine remains unknown in the remaining dinosaur groups of the proposed clade and, in fact, in most other theropods. On the other hand, a large subsidiary fenestra occurs in a tyrannosaurid, *Daspletosaurus* (Russell, 1970; R. E. Molnar, personal communication), which is outside the clade this character was adduced to define. The subsidiary fenestra may, therefore, be a common, possibly symplesiomorphic theropod character rather than a synapomorphy of one clade within the theropods.

The structure of the maxilla and the details of tooth implantation in *Archaeornithoides* show consistent similarities to *Baryonyx* (Charig and Milner, 1990), Troodontidae (Currie, 1987; Osmólska and Barsbold, 1990), *Lisboasaurus* (Milner and Evans, 1991), and birds including *Archaeopteryx* (Wellnhofer 1974, 1988, 1992) and *Hesperornis* (Witmer, 1990; Elzanowski, 1991).

The premaxilla-maxilla suture with rostral projections of the maxilla is well known in the carnosaurs (Madsen, 1976, pl. 6) but seldom exposed and thus poorly known in most of the other theropods. Based on what is visible in the lateral view, *Archaeornithoides* is specifically similar to *Baryonyx* in having two maxillary knobs that line up above one another and fit into the corresponding fossae in the premaxilla (Charig and Milner, 1990, fig. 9.1). Both knobs of *Baryonyx* and only the dorsal knob of *Archaeornithoides* are exposed in the lateral view. In both *Baryonyx* and *Archaeornithoides,* there is a sharp turn of the premaxilla-maxilla suture that separates the vertical, interdigitated part from the horizontal dorsal overlap of the maxilla by the premaxilla. Judging from the sharp turn of the suture (Wellnhofer, 1988, fig. 16; 1992, fig. 19), a comparable, complex premaxilla-maxilla articulation may be present in *Archaeopteryx.*

The conformation of the premaxilla-maxilla articulation is necessarily affected by the ventral tilt of the rostromedial processes that meet at, or at least approach, the midline to form a median ridge that certainly continued onto the premaxillary palatal shelves. The only known dinosaur with a median ridge in the rostral part of the palate is *Baryonyx* (Taquet, 1984, fig. 1; Charig and Milner, 1990, fig. 9.2). A median ridge in the rostral part of the palate may be an adaptation for crushing hard food items. This part of the palate remains totally unknown in *Archaeopteryx.*

Archaeornithoides differs from most of the theropods (Currie, Rigby, and Sloan, 1990) in lacking the interdental plates and in having the interdental septa sloping labiolingually. The interdental plates are positively absent in *Baryonyx, Spinosaurus,* Troodontidae, *Lisboasaurus,* and Dromaeosauridae (Ostrom, 1990). Currie (1987) proposed that the lingual, highly vascularized bony wall of the alveoli in the Dromaeosauridae incorporates or derives from the interdental plates. This is a valid morphological hypothesis which, however, should not be substituted for observable osteological facts at the risk of circular reasoning. *Archaeornithoides,* Troodontidae (Currie, 1987), and *Baryonyx* (personal observation) have the lingual wall of the dentary lower than the labial wall. Another striking feature shared by *Archaeornithoides,* Troodontidae (Currie, 1987, fig. 3b), *Baryonyx* (Charig and Milner, 1990, fig. 9.3), and *Spinosaurus aegyptiacus* (Stromer, 1915, fig. 12b) is the presence of the paradental groove that separates the interdental septa from the lingual wall of the dentary.

Lisboasaurus, hypothesized to belong within "the troodontid dinosaur-bird clade" (Milner and Evans, 1991), is more theropod-like than *Archaeornithoides* in having a higher number of densely spaced maxillary teeth with carinae. In addition, *Lisboasaurus* shares two more characters with the Troodontidae: tooth crowns with depressions on the lingual face and constrictions between the crowns and roots of the maxillary teeth. Both *Archaeornithoides* and, contrary to Milner and Evans (1991), *Archaeopteryx* differ from both *Lisboasaurus* and troodontids, in having unconstricted maxillary teeth (Howgate, 1984; Wellnhofer, 1988, 1992). There is no indication of the lingual depression in the front view of the dentary tooth of *Archaeornithoides,* and the lingual depressions are positively absent from the tooth crowns of *Archaeopteryx* as attested by the lingual views of the right maxillary teeth in the London specimen (Howgate, 1984, figs. 4 and 5) and the left dentary teeth, visible through the antorbital fossa and nasal opening, in the Eichstätt specimen (Wellnhofer, 1974, p. 184 and fig. 5A and B). Although likely to be close to avian ancestry, *Lisboasaurus* has retained plesiomorphic character states in comparison with *Archaeornithoides* and thus seems to be more distantly related to birds than is *Archaeornithoides.*

The combination of juvenile age and similarity to the Troodontidae, which are represented in the same locality by *Saurornithoides* (Osmolska, 1980), raises the possibility of *Archaeornithoides* being a juvenile troodontid. In fact, the maxilla in lateral view is similar to that of *Saurornithoides* (Osmolska and Barsbold, 1990) in having a slender jugal (subfenestral) ramus that tapers caudally. Also, the footing for the lateral wall of the caudal sinus is compatible with the presence of a mid-length pillar in the antorbital fenestra (see Description). However, *Archaeornithoides* is unlikely to be a juvenile troodontid due to a number of striking differences that are difficult to account for in terms of postembryonic development. The maxillae of troodontids do not show any indication of either particularly broad palatal shelves (Currie, 1987, fig. 2) or a rostral median ridge in the palate (Osmólska and Barsbold, 1990, fig. 11.1B). The troodontids have 15 to 20 teeth in each maxilla, which are strongly serrated, the denticles being relatively large. The teeth of young troodontids are at least as strongly serrated as those of large individuals and are even more recurved caudally than are grown up teeth (Carpenter, 1982; Barsbold, Osmólska, and Kurzanov, 1987). Although the teeth of *Archaeornithoides* are about half the size of the smallest known troodontid teeth (Carpenter, 1982, figs. 3b, c), nothing foreshadows a dramatic change in their morphology that would turn them into the heavily serrated and compressed maxillary teeth of *Saurornithoides.* The theropod teeth are known to show little ontogenetic variation in both their number and morphology. The juvenile teeth are scaled down versions of teeth in grown up individuals, and their denticles tend to be even relatively larger (Currie, Rigby, and Sloan, 1990). We believe, therefore, that the simple form of teeth of *Archaeornithoides* is representative of the adult as well as of the juvenile stages, although the appearance of fine surface differentiations at an old age is not unlikely as suggested by the development of fine serrations in the old individuals of some varanids (Mertens, 1942, p. 141–142).

Although the cross section of most maxillary teeth cannot be precisely determined in *Archaeornithoides,* and some of them seem to be labiolingually compressed, some of the distal (caudal) maxillary teeth are perfectly conical as revealed by their circular cross sections. Whereas the premaxillary and front dentary teeth tend to be rounded in some theropods (Currie, Rigby, and Sloan, 1990), the maxillary and distal dentary teeth in nearly all theropods are laterally compressed. Among few notable exceptions are the rounded maxillary teeth of *Baryonyx,* which are finely serrated (Charig and Milner, 1990, figs. 9.2 and .3), and *Spinosaurus,* which have smooth carinae (Stromer, 1915). Rounded maxillary alveoli are said to be present in *Dryptosaurus aquilunguis* (Molnar, 1990).

Archaeornithoides resembles *Archaeopteryx* in having pointed, maxillary teeth (fig. 3) which, in contrast to those of most theropods, are widely spaced, conical, or only slightly compressed labiolingually, and lack both serrations and carinae. The maxillary teeth of *Archaeornithoides* lack constrictions between crowns and roots, which also holds true for most maxillary teeth of *Archaeopteryx*, with the possible exception of one or two rostral teeth (Ostrom, 1991). In contrast to the troodontids, however, the constrictions of the premaxillary and rostralmost maxillary teeth in *Archaeopteryx* are poorly defined, not uniform (Ostrom, 1991), and even their location between the crown and the root is open to question (Howgate, 1984; Wellnhofer, 1988).

What best distinguishes *Archaeornithoides* from all the theropods is the broad palatal shelf with its pneumatic sinuses. Whereas in the theropods, including the troodontids, the palatal shelf of the maxilla is relatively narrow (Madsen, 1976, pl. 6; Currie, 1985, fig. 2), in *Archaeornithoides* it is so expanded that the subfenestral part of the maxilla is distinctly broader than it is high (table 1). A comparable broad palatal shelf is found in the same position relative to the nasal process in *Archaeopteryx* (Wellnhofer, 1974, fig. 5B "mpl"; Witmer, 1990, fig. 14A, "pal pr max") and the primitive neornithines including *Hesperornis* (Witmer, 1990, fig. 7; Elzanowski, 1991, fig. 3). The expanded palatal shelf seems therefore to represent a primitive avian character. The palatal shelf is also expanded, at least rostrally, in *Lisboasaurus* (Milner and Evans, 1991, fig. 2).

Probably in correlation with the large size of the palatal shelf, the entire configuration of a small rostral sinus, a large caudal, medially bulging sinus, and the nasal process with an opening to the supraalveolar canal just behind its base is strictly comparable in *Archaeornithoides* and *Hesperornis* (Witmer, 1990, fig. 7) but unknown in the theropods. The presence of the supraalveolar canal has been documented only in *Troodon* (Currie, 1985, fig. 2b, and c) and *Lisboasaurus* (Milner and Evans, 1991; fig. 2B) but may have gone unnoticed in other theropods (Ostrom, personal communication). In *Troodon* it opens dorsally by a number of foramina that pierce the palatal shelf, one of which is inside the apparently single maxillary sinus, medial to its lateral wall, whereas in *Archaeornithoides* the single opening is more marginal, lateral to, rather than inside the sinuses. A likely homologue of the supraalveolar canal opening is present (but unlabelled) lateral to the rostral sinus, near the base of the nasal process in *Hesperornis* (Witmer, 1990, fig. 7). If present in *Archaeopteryx*, this opening would not be visible due to the transverse flattening of all known cranial specimens. While the presence of the supraalveolar canal in *Hesperornis* needs to be verified, there can be little doubt that the rostral and caudal sinuses, which occupy the same position relative to one another and to the nasal process, are homologous in *Archaeornithoides* and *Hesperornis*.

CONCLUSIONS

Archaeornithoides represents a novel group of theropods, at the family level at least (Elzanowski and Wellnhofer, 1992). We were unable to confirm its aublysodontid affinities proposed by Paul (1988, p. 324). The avian features of the maxillary palatal shelf and dentition distinguish *Archaeornithoides* from all other potential sister groups of birds (Witmer, 1991), suggesting that *Archaeornithoides* is the closest known theropod relative of birds. However unexpected, its consistent similarities to *Baryonyx, Spinosaurus,* and troodontids seem to be synapomorphic since none of them is shared with the Ceratosauria (Welles, 1984) which is currently considered to be the plesiomorphic sister taxon of all other theropods (Gauthier, 1986; Benton, 1990). The presence of laterally compressed teeth in the primitive archosaurs (Benton, 1990) lends additional phylogenetic weight to the opposite character state (rounded teeth) found in *Archaeopteryx, Archaeornithoides, Baryonyx,* and *Spinosaurus*. Thus, the character distribution along the currently accepted cladograms suggests that these four taxa, the troodontids, and possibly *Lisboasaurus* together form a monophyletic taxon. This conclusion is consistent with the independent evidence for the avian relationships of the troodontids (Currie, 1987), the troodontid similarities of *Lisboasaurus* (Milner and Evans, 1991), and the demonstrated close relationships of *Baryonyx* and *Spinosaurus* (Buffetaut, 1989, 1992).

However, the current classification of theropods is still in a state of flux and any interpretations based on it have to remain tentative. While four or five out of six available *Baryonyx* characters support its branching off after the ceratosaurs (Charig and Milner, 1990), the *Baryonyx-Spinosaurus* clade does not fit Gauthier's (1986) subdivision of the remaining theropods (Tetanurae) into the carnosaurs and coelurosaurs, with birds and other maniraptorans as the most recent branches of the coelurosaurs. This opens up the possibility that the avian lineage branched off further back in the theropod phylogeny than suggested by Gauthier's phylogenetic scheme. Whatever the phylogenetic status of the theropod similarities of *Archaeornithoides,* they narrow down the ancestry of birds to the theropods that possess more or less rounded teeth and the paradental groove and that lack interdental plates.

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