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A New Skull of *Gobipteryx minuta* (Aves: Enantiornithes) from the Cretaceous of the Gobi Desert

LUIS M. CHIAPPE,[1] MARK NORELL,[2] AND JAMES CLARK[3]

ABSTRACT

We describe an exquisitely preserved new skull of a bird from the Late Cretaceous sandstones of Ukhaa Tolgod, southern Mongolia. Derived similarities shared between this skull and the holotype of *Gobipteryx minuta,* also from the Late Cretaceous of the Gobi Desert, support the assignment of the new cranial material to this avian taxon. The new skull also proves indistinguishable from that of the enantiornithine *Nanantius valifanovi* from the Late Cretaceous of Mongolia. The identification of the new skull as that of *Gobipteryx minuta* and its correspondence to that of *Nanantius valifanovi* indicate that the latter taxon is a junior synonym of *Gobipteryx minuta.* This taxonomic conclusion is crucial for understanding the phylogenetic relationships of *Gobipteryx minuta* because the undoubtedly enantiornithine postcranial morphology of *Nanantius valifanovi* provides the first uncontroversial evidence of the enantiornithine relationship of *Gobipteryx minuta.* The new skull from Ukhaa Tolgod and our reinterpretation of cranial aspects of the previously published material of *Gobipteryx minuta* and *Nanantius valifanovi* permit an accurate reconstruction of the palate of this enantiornithine bird, thus adding significant data for understanding the poorly known palatal structure of Mesozoic birds.

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INTRODUCTION

In the early 1970s, the Polish-Mongolian Paleontological expeditions (Kielan-Jaworowska and Barsbold, 1972) collected two fragmentary small skulls from beds of the Late Cretaceous Barun Goyot Formation of Khulsan (Aka Ikh Khongil), in the Nemegt Valley of the Mongolian Gobi Desert. [See Gao and Norell (2000) for a discussion of the age and stratigraphic relations of this and other Late Cretaceous units from the Gobi Desert.] These skulls were used to establish a new avian (avialan of others; e.g., Gauthier, 1986) taxon, *Gobipteryx minuta* (Elzanowski, 1974, 1976, 1977). Having been found at a period in the history of Mesozoic paleornithology when little was known aside from the classic discoveries of the 19th century (i.e., *Archaeopteryx, Hesperornis, Ichthyornis*), the avian status of *Gobipteryx* supported by Elzanowski was immediately criticized (e.g., Brodkorb, 1976, 1978). Although discoveries of other basal birds in the 1980s and 1990s corroborated the avian relationship of *Gobipteryx* (e.g., Martin, 1983; Cracraft, 1986; Chiappe, 1995; Elzanowski, 1995), the paucity and poor preservation of the specimens clouded its specific relationships among birds.

In 1996, a second avian taxon was described from the Barun Goyot Formation of the Southern Gobi. The partial skull and postcranium of the holotype and single specimen of *Nanantius valifanovi* (Kurochkin, 1996) were discovered at Khermeen Tsav, a locality some 100 km west southwest of Khulsan. Although *Nanantius valifanovi* was described as a distinct taxon, its skull is in fact very like that of *Gobipteryx minuta*. These similarities become obvious once it is realized that the maxilla and dentary were mistakenly identified by Kurochkin (1996); see below.

During the 1994 American Museum of Natural History–Mongolian Academy of Sciences expeditions, a small skull was found at the Nemegt Valley locality of Ukhaa Tolgod (for description of the locality see Dashzeveg et al., 1995; Loope et al., 1998). Upon preparation, it became evident that this exquisitely preserved skull was referable to *Gobipteryx minuta*. In this paper we provide a full description of the new skull and review the anatomy and affinities of this avian taxon.

SYSTEMATIC PALEONTOLOGY

AVES (=AVIALAE SENSU GAUTHIER, 1986) LINNAEUS, 1758

ORNITHOTHORACES CHIAPPE AND CALVO, 1994

ENANTIORNITHES WALKER, 1981

Gobipteryx minuta Elzanowski, 1974

HOLOTYPE: ZPAL-MgR-I/12, fragmentary and distorted skull and mandible (Elzanowski, 1974); the rostral portion of the snout, the quadrate, and the mandible are the only portions providing reliable information.

REFERRED SPECIMENS: ZPAL-MgR-I/32 (Elzanowski, 1976, 1977), poorly preserved preorbital portions of the skull and mandible, with portions of palatal bones; PIN-4492 (Kurochkin, 1996), partial skeleton preserving the rostral portion of the snout and mandible, and the two pterygoids in articulation with the parasphenoid rostrum [this specimen was used as the holotype of *Nanantius valifanovi* (Kurochkin, 1996); the synonymy of this name and the referral of this specimen is discussed below]; IGM-100/1011, nearly complete preorbital region of the skull, scleral ossicles, and portions of the mandibular rami.

LOCALITY AND HORIZON: The Barun Goyot Formation localities of Khulsan (ZPAL-MgR-I/12, ZPAL-MgR-I/32) and Khermeen Tsav (PIN-4492), and the Djadokhta Formation locality of Ukhaa Tolgod (IGM-100/1011). These localities are within the Nemegt Valley in southern Mongolia; the Barun Goyot and Djadokhta are regarded as Campanian age formations (Jerzykiewicz and Russell, 1991; Gao and Norell, 2000).

DIAGNOSIS: Toothless enantiornithine bird, with the derived presence of upturned rostrum, premaxilla with a large, horseshoe-shaped palatal chamber, a diamond-shaped maxillary facet on its ventrocaudal corner, and longitudinal grooves on each side of the midline of its dorsal surface.

DESCRIPTION OF THE NEW SKULL

IGM-100/1011 was found within a small sandstone concretion; such concretions are

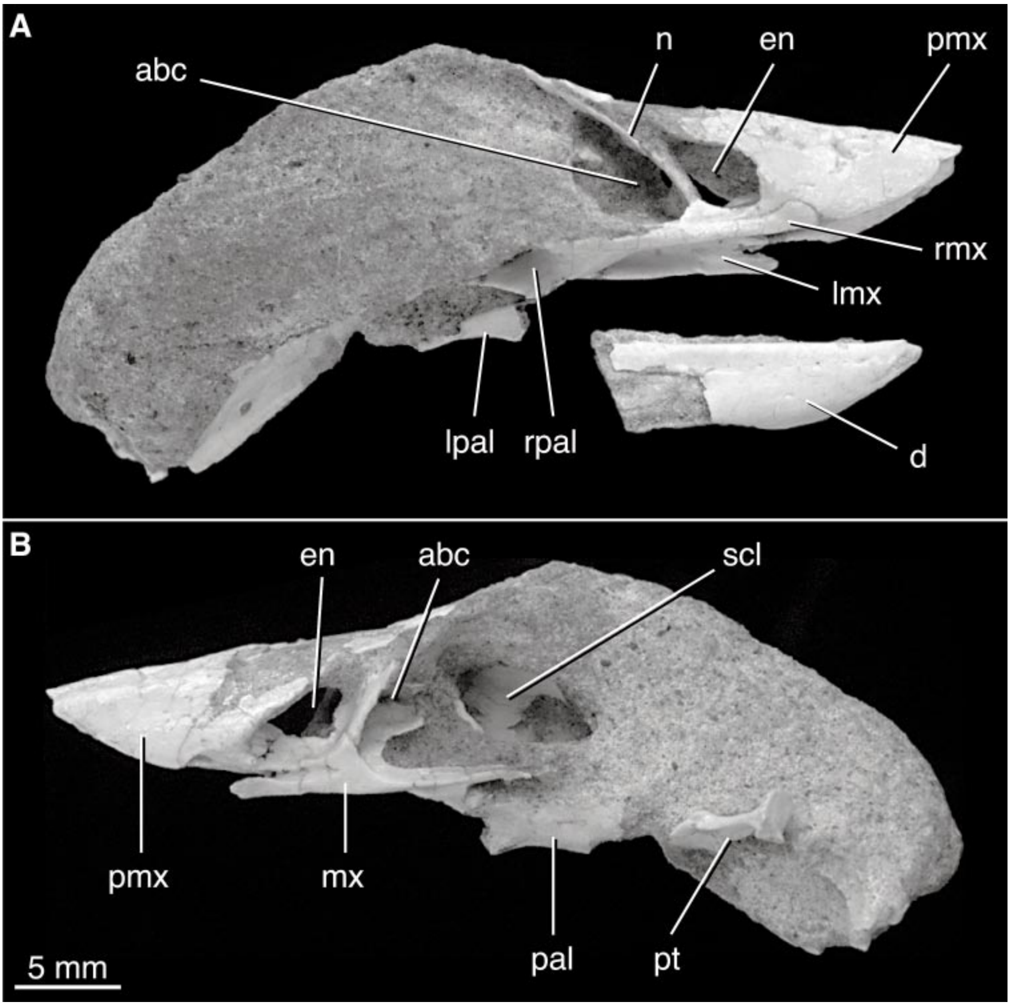

Fig. 1. Skull and mandible of *Gobipteryx minuta* (IGM-100/1011) in right **(A)** and left **(B)** lateral views. Abbreviations are spelled out in the appendix.

characteristic of the fossil-bearing deposits of Ukhaa Tolgod and other localities of the Barun Goyot and Djadokhta formations. IGM-100/1011 is composed of an articulated rostrum and palate associated with the left pterygoid, the rostral portion of the right dentary, a fragment of the left mandibular ramus, and some indeterminate bones. The preservation of IGM-100/1011 is excellent and all sutures between bones are distinct. This condition contrasts with the poor preservation of the first described skulls of *Gobipteryx minuta* (ZPAL-MgR-I/12 and ZPAL-MgR-I/32) and the incompleteness of PIN-4492.

CRANIAL CAVITIES

EXTERNAL NARES: The external nares are tear-shaped with their main axis directed rostroventrally (fig. 1). They are bounded dorsally, rostrally, and rostroventrally by the premaxilla, caudoventrally by the maxilla, and caudally by the maxillary process of the nasal. The dorsocaudal corner of the nares wedges in between the maxillary process of the nasal and the frontal process of the premaxilla (as indicated by impressions of these bones). Thus, the nares of *Gobipteryx* approach the schizorhinal condition of paleog-

Fig. 2. Skull of *Gobipteryx minuta* (IGM-100/1011) in palatal (ventral) view and interpretive drawing.

naths, charadriiforms, and some other extant lineages.

ANTORBITAL CAVITY: The caudal boundary of the antorbital cavity is not well preserved, yet it is clear that this cavity is subtriangular and larger than the external nares (fig. 1). This latter condition is primitive for ornithurine birds; in most ornithurines the antorbital cavity is significantly smaller than the external nares (Chiappe, 1996). The antorbital cavity is bounded by the maxillary process of the nasal rostrally, and the maxilla ventrally and rostroventrally. On the right side, this cavity is walled caudally by a fragmentary, thin ossification, perpendicular to the sagittal plane of the skull, which originates immediately caudal to the end of the vomers. Its topographic position suggests that this bone is most likely the ectethmoid.

CHOANA: The choanae are small and subelliptical (fig. 2). They are rostrally and laterally bounded by the maxilla, caudally by the palatine, and medially by the vomer. The rostral margin of the choana is directly beneath that of the external nares. The choana of *Gobipteryx* is thus more rostrally positioned than that of extant birds, where it typically opens at the level of the antorbital cavity–orbit junction (Huxley, 1867; Jollie, 1957).

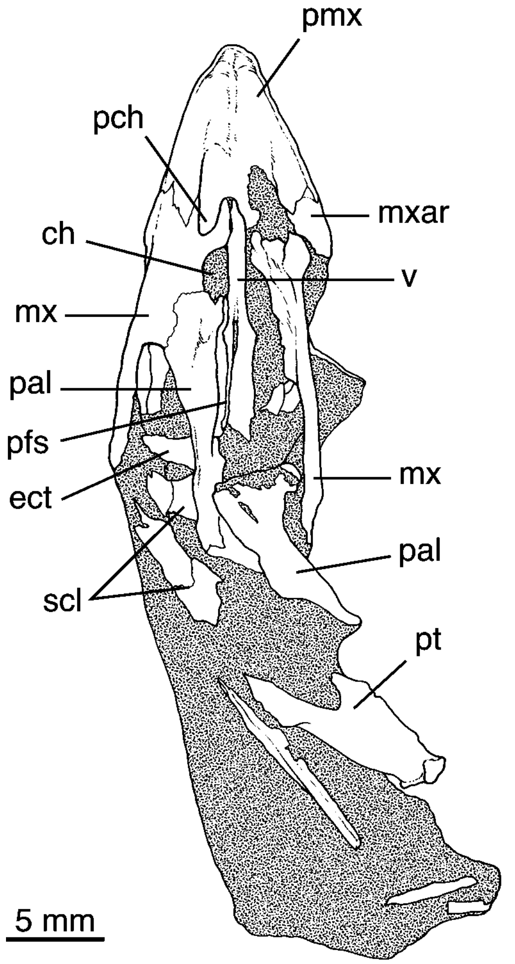

Fig. 2. Continued. Abbreviations are spelled out in the appendix.

PALATAL SUBSIDIARY FENESTRA: A narrow palatal opening is visible between the caudal half of the vomer and the main body of the palatine (fig. 2). Our interpretation of the pterygoid and its articulation to the palatine suggests that this opening widened caudally, reaching an ample notch defined by the mediodorsal and lateroventral (palatine) processes of the pterygoid.

CRANIAL AND MANDIBULAR BONES

PREMAXILLAE: The premaxillae lack teeth and their ventral margin forms a robust but sharp tomial crest (figs. 1, 2). This edge is less obvious in both ZPAL-MgR-I/12 and ZPAL-MgR-I/32, a difference probably resulting from postmortem compression of the latter. In lateral view, the tomial crest is nearly straight, although the rostral portion ascends so that the tip of rostrum is dorsal to the ventral border of the maxilla.

In dorsal view, the rostrum broadens caudally (fig. 3). At the junction of the steep lateral sides with the flat, dorsal surface there is a rostrocaudal groove on each side, which parallels the dorsal profile of the snout in lateral view. Comparable, but weaker, grooves are visible in ZPAL-MgR-I/12; in this specimen the grooves contain several nutrient foramina. These grooves are even weaker in ZPAL-MgR-I/32, although two medial rows of nutrient foramina, one on each side of the sagittal plane, are located in an identical position (Elzanowski, 1977). Some nutrient foramina also can be seen within the grooves of IGM-100/1011 (fig. 3); smaller nutrient foramina are randomly distributed across the rostrum. The dorsal surface between grooves and/or rows of nutrient foramina in ZPAL-MgR-I/12 and ZPAL-MgR-I/32 is somewhat more convex than that of IGM-100/1011.

In rostral view the two premaxillae define a subtriangular cross section, with steep lateral sides, a narrow, flat dorsal border, and a strongly arched palatal vault. A similar configuration is present in ZPAL-MgR-I/12, ZPAL-MgR-I/32, and PIN-4492. As a consequence of their postmortem compression, the premaxillae of ZPAL-MgR-I/12 and ZPAL-MgR-I/32 are slightly more depressed, with less steep lateral sides and shallower palatal vaults.

The premaxillae are fused to each other only rostrally (fig. 3). In IGM-100/1011 and ZPAL-MgR-I/12 they are fused to a level that is at least caudal to the rostral margin of the external nares. In ZPAL-MgR-I/32, however, there is a clear suture separating the premaxillae immediately rostral to the narial margin. The unfused dorsal processes of the premaxillae of IGM-100/1011 extend beyond the level of the caudal margin of the antorbital cavity. Elzanowski's (1977) description of these processes is inaccurate as it was based on the fragmentary ZPAL-MgRI/32. Conversely to what was stated by Elzanowski (1977), the frontal processes of the premaxillae do not taper strongly toward their caudal end; they are of approximately uni-

Fig. 3. Skull of *Gobipteryx minuta* (IGM-100/1011) in dorsal view and interpretive drawing.

form width throughout their length (fig. 4). In IGM-100/1011, the caudal extension of these processes is comparable to that reported by Elzanowski (1977). In IGM-100/1011, a skull slightly larger than ZPAL-MgRI/32, these processes extend 26 mm from the rostral end of the premaxillae, while in ZPAL-MgRI/32 they extend for about 22 mm (Elzanowski, 1977). The premaxillae of PIN 4492-1, where observable, conform to all of the above features. Unfortunately, Kurochkin (1996) described the specimen upside down, confusing the premaxilla with the dentary and vice versa (fig. 5).

The palatal vault is shallow rostrally and abruptly opens into a large chamber caudally (fig. 2). A low but distinct ridge sagittally dissects the palatal vault. On each side of this ridge on the internal surface of the premaxilla the wall of the premaxilla thins to form shallow oval excavations. Ventrally this chamber opens into the oral cavity through a large opening. This opening is a unique feature of *Gobipteryx,* as can be determined from IGM-100/1011. The opening is horseshoe-shaped with a rostral apex. Caudally, the opening is defined by the vomerine and medial edge of the premaxillary and processes of the maxilla and the vomer (fig. 2). The function of this opening and associated structures is unclear. Lateral to this opening the tomial edge of the premaxilla projects medially as a longitudinal trough that is limited to the caudal half of the premaxilla.

The premaxillary-maxillary articulation is complex (figs. 1, 2). The maxillary process

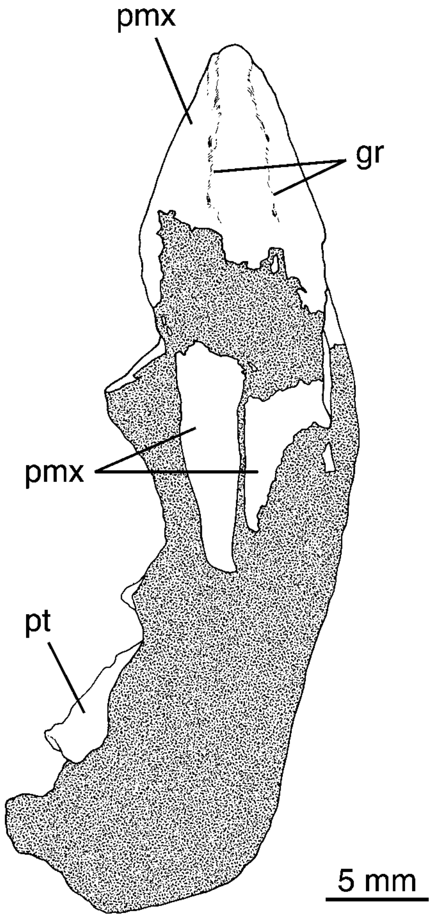

Fig. 3. Continued. Abbreviations are spelled out in the appendix.

is short and narrow, and it firmly articulates into a dorsal groove on the maxilla, which defines the ventral margin of the external nares; vestiges of this groove can be seen on the right side of ZPAL-MgR-I/12 (fig. 6). Ventrally, a zigzag suture runs transversely on the premaxillary-maxillary contact (fig. 2). On the lateral side, the ventrocaudal corner of the premaxilla bears a deeply indented, diamond-shaped facet for the articulation of a robust, lateral tongue of the premaxillary process of the maxilla—a portion of this facet is also exposed laterally and can be seen in both ZPAL-MgR-I/12 and ZPAL-MgR-I/32. On the medial side, the ventrocaudal corner of the premaxilla abuts against a thinner projection of the premaxillary process of the maxilla. A short wedge of the premaxilla fits ventrally between these two maxillary projections. Although poorly preserved, a similar premaxillary-maxillary contact can be seen ventrally on the right side of ZPAL-MgR-I/32. The maxilla separates the premaxilla from contacting the vomer and the palatine (fig. 2).

MAXILLA: Both maxillae are preserved. The right maxilla is articulated to the premaxilla, vomer, and palatine. The left maxilla, although complete, is disarticulated from other palatal elements, medially shifted, and rotated.

The maxilla is tetraradiate and toothless, forming more than half of the side of the rostrum (figs. 1, 2). A rostral, forked premaxillary process forms the complex articulation with the premaxilla described above. The lateral ramus of this fork is dorsally expanded, abutting against the diamond-shaped facet of the premaxilla—this articulation is preserved on the right side of ZPAL-MgR-I/32. Rostromedially, the maxilla possesses a short, thin vomerine process, which expands medially to abut against the rostral tip of the vomer (fig. 2). The vomerine process separates the choana from the rostral horseshoe-shaped chamber described above. The caudolateral process of the maxilla is slender and elongate, forming the ventral margin of the antorbital cavity. Dorsally, the caudal end of this process displays a deep groove below the caudal extremity of the antorbital cavity (fig. 1B). This groove probably received the rostral end of the jugal, the latter not being preserved. In nonavian theropods and basal avians, the jugal, lacrimal, and maxilla often contact in this position near the caudal end of the antorbital fossa.

Caudomedially, the maxilla has an extensive laminar process that approaches and undoubtedly contacted the vomer. This process is underlain by the rostral portion of the palatine and, along with the palatine, defines the caudal margin of the choana.

The main body of the maxilla is slightly concave in ventral view. Just caudal to the end of the dorsal groove for the premaxilla, the maxillary process projects caudodorsally to form a short, pyramidal nasal process that contacts a long, transversely extensive maxillary process of the nasal (fig. 1). A small pocket or foramen excavates the laterocaudal

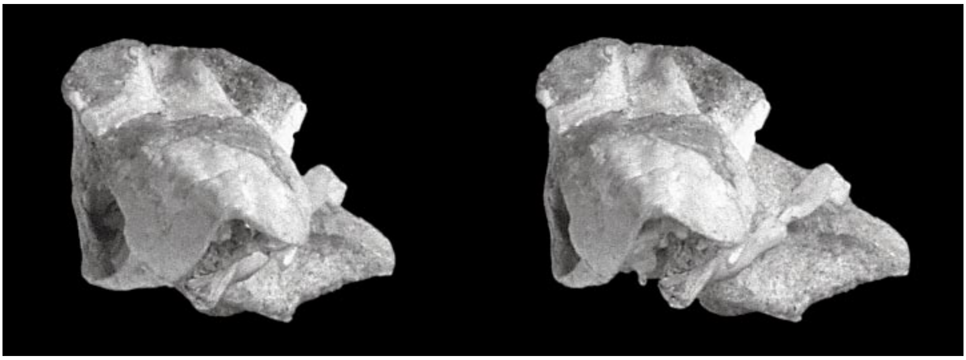

Fig. 4. Skull of *Gobipteryx minuta* (IGM-100/1011) in rostral view and interpretive drawing.

corner of the nasal process of the maxilla. This oblique maxillary-nasal bar completely separates the external nares from the antorbital cavity. The initial reconstruction by Elzanowski (1977) of a common opening for the external nares and the antorbital cavity later was corrected after additional preparation of ZPAL-MgR-I/32 (Elzanowski, 1995).

In contrast to most nonavian theropods and other basal birds such as *Archaeopteryx* and *Confuciusornis,* the nasal process of the maxilla of *Gobipteryx* does not form a recessed, medial wall lining the rostral end of the antorbital cavity. Instead, as in present-day birds, the internal and external antorbital fenestrae are subequal in size and the antorbital cavity is devoid of accessory fenestrae (see Witmer, 1997). Caudal to the nasal process, the concave dorsal surface of the caudomedial process of the maxilla forms the floor of the antorbital cavity. The caudal base of the nasal process forms a deep pocket although no pneumatic foramina perforate the maxilla in this area. The right and left maxillae do not contact each other on the ventral midline, being separated by the vomers (fig. 2).

NASAL: Only the rostroventrally directed maxillary process of each nasal is preserved. Each forms a long, thin, and transversally expanded lamina that contacts the short nasal process of the maxilla (figs. 1, 4). Based on the somewhat crushed ZPAL-MgR-I/32, Elzanowski (1977) described a premaxillary process of the nasal extending to the rostral end of the nares, underlying the frontal process of the premaxilla. In the revised study of ZPAL-MgR-I/32, Elzanowski (1995) implied that, in addition to the nasal process underlying the frontal process of the premaxilla, the nasal participates in the bar separating the nares from the antorbital fenestra. IGM-100/1011 does not support the presence of the nasal process that Elzanowski (1977, 1995) described as underlying the frontal process of the premaxilla. Based on IGM-100/1011, the only area of contact between the nasal and the premaxilla is caudal to the external nares (fig. 1). The long bones crossing both external nares of ZPAL-MgRI/32 (fig. 7) are probably portions of the frontal processes of the premaxilla, displaced by the obvious dorsal crushing of this specimen in this area. The well-preserved dorsocaudal end of the right nasal of IGM-100/1011 underlies the frontal process of the right premaxilla and indicates that dorsally, this premaxillary process must have covered a good portion of the body of the nasal.

VOMER: The vomers are in place and articulated to the right maxilla and palatine. The two vomers are fused throughout their rostral half, forming a rodlike central element that defines the medial margin of the choana (fig. 2). At the tip of this element, on each side, articulate the rostral ends of the vomerine process of the maxilla. Unlike paleognaths and perhaps *Archaeopteryx* (Witmer and Martin, 1987), the vomers of *Gobipteryx* do not appear to contact the premaxillae, as inferred from the fact that the rostral ends of the vomers appear to be complete and the premaxilla lacks any evidence of a vomerine facet.

The caudal halves of the vomers diverge slightly forming a narrow fork (fig. 2). This

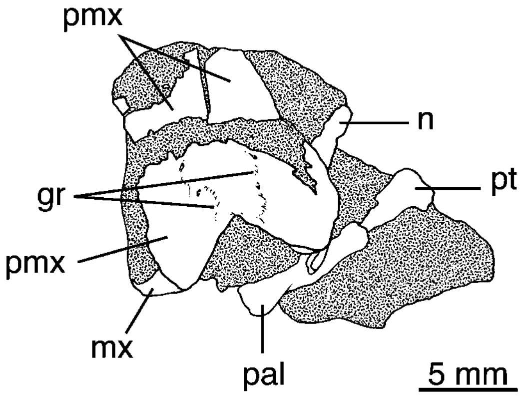

Fig. 4. Continued. Abbreviations are spelled out in the appendix.

separation starts at the level of the caudal margin of the choana. The overall shape of the vomers is different from that described by Elzanowski (1977, 1995); instead of being triangular, the vomers are parallel-sided with the fused portion narrower than the forked portion. Each vomer forms a vertically expanded lamina that caudally contacts a dorsal flange of the palatine. A similar morphology of the vomers is visible in ZPAL-MgR-I/32. The vomers in IGM-100/1011 are longer than the length given by Elzanowski (1977) (13 mm vs. 9 mm), although this is consistent with the somewhat larger size of IGM-100/1011. Elzanowski (1995) reconstructed the vomers with their fused portion much longer than their caudal, forked portion (fig. 8). The complete vomers of IGM-100/1011, however, indicate that the forked portion is indeed somewhat longer than the rostral fused section and the proportion between these two parts is similar to Elzanowski's (1977: fig 2: 1a) initial reconstruction.

PALATINE: Both palatines are preserved. The right palatine is in articulation with the right maxilla and vomer. Only the caudal half of the left palatine is preserved. It is disarticulated on top of the caudal portion of the right palatine, exposing its ventrolateral surface.

The palatine is an elongate bone with a dorsomedial flange. The rostral half of the palatine is an expanded, paddlelike lamina that ventrally overlaps the caudomedial process of the maxilla (fig. 2). The rostral end of the palatine borders the choana caudally. The medial margin of this end contacts the vomer, but caudal to this contact, there is a narrow gap separating the vomer from the palatine. At the approximate midpoint of the palatine lies the laminar and medially displaced dorsal process. This process bounds the caudal extension of the caudomedial process of the maxilla. The caudal edge of this process contacts a transverse lamina, which may be a fragment of the ectethmoid.

Elzanowski (1977) described a broad contact between the medial margin of the palatine and an unidentifiable bone (interpreted as a pterygoid by Elzanowski) immediately caudal to the vomers. However, the well-preserved right palatine of IGM-100/1011 did not contact any other bone immediately behind the vomers. The contact illustrated by Elzanowski (1977) is likely the medially displaced dorsal process of the palatine abutting against dislocated unidentifiable palatal elements. The caudal half of the palatine is laterally compressed and forms a nearly vertical flange. Caudal to the vomers, the palatines are separate from each other (fig. 2). The lateral surface of the caudal half of the palatine is convex; the medial surface is generally concave but bears a central, longitudinal ridge. Ventral to this ridge there is a well-defined concave area that probably accommodated the rostral portion of the pterygoid. The caudal tip of both palatines is missing and the palatopterygoid contact is not preserved.

PTERYGOID: A disarticulated pterygoid that we identify as the right element is preserved in ventral view (figs. 1, 2). The rostral end of this laminar, compressed bone forms a broad notch between two processes, one much longer than the other (fig. 2), greatly different from the rodlike pterygoid of extant birds (Huxley, 1867). Based on the presence of identical bones in articulation with a median element (identified as the parasphenoidal rostrum and a portion of its lamina by the daggerlike shape and terminal expansion; see Bellairs and Jenkin, 1960) in PIN-4492 (fig. 5), the shorter process is regarded to be medial and more dorsal than the longer process. The latter, laterally and more ventrally positioned, is interpreted to have overlapped the ventromedial surface of the caudal half of the palatine. If so, the rostral processes

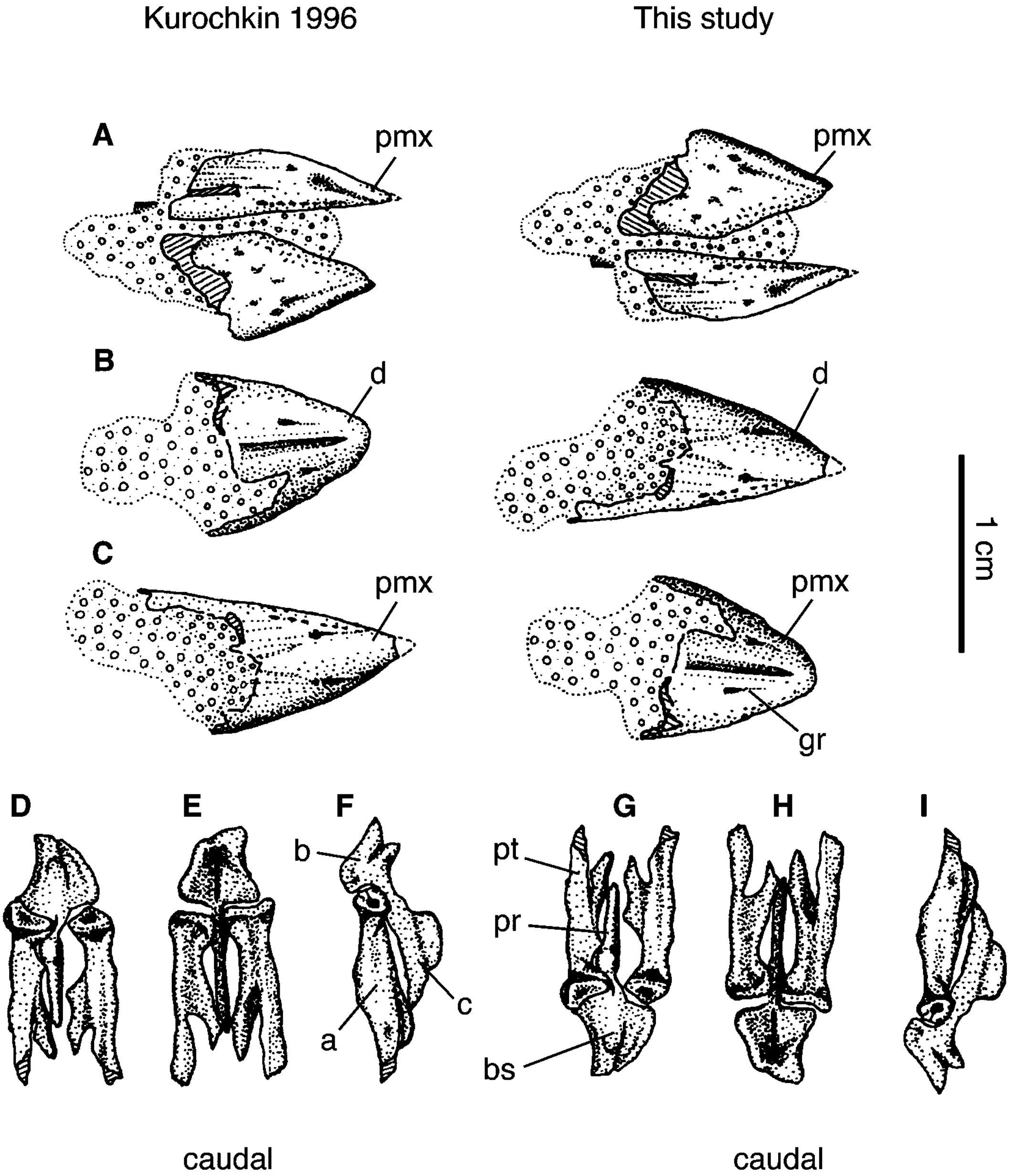

Fig. 5. Skull and mandible of *Gobipteryx minuta* (PIN-4492) as illustrated by Kurochkin (1996) and as interpreted in this study. **A,** Premaxilla and dentary in lateral view. **B,** Dentary in ventral view. **C,** Premaxilla in dorsal view. **D–I,** Pterygoids, parasphenoid rostrum, and basipterygoid in dorsal (D, G), ventral (E, H), and lateral (F, I) views. Modified from Kurochkin (1996: fig. 2). Kurochkin (1996: 10) provided the following with items D, E, and F: paired elements (**a**) rostral portions of pterygoid or pterygoid process of palatine bone; unpaired element (**b**) fused caudal portions of vomers or rostral portions of pterygoids; unpaired element (**c**) rostral portion of parasphenoidal rostrum or nasal septum of mesethmoid. Abbreviations are spelled out in the appendix.

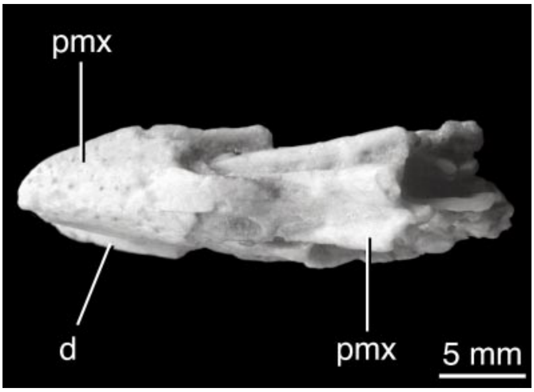

Fig. 6. Skull of *Gobipteryx minuta* (ZPAL-MgRI/32) in dorsal view. Abbreviations are spelled out in the appendix.

and main body of the pterygoid would have been oriented subvertically, with the shorter process much more dorsally positioned than the longer one. Caudal to the notch defined by these two processes, the pterygoid narrows slightly. Immediately caudal to the base of the shorter process, on what we interpret as the dorsolateral surface of the pterygoid, is a small tubercle. The caudal end of the pterygoid bears a large, elliptical facet with its main axis perpendicular to the plane of the pterygoid's body. As seen on PIN-4492, this facet is the basipterygoid articulation surface (Kurochkin, 1996). The medioventral corner of this facet is broken. This point may be the base of the quadrate flange of the pterygoid, which would have been caudodorsally projected as in nonavian theropods (e.g., *Deinonychus*, *Allosaurus*; see Ostrom, 1969; Madsen, 1976).

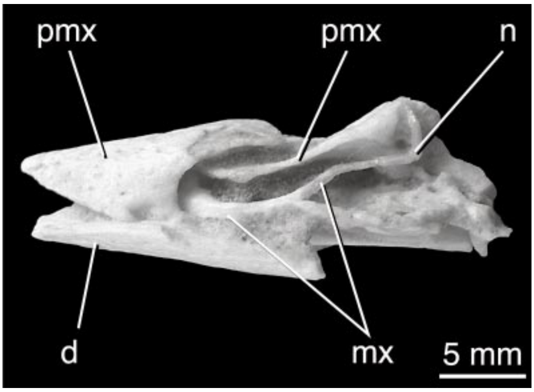

Fig. 7. Skull of *Gobipteryx minuta* (ZPAL-MgRI/32) in left lateral view. Abbreviations are spelled out in the appendix.

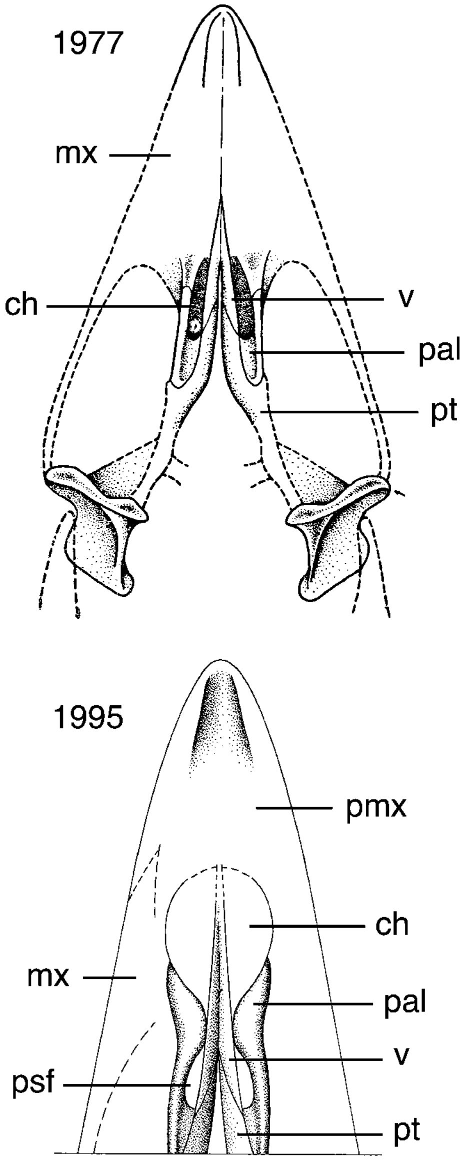

Fig. 8. Elzanowski's (1977, 1995) palatal reconstructions of *Gobipteryx minuta.* Abbreviations are spelled out in the appendix.

ECTETHMOID: A vertical, transverse bony lamina forms the caudal wall of the antorbital cavity separating it from the orbit. This element is interpreted as the ectethmoid, an ossification that in modern birds projects laterally from the interorbital septum (Cracraft, 1968). An ossification tentatively interpreted as an ectethmoid was reported for the alvarezsaurid *Shuvuuia* (Chiappe et al., 1998). Aside from this tentative report, the putative ectethmoid of *Gobipteryx* is the only known ectethmoid among Mesozoic theropods.

SCLEROTIC OSSICLES: A nearly complete sclerotic ring is preserved at the level of the caudal end of the palatine (figs. 1, 2). It appears to be that of the right orbit and it is composed of at least nine individual scleral ossicles. These ossicles are concave in lateral view, a condition typical of tubular eyes as in owls (Martin, 1985).

DENTARY: The rostral portion of the right dentary is preserved and exposed in lateral view. The tomial crest is straight and edentulous (fig. 1). On the lateral surface, somewhat ventral to the tomial crest and parallel to it, is a row of sparse mental foramina. The dentary is thicker at the symphysial region, which also constitutes the higher area of the preserved fragment. In lateral view, the ventral margin of the dentary slopes ventrocaudally at an angle of roughly 45° (fig. 1). The symphysial articulation is straight in ventral view and also angled at 45° in medial view. A scarred surface distinguishable on the medial surface of the mandible indicates that in IGM-100/1011 the two rami were not fused to each other but were firmly ankylosed. In this respect, IGM-100/1011 differs from ZPAL-MgR-I/12, ZPAL-MgR-I/32, and PIN-4492-1 in which the two rami are completely fused at the symphysis (Elzanowski, 1977; Kurochkin, 1996).

DISCUSSION

IGM-100/1011 is remarkably similar to ZPAL-MgR-I/12, ZPAL-MgR-I/32, and PIN-4492-1. ZPAL-MgR-I/12, the holotype of *Gobipteryx minuta*, is an extremely fragmentary specimen in which very few features can be interpreted with confidence. Nonetheless, IGM-100/1011 and ZPAL-MgR-I/12 share the presence of a vaulted premaxillary chamber, the grooves that lie on each side of the midline of the dorsal surface of the premaxillae, and the straight dorsal margin of the dentary. ZPAL-MgR-I/32 (figs. 6, 7) is more complete and better preserved than the holotype. All the features common to ZPAL-MgR-I/12 and IGM-100/1011 are also present in ZPAL-MgR-I/32. In addition, ZPAL-MgR-I/32 and IGM-100/1011 share the derived morphology of the complex premaxillary-maxillary articulation, the upturned tip of the premaxilla, the trough along the caudolateral edge of the premaxilla, and the pyramidal nasal process of the maxilla.

The partial skeleton described by Kurochkin (1996) as the holotype of *Nanantius valifanovi* (PIN-4492-1) includes portions of the rostral end of the premaxillae and dentaries as well as of the braincase and palate. PIN-4492-1 is essentially identical to IGM-100/1011, ZPAL-MgR-I/12, and ZPAL-MgR-I/32 in all features that co-occur in these specimens (i.e., sagittal grooves on each side of the midline of the dorsal surface of the premaxillae, straight dorsal margin of the dentary, upturned tip of the premaxilla, forked rostral portion of the pterygoid). Clearly, the differences that Kurochkin (1996) pointed out between PIN-4492-1 and *Gobipteryx minuta* (ZPAL-MgR-I/12 and ZPAL-MgR-I/32) were influenced by his mistaken interpretation of the premaxillae and dentaries. The single cranial character used in the diagnosis of *Nanantius valifanovi* is the presence of a longitudinal groove on the ventral side of the mandible (fig. 5). If this is attributed to the premaxilla, to correct Kurochkin's (1996) confusion of these elements, it may be a diagnostic feature of this taxon. However, examination of Kurochkin's (1996) plates 1c and 1d, indicates that this groove is not median but rather is displaced laterally and represents one of the pair of rostrocaudal grooves present on the dorsal surface of the premaxillae of IGM-100/1011, ZPAL-MgR-I/12, and to some extent, ZPAL-MgR-I/32. We find no evidence to recognize PIN-4492-1 as a different taxon from *Gobipteryx minuta. Nanantius valifanovi* is therefore a junior synonym of *Gobipteryx minuta.*

Perhaps the most interesting feature of IGM-100/1011 is its well preserved and articulated palate. Combined with information from other specimens, IGM-100/1011 allows an accurate reconstruction of the palate of *Gobipteryx minuta.* Based on the study of ZPAL-MgR-I/12 and ZPAL-MgR-I/32, Elzanowski reconstructed the palate of *Gobipteryx minuta* several times. The initial cursory reconstruction (Elzanowski, 1974) was emended with information provided by the discovery of ZPAL-MgR-I/32 (Elzanowski, 1976, 1977) (fig. 8). Elzanowski's 1977 reconstruction differs from his latest reconstruction (Elzanowski, 1995) mainly in the position of the choana. Whereas in 1977 he identified a pair of openings between the vomer and the palatines as the choana, in 1995 he correctly regarded these as the subsidiary palatal fenestrae and placed the choana in a more-rostral position (fig. 8). The well-preserved and articulated palate of IGM-100/1011 indicates that the choana of *Gobipteryx* opens caudal to a novel, horseshoe-shaped chamber separated from the choana by the vomerine process of the maxilla. The horseshoe-shaped chamber and the choana together composed Elzanowski's 1995 choana, because in ZPAL-MgR-I/32 the vomerine processes are not apparent.

The only pterygoid preserved in IGM-100/1011 is virtually identical to the pterygoids described by Kurochkin (1996) for PIN-4492-1. Kurochkin (1996) provided a wide range of interpretations for the identification of the palatal bones of PIN-4492-1. In all instances he identified an expanded bone attached to the parasphenoid (fig. 5) as the rostralmost element. Clearly, this element is caudal to the pterygoids and represents the basisphenoid, which forms an expansion fused to the caudal end of the parasphenoid as in extant birds (Bellairs and Jenkin, 1960). Importantly, the paired pterygoids lie in articulation with the basipterygoid processes, allowing determination of their orientation. Previous palatal reconstructions of *Gobipteryx* (Elzanowski, 1976, 1977, 1995) depict a pterygoid-vomer contact between the palatines (see also Witmer and Martin, 1987). Yet, the morphology of the nearly complete pterygoid of IGM-100/1011 suggests that this bone did not contact the vomer. In contrast to the alleged elongate pterygoids of previous reconstructions of *Gobipteryx* (e.g., Elzanowski, 1977; Witmer and Martin, 1987), the pterygoid of IGM-100/1011 is evidently too short to allow a pterygoid-vomer contact. Previous considerations of an elongate pterygoid in *Gobipteryx* are likely incorrect.

Previous to this study, *Gobipteryx minuta* was represented only by cranial material. Placement of *Gobipteryx minuta* within Enantiornithes had been based on the provisional assignment of a series of embryos from the Barun Goyot Formation of Khermeen Tsav to this species (Elzanowski, 1981) and the recognition of these embryos as enantiornithines (Martin, 1983; Elzanowski, 1995). Although unquestionably enantiornithines, morphological evidence for the identification of these embryos as *Gobipteryx minuta* had been rather weak given the lack of postcranial skeletons of the previously known material of *Gobipteryx minuta* and the poor preservation of the embryonic skulls (Elzanowski, 1981). Strong support of the placement of *Gobipteryx minuta* within Enantiornithes is provided by the synonymy of *Nanantius valifanovi* (PIN-4492-1) and *Gobipteryx minuta*. The postcranial morphology of PIN-4492-1 reveals several unquestionable synapomorphies of Enantiornithes, including the presence of a broad and deep fossa on the dorsal surface of the coracoid, a ventral margin of the furcula that is distinctly wider than the dorsal margin, a well-developed hypocleideum, a long axial groove on the interosseous surface of the radial shaft, the metacarpal III projecting distally more than the metacarpal II, and a metatarsal IV significantly thinner than the metatarsals II and III (Chiappe and Walker, in press).

Traditionally, palatal anatomy has played an important role in avian systematics (Huxley, 1867; Pycraft, 1900; Bock, 1963; Zusi, 1993). Yet, our knowledge of the palatal structure of basal birds is extremely poor (Witmer and Martin, 1987). The discovery and description of IGM-100/1011, along with the reinterpretation of PIN-4492-1 as *Gobipteryx minuta,* adds to our knowledge of the palatal structure of Mesozoic birds, and therefore, the early evolution of the avian palate.

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APPENDIX: ANATOMICAL ABBREVIATIONS

abc	antorbital cavity
bs	basisphenoid
ch	choana
d	dentary
ect	ectopterygoid
en	external nostril
gr	grooves
lmx	left maxilla
lpal	left palatine
mx	maxilla
mxar	maxillary articulation
n	nasal
pal	palatine
pch	horseshoe-shaped palatal chamber
pmx	premaxilla
pr	parasphenoidal rostrum
psf	palatal subsidiary fenestra
pt	pterygoid
rmx	right maxilla
rpal	right palatine
scl	sclerotic
v	vomer

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