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The Perinate Skull of *Byronosaurus* (Troodontidae) with Observations on the Cranial Ontogeny of Paravian Theropods

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ABSTRACT

The skulls of two perinate paravians from Ukhaa Tolgod, Djadoktha Formation, Mongolia, are described here. The skulls are nearly unique in their combination of ontogenetic age and preservational quality and provide us with the first look at the morphology of such important anatomical regions as the rostrum, palate, and braincase at or near the onset of postnatal development in a nonavian paravian coelurosaur. Based on a number of derived characters, the skulls are allocated to a derived position within Troodontidae that is outside the clade consisting of *Saurornithoides mongoliensis*, *Saurornithoides junior*, *Troodon formosus*, and probably *Sinornithoides youngi*. A single synapomorphy, presence of a lateral maxillary groove, supports the Ukhaa perinates as *Byronosaurus*. The comparative morphology of the Ukhaa perinates with adult troodontids indicates a number of significant postnatal transformations (e.g., elongation and flattening of the rostrum, increase in the number of maxillary and dentary teeth, restructuring of the occipital plate and paroccipital process). These comparisons demonstrate that many characters historically considered important for phylogenetic and taxonomic assessments of adult maniraptorans are present at a relatively early stage of ontogeny. Differences in the developmental timing of various cranial characters have important implications for interpreting the fossil record as well as for understanding the role heterochrony has played in the evolution of derived coleurosaurs, including birds. The ontogenetic information provided by the Ukhaa perinates also allow us to comment on the enigmatic paravian *Archaeornithoides deinosauriscus*, which has been considered both the sister taxon to Avialae and a juvenile specimen of the troodontids *Saurornithoides mongoliensis* and *Byronosaurus jaffei*. We found no unique characters that support a priviledged relationship of *Archaeornithoides deinosauriscus* with avialans and only weak character support for this taxon as a basal troodontid—there is no known character evidence supporting it as a juvenile of either *Saurornithoides* or *Byronosaurus*.

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INTRODUCTION

The remains of embryonic, neonate, and juvenile dinosaurs are emerging from the fossil record with increasing frequency (e.g., Norell et al., 1994; Mateus et al., 1997; Xu et al., 2001; Reisz et al., 2005; Goodwin et al., 2006; Schwarz et al., 2007; Balanoff and Rowe, 2007; Balanoff et al., 2008; Kundrát et al., 2008). This generalized trend is less obvious within Theropoda, where the number of known specimens representing these relatively early stages of skeletal ontogeny—especially those with well-preserved cranial material—continues to be extremely limited (Rauhut and Fechner, 2005). Our understanding of skeletal development and its phylogenetic patterns in this important clade, which includes the origin of birds, is equally limited. Establishing the nature and pattern of skeletal development, and the phylogenetic distribution of the features defining that development, is necessary to fully understand the characters through which we interpret the evolutionary history of this, or any, group. The implications of this understanding—or lack thereof—range from the accuracy with which specimens of different ontogenetic ages are identified taxonomically, to the precision with which the characters we use to build phylogenetic hypotheses are defined, to our ability to recognize transformations in developmental patterns. In other words, our understanding of skeletal development and its phylogenetic patterns has implications for our ability to effectively carry out many of the core objectives of morphological research. The only way to establish ourselves on the right side of these implications is by finding new ontogenetically and phylogenetically informative specimens and describe them in detail.

During the 1993 field season of the American Museum–Mongolian Academy of Sciences joint expeditions (Novacek et al., 1994), a weathered theropod nest was encountered at the rich Late Cretaceous fossil locality of Ukhaa Tolgod. This nest contained an embryo of a near hatchling oviraptorid (Norell et al., 1994, 2001a). Associated with the clutch of oviraptorid eggs were two skulls of a nonoviraptorid theropod, the extremely small size and morphology of which suggests they are either late-stage embryos or hatchlings (i.e., perinates). These specimens were noted in a short paper (Norell et al., 1994) where they were referred to as dromaeosaurids.

The purpose of this paper is to provide a detailed description of these two skulls, and in the process, critically assess both their taxonomic status and importance for our understanding of ontogenetic and phylogenetic transformations in theropod cranial morphology. The relatively high preservational quality of these skulls provides us with the first opportunity to study several aspects of cranial anatomy in a highly derived, nonavian theropod. For example, the presence of a well-preserved braincase in one of these specimens gives us our first look at many features of the otic capsule not previously described in non-avialan Maniraptora. The Ukhaa perinate skulls also allow us to comment on the status of other small, but more fragmentary, Mongolian theropods. Chief among these is *Archaeornithoides deinosauriscus*, which is based on a juvenile nonavian theropod that originally was given a privileged relationship with birds (Elzanowski and Wellnhoffer, 1992, 1993).

OCCURRENCE

The perinate skulls (IGM 100/972 and IGM 100/974; figs. 1–4) were found in a weathered nest of at least six eggs in the Late Cretaceous Xanadu sublocality of Ukhaa Tolgod, Djadoktha Formation, Mongolia (Loope et al., 1998; Norell et al., 1994; Dingus et al., 2008; fig. 5). This number probably represents only part of the total number of eggs originally deposited in the nest. Our experience at Mongolian Djadoktha and Djadoktha-like localities (Norell et al., 1995) and the observations of others (Sabath, 1991; Mikhailov et al., 1994) show that nests of this type usually contain 10 or more eggs. Because embryonic remains of an oviraptorid theropod were found inside one of the eggs (Norell et al., 1994) and other occurrences of adult oviraptorids associated with eggs of this eggshell type are documented (Osborn, 1924; Currie et al., 1993; Norell et al., 1995; Dong

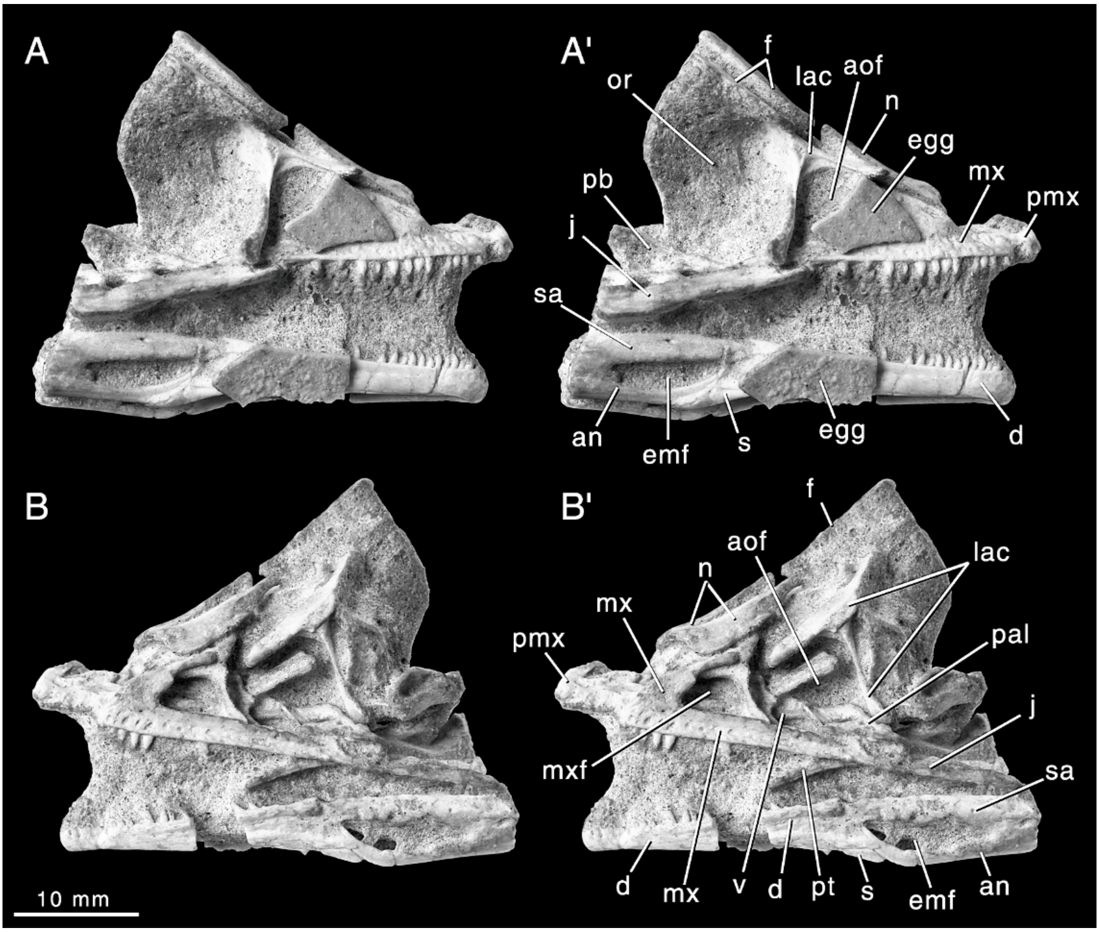

Fig. 1. Right (A, A′) and left lateral (B, B′) views of IGM 100/972, a Late Cretaceous perinate troodontid from Ukhaa Tolgod, Mongolia.

and Currie, 1996), the nest is inferred to be that of an oviraptorid dinosaur.

TAXONOMIC IDENTIFICATION

The presence of numerous teeth, a close packing of the dentition within the dentary near the rostral tip of the lower jaw, a distinct groove for the neurovascular foramina on the buccal surface of the dentary, a dorsoventrally flattened internarial bar, absence of a basisphenoid recess, and a short, largely apneumatic paroccipital process are synapomorphies present in the perinate skulls that diagnose them as Troodontidae (Xu et al., 2002; Makovicky et al., 2003; fig. 6). Within Troodontidae, these specimens are allocated to the clade comprised of all known troodontids besides *Sinovenator changii*, *Mei long*, and probably *Jinfengopteryx elegans* based on the derived presence of an extensive supraantorbital process of the lacrimal, a supraorbital shelf of the lacrimal, a wedge-shaped nasal-frontal suture, a highly pneumatized base of the cultriform process, pneumatized basipterygoid processes, and a constricted neck of the occipital condyle. Within this derived clade, the perinates lack a series of synapomorphies that would support their inclusion in the clade comprised of *Troodon formosus*, *Saurornithoides mongoliensis*, and *Saurornithoides junior*, and probably *Sinornithoides youngi*. The synapomorphies supporting the monophyly of *Saurornithoides*, *Troodon*, and *Sinornithoides*

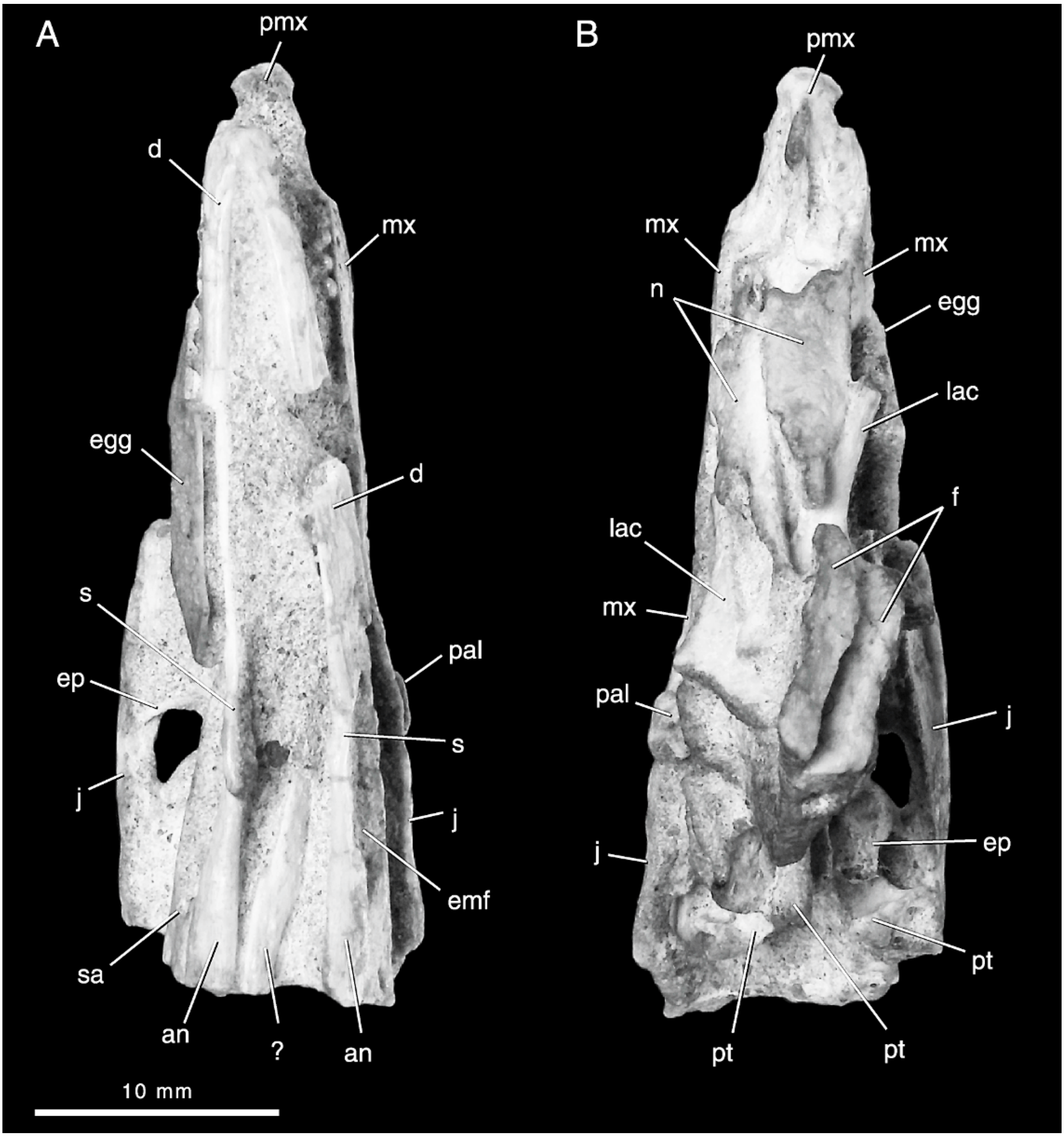

Fig. 2. Dorsal (A) and ventral (B) views of IGM 100/972.

to the exclusion of the Ukhaa perinates include a medially recurved dentary symphysis and serrated teeth. Absence of these synapomorphies does not support the allocation of the Ukhaa perinates to *Byronosaurus jaffei*—the possible sister taxon to the *Saurornithoides*-*Troodon*-*Sinornithoides* clade and the only other named taxon in this area of the tree—but it does support the Ukhaa perinates as either *Byronosaurus jaffei*, the sister taxon to *Byronosaurus jaffei*, or the sister taxon to the *Saurornithoides* et al. clade.

Byronosaurus jaffei was diagnosed as a new troodontid based on the presence of unserrated teeth, an interfenestral bar that is not recessed from the plane of the maxilla, and a shallow groove along the buccal margin of the maxilla (Norell et al., 2000; Makovicky et al., 2003). The Ukhaa perinates possess unserrated teeth and a buccal maxillary groove but

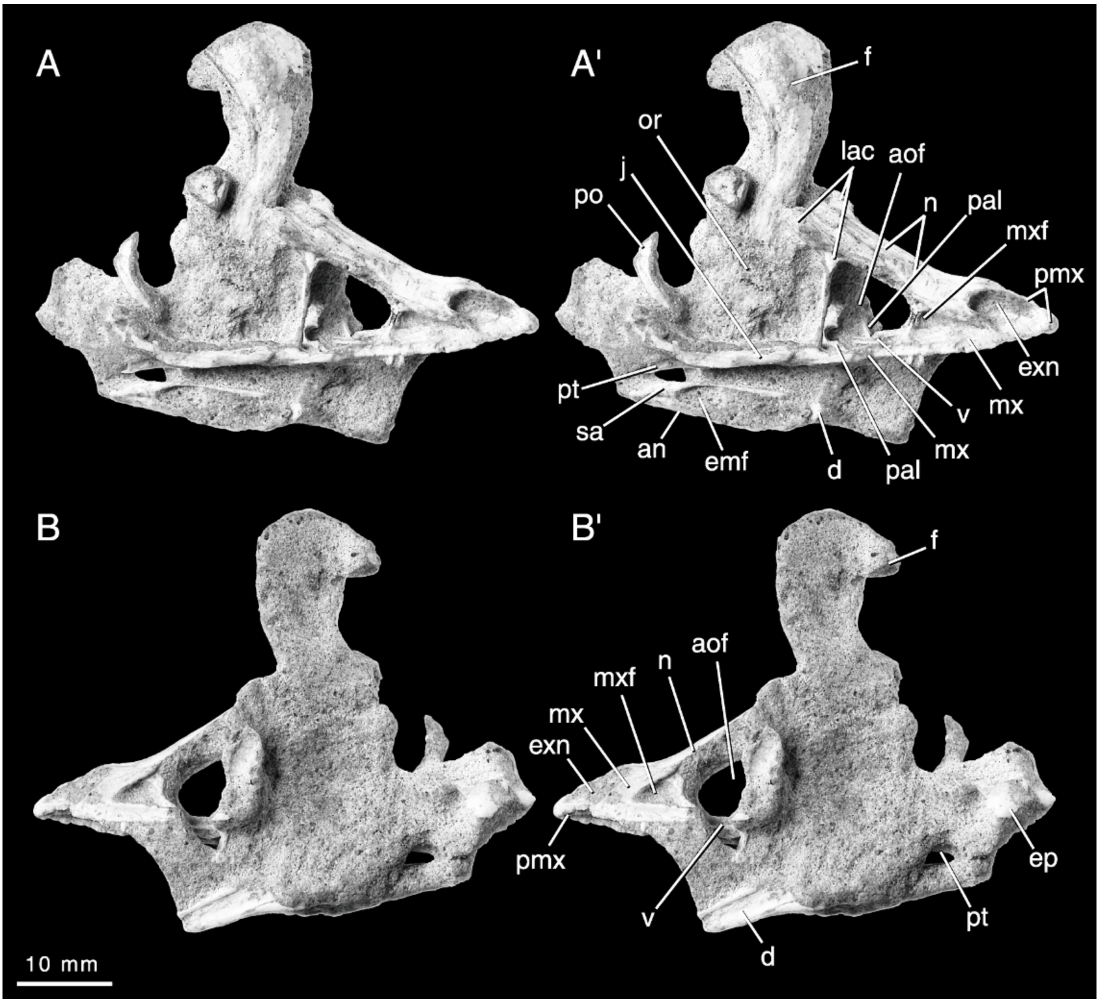

Fig. 3. Right (A, A′) and left lateral (B, B′) views of IGM 100/974, a Late Cretaceous perinate troodontid from Ukhaa Tolgod, Mongolia. The partial braincase preserved with this specimen was removed and prepared separately.

clearly have a recessed interfenestral bar. Unserrated teeth are no longer restricted to *Byronosaurus* within Troodontinae—present in *Mei long* (Xu and Norell, 2004), EK troodontid IGM 100/44, and *Urbacodon itemirensis* (Averianov and Sues, 2007). Based on this distribution and the lack of serrations in other paravians, such as *Buitreraptor gonzalezorum* (Makovicky et al., 2005), *Rahonavis ostromi* (Forster et al., 1998), and *Archaeopteryx lithographica*, unserrated teeth may be plesiomorphic for Troodontidae (with the serrated teeth of *Sinovenator changii*, *Sinornithoides youngi*, *Troodon formosus*, and both species of *Saurornithoides* representing a convergently derived condition within troodontids). As noted above, the lack of serrated teeth restricts the Ukhaa perinates from the *Saurornithoides*-*Troodon*-*Sinornithoides* clade.

The presence of a buccal maxillary groove and recessed interfenestral bar can be interpreted a number of ways. A distinct buccal groove is a derived character within troodontids found only in *Byronosaurus jaffei* and the perinate skulls and thus supports a close phylogenetic relationship between these specimens. The plesiomorphic retention of a recessed interfenestral bar may represent intra-

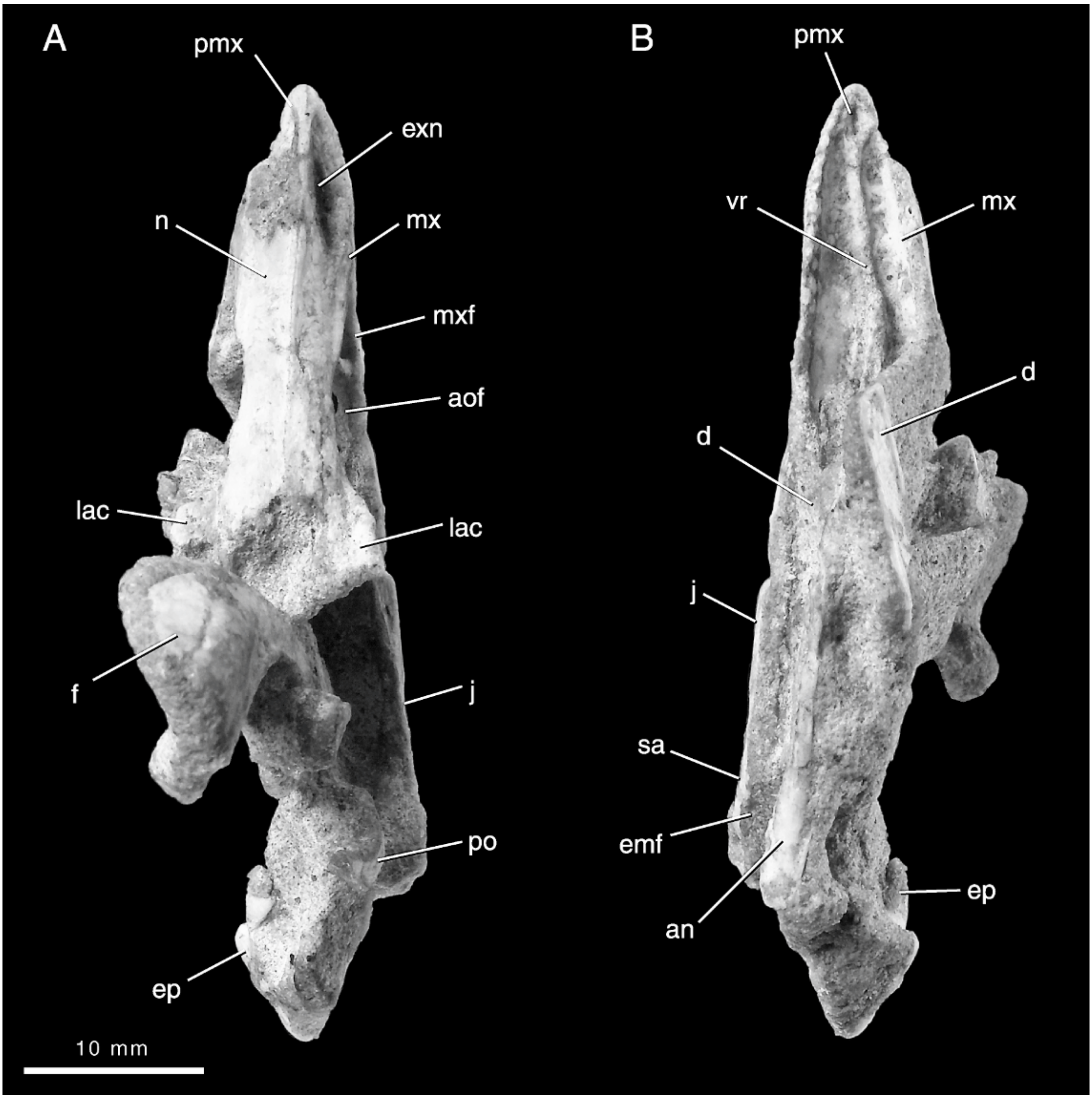

Fig. 4. Dorsal (A, A′) and ventral (B, B′) views of IGM 100/974.

specific variation within *Byronosaurus jaffei* (possibly a postnatal ontogenetic transformation). It also is possible that a buccal maxillary groove is diagnostic of a more inclusive clade that includes *Byronosaurus jaffei* and the Ukhaa perinates, with an unrecessed interfenestral bar optimized as an autapomorphy of *Byronosaurus jaffei*. In the latter interpretation, the perinate skulls could be referred to a new species of *Byronosaurus* diagnosed by the presence of the *Byronosaurus* synapomorphy (i.e., buccal maxillary groove) and the plesiomorphic lack of the *Byronosaurus jaffei* autapomorphy (i.e., recessed interfenestral bar). Considering the early ontogenetic age of the perinate skulls and the lack of a clear autapomorphy, we are conservative and refrain from naming a new species based on these specimens. Ontogenetic transformations derived from comparisons between the Ukhaa perinates and the holotype of *Byronosaurus jaffei* are optimized at the taxonomic level of *Byronosaurus* rather than *Byronosaurus jaffei*. This does not necessarily affect the implications

Fig. 5. Map of Mongolia showing the geographic position of Ukhaa Tolgod (Late Cretaceous, Djadoktha Formation).

of these interpretations but does convey our recognition that these transformations are likely to be informative at a deeper position on the troodontid tree than *Byronosaurus jaffei*.

DESCRIPTION

The preservational nature of the Ukhaa perinates restricts comparison of most standard cranial measurements. The two skulls, however, are nearly identical in size based on qualitative comparison and the few comparable measurements available (table 1). For example, greatest length of the maxilla in IGM 100/972 and IGM 100/974 (measured buccally) is 18.9 and 19.2 mm respectively, which is approximately the same as *Troodon formosus* (18 mm; Varricchio et al., 2002) and slightly smaller than the perinate holotype of *Archaeornithoides deinosauriscus* (24.5 mm; Elzanowski and Wellnhofer, 1992, 1993). Greatest length of the right maxilla in the adult holotype of *Byronosaurus jaffei* is approximately 97 mm, which is approximately 82% (5.5×) greater than the perinate maxillae. The length of the entire upper jaw (tip of rostrum to caudal margin of maxilla) in IGM 100/974 is approximately 25 mm. The ratio between this length and greatest skull length is 0.5–0.6 in *Archaeopteryx lithographica*, *Saurornithoides mongoliensis*, and *Velociraptor mongoliensis* (Elzanowski and Wellnhofer, 1993). Based on this index, greatest skull length in IGM 100/974 was approximately 5 cm (the same as estimated for *Archaeor-*

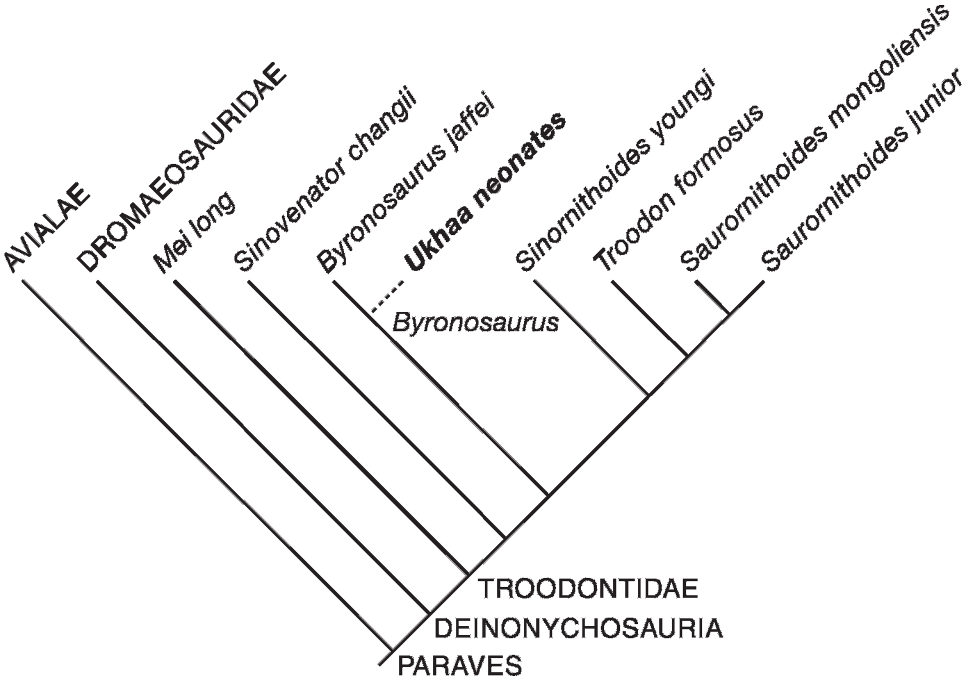

Fig. 6. Phylogenetic relationships of selected paravian taxa (after Makovicky et al., 2003). The inferred position of the Ukhaa Tolgod perinates as *Byronosaurus* is based on a series of derived characters (see text).

TABLE 1

Measurements (mm) of the perinate skulls of *Byronosaurus* from Ukhaa Tolgod

* estimated. The two measurements for length of the maxillary fenestra in IGM 100/974 refer to the right and left sides respectively.

	IGM 100/972	IGM 100/974
Length from preorbital bar to tip of rostrum	22.6	25.4
Length of maxilla	18.9	19.2
Length of upper tooth row*	20.8	21.5
Length of dentary tooth row*	?	21.1
Length of antorbital fenestra	8.7	8.3
Length of antorbital fenestra (com)	16.0*	16.9
Length of external nares	7.6	7.9
Length of maxillary fenestra	5.0	7.3, 5.0

nithoides deinosauriscus; Elzanowski and Wellnhofer, 1993).

IGM 100/972 (figs. 1, 2) is composed of a preorbital rostral region that includes at least portions of the midline vomer, right ectopterygoid, and right and left premaxillae, maxillae, nasals, frontals, lacrimals, jugals, palatines, and pterygoids. No elements caudal to the orbit are present. The preserved elements lay in loose articulation and most are slightly displaced. Two small pieces of eggshell adhere to the right rostral region. The mandibular rami are preserved back to and including the mandibular fenestrae. The preserved mandibular elements are preserved in articulation and include at least portions of the right and left dentaries, splenials, prearticulars, angulars, and surangulars.

IGM 100/974 (figs. 3, 4) is more complete than IGM 100/972 in that an unbroken right frontal is preserved, as are details of the secondary palate and braincase. The articulated shape of the rostrum exhibits little distortion. The bones of IGM 100/974, however, are less well preserved than the corresponding elements of IGM 100/972. The individual braincase elements, which include the right exoccipital/opisthotic, left prootic, and midline parabasisphenoid were removed and prepared individually. Postdentary bones of both lower jaws are present but poorly preserved in IGM 100/974.

Our description is based on a composite of IGM 100/972 and IGM 100/974. Cases of ambiguity are indicated. Comparisons with the type and referred specimen of *Byronosaurus jaffei* are based on Norell et al. (2000), Makovicky et al. (2003), and new observations. Comparisons with *Sinovenator changii*, *Mei long*, *Sinornithoides youngi*, *Saurornithoides junior*, and *Troodon formosus* are based on Xu et al. (2002), Xu and Norell (2004), Russell and Dong (1993), Barsbold (1974), Norell et al. (2009), and Currie (1985), Currie and Zhao (1993), respectively. Comparisons with *Saurornithoides mongoliensis* are based on Barsbold et al. (1987), Makovicky et al. (2003), Norell et al. (2009), and personal observations. Additional comparisons are cited independently.

ROSTRUM AND PALATE

PREMAXILLA: The paired premaxilla is attenuate rostrally (figs. 7, 8; more so than the referred specimen of *Byronosaurus jaffei*, IGM 100/984). As in other troodontids, the premaxilla is significantly smaller than the external nares (Xu et al., 2002). The premaxilla contacts the opposing premaxilla medially, maxilla caudolaterally, and nasals caudomedially. The lateral surfaces are heavily degraded; however, an identical sutural contact with the maxilla positioned rostral to the longitudinal midpoint of the narial opening is visible on both specimens. The degraded nature probably reflects fragility of perinate bone, as there is little chance the bone was subjected to surficial erosion. Both specimens were collected inside concretions and the taphonomic processes at the site are thought to be burial alive (Dingus et al., 2008).

The nasal process is thin and defines the rostrodorsal margin of the external naris. It cannot be determined definitively whether this process separates the nasals rostrally as in *Byronosaurus jaffei*, *Saurornithoides junior*, and *Velociraptor mongoliensis* (AMNH 6515). It is apparent that the nasal process meets the premaxillary process of the nasal rostral to the caudal boundary of the external naris and therefore contributes to the dorsoventrally flattened internarial bar. A flattened internarial bar is derived for Troodontidae but also is found in ornithomimids and the alvarezsaur *Shuuvia deserti*.

The maxillary process is short and pitted as in the adult. Also in agreement with *Byronosaurus jaffei* and other troodontids besides *Sinovenator changii*, the maxillary process does not exclude a nasal-maxillary contact as it does in adult dromaeosaurs and ornithomimids. The floor of the narial chamber is formed largely by the narial ramus of the premaxilla, with only a short, caudal, maxillary contribution. This morphology is similar to *Troodon formosus* but contrasts somewhat to *Byronosaurus jaffei*, in which the maxilla contributes more significantly to the narial floor. A short but distinct sagittal ridge runs along the floor of the nasal chamber. The ridge terminates caudally above a notch that is formed between the opposing premaxillae and likely marks the contact with the vomer. A longitudinal trough excavates the floor of the narial chamber on either side of the sagittal crest. It is unclear whether this excavation represents a simple concavity or a penetration of the narial ramus.

EXTERNAL NARIS: The paired external naris is approximately 8.0 mm long and 3.5 mm tall giving it a long and elliptical appearance (fig. 7). Its relative length is abbreviated compared to that of *Byronosaurus jaffei*, which extends for more than half the maxillary tooth row (this expanded adult condition previously was described as an autapomorphy of *Mei long* [Xu et al., 2002] but may be basal for Troodontidae). As in other troodontids, with the exception of *Sinovenator changii* and *Mei long*, the caudal margin of the external naris fails to overlap with the antorbital fenestra, although it does overlap with the maxillary fenestra. The nasal and maxillary processes of the premaxilla delineate the rostral margin of the naris (dorsally and ventrally, respectively), while the nasal forms the posteriorly convex caudal boundary. The ascending process of the maxilla contributes to the caudoventral narial margin—an apparently derived condition present in all troodontids besides *Sinovenator changii*, where the plesiomorphic exclusion of a maxillary participation

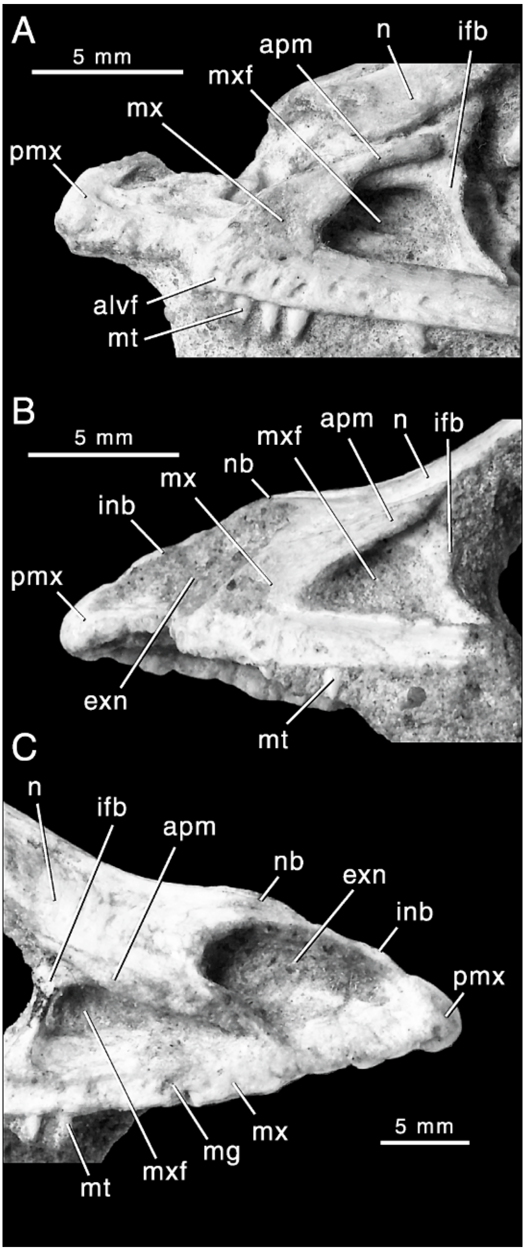

Fig. 7. Left lateral views of the rostrum in IGM 100/972 (A) and IGM 100/974 (B) and a dorsolateral view of the right side of the rostrum in IGM 100/974 (C).

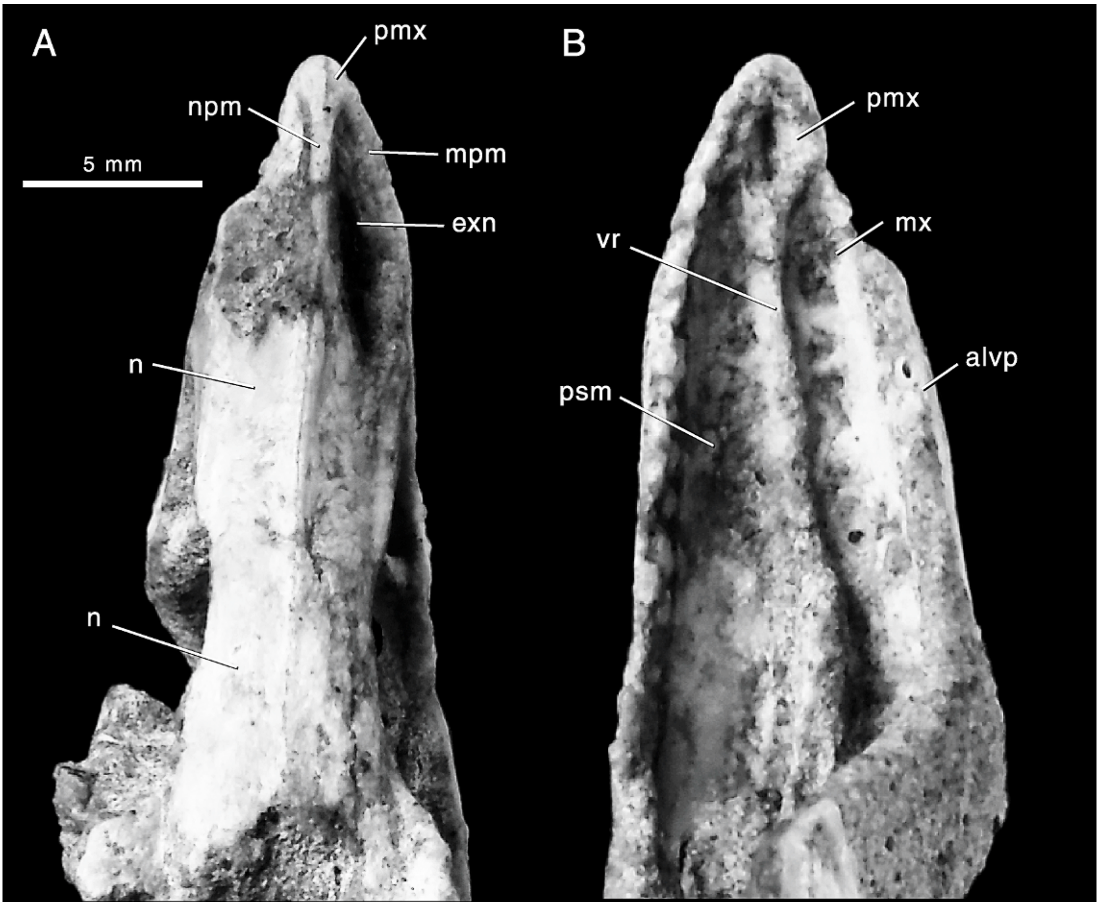

Fig. 8. Dorsal (A) and ventral (B) views of the rostrum in IGM 100/974.

in the narial border by the premaxilla is retained.

Maxilla: The triangular maxilla (lateral view; fig. 7) includes a prominent ascending process, alveolar process, and palatal shelf. The maxilla contacts the premaxilla rostromedially, vomer medially, nasal and lacrimal dorsally, and the jugal, ectopterygoid, and palatine caudally. The ascending and alveolar processes are thin compared to those of *Byronosaurus jaffei* and dromaeosaurids—more comparable in relative size to those of *Troodon formosus* (Russell, 1969; Currie, 1985). The ascending process in both the perinate and adult of *Byronosaurus* narrows distally to a fingerlike terminus that fails to contact the rostral ramus of the lacrimal (a narrow contact occurs in *Troodon formosus*; Currie, 1985). The perinate ascending process differs from that of the adult by projecting caudodorsally along a curved rather than linear trajectory (i.e., the ascending process is vertical as in other embryonic or neonate theropods [Norell et al., 1994; Dal Sasso and Signore, 1998; Rauhut and Fechner, 2005]). The alveolar ramus is laterally concave and narrows caudally into a longitudinal facet that lies medial to the jugal. The lateral concavity houses a series of foramina that correspond with maxillary tooth positions and likely transmitted branches of the maxillary nerve (CN V) and associated vasculature from the supraalveolar canal as described for *Troodon formosus* (Currie, 1985).

The interfenestral bar (pila interfenestralis) is distinctly recessed from the lateral maxillary surface (fig. 7). As noted above, the recessed condition is plesiomorphic within

Troodontidae and is present in all troodontids except the holotype of *Byronosaurus jaffei*. The overall shape of the perinate interfenestral bar differs distinctly from that of the adult, which is relatively shorter and wider. The interfenestral bar in the perinate and adult is slightly concave rostrally and oriented along a rostrodorsal-caudoventral angle. This morphology likely is plesiomorphic for *Byronosaurus* as it is present in *Troodon formosus*, *Saurornithoides mongoliensis*, and dromaeosaurids. It differs from the autapomorphically straight and vertical interfenestral bar of *Sinovenator changii* (Xu et al., 2002). The caudal margin of the perinate interfenestral bar lacks the distinct emarginations marking the caudal openings of the narial passage (dorsally) and interfenestral canal (ventrally) in the adult. The openings themselves, however, are present and described with the antorbital and maxillary fenestrae below. The interfenestral bar lies dorsal to the 9th or 10th maxillary tooth—well in front of the same landmark in *Byronosaurus jaffei* and other troodontids (e.g., above the 20th maxillary tooth [approximately] in *Sinovenator changii*). The position is similar to the dromaeosaur condition (e.g., above maxillary tooth 4 or 5 in *Velociraptor mongoliensis* [Barsbold and Osmólska, 1999], 5 or 6 in *Deinonychus antirrhopus* [Ostrom, 1969a, 1969b], and probably 3 in *Dromaeosaurus albertensis*). These comparisons are complicated by the larger, less closely packed teeth of dromaeosaurs.

The perinate maxillae have extensive, but thin, palatal shelves that contribute significantly to the formation of a complete secondary palate (fig. 8). The shelves form the rostral margin of the choanae caudally (as in *Byronosaurus jaffei*, *Velociraptor mongoliensis*, and *Tsaagan mangas*; the palate is largely unknown in other troodontid taxa, but from CT data it is apparent this architecture also is present in both species of *Saurornithoides* [Norell et al., 2009]). The shelves are individually concave and appear to join along the sagittal midline to form (in part) a conspicuous vomerine ridge that terminates rostrally just behind the tip of the snout. This termination probably occurs on the palatal surface of the premaxillae (the premaxilla-maxilla suture is indistinct). The height of the vomerine ridge may be exaggerated due to mediolateral compression—the right maxilla is pushed slightly under the left—but the ridge itself appears to be real. The dorsal surface of the palatal shelves helps floor the antorbital cavity and maxillary antrum and is described with those structures below.

NASAL: The paired nasals exhibit a midlength constriction and thus a slight hourglass shape in dorsal view (fig. 8A). The nasals are wider rostral to this constriction where they contact the ascending processes of the maxilla ventrally (fig. 7). Like the other rostral bones, the nasal is proportionally shorter than in adult paravians (including *Byronosaurus jaffei*). A distinct midline ridge achieves its greatest development directly above the nares. In lateral view, the dorsal margin of the nasal is arched rostrally but grades into a nearly flat surface caudally. This rostral arch forms a distinct nasal boss (fig. 7B, C) that may reflect an expansion of the underlying nasal cavity (visible only in IGM 100/974). This boss is not present in *Byronosaurus jaffei* but is to some degree in *Sinovenator changii* and *Mei long*. The nasal narrows caudally to a fingerlike process that cups the triangular rostral margin of the frontal (fig. 8A). The shape of this suture compares closely with *Byronosaurus jaffei* and *Saurornithoides junior* (Barsbold, 1974), whereas a transverse suture is present in *Mei long*, dromaeosaurs, and basal avialans. The rostral margin of the nasals is deeply concave where it forms the caudal margin of the external nares. Despite a dramatic postnatal elongation of the snout, the perinate nasals agree with those of the adult in terminating just behind the preorbital bar.

A sharp demarcation between the dorsal and lateral nasal surface is not apparent except where the nasal overlies the ascending process of the maxilla. In this region, the lateral margin is deflected, so it faces dorsally rather than laterally and forms a small shelf (fig. 8A). This deflected condition is similar to that described for *Sinovenator changii* (Xu et al., 2002) and more dramatic than the slightly deflected condition of most other theropods, including *Byronosaurus jaffei*. A row of small foramina lies within the nasal on the dorsal surface of the rostrum. These foramina parallel the nasal-maxillary suture as in *Byronosaurus jaffei*, *Troodon formosus*, *Velociraptor mongoliensis* (Sues, 1977), *Tsaagan mangaas* (Norell et al., 2006), and *Deinonychus antirrhopus* (Ostrom, 1969b). The foramina likely are not pneumatic as a pneumatic recess of the nasal is not visible (unknown in troodontids even with CT data; Witmer, 1997a; Norell et al., 2009). The nasal overlies the rostral process of the lacrimal caudally. The lacrimal contact extends for nearly half the preserved length of the nasal.

LACRIMAL: The paired lacrimal is a slender, T-shaped element (fig. 9). The lacrimal contacts the nasal rostromedially, frontal medially and caudomedially, and the jugal (and possibly palatine) ventrally. The ventral ramus (preorbital bar) separates the orbit from the antorbital fossa and is compressed rostrocaudally with a transverse breadth that is expanded relative to the slender dromaeosaur condition (Ostrom, 1969b; Sues, 1977). The shaft of the preorbital bar twists slightly and widens ventrally before contacting the jugal. A ridge, comparable to that described for *Troodon formosus* (Currie, 1985), extends down the rostrolateral margin. The vertical angle of the preorbital bar in both perinate skulls supports the same morphology in the adult, whose vertical orientation was considered to possibly be the result of postmortem distortion (Makovicky et al., 2003). A vertical preorbital bar is a potential synapomorphy of *Byronosaurus* as it is angled in other troodontids (e.g., *Saurornithoides junior* and *Mei long*). The ventral articulation with the jugal occurs along a horizontal surface that is expanded relative to the shaft. The vertically oriented, lateral facet described for *Troodon formosus* (Currie, 1985) is not evident in *Byronosaurus*, although, a small, medial articulation with the palatine may have been present in the perinates. The foramen described as opening caudolaterally near the lacrimal-jugal contact in *Bryonosaurus jaffei* (Makovicky et al., 2003), and likely housing a diverticulum of the antorbital sinus (Witmer, 1997a), is not apparent in either perinate skull.

The lacrimal exhibits extensive dorsal exposure that is exaggerated caudally where a shelflike process overhangs the rostrodorsal margin of the orbit (derived condition known in *Byronosaurus jaffei*, *Troodon formosus*, and *Saurornithoides junior*; fig. 9A). The caudal margin of the supraorbital process (caudal ramus) lies in a transverse plane that is well posterior to the caudal margin of the nasal (as in the adult; Makovicky et al., 2003). The supraantorbital process (rostral ramus) also is extensively developed but, in contrast to the dorsoventrally compressed caudal ramus, is cylindrical in cross-sectional shape. The rostral ramus forms the entire dorsal margin of the antorbital fenestra in IGM 100/972, whereas in IGM 100/974 the same process forms only the caudal half of this margin (with the rostral half formed by the nasals). This may reflect postmortem damage or variation in the extent of ossification. The rostral ramus is longer than the caudal ramus in agreement with *Byronosaurus jaffei*, *Troodon formosus*, *Saurornithoides junior* and *mongoliensis*, and *Sinornithoides youngi* and in contrast to *Mei long*, dromaeosaurs, and avialans. The lateral margin of the rostral ramus is visible dorsally, whereas its medial margin is overlain by the nasal.

A lacrimal boss (fig. 9A, B) overhangs the preorbital bar and although more distinct in IGM 100/974 (where it results in a triangle-shaped dorsal surface), it is less prominent in the perinates than in *Byronosaurus jaffei*. A recess lies below this boss in the junction between the rostral ramus and preorbital bar. The recess delineates the caudodorsal corner of the antorbital fossa and likely housed a diverticulum of the antorbital sinus (recessus pneumaticus lacrimalis; Witmer, 1997a). A foramen lies in the deepest part of the recess in the left lacrimal of IGM 100/972 and the only visible lacrimal of IGM 100/974 (right), and just outside the recess in the right lacrimal of IGM 100/972. This position corresponds to the nasal aperture of the nasolacrimal canal as described for *Byronosaurus jaffei* (Makovicky et al., 2003). The typical course in theropods, including *Troodon formosus* (Currie, 1985), is for the nasolacrimal canal to penetrate the lacrimal on the medial surface of the rostral ramus and pass posterolaterally (Sampson and Witmer, 2007). The perinate foramen is thus interpreted to be the caudal opening of the nasolacrimal canal. It should be noted that the lacrimal of *Troodon formosus* lacks any lateral

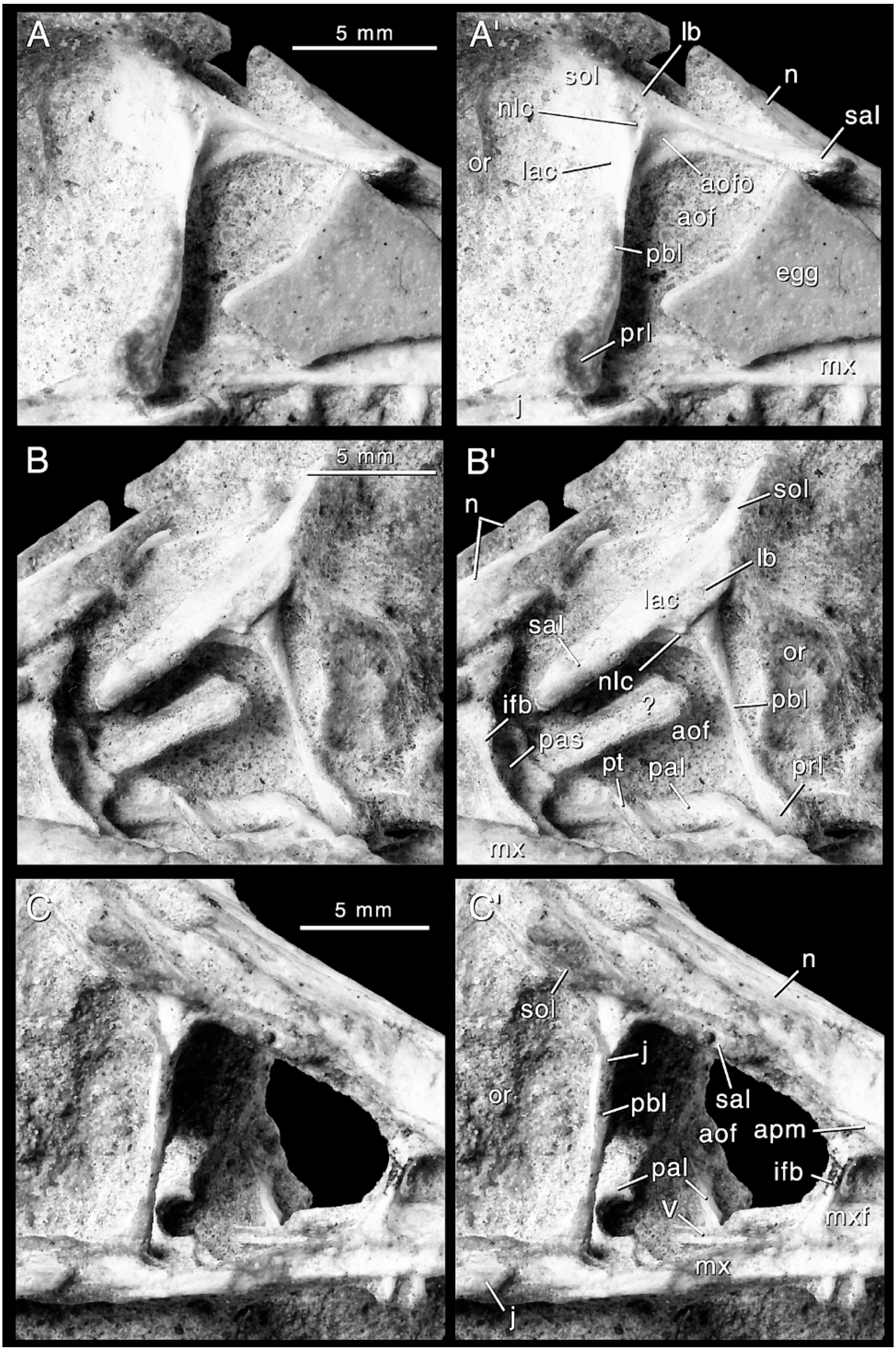

Fig. 9. Lacrimal and surrounding region of IGM 100/972 (A, A′ right; B, B′ left) and IGM 100/974 (C, C′, right).

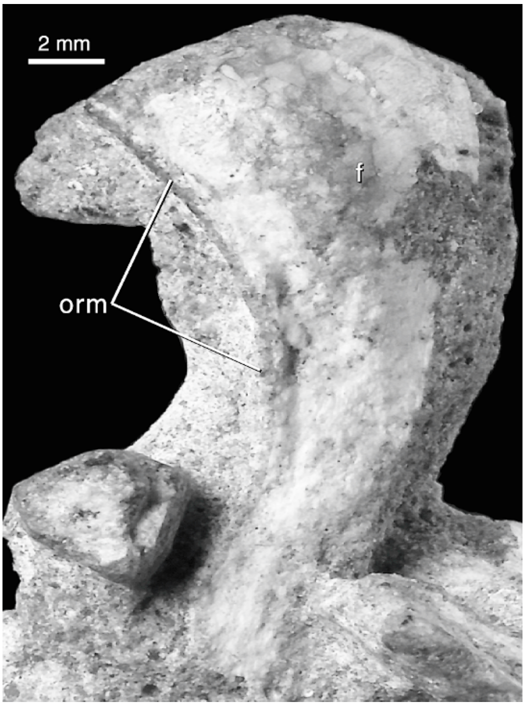

Fig. 10. Dorsal view of right frontal of IGM 100/974.

apertures; Currie, 1985; Witmer, 1990). As noted by Makovicky et al. (2003), a nasolacrimal duct (or at least its osteological correlate) previously was considered absent in troodontids (Currie and Dong, 2001), suggesting its presence in *Byronosaurus* may be derived within troodontids. The condition in *Mei long* and *Sinovenator changii* is difficult to interpret, but a nasolacrimal canal also appears to be present in *Troodon formosus* and both species of *Saurornithoides*. There is no evidence of a groove on the medial surface of the lacrimal (or the nasal) in either of the Ukhaa perinates indicative of a suborbital nasal gland (Witmer, 1997a), however, these surfaces are largely obscured by matrix making their absence far from definitive.

FRONTAL: The right and left frontal in IGM 100/972 are represented by poorly preserved fragments that lie above the orbit and meet each other along a clearly visible midline suture. These fragments extend rostrally to a position adjacent to the anterior orbital margin. Their articulation with the nasals is not retained. A nearly complete, although displaced, right frontal is present in IGM 100/974 (figs. 3, 10). This element is more complete than in *Byronosaurus jaffei* and thus provides novel information for this part of the troodontid tree. The frontal is elongate with a strongly curved lateral margin that contributes significantly to the dorsal orbital boundary. The medial margin, which formed the apparently unfused suture with the opposing frontal, is relatively straight but with a slight medial bow. The frontal is narrow rostrally but with an overall triangular shape comparable to the frontal of *Troodon formosus* (Currie, 1985). The caudal margin, which in *Troodon formosus* articulates with the parietal medially and contributes to the rostral margin of the supratemporal fenestra laterally, is rounded in outline and lacks a clear distinction between the parietal suture and supratemporal boundary. This is in contrast to the heavily angled caudal margin of *Troodon formosus* and likely is due, at least in part, to the ontogenetic age of IGM 100/974. For example, the frontoparietal fontanelle, which closes postnatally in at least some ratite birds (Balanoff and Rowe, 2007), may not be completely closed in the Ukhaa perinates. The caudodorsal surface of the frontal lacks the distinct sculpturing that marks the rostral origins of the temporal musculature in *Troodon formosus*. The dorsal surface, in general, is more convex and bulbous than that of *Troodon formosus*—frontal shape apparently reflects the shape of the forebrain early in ontogeny before thickening and flattening during postnatal growth. The supraciliary rim is preserved as a slightly everted crest bounded laterally by a shallow but distinct trough. This margin reveals no distinct foramina or fine grooves that may reflect the presence of a birdlike supraorbital nasal gland (Gauthier, 1986; Witmer, 1997a) as described for *Troodon formosus* (Currie, 1985). The osteological correlates of a supraorbital nasal gland also are lacking in *Sinornithoides youngi* (Russell and Dong, 1993). Also in apparent agreement with *Sinornithoides youngi* and the observations of Makovicky and Norell (2004), the lateral frontal margin in IGM 100/974 shows no evidence of a separate prefrontal ossification as described for *Troodon formosus* (Currie, 1985). The vertical lamina of the frontal that borders the lacrimal in *Sinovenator changii* is absent in IGM 100/974, *Byronosaurus jaffei*, *Mei long*, and more derived troodontids.

JUGAL: The jugal is best preserved on the right side of IGM 100/972 (figs. 1A, 11). As in the adult, it is thin, elongate, horizontally oriented and forms visible contacts with the maxilla and palatine rostromedially, ectopterygoid and pterygoid caudomedially, and lacrimal rostrodorsally. The jugal forms the caudoventral corner of the external antorbital fenestra and the ventral orbital margin. The jugal's contribution to the antorbital fossa is dorsoventrally flattened and contains a distinct fossa. This fossa rotates slightly as it extends caudally so that it opens dorsolaterally as a troughlike groove below the orbit (fig. 11). The fossa gradually shallows as the jugal assumes a mediolaterally compressed shape near its ectopterygoid contact. The fossa likely housed a portion of the antorbital sinus (at least rostrally). There is no visible penetration that would suggest internal pneumatization (as in *Deinonychus antirrhopus* [Witmer, 1997a], *Tsaagan mangaas* [Norell et al., 2006], and a large number of other theropod taxa—including *Saurornithoides junior* [Norell et al., in 2009]).

ECTOPTERYGOID: The troodontid ectopterygoid is not well known and is unknown for *Byronosaurus jaffei*, so its presence in IGM 100/972 provides important new information. The perinate ectopterygoid (fig. 11) is triradiate with prominent jugal, pterygoid, and maxillary processes as in dromaeosaurs and other closely related maniraptorans (Ostrom, 1969b; Sues, 1978; Currie, 1995). The lateral jugal process has a strong caudal hook. The medial pterygoid flange is large and inflated relative to that of *Saurornithoides junior* and adult dromaeosaurs (Currie and Zhao, 1993). A ventrally positioned recess marks the position through which a diverticulum (likely from the suborbital air sac) pneumatized an internal cavity within this process (Currie and Zhao, 1993; Witmer, 1997a). A similar ventral recess is present in *Saurornithoides junior*; however, it is blind with no associated internal pneumatic cavity. A dorsal trough lies medial and rostral to the inflated part of the pterygoid flange. This trough deepens caudally and in this sense is similar to the conspicuous "pit" on the dorsal surface of the ectopterygoid in *Saurornitholestes langstoni* (Sues, 1978) and *Deinonychus antirrhopus* (Ostrom, 1969b). This dorsal recess also may be associated with the suborbital sinus (more likely for the dorsal than ventral recess; with the latter possibly formed from a middle ear sac or novel diverticulum; Witmer, 1997a). The dorsal and ventral recesses do not communicate in *Byronosaurus* (in agreement with *Deinonychus antirrhopus*). The dorsal recess could not previously be scored in any troodontid, but its presence appears to be derived for Deionychosauria with an apomorphic loss in *Dromaeosaurus albertensis*.

VOMER: The vomer is a midline element that contacts the maxillae rostrolaterally and palatines laterally (fig. 9B, C). The vomer is mediolaterally compressed where it forms the medial margin of the choanae. The vomer is preserved behind the secondary palate, but its caudal terminus is not preserved in either of the perinates. The relationship of the vomer to the vomerine ridge (fig. 8B) is unclear. Also unclear is whether the vomer extended the entire length of the palate to contact the premaxillae rostrally as in many nonavian theropods (e.g., *Allosaurus fragilis* [Madsen, 1976], *Velociraptor mongoliensis* [Barsbold and Osmólska, 1999], *Tsaagan mangaas* [Norell et al., 2006]); however, as noted above, the vomerine ridge terminates just behind the tip of the snout on the premaxilla. The vomer in *Byronosaurus jaffei* was interpreted to terminate at a position caudal to the external nares (Makovicky et al., 2003).

PALATINE: The palatines are poorly preserved in *Byronosaurus jaffei* making their presence in the perinates especially important. The paired palatine (fig. 12) is a relatively flat element lying medial and just rostral to the preorbital bar of the lacrimal. It contacts the alveolar process of the maxilla laterally, jugal caudolaterally, vomer medially, and probably the pterygoid caudomedially—the latter articulation is not preserved in either perinate specimen, probably due to displacement of the pterygoids. The most distinctive feature is a large, rostrally positioned U-shaped notch that forms the caudal choanal margin and is defined by a vomeropterygoid process medi-

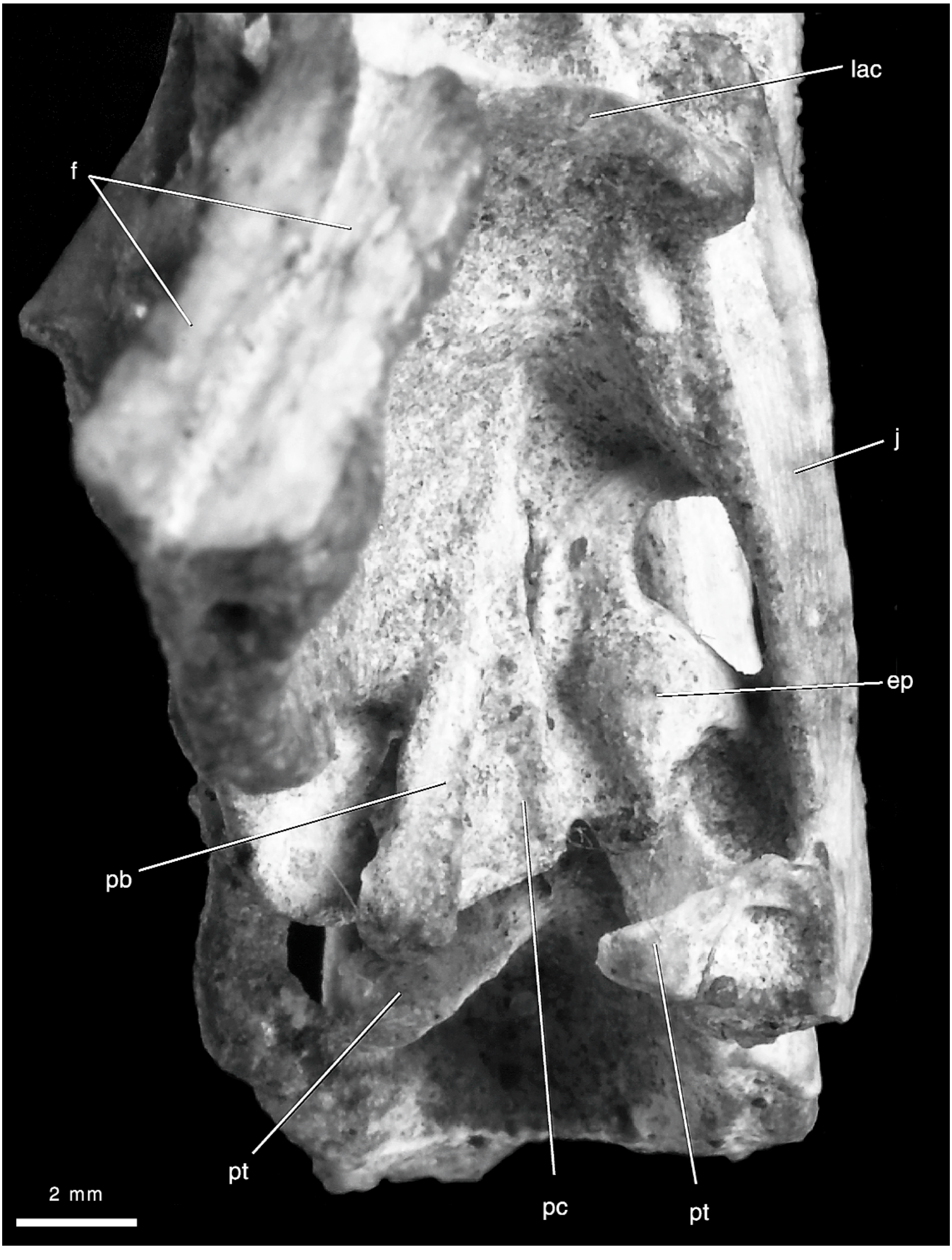

Fig. 11. Right dorsolateral view of the caudal half of IGM 100/972 showing the right ectopterygoid and jugal, the caudal ends of both pterygoids, and the rostral end of the parasphenoid process of the parabasisphenoid.

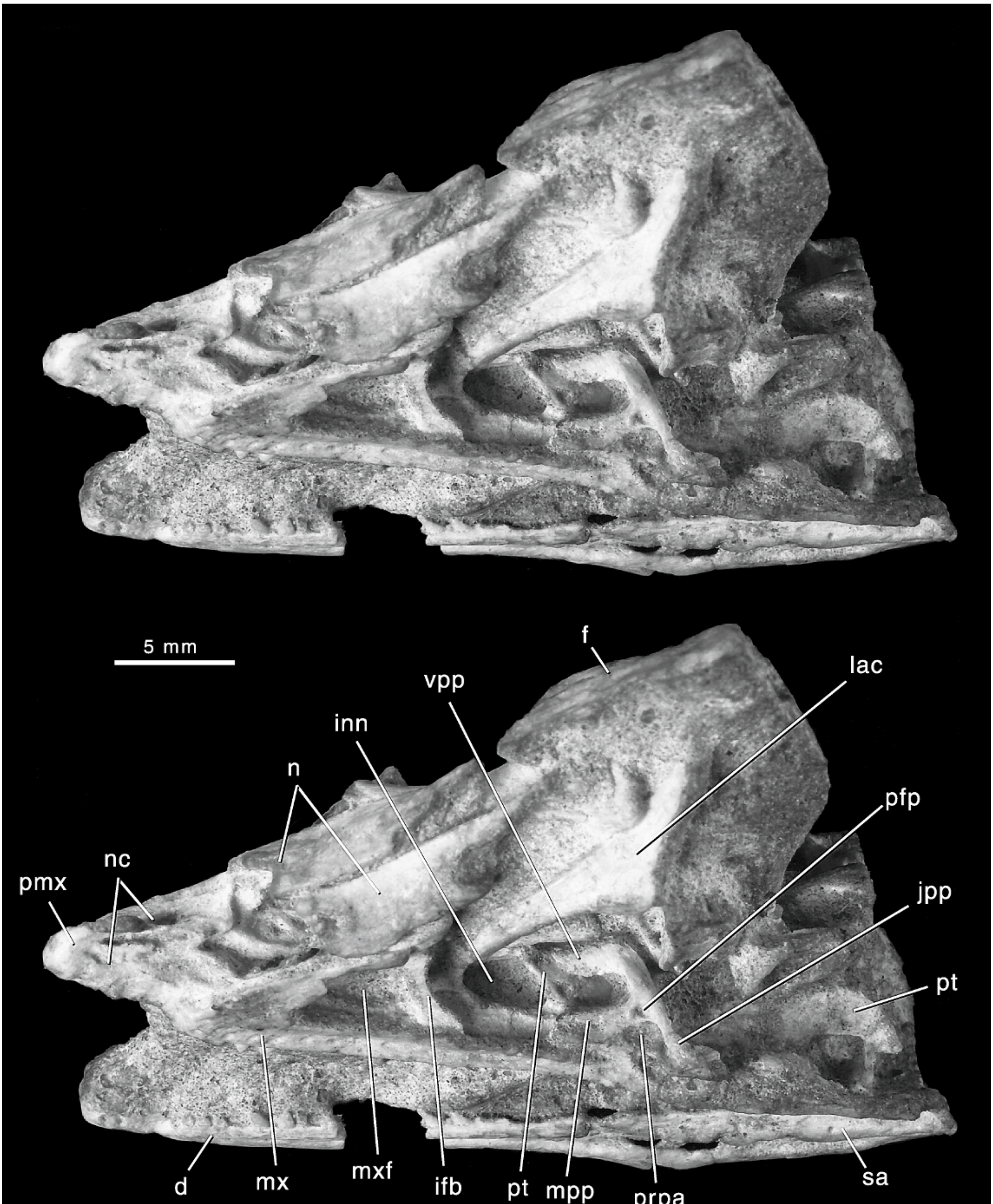

Fig. 12. Left dorsolateral view of IGM 100/972. Note the broad lacrimal shelf and well-preserved left palatine.

ally and maxillary process (facies articularis maxillaris) laterally. Both processes are significantly broader mediolaterally than the fingerlike processes of *Deinonychus antirrhopus* (Ostrom, 1969b; Witmer, 1997a). The rostral margins of both processes slant caudomedially. A dorsal ridge along the caudal margin of the choana slopes medially and laterally to the base of the vomeropterygoid and maxillary processes, respectively.

The maxillary process contains a short, dorsal ridge that parallels the lateral margin of the choana and delimits a shallow trough. A foramen lies at the caudal end of the trough directly adjacent to a prominent, caudomedially directed cavity. This cavity (recessus pneumaticus palatinus) agrees in general position with the same structure in *Deinonychus antirrhopus* (Ostrom, 1969b), *Velociraptor mongoliensis* (Norell et al., 2004), *Archaeopteryx lithographica* (Elzanowski and Wellnhofer, 1996; Witmer, 1997a), and *Saurornithoides mongoliensis* (Norell et al., 2009), and is interpreted as having housed a diverticulum of the antorbital sinus. The single foramen adjacent to the recess also is interpreted to be pneumatic in origin and likely opens into an internal pneumatic cavity. A single pneumatic foramen on the dorsal surface of the palatine is known in a small number of coelurosaur taxa (e.g., *Tyrannosaurus rex*; AMNH 5027) but was previously undescribed in a troodontid (Witmer, 1997a).

The caudal margin of the palatine has a transverse orientation medially but curves posteriorly to form a lateral jugal process. The long medial surface and distinct pterygoid process of other theropods (e.g., *Deinonychus antirrhopus*; Ostrom, 1969b) is absent. The jugal process is shorter than in *Deinonychus antirrhopus*. The medial surface of this process is deeply excavated—probably by the antorbital sinus. The resultant fossa is not visible in a strict dorsal view but opens ventrolaterally. The fossa is positioned caudoventral and lateral to the aforementioned recessus pneumaticus palatinus. The lengths of these two pneumatic fossae overlap but are not wholly confluent—being separated by a small longitudinal ridge. A much larger dorsal ridge separates these cavities from a small but distinct fossa that excavates the caudomedial surface of the jugal process. This fossa is an osseous signature of the m. pterygoideus pars dorsalis and is considerably smaller than the same fossa in *Deinonychus antirrhopus* (possibly reflecting the small size and early ontogenetic age of the Ukhaa perinates). The lack of a distinct pterygoid process eliminates an osseous demarcation of the space housed by the dorsal pterygoideus laterally and subsidiary palatal fenestra medially (compare to *Archaeornithoides deinosauriscus* [Elzanowski and Wellnhofer, 1993; fig. 4c]).

Pterygoid: The pterygoids are not visible in IGM 100/974 and are not preserved in *Byronosaurus jaffei*. The right and left pterygoid are present in IGM 100/972 and are preserved (at least approximately) in their expected life positions at the caudal end of the palate (figs. 11, 12). Some displacement, however, certainly has occurred making the exact positional relationships and bony contacts difficult to interpret. The dorsal surface of the left pterygoid is visible for most its length, although its medial surface is embedded in matrix. The rostral extent of the right pterygoid and the entire ventral surface of both pterygoids are obscured by matrix. A short length of a dorsoventrally compressed bone that tapers to a point is visible through the left choana. This element appears to be displaced and may represent the broken rostral tip of the right pterygoid.

The pterygoids do not meet along the midline caudally and thus a long interpterygoid vacuity is retained. It is unclear whether a midline contact occurred rostrally; however, based on the shape of the left pterygoid, such a contact is unlikely. If a rostral contact did occur, it probably did not form at the extreme tip (as in *Allosaurus fragilis*), but rather in the anterior half of the pterygoid with subsequent rostral divergence. The pterygoids of *Saurornithoides mongoliensis* lack a medial contact (Norell et al., 2009). The tapered rostral tip of the pterygoid is cylindrical in cross-sectional shape. This shape transforms caudally into a dorsoventrally compressed plate. This platelike morphology is most obvious where the pterygoid contacts the ectopterygoid along a distinct caudolateral flange (the rostral margin of this "pterygoid flange" may also contact the palatine), and is similar to that of *Deinonychus antirrhopus* (Ostrom, 1969b) and *Dromaeosaurus albertensis* (Currie, 1995). The caudal end of the flange curves dorsolaterally to form a flat, posteromedially facing facet that articulates with the basipterygoid process of the basisphenoid. A well-developed pterygoid flange previously was scored only for *Saurornithoides mongoliensis* within Troodontidae (Turner et al., 2007a, 2007b). A thin, ventrolaterally projecting process defines a lateral notch that accepts the pterygoid ramus of the quadrate rostral to the basipterygoid articulation.

ANTORBITAL AND MAXILLARY FENESTRA: The lateral rostral surface is characterized by a large, polygonal external antorbital fenestra and a smaller, triangular maxillary fenestra (subsidiary antorbital fenestrae; see Witmer, 1997a). These fenestrae (figs. 1, 3, 7, 9, 13) are less elliptical and elongate than those of *Byronosaurus jaffei* and other troodontids whose long and low maxillary fenestra was considered a derived shape shared with ornithomimosaurs (Witmer, 1997b).

The external antorbital fenestra is delineated by the lacrimal caudally (preorbital bar) and caudodorsally (supraantorbital process), and the maxilla rostrally (interfenestral bar) and ventrally (alveolar process). The nasal contributes to the dorsal margin—between the supraantorbital process of the lacrimal and ascending process of the maxilla. The rostral tip of the maxillary process of the jugal emerges from beneath the distal end of the preorbital bar to form the caudodorsal corner of the fenestra. Because the interfenestral bar is recessed, the external antorbital fenestra technically extends to the ascending ramus of the maxilla, with the maxillary fenestra lying medial to it. To ease comparisons with the adult (where the bar is not recessed), we describe the rostral and caudal limits of the perinate antorbital and rostral fenestrae respectively based on the position of the interfenestral bar. The internal antorbital fenestra is not well ossified leaving a broad communication between the antorbital and nasal cavities. The antorbital fossa (as defined by Witmer, 1997b) is relatively narrow mediolaterally. The lacrimal antorbital fossa is characterized by a dorsal and ventral widening

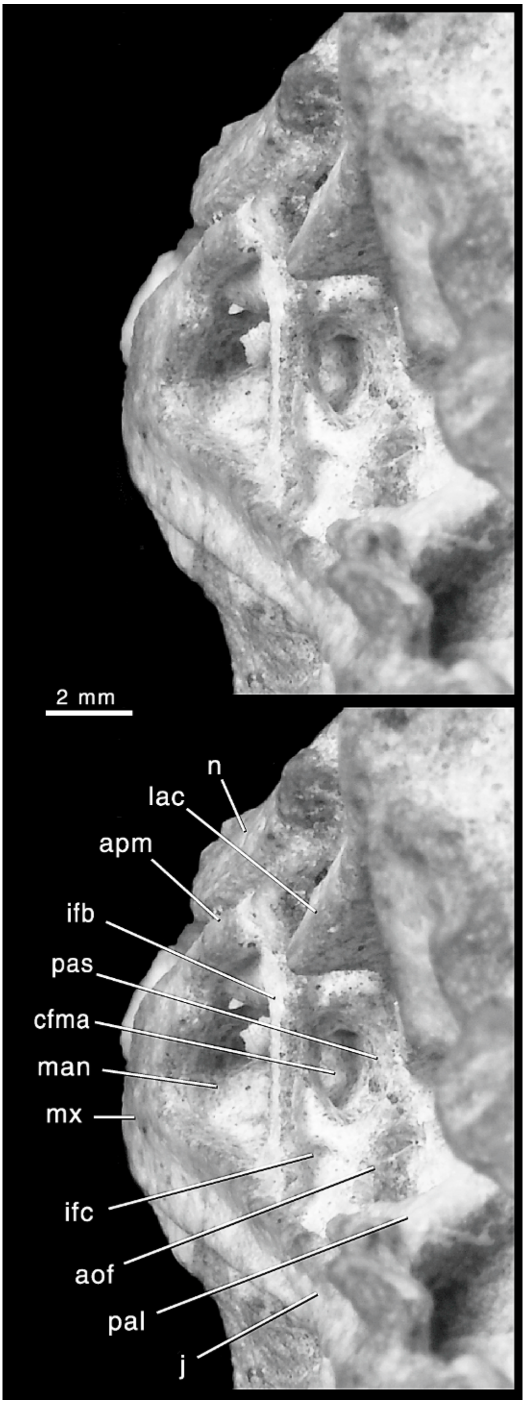

Fig. 13. Left caudolateral view of the rostrum of IGM 100/972 showing the rostral walls of the antorbital fossa and maxillary antrum.

of the preorbital bar (fig. 9A). The dorsal widening forms a distinct pocket (recessus pneumaticus lacrimalis) that housed a diverticulum of the antorbital sinus as well as the caudal aperture of the nasolacrimal canal (see above). No pneumatic foramen or internal pneumatic cavities are associated with this recess (also lacking in *Troodon formosus*). The lacrimal pneumatic recess is delineated medially by a short, oblique crest (forming the caudodorsal corner of the internal antorbital fenestra) and laterally by the vertical ridge that extends along the rostrolateral margin of the preorbital bar (fig. 9). The maxillary antorbital fossa is characterized by a ventral widening of the interfenestral bar. As noted above, this surface is penetrated by a foramen and canal (fig. 13; interfenestral canal of Makovicky et al., 2003). The foramen actually is a slitlike opening that begins in the dorsal surface of the alveolar ramus of the maxilla and widens rostrodorsally where it extends into the base of the interfenestral bar. A series of small openings pierce the maxilla along this slitlike structure culminating with the large interfenestral canal between the antorbital fossa and maxillary antrum. The smaller foramina, which penetrate the alveolar ramus of the maxilla, are interpreted as having communicated branches of the maxillary nerve (CN V) and its associated vasculature into the supraalveolar canal. The interfenestral canal likely communicated a diverticulum of the antorbital sinus, although portions of the maxillary vasculature also may have traversed this opening. The fenestra's ventral position indicates the m. pterygoideus pars dorsalis extended well into the antorbital fossa but did not fill it—the neurovascular bundle consistently lies dorsal to this muscle in sauropsids (Witmer, 1997a). The interfenestral canal is positioned more ventrally in the perinates than in the holotype of *Byronosaurus jaffei*.

The floor of the antorbital cavity is largely unossified. The choana lies directly adjacent to the antorbital fossa (as in *Archaeopteryx lithographica*), and the length of this opening corresponds almost exactly to the length of the antorbital cavity (fig. 12). The palatal ramus of the maxilla partially floors this space rostrally and laterally. This floor is slightly more extensive in IGM 100/972 than IGM 100/974, but this may reflect the region's poor preservation in the latter specimen. The dorsal surface of the palatine contributes to the floor of the antorbital cavity (contribution restricted to the caudal margin). The palatine contribution to this floor is characterized by three distinct fossae described above—two of which are excavated by pneumatic diverticula of the antorbital sinus and the third is an osseous signature of the dorsal pterygoideus (fig. 12). The palatal ramus of the maxilla extends medially from the interfenestral canal to define the rostral choanal margin and meet the vomer near the cranial midline. Just lateral to the vomer contact, a maxillary flange curves dorsally to form the medial wall of a large rostrocaudal communication between the antorbital cavity and maxillary antrum (fig. 13). The opening is interpreted as the caudal fenestra of the maxillary antrum with its medial wall formed by the postantral strut (Witmer, 1997b). The dorsal margin of the strut curves laterally to meet the interfenestral bar above the caudal antral fenestra. The diameter of the fenestra narrows rostrally. Fenestration of the postantral strut was not reported previously in troodontids (known largely in tyrannosaurids; absent in *Ornitholestes hermanni* and *Deinonychus antirrhopus* Witmer, 1997a). The postnasal fenestra is preserved in IGM 100/974 medial to the caudal ramus of the lacrimal and dorsal to the palatine. The medial margin of this broad communication between the antorbital fossa and the orbit, however, is not visible in either specimen and probably was delimited by the caudal extent of the cartilaginous nasal capsule (Witmer, 1995, 1997a).

The external maxillary fenestra is delineated solely by the maxilla and lies at, rather than behind, the rostral border of the antorbital fossa, in contrast to *Saurornithoides mongoliensis* and a variety of dromaeosaurs and other theropods. The rostral margin of the maxillary fenestra, which is formed by the lateral ramus of the ascending process of the maxilla, is less rounded in both the perinates and adults of *Byronosaurus* than in *Troodon formosus*—in this respect, *Byronosaurus* more closely resembles *Saurornithoides junior* (Barsbold, 1974; Currie, 1985). The interfenestral bar forms the caudal margin of the maxillary fossa, but as noted above, the antorbital and maxillary fossae communicate lateral to the bar due to its recessed position. The interfenestral canal is confluent rostrally with a distinct groove in the floor of the mediolaterally deep maxillary antrum. A similar groove is located in the medial wall of the maxillary antrum rostral to the caudal antral aperture. These excavations may penetrate the floor and medial wall of the maxillary antrum. A series of foramina are present on the roof of the palate; however, these are largely directed laterally toward the alveolar ramus. The ceiling of the maxillary antrum extends medial to the ascending maxillary ramus, but a distinct epiantral recess near the junction between the interfenestral bar and postantral strut as found in tyrannosaurids does not appear to be present. The medial wall of the maxillary antrum is complete (as in *Ornitholestes hermanni* and *Deinonychus antirrhopus*; Witmer, 1997a).

The front wall of the maxillary antrum (pila promaxillaris) is pierced by a relatively large opening that communicates rostrally with a deep fossa lying beneath the rostral margin of the nasal passage. This fossa is interpreted to be the promaxillary recess, with its communication with the maxillary antrum being the fenestra communicans. The fenestra communicans was not reported previously in troodontids, but its presence is known in such taxa as *Allosaurus fragilis* and *Deinonychus antirrhopus* (Witmer, 1997a). The right and left promaxillary recesses are widely confluent with each other medially and with the external nares rostrodorsally. The maxillary shelf separating the promaxillary recess (ventrally) from the nasal passage (dorsally) is penetrated by a large opening on the left side of IGM 100/972 that may be a preservational artifact (the shelf is extremely thin).

The fenestra promaxillaris, which is present as a slitlike opening in the caudal margin of the ascending ramus of the maxilla in *Troodon formosus* (Currie, 1985; Witmer, 1997a), *Sinornithoides youngi* (Russell and Dong, 1993), *Saurornithoides junior* (Barsbold, 1974), and *Sinovenator changii* as well as in *Archaeopteryx lithographica*, *Deinonychus antirrhopus*, and *Velociraptor mongoliensis* (Witmer, 1997a), is not immediately visible in IGM 100/972. The fenestra was scored as absent in *Saurornithoides mongoliensis* and unknown in *Mei long* (Turner et al., 2007a, 2007b). The internal surface of the ascending ramus adjacent to the promaxillary recess is inflated and appears to house a cavity (or potentially multiple cavities). There is no visible communication between this cavity and the maxillary antrum (i.e., no visible fenestra promaxillaris), but a medial communication with the promaxillary recess is present. At least the rostral portion of this cavity is interpreted as the vestibular bulla, which is present in *Troodon formosus* (Currie, 1985; Witmer, 1997b). The vestibular bulla and its associated cavities in the ascending ramus of the maxilla may be pneumatized by a diverticulum entering through the medial communication with the promaxillary recess or they may be pneumatized by a diverticulum from the maxillary antrum (with the requisite fenestra promaxillaris concealed by matrix). If a promaxillary fenestra is present then it is recessed behind the lateral ramus of the ascending maxillary process, as in *Troodon formosus* and in contrast to *Sinornithoides youngi* and *Saurornithoides junior* (Witmer, 1997a). The rostral terminus of the supraalveolar canal is present along the maxillary margin near or within the premaxilla-maxilla suture. The foramen is visible rostrally but not laterally. The same opening was described in *Byronosaurus jaffei* as the subnarial foramen (Makovicky et al., 2003), which previously had been considered absent in troodontids (Sereno, 2001). A subnarial foramen also is present in the purported troodontid *Archaeornithoides deinosauriscus* (Elzanowski and Wellnhofer, 1993) and in the alvarezsaur *Shuuvia deserti*.

BRAINCASE

Elements of the otic capsule and neurocranium preserved in IGM 100/974 include the right exoccipital/opisthotic and prootic, and the midline parabasisphenoid. No other braincase elements, including ossifications of the interorbital septum were recovered.

EXOCCIPITAL/OPISTHOTIC: The exoccipital/opisthotic is a thin, irregularly shaped compound element composed of the caudal exoccipital and rostral opisthotic (fig. 14). A small length of the suture between the two elements is retained dorsomedially (above the foramen magnum; fig. 14A, B).

The caudal surface is marked by a broadly concave medial margin that represents a relatively large foramen magnum. Based on this surface only, the foramen magnum is less elliptical than that of the adult—although it does appear to be taller than wide in agreement with the adult condition and that of most troodontids (e.g., *Sinovenator changii*) but differing from the subcircular foramen magnum of *Troodon formosus* (Currie and Zhao, 1993). An exoccipital/opisthotic contribution to the occipital condyle is present as a small knob. It is unclear whether this contribution met that of the opposing exoccipital/opisthotic to prevent basioccipital participation in the foramen magnum. The occipital condyle is not preserved in the adult holotype of *Byronosaurus jaffei*; however, a midline contact of the exoccipital/opisthotics at the occipital condyle is absent in *Troodon formosus* and uncommon in coelurosaurs (Osmólska et al., 1972; Currie, 1985). The perinate occipital condyle lacks a distinct neck (fig. 14C)—in agreement with *Troodon formosus*, *Saurornithoides mongoliensis*, and *Saurornithoides junior*.

Lateral and slightly ventral to the occipital condyle is a broad surface penetrated by three foramina. The two medial-most foramina communicate directly with the endocranial floor and likely transmitted branches of the hypoglossal nerve (CN XII). There is no evidence of the third hypoglossal foramen present in *Itemirus medularis*, *Troodon formosus*, and *Hesperornis regalis* (Kurzanov, 1976; Elzanowski, 1991; Currie and Zhao, 1993). The first (medialmost) hypoglossal foramen is positioned slightly dorsal to, and is distinctly larger than, the second (in agreement with *Byronosaurus jaffei*, *Troodon formosus*, and birds). Lateral and slightly dorsal to the hypoglossal foramina is a foramen comparable in size to the largest of the hypoglossal foramina. This opening is confluent with the postnatal remnant of the metotic fissure (cavum metoticum) and thus is the jugular (vagus) foramen. The relative position of this opening differs from that of adult *Bryonosaurus jaffei* and juvenile *Struthio camelus* where the jugular foramen lies distinctly below the dorsomedial hypoglossal foramen and roughly in line with the smaller, posterolateral foramen of CN XII. The external surface through which the hypoglossal and vagus nerves pass is slightly concave, but is not the bowl-like depression of more basal tetanurans, some dromaeosaurs, and *Oviraptor philoceratops* (Turner et al., 2007a).

The absence of additional foramina in the caudal surface of the occipital plate suggests the jugular foramen transmitted both the vagus (CN X) and spinal accessory (CN XI) nerves. The path of the glossopharyngeal nerve (CN IX) is unclear, but it either exited through the jugular foramen or traversed the more rostral fenestra pseudorotunda (fenestra cochleae; see below). The latter condition generally is assumed in nonavian theropods (Currie, 1997), whereas CN IX generally exits with CN X in *Rhea americana*, *Struthio camelus*, and crocodilians (Müller, 1961; Iordansky, 1973; Bellairs and Kamal, 1981; Walker, 1985). A groove or foramen in the prevagal strut (crista tuberalis of many authors; metotic buttress of Walker, 1985; metotic strut of Witmer, 1990; Baumel and Witmer, 1993; see discussions in Gower and Weber [1998] and Sampson and Witmer [2007]) rostrolateral to the jugular foramen marks an independent path of the glossopharyngeal nerve in many neognath birds and at least some nonavian coelurosaurs, including *Troodon formosus* (Witmer, 1990; Currie and Zhao, 1993; Sampson and Witmer, 2007). As noted by Mackovicky et al. (2003), a distinct, but unidentified, foramen is present in the left prevagal strut of the holotype of *Byronosaurus jaffei* but is absent from the right side of the same skull. A small groove, however, is present on the rostral face of the right strut of this specimen. Considering the comparative framework, it appears likely this foramen and groove in *Byronosaurus jaffei* mark the passage of the glossopharyngeal nerve out of the cavum metoticum. The same path of CN IX, therefore, is inferred for the perinates—with the associated bony signature developing as the ossified prevagal strut thickens during postnatal ontogeny.

The ventral margin of the exoccipital/opisthotic extends away from the occipital

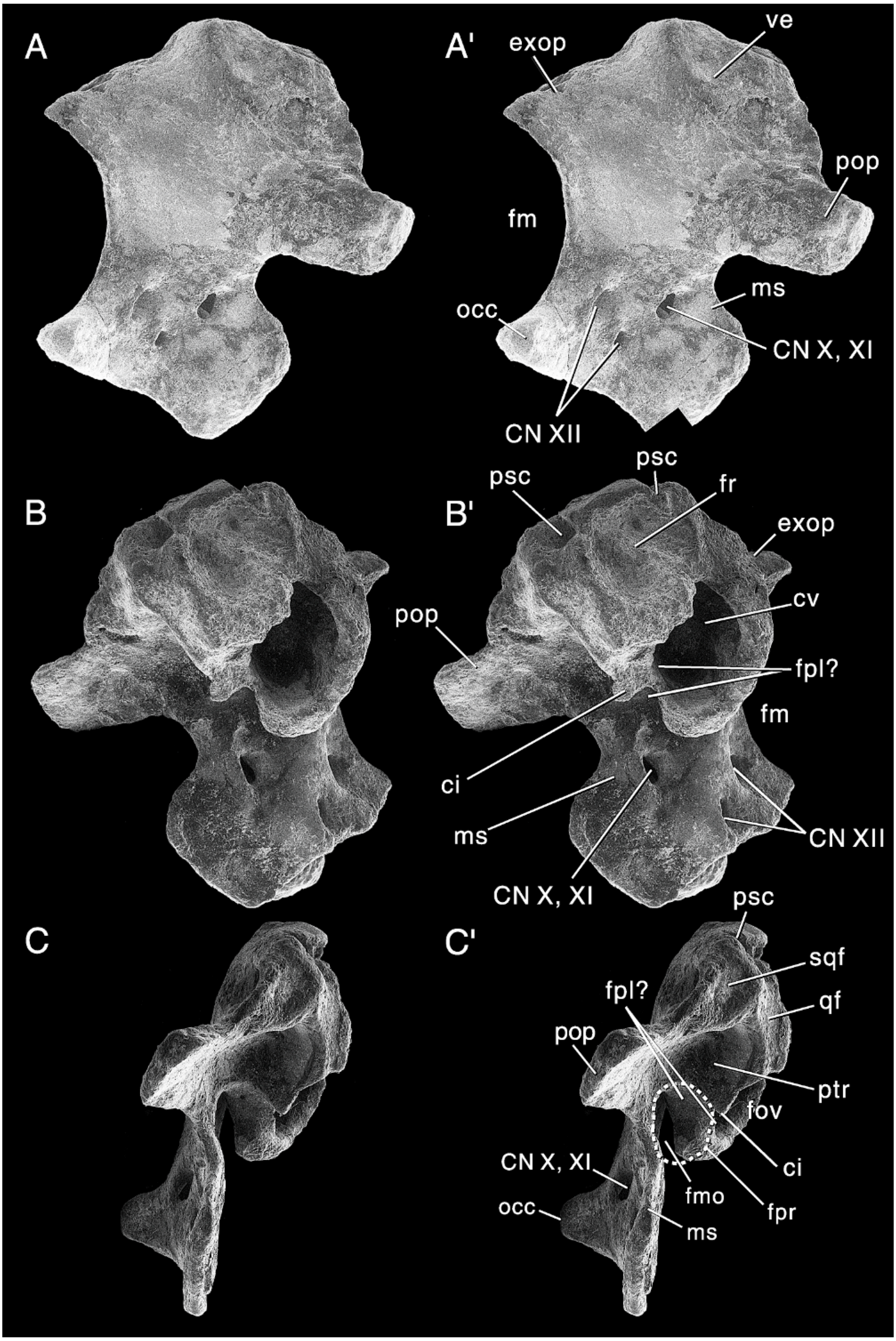

Fig. 14. Right exoccipital/opisthotic of IGM 100/974 in caudal (A, A′), rostral (B, B′) and lateral (C, C′) views.

condyle past the position of the hypoglossal and jugular foramina to form a distinct lateral surface. This surface contributes to a prominent notch that is confluent rostrally with the fenestra pseudorotunda and whose dorsal margin is formed by the paroccipital process (fig. 14). The notch is less prominent in the adult where the paroccipital process is dorsoventrally deeper (see below). The ventrolateral process of the exoccipital/opisthotic, which flanks the basal tubera of the basioccipital in many theropods (Rauhut, 2004), is absent in IGM 100/974. A modestly expanded surface that borders the reduced and medially positioned basal tubera exists in *Byronosaurus jaffei*, but unlike in most other theropods (e.g., *Gallimimus bullatus*; Osmólska et al., 1972), this surface fails to narrow to a discrete ventrolateral process. The absence of discernible sutures in the holotype of *Byronosaurus jaffei* further complicates the development of this region because this surface may be an extension of the basioccipital rather than exoccipital/opisthotic.

The paroccipital process in both IGM 100/974 and *Byronosaurus jaffei* exhibit the relatively short, rostrocaudally compressed, and dorsoventrally deep morphology typical of troodontids. This shape is less exaggerated in the perinate than in the holotype. A broad yet shallow depression separates the base of the paroccipital process from the foramen magnum (also present in *Mei long*; Xu and Norell, 2004). A low, horizontal ridge excludes this depression from the more ventral concavity housing the hypoglossal and jugular foramina, whereas in the adult these depressions are fully confluent. The ventral margin of the paroccipital process in the perinate and adult extends laterally at a subtle downward angle (in agreement with *Troodon formosus*; Currie and Zhao, 1993) and lies along a transverse plane that approximates the dorsoventral midline of the foramen magnum (in contrast to *Troodon formosus* whose ventral margin lies below the foramen magnum). The distal extremity of the paroccipital process is twisted, so that the dorsal border is rostral to the ventral border giving the perinate and adult process surfaces that are oriented caudodorsally and rostroventrally (fig. 14C; this torsion is more extreme in *Byronosaurus jaffei*).

The paroccipital process lacks any hint of a foramen on either its rostral or caudal surface and exhibits no degree of inflation. This is in contrast to the slightly inflated process of the adult whose base is pierced by a pair of rostral foramina (Makovicky et al., 2003). This external morphology suggests the paroccipital process of *Byronosaurus jaffei* was pneumatized, at least to some degree, by a diverticulum associated with a posterior (caudal) tympanic recess—a feature common in derived theropods (Witmer, 1997b) but one considered secondarily lost in troodontids (Currie and Zhao, 1993; Turner et al., 2007a, 2007b). The presence of a cavity within the paroccipital process of *Byronosaurus jaffei* associated with the rostral foramina and therefore inferred to be pneumatic is confirmed by CT data (fig. 15). The paroccipital process of *Saurornithoides junior* contains a similar pneumatic signature (Norell et al., 2009). The distal end of the perinate process is not distinctly expanded as in *Byronosaurus jaffei*, *Troodon formosus*, and *Mei long*, and lacks the diagonal ridge that divides the process into medial and lateral components in the adults. The degree to which these features are dependent on pneumatization of the paroccipital is not clear; however, *Mei long* was described as having an apneumatic process that exhibits distal expansion.

The rostral surface of the paroccipital process is smooth and gently concave (fig. 14C), but lacks the well-defined columellar sulcus of *Byronosaurus jaffei*, adult specimens of *Velociraptor mongoliensis* (Norell et al., 2004), and *Dromaeosaurus albertensis* (Currie, 1995). The rostral concavity continues medially as a broad and relatively deep depression in the lateral surface of the exoccipital/opisthotic that widens to include the area directly above the fenestra pseudorotunda (fig. 14C). The rostral concavity and its associated medial fossa are interpreted as having housed the pneumatic sac associated with the posterior tympanic recess (Walker, 1985). If correct, this sac, whose origins are unclear (Witmer, 1997b; Rauhut, 2004), was present in the caudal margin of the perinate tympanic cavity despite its failure to invade and inflate the paroccipital process (a condition similar to that described for the basal

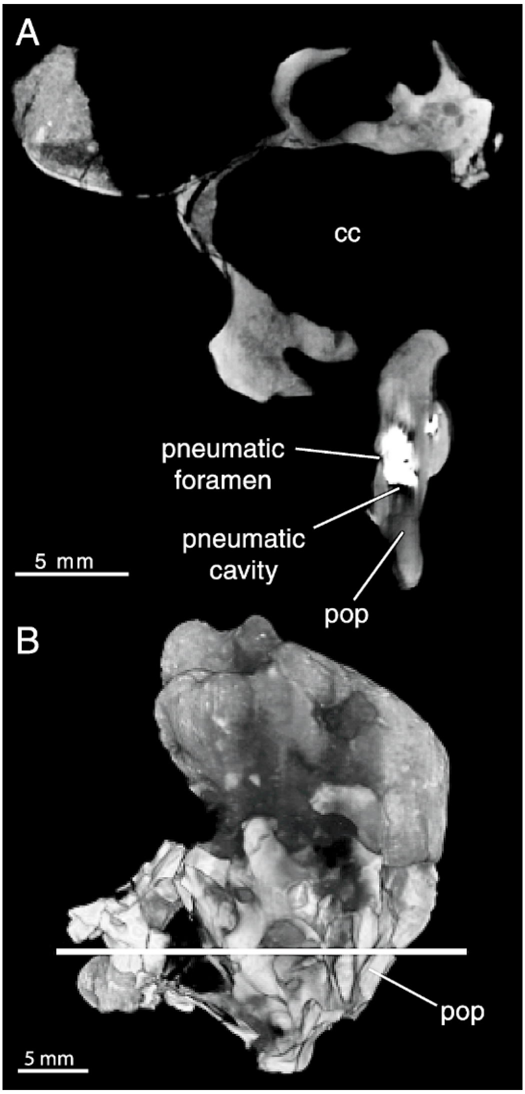

Fig. 15. Horizontal slice (A) through the braincase of the holotype of *Byronosaurus jaffei* (IGM 100/983) (B) showing the presence of pneumatic cavity in the base of the paroccipital process. The cavity is associated with a pair of rostral foramina and is inferred to result from invasion of the paroccipital process by diverticula of a posterior tympanic sinus residing in the posterior tympanic recess. The pneumatic cavity in the paroccipital process is largely infilled with a mineral inclusion that renders as a bright white in the figure. The white, horizontal line through the braincase (B) shows the position of the slice (A). Rostral is to the left, dorsal to the top.

theropod *Syntarsus rhodesiensis*; Raath, 1985). This medial fossa is partially divided into dorsal and ventral compartments resulting in an hourglass shape when viewed laterally and indicating at least some morphological complexity at this early stage of postnatal ontogeny. The rostral margin of this fossa is sharply delimited and, in contrast to the adult, does not extend onto the surface above the crista interfenestralis (accessory tympanic recess; Norell et al., 2001b). Broad surfaces positioned caudodorsal and rostrodorsal to the medial concavity of the posterior pneumatic cavity probably represent articular facets for the squamosal and quadrate, respectively (as in *Troodon formosus*; Currie and Zhao, 1993). A relatively diminutive posterior tympanic recess therefore is present in *Byronosaurus* (following Makovicky et al., 2003; contra the matrix of Turner et al., 2007a, 2007b). The recess has an osseous signature early in postnatal ontogeny as it excavates a prominent cavity in the perinate opisthotic above the fenestra pseudorotunda. The perinate paroccipital process, however, does not contain a pneumatic cavity nor is the area above the crista interfenestralis pneumatized (both of which are in contrast to the adult condition of *Byronosaurus jaffei*).

The caudal surface of the exoccipital/opisthotic dorsal to the foramen magnum is broadly convex but with a distinct concavity directly above the paroccipital process (fig. 14A). This concavity may be related to the insertion of transversospinalis muscles (Tsuihiji, 2005), whereas the broad convexity reflects the general expansion of the underlying inner ear. The inner ear contains a deeply excavated cavum vestibulare that reaches (but does not penetrate) the caudodorsal margin of the exoccipital/opisthotic and continues into the prootic through a large, ovoid, rostral opening. The medial wall of the vestibule contains a small horizontal ridge that partially divides the chamber into dorsal and ventral portions—this partial division may reflect the relative positions of the utriculus and sacculus within the vestibular cavity.

Dorsal to the rostral opening of the vestibule, the roof of the inner ear is excavated by a deep and well-defined depression that is partially divided into caudomedial and rostrolateral halves by an oblique ridge in its floor. This recess probably represents, at least in part, a deep auriculae cerebelli that would have housed an expanded floccular lobe (as described in *Troodon formosus*; Currie and Zhao, 1993). The caudal wall of this concavity is marked by two circular openings—one positioned at its lateral margin, one at its medial margin—that mark the posterior semicircular canal. The vestibular cavity remains partially open dorsally, which may correspond to the notch along the opisthotic-prootic suture described in juvenile birds and the London specimen of *Archaeopteryx lithographica* (Walker, 1985).

The medial, lateral, and caudal walls of the otic capsule are relatively thick. The caudal wall separates the cavum vestibulare from the postnatal remnant of the metotic fissure. The small foramen inferred as transmitting the endolymphatic duct posteromedially through the vestibular wall into the endocranial space in *Byronosaurus jaffei* (Makovicky et al., 2003) and *Troodon formosus* (Currie and Zhao, 1993) is not preserved in IGM 100/974 and likely passed through the unossified space between the prootic, opisthotic, and epiotic (vestibular pyramid; see below). The cavum metoticum opens into the endocranial space through a dorsoventrally elongate medial aperture that narrows laterally and widens ventrally (fig. 14C). There is no indication this space is divided medially—in agreement with *Byronosaurus jaffei* and crocodilians (Iordansky, 1973; Rieppel, 1985) but differing from hatchling *Struthio camelus*, in which the internal opening of the jugular foramen is positioned more medially and communicates directly with the endocranial space (fig. 16). Cranial nerves IX, X, XI, as well as the jugular (posterior cerebral) vein, all are interpreted as having passed out of the endocranial space through this medial aperture. The medial aperture of the cavum metoticum is recessed laterally from the medial margin of the vestibular eminence and foramen magnum. This recessed position results in a depression that leads into the medial aperture laterally and likely housed a ganglion for CN IX, X, and XI (fovea ganglii vagoglossopharyngealis of Currie and Zhao, 1993). The jugular vein presumably passed through the constricted dorsal portion of the fovea before traveling ventrally to enter the medial aperture through which it was transmitted with the aforementioned cranial nerves below the otic capsule to the lateral surface of the braincase. The slitlike medial aperture of the cavum metoticum (in medial view) is similar in shape to that of *Troodon formosus* (Currie and Zhao, 1993) and differs from the more rounded medial aperture of *Itemirus medularis*, *Dromaeosaurus albertensis*, *Velociraptor mongoliensis*, *Tsaagan mangas*, and *Bambiraptor feinbergi*. There is a slight medial constriction resulting in an hourglass-shaped medial aperture in *Byronosaurus jaffei* and *Troodon formosus* that is absent in the perinate. The vestibule communicates with the endocranial space rostral to the medial aperture of the cavum metoticum through what appears to be an ovoid window that is completed rostrally by the prootic and dorsally by the unpreserved, probably unossified, epiotic. This window differs from that of most known coelurosaurs, including *Byronosaurus jaffei*, where this medial opening is more triangular in shape (vestibular pyramid)—this difference likely reflects the reduced ossification of the otic capsule in IGM 100/974.

The caudolateral margin of the cavum vestibulare is delimited by an expanded lateral surface that marks the insertion of the footplate of the columella into the fenestra ovalis (fig. 14B, C). This surface (crista interfenestralis) is confluent with the lateral surface of the opisthotic and prootic rather than distinctly depressed within the middle ear. This plesiomorphic lateral position also is present in *Byronosaurus jaffei*, *Sinovenator changii*, *Mei long*, and *Saurornithoides mongoliensis* (Barsbold et al., 1987), whereas the derived recessed condition is expressed in *Troodon formosus*, *Citipati osmolskae*, and dromaeosaurids (Turner et al., 2007a, 2007b). The crista interfenestralis is not well preserved in the perinate perhaps due to delayed ossification of this portion of the opisthotic. The crista interfenestralis separates the fenestra ovalis from the cavum metoticum. The crista interfenestralis also forms the dorsolateral margin of a large, well-defined notch (see rostral view). In adult *Byronosaurus jaffei* and juvenile *Struthio camelus*, this

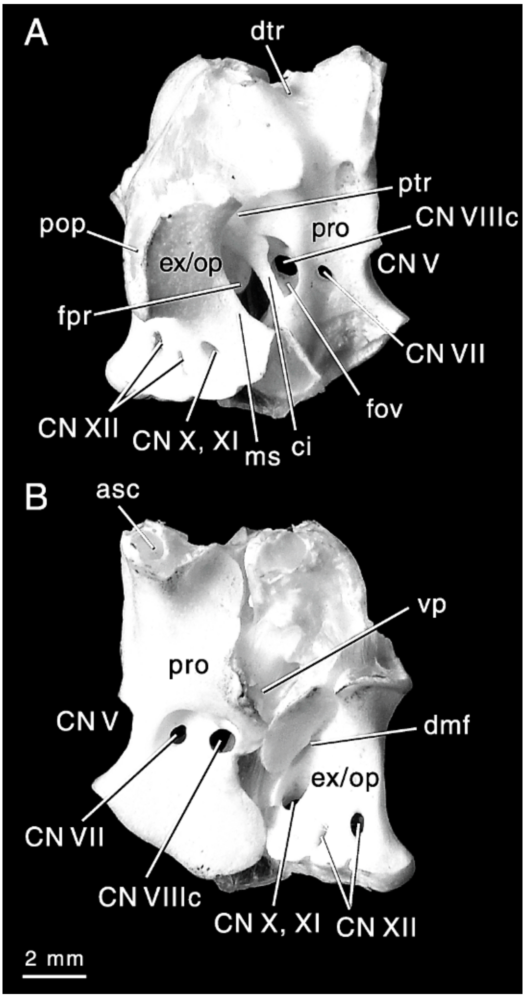

Fig. 16. Lateral (A) and medial (B) views of an articulated prootic and exoccipital/opisthotic in a perinate *Struthio camelus*. Note the medial opening of the metotic fissure is divided—in contrast to the undivided metotic foramen of IGM 100/974.

"notch" is present as a large communication between the middle ear and metotic fissure. It is unclear what structure, if any, passed through this space. The perilymphatic duct of *Byronosaurus jaffei* was interpreted to enter the cavum metoticum through a small, medial foramen (Makovicky et al., 2003). A foramen similar in size and position to the inferred foramen perilymphaticum of the adult is present in the IGM 100/974 and juvenile *Struthio camelus*. If the perilymphatic duct traversed the large opening, a structure whose identity is unclear, formed the small, medial foramen.

The prevagal strut of the perinate separates the jugular foramen from the fenestra pseudorotunda thereby dividing the lateral portion of the cavum metoticum (fig. 14). This lateral division of the embryonic metotic fissure is likely plesiomorphic in *Byronosaurus* and paravians in general, as it is present in more basal tetanurans (e.g., *Majungasaurus*; Sampson and Witmer, 2007). The prevagal strut, which may represent the ossified metotic cartilage of birds (de Beer, 1937) and perhaps the subcapsular process of crocodiles (Baird, 1970; see Rieppel, 1985), is relatively small in the perinate. The ventral margin of the fenestra pseudorotunda is open in IGM 100/974 but may have been closed by the caudodorsal margin of the basisphenoid as in the adult. This is in contrast to the condition in *Archaeopteryx lithographica* and many extant birds in which the crista interfenestralis either curves caudally to contact the rostral face of the prevagal strut or the strut exhibits a distinct rostroventral expansion that contacts a vertical crista interfenestralis (the former being present in *Archaeopteryx lithographica*; Walker, 1985). Perinate *Struthio camelus* exhibit a prevagal strut with a strong rostroventral expansion that approximates but fails to contact the crista interfenestralis (fig. 16). A shallow groove extends from a position below the otic capsule ventrolaterally along the caudal wall of the cavum metoticum to the internal opening of the jugular foramen. This groove is inferred to mark the path of CN X and CN XI through the lateral portion of the cavum metoticum to the caudolateral surface of the braincase.

The ventral margin of the prevagal strut lacks any expansion that would indicate the presence of a subotic recess (although this recess would have resided mainly in the unpreserved basioccipital). The subotic recess is present in the adult *Byronosaurus jaffei* and therefore may develop relatively late in postnatal ontogeny (or at least its progression onto the exoccipital/opisthotic occurs relatively late). The presence of a subotic recess was considered a synapomorphy of Troodontidae (present in *Byronosaurus jaffei*, *Troodon formosus*, *Saurornithoides junior*, *Saurornithoides* *mongoliensis*), but is shared with some derived ornithomimids, *Velociraptor mongoliensis*, and *Allosaurus fragilis*. A subotic recess is absent in basal avialans, alvarezsaurids, oviraptorosaurs, and most dromaeosaurids (Norell et al., 2001b; Hwang et al., 2004; Turner et al., 2007b).

PROOTIC: The prootic in medial and lateral views is a triangle-shaped element whose corners are formed by three strong processes (fig. 17). The paroccipital ramus is positioned caudodorsally and forms a dorsal articulation with the exoccipital/opisthotic. The ramus is curiously short compared to that of basal avialians (e.g., *Hesperornis regalis*; Witmer, 1990; Elzanowski, 1991) and nonavialian theropods. A short paroccipital ramus also is present in *Byronosaurus jaffei* suggesting the restricted length is a derived feature within Coelurosauria rather than an ontogenetic variation. Internally, the paroccipital ramus houses (in part) the prootic contribution to the vestibular cavity.

The articular surface with the laterosphenoid lies at the rostrodorsal margin of the prootic. This surface is separated from the paroccipital ramus by a saddle-shaped depression (fig. 17C) that lies in a position homologous to the dorsal tympanic recess of *Archaeopteryx lithographica*, modern birds (Walker, 1985; Witmer, 1990), and perhaps the alvarezsaurid *Shuuvia deserti*. Considering its presence in these taxa, it is not surprising this area has received considerable attention in nonavian theropods. Witmer (1997b) considered this recess present in ornithomimids, velociraptorine dromaeosaurids, and all known avialians, whereas a much wider taxonomic distribution was argued by Rauhut (2004), who interpreted the dorsal tympanic recess to be derived at a relatively deep node in theropod evolution (Neotheropoda). A small depression referred to as a nascent dorsal tympanic process (Walker, 1985) characterizes this region in *Dromaeosaurus albertensis*, *Archaeopteryx lithographica*, and other known troodontids. This is in contrast to the same area in adult *Velociraptor mongoliensis* that houses a large excavation bounded completely by the prootic (Sues, 1977; Norell et al., 2004). The extent of this depression in *Byronosaurus*—both the perinate and adult—is more comparable to that of adult *Velociraptor mongoliensis* and *Tsaagan mangaas* and therefore larger than the recess of most non-metornithine theropods. No foramen is associated with this concavity in either IGM 100/974 or *Byronosaurus jaffei*, which agrees with *Archaeopteryx lithographica* (Walker, 1985) and *Chilantaisaurus ashuikouensis* (see Rauhut, 2004). The presence of a pneumatopore on this surface is intraspecifically variable in *Troodon formosus* (Currie and Zhao, 1993). A mediolaterally elongate groove lies within this recess along the medial margin of the perinate laterosphenoid articular surface. This groove conforms in both size and shape to a pneumatic depression found in perinate *Struthio camelus*.

The rostral margin of the prootic below the laterosphenoid contact is marked by a deeply excavated depression forming the caudal margin of the trigeminal fenestra (fig. 17A). The laterosphenoid was not recovered in either the perinate or adult but almost assuredly formed the rostral margin of the trigeminal fenestra as in *Troodon formosus* (Currie and Zhao, 1993; contra Currie, 1985) and most archosaurs (Clark et al., 1993). The depth of the lateral concavity associated with the trigeminal fenestra in both the perinate and adult suggest the gasserian ganglion (CN V) was positioned extracranially in *Byronosaurus* (in agreement with *Saurornithoides junior*, *Saurornithoides mongoliensis*, *Dromaeosaurus albertensis*, and most nonavian theropods). In contrast, the gasserian ganglion of *Troodon formosus*, allosaurids, tyrannosaurids, and the majority of avialians (including modern birds) lies within the endocranial space (Madsen, 1976; Currie and Zhao, 1993; Brochu, 2003) and exits the braincase through a pair of openings—the ophthalmic branch passing through the laterosphenoid.

The trigeminal fenestrae of the perinate and *Byronosaurus jaffei* are relatively large compared to the same structure in adult specimens of *Troodon formosus* and *Saurornithoides junior*. A distinct rostral process forms the ventral margin of the perinate trigeminal fossa. The rounded lateral margin probably represents a portion of the otosphenoidal crest. The crest is short, but this appears to be a reflection of ontogenetic scaling in which

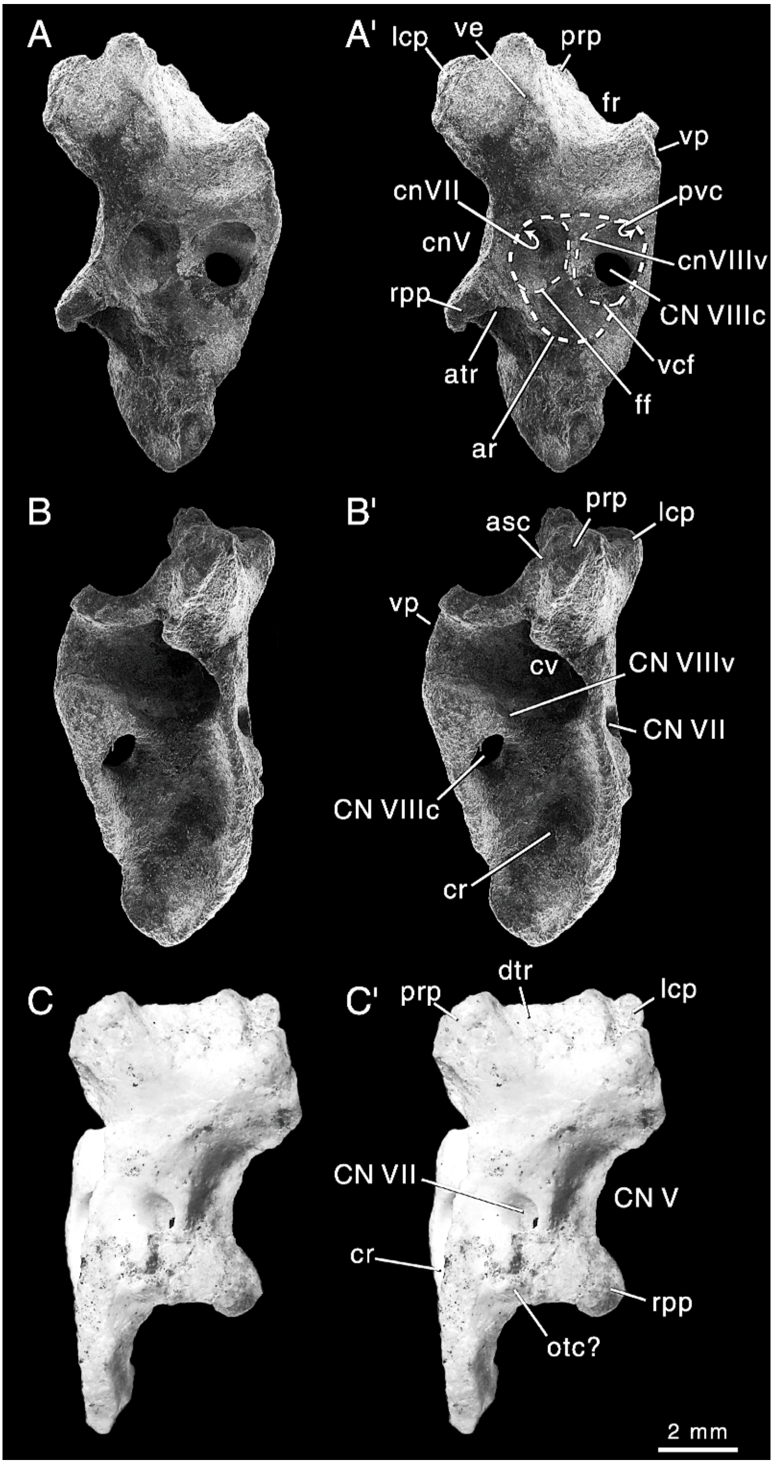

Fig. 17. Left prootic of IGM 100/974 in caudal (A, A′), rostral (B, B′) and lateral (C, C′) views.

the entire lateral surface of the prootic is short relative to that of the adult, rather than allometric development of the anterior tympanic recess (which delineates this recess rostrodorsally). The rostral surface of the prootic below the trigeminal fenestra houses a well-defined, blind cavity in the perinate. In an articulated skull, this surface lies adjacent to a deeply excavated pneumatic fossa of the parabasiphenoid that is considered part of the anterior tympanic recess (see below). A pneumatic diverticulum from within the anterior tympanic recess likely excavated this rostroventral cavity. The timing and progression of this structure's development is of phylogenetic interest as the presence of a large otosphenoidal crest defining a lateral depression on the side of the braincase may be a synapomorphy of a monophyletic Troodontidae (Makovicky et al., 2003).

A small but distinct canal that transmitted the facial nerve (CN VII) from the endocranial space penetrates the lateral surface of the prootic behind the trigeminal fenestra (fig. 17C). The facial foramen lies completely within the prootic as in *Byronosaurus jaffei* and *Troodon formosus* and presumably transmitted both the palatine and hyomandibular branches of CN VII. The foramen opens caudolaterally and is confluent with a shallow groove that turns caudally and presumably marks the path of the hyomandibular ramus above the acoustic recess, as is typical of maniraptorans. A subtle vertical groove extends ventrally from the area behind the facial foramen. This structure may reflect the path of the palatine branch (Currie, 1985). If so, this nerve passed rostrally below the trigeminal fenestra rather than traversing the fenestra as was speculated for *Troodon formosus* (Currie and Zhao, 1993). The medial opening of the facial canal is significantly smaller than its lateral counterpart—perhaps reflecting the position of the geniculate ganglion on the lateral surface of the prootic. The facial foramen lies at a level just above the ventral border of the trigeminal fossa as in the oviraptorosaur *Conchoraptor gracilis* (Balanoff and Norell, in prep.) and *Struthio camelus*. This position is dorsal to that of most adult maniraptorans (e.g., *Velociraptor mongoliensis* and *Dromaeosaurus albertensis*) including other troodontids (e.g., *Troodon formosus*) where the facial foramen lies fully below the trigeminal opening. The condition in *Byronosaurus jaffei* is intermediate with the facial foramen positioned in line with the ventral margin of the trigeminal fenestra. This difference with other maniraptorans may reflect the relatively large trigeminal opening in *Byronosaurus*. Below the facial foramen is a small but highly rugose surface. This rugosity lies in the same position as the terminus of the otosphenoidal crest in *Byronosaurus jaffei* and therefore may represent the early development of this structure. The adult trigeminal and facial openings lie in a shallow but wide trough delineated by a strongly developed otosphenoidal crest ventrally and a lateral expansion of the braincase dorsally (Makovicky et al., 2003). This trough is absent in the perinate due to the lack of a well-defined otosphenoidal crest. The facial foramen in *Byronosaurus* lies dorsal to the anterior tympanic recess rather than within it as in both species of *Saurornithoides* and *Troodon formosus* (Barsbold, 1974; Currie and Zhao, 1993; see Norell et al., 2009).

The caudal edge of the perinate prootic forms the rostral border of the fenestra ovalis. This margin is sharply delimited but is not markedly concave at the point of insertion for the columella auris (unlike the adult and perinate *Struthio camelus*; fig. 16). This margin continues ventrally as the caudal edge of the long, medially curved cochlear recess (fig. 17B).

A saddle-shaped area in the caudodorsal region of the medial surface (fig. 17A) is the prootic contribution to the floccular recess. Rostral to this recess, the base of the laterosphenoid contact is markedly convex reflecting the rostrodorsal extension of the underlying vestibular cavity (medial vestibular eminence). There is no visible signature of the middle cerebral vein. Caudoventral to the floccular recess is a second inflated area representing an emargination of the prootic contribution to the vestibular pyramid. The dominant feature on the medial surface is a broad acoustic recess that houses the lateral openings of both the facial and vestibulocochlear (CN VIII) nerves. The facial foramen lies near the rostral margin of this recess within a deep secondary fossa (facial fossa). This fossa is slightly larger than a similar secondary fossa (vestibulocochlear fossa) positioned caudally and housing the ganglion and associated foramina of CN VIII. The facial fossa is confluent with the surface lying ventral to it and is separated from the vestibulocochlear fossa by a vertical ridge that becomes less distinct ventrally.

The vestibulocochlear fossa is penetrated by two foramina that transmitted branches of CN VIII into the inner ear. The larger of these openings lies at the ventral margin of the acoustic recess (at approximately the same dorsoventral position as the facial foramen—as noted for the *Byronosaurus jaffei*; Makovicky et al, 2003). This foramen conveyed the cochlear branch of CN VIII into the caudodorsal margin of the cochlear recess at a slightly downward angle. The foramen is bordered internally by a ventral surface that lies behind the primary chamber housing the cochlear duct (fig. 17B). The cochlear recess, which ossifies around the cochlear duct and is open caudally, is bulbous, medially curved, and long. The oblique, medial ridge partly dividing the cochlear recess into proximal and distal parts in the adult is not present in the perinate.

The second acoustic foramen, which transmitted the vestibular branch of CN VIII, is similar in size to the facial foramen and thus much smaller than the cochlear foramen. The vestibular foramen is positioned above the cochlear foramen along the rostral margin of the vestibulocochlear fossa. Internally, this foramen opens onto the floor of the vestibule, which extends into the paroccipital ramus as a largely horizontal, cylindrical cavity (cavum vestibulare). A relatively small secondary chamber, which is widely confluent with the greater vestibular cavity, is present in the dorsolateral region of the inner ear. This secondary chamber probably housed the ampulla of the anterior and horizontal semicircular ducts. The dorsal foramen for the anterior semicircular canal resides in the caudal margin of the paroccipital ramus. The canal is closed, but a groove marks its vertical length. A strong horizontal ridge separates the vestibular cavity from the more vertical cochlear recess. This ridge also separates the vestibular and cochlear foramina internally.

The vestibulocochlear fossa continues as a deep cavity caudal and dorsal to the foramina of CN VIII. This extension also is present in perinate *Struthio camelus*, but unlike in the ostrich, in which this cavity is pierced by a foramen that opens caudally into the medial margin of the vestibule, the extension in IGM 100/974 ends as a blind pocket. Two additional foramina, also not present in IGM 100/974, penetrate the floor of the vestibular cavity in *Struthio camelus*. These foramina enter the vestibule through the dorsal margin of the facial fossa. The expanded fossae surrounding CN VII and VIII are shared features of the perinate *Byronosaurus* and *Struthio camelus*, although the additional pneumatic foramina that penetrate these fossae in the latter are absent in the former. The anatomical origin of these similarities and differences, as well as their phylogenetic polarity within Coelurosauria, is currently unclear.

PARABASISPHENOID: The parabasisphenoid is an elongate element whose left side is badly damaged exposing the internal surfaces of the right side (fig. 18). The parabasisphenoid is inferred as divided indistinguishably into an anterior parasphenoid, which forms a prominent rostrum, and the more compact basisphenoid. The fusion of this compound element likely occurred prenatally as it does in the modern reptiles whose skeletal development has been surveyed (Bellairs and Kamal, 1981). The basioccipial is not preserved, but a small triangular surface lying at the caudoventral margin of the dorsum sellae represents the basioccipital-parabasisphenoid contact. The triangular shape of this concave surface suggests that at least the lateral margins of the basicranial fenestra (de Beer, 1937) remained unossified (as in specimens of similarly aged *Struthio camelus*, but in contrast to *Aepyornis* where this fontanelle closes prenatally; Balanoff and Rowe, 2007).

The cultriform process (parasphenoid rostrum) is prominently elongate and tapers rostrally to a thin apex. This structure is not preserved in the holotype of *Byronosaurus jaffei*. A small but distinct secondary process (parasphenoid process of Colbert and Russell, 1969) lies rostral to the hypophyseal fossa and roughly approximates the caudal margin of the cultriform process and probably the caudoven-

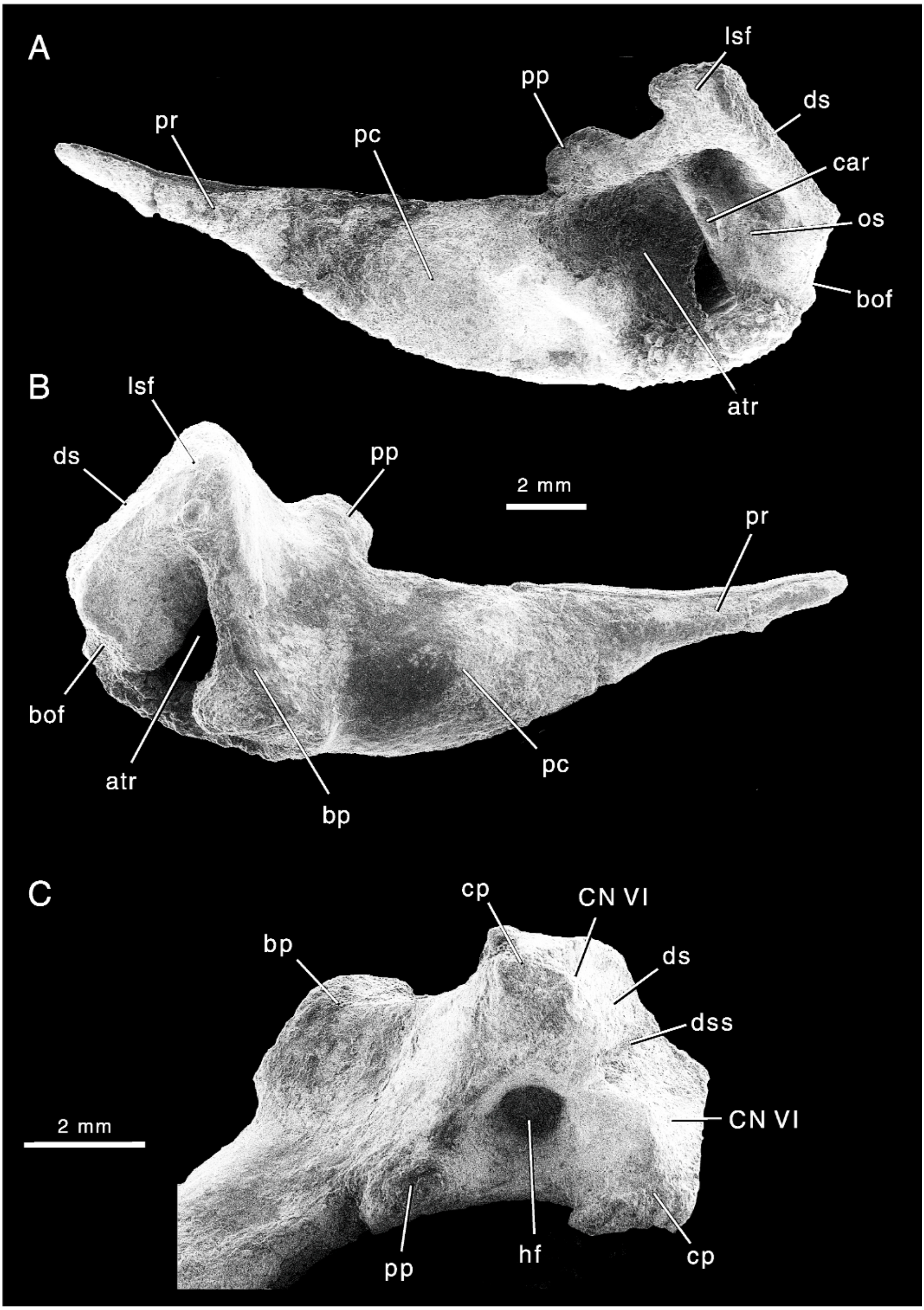

Fig. 18. Parabasisphenoid of IGM 100/974 in left lateral (A, A′), right lateral (B, B′), and rostrodorsal (C, C′) views.

tral extent of the interorbital septum (Currie, 1985). The parasphenoid process is bilaterally symmetrical with a distinct sagittal keel. There is no indication of a midline suture, in agreement with *Saurornithoides mongoliensis*, although the same process in a specimen of *Troodon formosus* was described as paired (Currie, 1985). The parasphenoid process also differs from that of *Troodon formosus* in being broadly rounded rather than forming a nearly vertical, fingerlike structure (Currie, 1985; Currie and Zhao, 1993). There is no evidence on the dorsal surface of the cultriform process of the narrow, longitudinal trough that houses the trabecular cartilages of the interorbital septum in other troodontids, dromaeosaurs, and ornithomimids (Currie, 1985).

The base of the cultriform process is pneumatized forming a bulbous parasphenoid capsule. The capsule is mediolaterally constricted directly rostral to the basipterygoid process; however, there is no evidence for a discrete basipterygoid recess (present in *Sinovenator changii* but absent in *Sinornithoides youngi*, *Saurornithoides mongoliensis* and *junior*, and *Troodon formosus*). The capsule likely is pneumatized by a diverticulum of the anterior tympanic air sac lying within the anterior tympanic recess (especially considering the absence of a basisphenoid recess, which also was implicated as pneumatizing the parasphenoid; see Currie and Zhao, 1993; Witmer, 1997a). Rauhut (2004) drew support for pneumatization of the capsule through the anterior tympanic recess based on the confluence of these cavities in *Sinovenator changii*. This confluence also was described in *Troodon formosus* (Currie, 1985; Currie and Zhao, 1993), and is partially present along the sagittal midline in the Ukhaa perinate. An irregularly shaped wall of bone positioned rostral and ventral to the hypophyseal fossa and medial to the basipterygoid process, however, at least partially separates the parasphenoid capsule and a rostral expansion of the anterior tympanic recess. Details of this bony partition are difficult to discern because of the presence of a small amount of matrix inside the cultriform process and the probable existence of postmortem damage to this area. Pneumatized parasphenoid capsules are known in several theropod lineages including troodontids (Barsbold, 1974; Osmólska and Barsbold 1990; Currie, 1985), ornithomimids (Osmólska et al., 1972; Barsbold, 1983), and therizinosaurids (Currie, 1997; see also Kurzanov, 1976; Clark et al., 1994; Holtz, 1994).

The right basipterygoid process is preserved (neither are preserved in *Byronosaurus jaffei*). The process has a strongly developed base and an ovoid, rostroventrally projecting distal end (a derived character shared with other troodontids, some ornithomimids, and *Apsaravis ukhaana*; Norell et al., 2001b; Hwang et al., 2004; Turner et al., 2007a, 2007b). Its length does not surpass the ventral margin of the cultriform process, which makes it considerably shorter than that of other troodontids. This may be due in part to a distal break or reduced ossification along its contact with the pterygoid. Relative to the hypophyseal fossa, the process is positioned further rostral than in *Troodon formosus* (Currie, 1985; Currie and Zhao, 1993). The perinate process is bulbous suggesting pneumatization. However, as noted above, there is no visible evidence of a basipterygoid recess or foramina that might have communicated pneumatic diverticula to its interior. The distal and medial surfaces of this structure are covered in a thin layer of matrix that might be obscuring such an opening(s) if one exists. Pneumatized processes are considered derived within Coelurosauria and are present in *Troodon formosus*, *Sinornithoides youngi*, *Saurornithoides mongoliensis*, *Saurornithoides junior*, oviraptorosaurs, and derived ornithomimids (Turner et al., 2007a, 2007b).

The ventral surface of the parabasisphenoid between the basipterygoid processes is only partially preserved but exhibits no evidence of the basisphenoid recess or more rostral subsellar recess that excavate this surface in other tetanurans (Witmer, 1997). The basisphenoid recess is absent in other known troodontids, the therizinosaurid *Erlikosaurus andrewsi* (Clark et al., 1994) and advanced avialians. Its loss was considered a synapomorphy of Troodontidae (Makovicky et al., 2003). Caudally, the ventral margin of the parabasisphenoid contacts the basioccipital and agrees with other troodontids in providing no bony struts to brace the presumably reduced basitubera (basitubera formed by both the basioccipital and basisphenoid is plesiomorphic within Coelurosauria; Currie and Zhao, 1993).

The hypophyseal fossa lies in the floor of a triangular sella turcica (differs from the more circular structure of dromaeosaurs; e.g., *Bambiraptor feinbergii*). The fossa is deep but did not communicate with the ventral surface of the parabasisphenoid via a craniopharyngeal canal (an embryonic communication that can be retained late into postnatal ontogeny in a wide variety of vertebrates; Edinger, 1942; Hauser and De Stefano, 1989). Two short ridges flank the hypophyseal fossa laterally and likely contacted the absent laterosphenoids and orbitosphenoids (as in *Troodon formosus* [Currie and Zhao, 1993] and *Saurornithoides mongoliensis* [Barsbold, 1974]), as well as providing a surface of origin for the retractor muscles of the eye. These ridges culminate in the clinoid processes, which are asymmetrically developed (left larger than right). There is no evidence of a retractor pit between the hypophyseal fossa and parasphenoid process. A small, bilaterally symmetrical tubercle projects laterally from the surface of the parabasisphenoid directly below these ridges and likely functioned to increase the surface area available to the external eye musculature.

This lateral tubercle lies at the dorsal margin of the anterior tympanic recess, which excavates the lateral surface of the parabasisphenoid caudal to the basipterygoid process. The resultant cavity continues medial to the basipterygoid process and possibly forms a midline communication with the parasphenoid capsule (described above). The right and left anterior tympanic cavities form a midline communication beneath the hypophyseal fossa rostral to the cerebral carotid canals. A second communication also may be present behind the hypophyseal fossa and cerebral carotid canals and in front of the dorsum sellae as in *Troodon formosus* (Currie and Zhao, 1993). This caudal confluence appears to exist in *Byronosaurus jaffei*, although poor preservation precludes confidently assessing the extent to which a bony lamina partitions these cavities (Makovicky et al., 2003). There does not appear to be an osseous subdivision of the anterior tympanic recess into a dorsal prootic and ventral subotic region as clearly is present in *Byronosaurus jaffei*. Disparity in the degree to which the rostrodorsal (see prootic above) and rostroventral regions are excavated in the perinate indicates at least some vertical partitioning of the anterior tympanic recess. Also difficult to assess is the presence/absence of a thin wall of bone contributed by the parasphenoid that encloses the anterior tympanic recess and part of the middle ear sac laterally in other troodontids, ornithomimids, and birds (Witmer, 1997b). Such a wall is not present in the perinate either because it had yet to ossify, was ossified but not preserved, or never developed.

The cranial carotid arteries were enclosed in osseous tubes passing through the anterior tympanic recess (the left tube is broken). Similar tubes were described in therizinosaur embryos and are known in some birds (Kundrát et al., 2008). These tubes meet ventral to the hypophyseal fossa (intrahypophyseal recess) and probably entered the fossa through a common canal—as in *Byronosaurus jaffei*, other troodontids, and *Itemirus medularis* (Kurzanov, 1976), but in contrast to the condition in *Dromaeosaurus albertensis* (Currie and Zhao, 1993) and *Gallimimus bullatus* (Osmólska et al., 1972). The common carotid canal of IGM 100/974 enters the hypophyseal fossa in a more ventral position than in *Struthio camelus*. There is no evidence of a separate foramen vidiani indicating that, as in most archosaurs including *Byronosaurus jaffei*, the palatine artery split from the internal carotid artery external to the parabasisphenoid and ran rostrally ventromedial to the basipterygoid processes (Currie, 1985; Walker, 1990; Rauhut, 2004). A shaft of bone in both the perinate and the adult angles from the rostral surface of the dorsum sellae to buttress the carotid canals at their apparent confluence below the hypophyseal fossa (fig. 18A). There is no indication of a lateral groove transmitting the oculomotor nerve (CN III).

Broad and relatively tall dorsum sellae delineates the caudal margin of the hypophyseal fossa and contribute to the floor of the endocranial space. The dorsum sellae is heart shaped in caudodorsal view with a ventral apex truncated by the basioccipital contact. A faint sagittal line divides the dorsum sellae caudally. The line suggests fusion of right and left ossification centers was incomplete at this stage of ontogeny (fig. 18C). This suture also is visible in the caudal wall of the sella turcica. A paired abducens canal (CN VI) penetrates the dorsum sellae near its dorsolateral margin. The rostral abducens foramina lie ventral to the clinoid processes, and thus open below the origins of the external eye musculature, which the abducens nerve innervates. There is no broad opening of the caudal wall of the hypophyseal fossa as described in some dinosaurs (e.g., *Piatnitzkysaurus floresi*, Rauhut, 2004; *Apatosaurus*, Balanoff et al., in press). The oblique orientation of the dorsum sellae together with the hypophyseal surface gives the basisphenoid a pyramidal shape when viewed laterally. This orientation also indicates the caudal floor of the perinate endocranial cavity was deeply concave as in the adult, which Makovicky et al. (2003) interpreted (in combination with a large foramen magnum) as reflecting an enlarged pons and medulla oblongata. If the hindbrain of *Byronosaurus* was large relative to other derived coelurosaurs than this expansion occurred relatively early in ontogeny. A remarkably deep braincase floor characterizes all known troodontids (Currie and Zhao, 1993). The lateral margins of the dorsum sellae contain an elongate articular surface for contact with the prootic.

The distal end of the cultriform process is preserved in IGM 100/972 as the only known braincase element of this specimen (fig. 11). The fragment includes a short length of the parasphenoid capsule, which compares closely with that of IGM 100/974 (the wall of the capsule may be slightly thicker in IGM 100/972).

MANDIBLE

DENTARY: The dentary has a subtriangular shape (in lateral view; fig. 19) that is shared with other troodontids (Currie, 1987), including *Byronosaurus jaffei*, and differs from the apomorphic subparallel dorsal and ventral margins in dromaeosaurs and *Archaeopteryx lithographica*. In ventral view (fig. 2A), the dentary is straight (up to and including the symphysis)—a condition present in *Byronosaurus jaffei*, *Sinornithoides youngi*, *Mei long*, *Sinovenator changii*, and adult dromaeosaurs (Ostrom, 1990). This contrasts with the derived condition in *Saurornithoides mongoliensis*, *Saurornithoides junior*, and *Troodon formosus* in which the dentary curves medially at the symphysis (Currie, 1987). The perinate dentary is expanded dorsoventrally and transversely at the symphysis. The lateral surface is marked by a shallow groove housing a row of nutritive foramina that communicate with the inferior alveolar canal (fig. 19). The groove delineates a small dorsal ridge that overhangs the remaining lateral surface of the dentary. The groove is not as deep as in other troodontids, including *Byronosaurus jaffei*, but this is likely an ontogenetic variation. Meckel's groove on the medial surface of the dentary also is relatively shallow. A groove housing nutritive foramina was considered a synapomorphy of Troodontidae, although it is present in a small number of other paravian taxa (e.g., *Buitreraptor gonzalezorum* [Makovicky et al., 2005]; *Archaeornithoides deinosauriscus*; Elzanowski and Wellnhofer, 1993). The lower dentition is housed in a thin, but deep, groove (see below). The dentary lacks a process that extends above the mandibular fenestra, in agreement with dromaeosaurs and *Archaeopteryx lithographica* but differing from *Mei long* and *Confuciusornis sanctus* (Chiappe et al., 1999).

SPLENIAL: As in dromaeosaurs and other troodontids (Osmólska and Barsbold, 1990), the perinate splenial is exposed laterally as an extensive triangular wedge. The rostral extent of this exposure is difficult to determine precisely but appears to have extended for more than half the dentary length, as in *Byronosaurus jaffei* and similar to *Velociraptor mongoliensis* and *Dromaeosaurus albertensis*. The splenial-angular articulation occurs along a concave margin. The splenial wraps around the ventral mandibular margin and is exposed as a large plate medially. The rostral extent of this medial exposure is concealed by matrix, however, the visible surface compares closely with the same triangle-shaped exposure in *Saurornithoides junior*, *Saurornithoides mongoliensis*, and dromaeosaurids (Currie, 1995) (cannot be determined in *Byronosaurus jaffei*; Makovicky et al., 2003). The splenial delineates the rostromedial margin of the mandibular fenestra. The caudal margin of the splenial's medial expo-

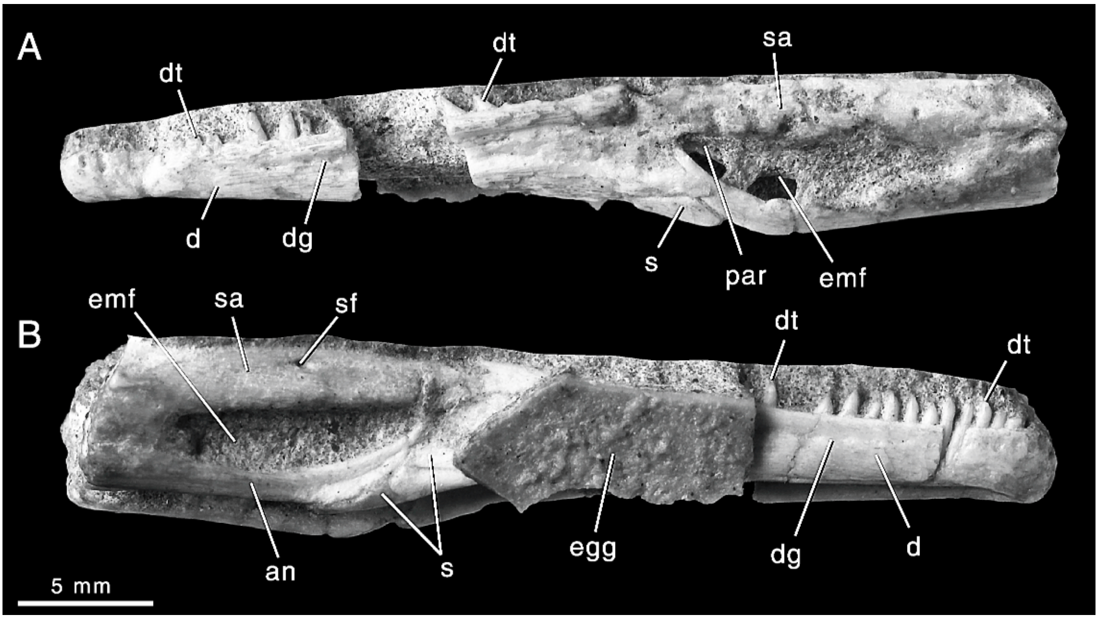

Fig. 19. Lateral views of the left (A) and right (B) mandibles of IGM 100/972.

sure inclines caudodorsally and does not fork, which differs from the forked condition of adult dromaeosaurs (e.g., *Dromaeosaurus albertensis* and *Deinonychus antirrhopus*).

PREARTICULAR, ANGULAR, AND SURANGULAR: Poor preservation obscures the intramandibular joint. The prearticular is present on the medial surface of the right mandible of IGM 100/972 as a broad, slightly convex bone that covers the dorsal half of the mandibular fenestra (fig. 19A). The slender, elongate angular has a straight ventral margin that helps form the mandibular fenestra. The rostral one-third of the angular curves dorsally following the fenestra and forms a broad contact with the caudoventral corner of the dentary and the concave caudal margin of the splenial. The angular-surangular contact lies slightly above the ventral margin of the mandibular fenestra. The angular meets the prearticular medially. The straight, dorsally convex surangular forms the roof of the external mandibular fenestra. Anteriorly, it meets the dentary at the rostral border of the mandibular fenestra. Posteriorly, it forms the caudal border of the same fenestra. The surangular lacks the T-shaped cross-sectional morphology exhibited by *Sinovenator changii*. A foramen pierces the lateral surangular surface directly above the midline of the mandibular fenestra. A laterally exposed surangular foramen is common in coelurosaurs although absent in *Shuuvia deserti*, oviraptorosaurs, and *Archaeopteryx lithographica* (Turner et al., 2007a, 2007b). The surangular foramen of *Byronosaurus jaffei* is much larger but similar in position to that of the perinates. Neither the coronoid nor the supradentary of *Dromaeosaurus albertensis* (Currie, 1995) can be observed.

MANDIBULAR FENESTRA: As in other troodontids, the external mandibular fenestra retains a basically oval shape, which is plesiomorphic for paravians. The dorsal margin is straight, the ventral margin concave. Laterally, the angular forms the ventral margin, the surangular the dorsal border (with no contribution from a caudal process of the dentary as in *Mei long*). The mandibular fenestra is proportionally larger than in adult deinonychosaurs.

DENTITION

The premaxillae bear four teeth—as in *Byronosaurus jaffei*, *Velociraptor mongoliensis* (contra Sues, 1977), and other dromaeosaurids (Currie, 1995; Ostrom, 1990; this likely is the plesiomorphic condition for Theropoda, Makovicky et al., 2003).

The dental border of the maxilla contains at least 13 tooth positions; if more are present, there is room only for an additional one or two teeth. This compares with 10 maxillary teeth in adult *Velociraptor mongoliensis*, 15 in *Deinonychus antirrhopus* (Ostrom, 1969b), nine in *Dromaeosaurus albertensis* (Currie, 1985) and more than 10 in *Saurornitholestes langstoni* (Currie et al., 1990). Within Troodontidae, *Mei long* contains approximately 24 maxillary teeth (Xu and Norell, 2004), with a similar number present in *Sinovenator changii* (Xu et al., 2002) and *Saurornithoides junior* (Barsbold, 1974). *Sinornithoides youngi* contains approximately 18 maxillary teeth (Russell and Dong, 1993) and whereas only nine tooth positions are preserved in *Troodon formosus*, much of the maxillary tooth row of that specimen is missing (Currie, 1985). At least eight and at most 11 maxillary teeth were described for *Archaeornithoides deinosauriscus*; although, like the Ukhaa perinates, the only known specimen of this taxon is ontogenetically young (Elzanowski and Wellnhofer, 1992, 1993). Makovicky et al. (2003) noted difficulty in determining the number of maxillary teeth in *Byronosaurus jaffei* but predicted the number may reach 30, based on spacing of the observable teeth. These comparisons support a relatively large number of maxillary teeth as a derived feature of adult troodontids. Approximately 18 or 19 tooth positions are located on the perinate dentary, which is significantly fewer than the conservative estimate of 30 for the adult (Makovicky et al., 2003).

The upper and lower teeth (fig. 20) in general exhibit straight, conical cusps that are mediolaterally compressed. Some teeth are slightly recurved and there is considerable variation with regard to the rostrocaudal length of the crowns (there is no obvious trend with regards to tooth-row position for either of these variables). Length of the tooth affects the crown shape, with the wider teeth having a vertical caudal margin and a posteroventrally sloping rostral margin. The teeth are constricted between the root and crown and lack any evidence of serrations—conditions that differ from the unconstricted and serrated teeth of dromaeosaurs. Absence of serrations also characterizes the teeth of *Mei long*, EK troodontid IGM 1000/44, *Archaeornithoides deinosauriscus* (Elzanowski and Wellnhofer, 1993), and *Urbacodon itemirensis* (Averianov and Sues, 2007), as well as a

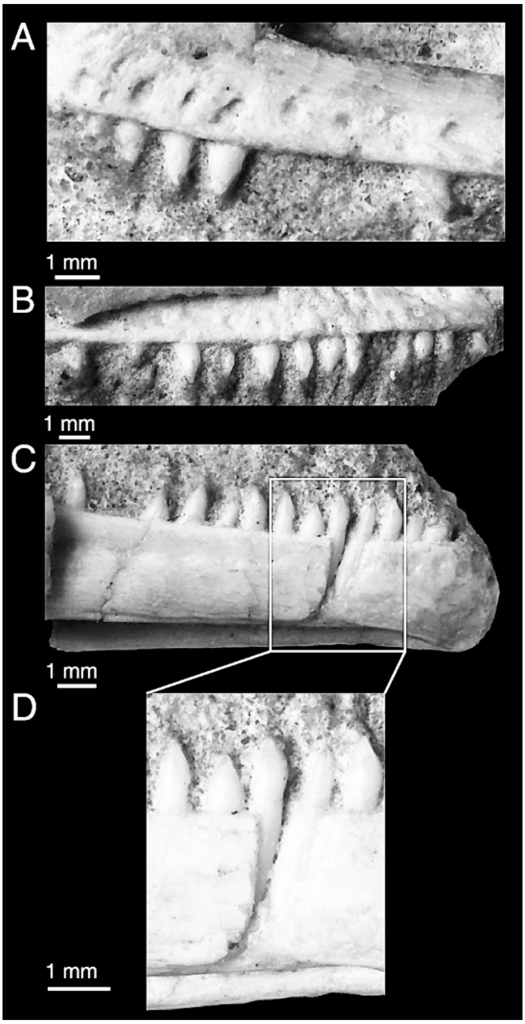

Fig. 20. Lateral views of the left maxillary (A), right maxillary (B), and right dentary (C) teeth of IGM 100/972. A fracture in the right dentary reveals the closely appressed rostral dentition of the lower jaw characteristic of troodontids and the restriction of the interdental septae to the base of the tooth roots.

number of non-troodontid paravians (e.g., *Buitreraptor gonzalezorum*, *Rahonavis ostromi*, *Archaeopteryx lithographica*, and other toothed avialans: Turner et al., 2007b).

The dentary teeth become smaller, more numerous, and more appressed rostrally, which is characteristic of troodontids (Currie, 1987). The teeth are set in a deep groove and separated by bony septae that appear to extend lingually as outgrowths of the dental groove's labial margin (fig. 21). The separation between the highly vascularized interdental bone and the labial surface of the dentary described in a specimen of *Dromaeosaurus* and figured in a specimen of *Troodon formosus* by Currie (1987; fig. 3b) is not apparent in IGM 100/972 (fig. 21). There is no sutural connection between these interdental septae and the lingual margin of the dental groove, except perhaps at the base of the groove—as described for *Troodon formosus* (Currie, 1987). This basal separation of the tooth roots is maintained even at the rostral end of the jaw where appression of the numerous dentary teeth results in the reduction of most of the length of the interdental septae (fig. 21C).

The phylogenetic identity of the interdental septae in paravians is one that is not immediately clear. Currie (1987) concluded that the interdental plates, so obvious in more basal coelurosaurs (e.g., tyrannosaurids; fig. 21E), are lost in troodontids and present, but fully fused, in dromaeosaurs (fig. 21D). This scenario is in contrast to Varricchio (1997b), who described troodontids as having interdental plates. Evidence for interdental plates in dromaeosaurs is drawn largely from the absence of a distinct disparity between the height of the dorsolabial and dorsolingual margins of the dental groove. The dorsolabial margin is significantly higher than the dorsolingual margin in troodontids and in taxa where interdental plates are present unambiguously. The relatively tall dorsolingual margin of dromaeosaurs, therefore, either is the result of fusion of the interdental plates into the labial margin of the dental groove (as argued by Currie, 1987) or the acquisition of a derived growth trajectory for these margins. Currie (1987) drew additional evidence for the retention of interdental plates in dromaeosaurs from a histological disparity between the highly vascularized interdental plates and the laminar bone of the dentary in a specimen of *Dromaeosaurus* (TMP 82.19.185). This disparity, however, is not obvious in *Dromaeosaurus albertensis* (AMNH FR 5356), *Velociraptor mongoliensis* (IGM 100/976), *Bambiraptor feinbergi* (AMNH FR 30556), or the perinate *Byronosaurus* (IGM 100/972). Complicating the issue, the interdental morphology of IGM 100/972 compares closely with that of the Munich specimen of *Archaeopteryx lithographica*, which is identified as retaining true interdental plates (Wellnhofer, 1993). Both specimens exhibit interdental septae set low in the dental groove and that extend from the relatively tall labial margin of the dental groove before expanding lingually. Depending on the number of characters that ultimately are shared with basal avialans, the phylogenetic implications of this problem may lie more in the accuracy of character definitions than in the phylogenetic position of dromaeosaurs and/or troodontids. For example, the dromaeosaur condition is autapomorphic among paravians regardless of whether the apomorphy lies in the fusion of retained interdental plates or the loss of these plates combined with an autapomorphic growth trajectory for the dorsolingual and dorsolabial margins of the dentary. The same is true for the troodontid condition, which either reflects a derived state in which the interdental plates are lost or simply reduced as the teeth become autapomorphically numerous and closely appressed within the jaw. The identity and evolutionary history of tooth implantation in derived coelurosaurs needs to be reviewed comprehensively—perhaps beginning with the nature of inter- and intraspecific variation in the histological signature of "true" interdental plates.

DISCUSSION

The perinate skulls collected in association with a nest of oviraptorid eggs and discussed previously as dromeosaurids (Norell et al., 1994) are herein allocated to the derived troodontid, *Byronosaurus*. The only other specimens currently allocated to *Byronosaurus* are the holotype skull of *Byronosaurus*

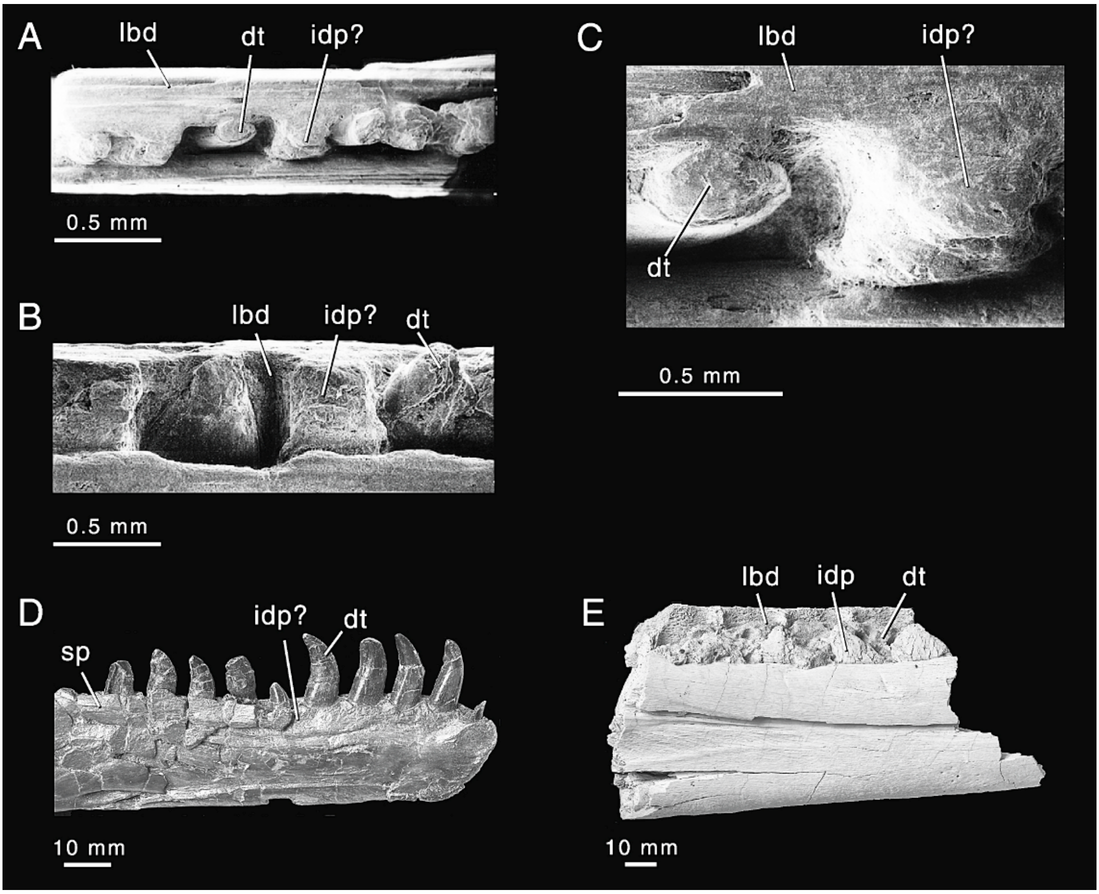

Fig. 21. Scanning electron microscopy images (A–C) of a portion of dentary and associated dentition removed from the left side of IGM 100/972. The teeth are set relatively low in a dental groove but are divided by interdental septae that appear to extend from the groove's labial margin. Medial view of the left mandible of *Dromaeosaurus albertensis* (AMNH FR 5356) (D). Note the similar height of the labial and lingal margins of the dental groove that characterizes dromaeosaurs (Currie, 1987) among coelurosaurs and the apparent lack of a distinct textural difference between the proposed fused interdental plates and laminar bone of the dentary. Medial view of a partial right mandible of the tyrannosaurid *Tarbosaurus baatar* (IGM 100/1841) (E) showing the distinct difference between the labial and lingual margins of the dental groove and a distinct textural difference between the interdental plates and dentary bone.

jaffei and a fragmentary rostrum (IGM 100/984), both of which are relatively large, skeletally mature, and considered to reflect the adult condition of this taxon (Makovicky et al., 2003). The Ukhaa perinates preserve cranial elements and structures that are not preserved in the adult specimens of *Byronosaurus* and are poorly understood in troodontids and derived maniraptorans in general. The ectopterygoid, pterygoid, and cultriform process of the parabasisphenoid were not preserved in the adult and therefore are described for the first time here. The frontal, lacrimal, and palatine are better preserved in the perinate than the adult, as are the palate and the internal morphologies of the rostrum, braincase, and otic capsule.

ONTOGENY

The ontogenetic age of the Ukhaa perinates provides a nearly unique opportunity to infer postnatal changes in the cranial morphology of a highly exclusive clade of nonavian coelurosaurs. This ontogenetic variation serves as baseline data for future comparisons of postnatal transformations in maniraptoran cranial morphology and therefore is an important step in establishing the role heterochrony has played in the morphological diversification of derived coelurosaurs (including birds).

That stated, establishing the biological source of observed morphological variation requires replication (Jones and German, 2005)—variation has to be studied at two hierarchical levels (at least) to say anything about one. For example, an observed difference between a male and female specimen may not represent a true sexual dimorphism but rather reflect an individual variation that occurs in both sexes but cannot be recognized without adequate samples of both males and females. The samples required for replication often are difficult to procure for extant vertebrate taxa much less extremely rare extinct lineages (Bever, 2009). Observed differences between the perinates and adults of *Byronosaurus* therefore may represent phylogenetic variation (the specimens may represent different species of *Byronosaurus*), sexual dimorphism, polymorphism, ontogenetic transformations, or some combination thereof. Considering the disparity in size and stage of development between the Ukhaa perinates and adults of *Byronosaurus*, however, we conclude that the vast majority of the observed differences between these specimens are likely to be highly correlated with ontogeny (meant here in the classical sense—all anatomical features and thus all variation have an ontogenetic history). This conclusion allows these comparative observations to serve as a series of hypotheses regarding what features of the *Byronosaurus* skull transform during postnatal ontogeny. The polarity of these transformations, the accuracy with which they predict ontogenetic transformations in other coelurosaur taxa, and the status of these observed variations as ontogenetic in origin will be established/rejected only with future study and new specimens.

GENERAL SIZE AND SCALING: Based on maxillary length, the Ukhaa perinates are approximately 20% the size of the adult holotype of *Byronosaurus jaffei*. The size disparity in *Byronosaurus* supports the conclusions of Rauhut and Fechner (2005) that perinates of derived coelurosaurs were precocially large relative to more basal tetanurans (e.g., allosaurids)—even when the adult body size of the former is considerably smaller than the latter. One of the most striking features of the cranial morphology of the perinate *Byronosaurus* (most obvious in IGM 100/974) compared to that of the adult is the disparity in the relative size of the circular orbit. A relatively large orbit in the perinate skull is expected considering that vertebrate species in general retain an ontogenetic trajectory (apparently derived at a deep node in chordate if not deuterostome phylogeny) in which the central nervous system develops at a faster rate than the surrounding skeleton (see Emerson and Bramble, 1993). This trend predicts that skeletal structures housing components of the central nervous system (e.g., orbit, braincase, trigeminal fenestra) appear larger in juveniles and then become relatively small during postnatal growth. In fact, both the braincase and trigeminal fenestra of the Ukhaa perinate IGM 100/974 is large relative to the same structures in the adult of most troodontids and other maniraptorans. For example, the convex and bulbous shape of the frontal in the perinate as compared to that of the adult *Troodon formosus* (the frontal of the adult *Byronosaurus* is not well preserved) likely is a reflection of the different postnatal growth trajectories of the frontal (positive allometry) and the underlying telencephalon (negative allometry). In contrast to these expected trajectories, the trigeminal fenestra of adult *Byronosaurus* retains its relatively large size. Makovicky et al. (2003) attributed this large size to allometry, which undoubtedly is correct. Based on comparisons with other troodontids and the expected relative size of this structure if plesiomorphic growth trajectories were fully retained, a large trigeminal fenestra in adult *Byronosaurus* reflects a derived transformation in the allometry of this region. The pattern of this transformation most closely resembles paedomorphosis (Alberch et al., 1979; Fink, 1982). Intra-versus extracranial positions of the gasserian ganglion seemingly would affect the allometry of this fenestra (an extracranial position is interpreted for this ganglion in *Byronosaurus* —in contrast to *Troodon formosus*; see above); however, we know of no studies that have examined these effects explicitly. The apomorphic retention of a large trigeminal fenestra combined with a plesiomorphic decrease in the relative size of the orbit and endocranial space in adult *Byronosaurus* suggests the ontogeny and phylogeny of these bony structures and the components of the central nervous system with which they are directly associated are decoupled at least to some degree.

ROSTRUM: Another component of the perinate skull of *Byronosaurus* that differs markedly from that of the adult is rostral shape. The perinate rostrum is short (rostrocaudally) and deep (dorsoventrally) with a markedly convex dorsal margin (when viewed laterally), whereas that of the adult is relatively elongate and flat. This indicates that significant shape change due to allometric growth within the rostrum (flattening) and between the rostrum and the rest of the skull (lengthening) is a morphological transformation that characterizes the postnatal development of *Byronosaurus*. Postnatal elongation of the rostrum is common among dinosaurs (Coombs, 1982; Horner and Currie, 1994; Varricchio, 1997b; Carr, 1999; Rauhut and Fechner, 2005), and archosaurs in general (e.g., Hall and Portier, 1994; Monteiro et al., 1997), and therefore its presence is plesiomorphic in *Byronosaurus*. The perinate rostrum of *Byronosaurus*, however, is more elongate than the perinate rostrum of more basal tetanurans (Rauhut and Fechner, 2005), which suggests that the growth trajectory of the snout of *Byronosaurus* is derived at some position within coelurosaurian phylogeny. Likewise, the rostrum of adult *Byronosaurus jaffei* is relatively long and flat (i.e., more shallow dorsoventrally) compared to other adult troodontids (e.g., *Mei long*, *Sinovenator changii*, and *Troodon formosus*; Makovicky et al., 2003). The apparently apomorphic shape of the rostrum in adult *Byronosaurus* therefore is the result of a growth trajectory that begins early in ontogeny (probably prenatally). Whether this adult shape ultimately is due to a derived elongation of the plesiomorphic allometric growth trajectory, or whether a change in the slope of allometric change is driving this apomorphic transformation in *Byronosaurus* cannot currently be determined.

A number of more specific characters that exhibit variation between the perinate and adult skull of *Byronosaurus* likely are correlated with the general transformation in rostral shape. These characters include rounding of the premaxillary symphysis, lengthening of the external naris, maxillary fenestra, and antorbital fenestra, a caudal shift in the position of the rostral margin of the antorbital cavity relative to the maxillary tooth row, a flattening of the caudodorsal trajectory of the ascending process of the maxilla, a shift in the primary contribution to the narial floor from the premaxilla to the maxilla, loss of a rounded boss on the dorsal surface of the nasals, deflection of the lateral margin of nasals so that they face dorsally, lengthening and flattening of the interfenestral bar, and scooping of the caudal margin of the interfenestral bar, so that the caudal openings of the nasal passage and interfenestral canal are visible laterally. The interfenestral canal, which is interpreted as having communicated branches of the maxillary nerve (CN V) and associated vasculature as well as a diverticulum of the antorbital sinus from the antorbital cavity to the supraalveolar canal and maxillary antrum respectively, has a more ventral position in the interfenestral bar of the perinates than the adult. This variation may be a correlate of the elongation and flattening of the rostrum during postnatal growth or perhaps the relative size of the dorsal pterygoideus muscle within the antorbital cavity increases during postnatal ontogeny causing a slight dorsal shift in the position of the neurovascular bundle and its associated interfenestral canal. These two possibilities are not mutally exclusive as the flattening of the rostrum in general and antorbital cavity in particular could result in a rostral expansion of the dorsal pterygoideus within the antorbital cavity. This expansion could, in turn, then result in a dorsal shift of the interfenestral canal.

DENTITION: The small number of maxillary teeth (13–15) in the Ukhaa perinates represents either the retention of the plesiomorphic paravian condition (based on comparison with dromaeosaurs) or a secondarily derived condition within troodontids. Based on the hypothesized position of the Ukhaa perinates within *Byronosaurus*, the latter interpretation likely is the correct one. A third possibility is that *Byronosaurus* exhibits a significant postnatal increase in the number of maxillary teeth. In agreement with adult *Byronosaurus jaffei*, the maxillary tooth row in the Ukhaa perinates extends approximately to the rostral margin of the antorbital fenestra and fails to reach the level of the preorbital bar (as in *Mei long*; Xu and Norell, 2004). Therefore, if the relatively small number of maxillary teeth in the Ukhaa perinates reflects the presence of a postnatal transformation in which the number of maxillary teeth increases significantly, then it appears to do so without a significant relative increase in the length of the maxillary tooth row (despite the aforementioned overall size increase in the length of the maxilla). Rauhut and Fechner (2005) noted an increase in the number of maxillary teeth in *Allosaurus fragilis* during postnatal ontogeny from 13 to 15 or 16. They considered this increase to be the plesiomorphic postnatal trajectory within Tetanurae, with coelurosaurs exhibiting a derived trajectory in which the maxillary dentition either was stable during postnatal growth or the number of teeth decreased (Varricchio, 1997b; Carr, 1999). A corollary of their hypothesis is that heterochrony in the form of paedomorphosis may have served to decrease the number of teeth in adult coelurosaurs. The number of maxillary teeth exhibited by the Ukhaa perinates complicates hypothesized trends in dental ontogeny and phylogeny in an area of the tree important for understanding the origin of birds—even if the morphology of these specimens reflects the apomorphic morphology of a new species of *Byronosaurus* within troodontids rather than evidence of a dramatic postnatal transformation.

BRAINCASE AND PNEUMATICITY: The plethora of anatomical features raises the possibility that the braincase will become increasingly important for understanding phylogenetic relationships among the derived coelurosarian taxa, including birds (Currie and Zhao, 1993). This phylogenetic potential makes understanding the developmental history of the braincase and the characters it contains all the more important.

The postnatal maturation of the vertebrate neurocranium and otic capsule in general is delayed relative to other cranial partitions. This plesiomorphic ontogenetic trajectory appears to be retained in *Byronosaurus* as the braincase exhibits a number of variations between the perinate and adult condition that likely represent postnatal transformations. Fusion of the exoccipital and opisthotic occurs relatively early in ontogeny in most if not all diapsid reptiles (de Beer, 1937; Bellairs and Kamal, 1981) and in birds generally is completed during prenatal development (although with probable exceptions, e.g., *Aepyornis* [Balanoff and Rowe, 2007]). The retention of a small length of suture in the dorsomedial surface of this compound element in IGM 100/974 suggests fusion of these elements occurred largely, but not wholly, during prenatal ontogeny in *Byronosaurus*. The dorsal position of the sutural remnant indicates fusion of these elements does not occur uniformly along their entire margin. The phylogenetic and/or functional information correlated with the timing and topological progression of this sutural obliteration is unclear. The midline suture between the paired ossifications constituting the adult dorsum sellae also is retained in IGM 100/974.

The occipital plate undergoes considerable postnatal restructuring. One of the primary transformations involves the development of an osseous flange, probably an extension of the exoccipital, below the hypoglossal foramina (this flange is absent in the perinate). Expansion of this region correlates with a shift in the position of the jugular foramen relative to the hypoglossal foramina. The absence of a ridge that in the adult partially obscures the jugular foramen in caudal view and is formed by the ventral margin of the paroccipital process is one of several transformations associated with the paroccipital process. The paroccipital process in general changes from being gracile in the perinate to relatively short and robust in the adult. The postnatal dorsoventral expansion of the paroccipital process is most obvious distally but also results in the concavities, which lie at the base of the process and are partitioned by a ridge in the perinate, becoming fully confluent in the adult. In contrast, a ridge develops during postnatal growth that partitions the caudal surface of the paroccipital process into medial and lateral components. The groove in the rostral surface of the paroccipital process that houses (in part) the stapedial shaft in the adult is absent in the perinate and therefore is inferred to develop postnatally.

One of the most notable differences between the perinate and adult braincase is the absence of a rostral foramen in the perinate paroccipital process and the inflation associated with pneumatization by the posterior tympanic sinus. A depression in the caudal margin of the tympanic cavity above the fenestra pseudorotunda and near the base of the paraoccipital process is interpreted as having housed the posterior tympanic sinus. The presence of this portion of the posterior tympanic recess combined with the absence of both an associated pneumatic foramen and inflation of the paroccipital process indicates that while the posterior tympanic sinus was present at this stage of ontogeny it had yet to invade the paroccipital process. The delayed invasion of the process by a diverticulum of the posterior tympanic sinus likely accounts for many of the described variations of the paroccipital process and occipital plate, and therefore has a number of morphological consequences.

The matrix of Turner et al. (2007a, 2007b) reflects the presence of a posterior tympanic recess in the basal troodontids *Sinovenator changii* (Xu et al., 2002) and *Mei long* (Xu and Norell, 2004), whereas the more derived troodontids *Sinornithoides youngi*, *Saurornithoides mongoliensis*, *Saurornithoides junior*, *Troodon formosus*, and *Byronosaurus jaffei* were scored as lacking this recess. The absence of a posterior tympanic recess in these latter taxa may be interpreted as a derived, secondary loss that diagnoses (in part) these five troodontids as a clade. However, based on the observations of Norell et al. (2009), Makovicky et al. (2003), and those presented here, *Saurornithoides mongoliensis* and *Byronosaurus* contain a posterior tympanic recess—albeit one that, in agreement with *Sinovenator changii* and *Mei long*, is reduced relative to that of most coelurosaurs (a posterior tympanic recess is known for ornithomimids, therizinosaurs, oviraptorids, avialians, and all dromaeosaurids; Witmer, 1997a). Phylogenetic analyses (e.g., Makovicky et al., 2003; Xu and Norell, 2004; Turner et al., 2007a, 2007b) determined *Byronosaurus jaffei* resides at a more derived position within Troodontidae than *Sinovenator changii* and *Mei long* but outside the *Saurornithoides-Troodon* clade. The presence of a posterior tympanic recess in dromaeosaurids and avialans, indicates the presence of this structure in *Sinovenator changii*, *Mei long*, *Byronosaurus*, and *Saurornithoides mongoliensis* is plesiomorphic, with its loss apomorphic in *Troodon formosus*, *Sinornithoides youngi*, and *Saurornithoides junior*. Based on these same comparisons, however, the diminutive nature of the posterior tympanic recess in *Sinovenator changii*, *Mei long*, and *Byronosaurus* would be derived, placing these taxa as morphological intermediates between dromaeosaurs and the more derived troodontids. The perinate posterior tympanic recess of *Byronosaurus* is even simpler than that of the adult in that its paroccipital process lacks any degree of pneumatization. This feature may be shared with the holotype of *Mei long*, which also is skeletally immature (Xu and Norell, 2004). The delayed onset of paroccipital pneumatization well into postnatal ontogeny as evidenced by IGM 100/974 may provide some insight into the nature of the transformation that results in the loss of the posterior tympanic recess in troodontids and the role that developmental timing might have played.

In contrast to the posterior tympanic recess, the anterior tympanic recess is present in the early stages of postnatal ontogeny in *Byronosaurus*. Excavation of the parabasisphenoid by the anterior tympanic recess in this specimen is significant and closely resembles the extent of pneumaticity present in adult *Byronosaurus jaffei* and adult specimens of other derived coelurosaurs. The dorsal extent of the anterior tympanic recess, however, appears to exhibit considerable ontogenetic variation in that the lateral surface of the prootic is not deeply excavated in the perinate (in contrast to the adult). A correlative of this lack of pneumaticity is the underdevelopment of the otosphenoidal crest on the lateral surface of the prootic. A deeply excavated rostroventral margin in the perinate represents the initiation of prootic excavation by the anterior tympanic recess. Development of the deep lateral recess, which characterizes the lateral wall of the braincase in most derived coelurosaurs, procedes ventral to dorsal.

Osteological correlates of the pneumatization of the perinate rostrum by diverticula of the paranasal sinus in general appear to correspond more closely with the adult condition than those associated with pneumatization of the braincase (either the anterior tympanic or posterior tympanic recesses). For example, the presence of an expanded cavity within the ectopterygoid of IGM 100/972 likely is due to pneumatization of this element by a diverticulum of the antorbital sinus relatively early in postnatal ontogeny followed by positive allometric growth of the surrounding bone. The well-defined osteological correlates of rostral pneumatization in the Ukhaa perinates support the conclusion of Rauhut and Fechner (2005) that this pneumatic system was established relatively early in the skeletal ontogeny of nonavian theropod dinosaurs (in agreement with extant crocodiles and birds; Witmer, 1995).

The disparity in development timing between the paranasal and the tympanic pneumatic systems in perinate *Byronosaurus* skull likely is due, at least in part, to differences in the relative maturity of the bones themselves rather than the timing of development of the actual sinuses (as noted above, maturation of the otic capsule and neurocranium generally lags behind that of the dermatocranium). That stated, it is apparent that rostral and braincase pneumatization in *Byronosaurus* was not uniform at the early posthatching stage of development, which is somewhat in contrast to the observations of Chure and Madsen (1996) and speculations of Rauhut and Fechner (2005) on the postnatal development of allosaurids. This lack of uniformity suggests that heterochrony may be an important vector for the phylogenetic transformation of these pneumatic systems and the skeletal characters they influence.

ARCHAEORNITHOIDES

Archaeornithoides deinosauriscus Elzanowski and Wellnhofer, 1992, was named based on a partial rostrum and mandible from the Djadokhta Formation at Bayn Dzak, Mongolia (Elzanowski and Wellnhofer, 1993). As recently reviewed by Averianov and Sues (2007), *Archaeornithoides deinosauriscus* originally was hypothesized as having a privileged phylogenetic relationship with birds among nonavian theropods. Support for this relationship was drawn from the absence of interdental plates and lack of serrations on the teeth, and the presence of a paradental groove on the dentary and wide palatal shelves on the maxilla. The presence of each of these "avian" characteristics is now known to occur within troodontids, with *Byronosaurus* (both the holotype of *Byronosaurus jaffei* and the Ukhaa perinates) exhibiting all four characters. The avialan status of *Archaeornithoides deinosauriscus* was challenged by Clark et al. (2002) who indicated the holotype probably had passed through the digestive tract of a larger animal. These authors considered the holotype to be a poorly preserved juvenile specimen of a nonavialan coelurosaurian taxon (Clark et al., 2002: 39). Currie (2000) suggested that the holotype of *Archaeornithoides deinosauriscus* might be a juvenile *Saurornithoides mongoliensis*, which also is known from Bayn Dzak. This possibility was considered by Elzanowski and Wellnhofer (1993) but rejected based on the presence of expanded palatal shelves of the maxillae in *Archaeornithoides deinosauriscus*—shelves that are present in basal avialans but also present in *Byronosaurus* (and probably both species of *Saurornithoides*). Averianov and Sues (2007) put forth the idea that *Archaeornithoides deinosauriscus* could be a juvenile *Byronosaurus jaffei*; however, they did not synonymize *Byronosaurus* under *Archaeornithoides* stating that it was preferable to retain both as distinct taxa until more information on troodontid ontogeny was available. The discovery and description of the Ukhaa perinates, which are highly comparable in size to the holotype of *Archaeornithoides deinosauriscus*, provide us with enough new information on troodontid skeletal ontogeny to reconsider this enigmatic taxon.

The presence of a distinct groove on the buccal surface of the dentary housing neurovascular foramina, a relatively large number of small teeth that are packed closely together (most notably at the rostral end of the lower jaw), dentary teeth that lie within a medially open groove, and a flat internarial bar are synapomorphies that are present in all known troodontids and that at least could be preserved in the holotype of *Archaeornithoides deinosauriscus*. The presence of each of these characters in the Ukhaa perinates establishes that in at least one troodontid lineage, these characters are present early in postnatal ontogeny and therefore likely present in *Archaeornithoides deinosauriscus* if that taxon is indeed a troodontid.

The morphology of the internarial bar of *Archaeornithoides deinosauriscus* cannot be discerned. The dentary teeth are larger than those of the Ukhaa perinates and are evenly spaced, with no obvious concentration at the rostral end of the lower jaw. The dentary teeth are described as sitting within distinct alveoli; however, the lingual margin of the tooth row is lower than the labial margin and is separated from the tooth row by a distinct paradental groove. The presence of an open groove for the dentary teeth as described by Currie (1987), therefore, may be present. The buccal surface of the lower jaw contains nutrient foramina lying within a distinct groove that is delimited dorsally by a ridge, as in the Ukhaa perinates. The groove is not as deep as that of adult troodontids but is similar in depth to the same structure in the Ukhaa perinates. The size and distribution of the dentary teeth suggests that *Archaeornithoides deinosauriscus* falls outside the troodontid clade defined by the most recent common ancestor of *Sinovenator changii* and *Troodon formosus*. The presence of a distinct groove on the buccal surface of the dentary is present in all troodontids but also is known in a small number of non-troodontid paravians (e.g., *Buitreraptor gonzalezorum*; Makovicky et al., 2005). If the dentary teeth actually do lie within an open groove, this may represent an unambiguous troodontid synapomorphy (see above). These two characters tentatively support the conclusions of Currie (2000) and Averianov and Sues (2007) that *Archaeornithoides deinosauriscus* is a troodontid—but one that is outside the clade comprised of the other currently recognized troodontid taxa. Further complicating the issue of *Archaeornithoides deinosauriscus* is its possession of unconstricted teeth. A continuous transition between root and crown is a derived feature within Paraves that is shared by dromaeosaurs. If *Archaeornithoides deinosauriscus* is a basal troodontid then unconstricted teeth may be plesiomorphic for Paraves with the apomorphically reversed condition of constricted teeth occurring in troodontids, avialians, and *Microraptor zhaoianus*. The perinate holotype of *Archaeornithoides deinosauriscus* indicates that the transformation from constricted to unrestricted teeth occurs relatively early in ontogeny, and if the presence of constricted teeth in adult troodontids and avialans does reflect a paedomorphic phylogenetic transformation then the transformation likely affected the embryological rather than postnatal development.

Archaeornithoides deinosauriscus, despite being based on a highly fragmentary single specimen, provides further complexity to the issue of ontogeny and phylogeny of paranasal pneumaticity in nonavian theropods. The antorbital fossa, maxillary antrum, and premaxillary recess all are present and well defined in the holotype. The palatine of *Archaeornithoides deinosauriscus*, however, exhibits no evidence of pneumatization—in stark contrast to the Ukhaa perinates. The palatine also differs from that of the Ukhaa perinates in its possession of a more plesiomorphic tetraradiate shape that includes a well-defined pterygoid process. The establishment of pneumatic-related rostral morphologies early in the postnatal ontogeny of crocodilians, birds, allosaurs, and the Ukhaa perinates, indicates that the apparent absence of pneumatic fossae in the palatine of *Archaeornithoides deinosauriscus* is a derived condition (either the palatine in this taxon lacks pneumatization or pneumatization is apomorphically delayed into latter stages of postnatal ontogeny).

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APPENDIX 1

Anatomical Abbreviations

alvf	alveolar foramina
alvp	alveolar process of maxilla
an	angular
aof	antorbital fenestra
aofo	antorbital fossa
apm	ascending process of maxilla
ar	acoustic recess
asc	anterior semicircular canal
atr	anterior tympanic recess
bof	facet for basioccipital on parabasisphenoid
bp	basipterygoid process
car	cerebral carotid canal
cc	cavum cranii
cfma	caudal fenestra of maxillary antrum
ci	crista interfenestralis
CN VI	abducens foramen (for cranial nerve VI)
CN VII	facial foramen (for cranial nerve VII)
CN VIIIc	vestibulocochlear foramen (for cochlear branch of cranial nerve VIII)
CN VIIIv	vestibulocochlear foramen (for vestibular branch of cranial nerve VIII)
CN X, XI	jugular foramen (for cranial nerves X and XI and jugular vein)
CN XII	hypoglossal foramen (for cranial nerve XII)
CN V	trigeminal fenestra (for cranial nerve V)
cp	clinoid process
cr	cochlear recess
cv	cavum vestibulare
d	dentary
dg	dentary groove
dmf	upper division of cavum metoticum
ds	dorsum sellae
dss	suture between right and left ossifications of the dorsum sellae
dt	dentary tooth
dtr	dorsal tympanic recess
egg	eggshell
emf	external mandibular fenestra
ep	ectopterygoid
ex/op	exoccipital/opisthotic
exn	external naris

exop	exoccipital/opisthotic suture
f	frontal
ff	facial fossa
fm	foramen magnum
fmo	medial aperture of cavum metoticum
fov	fenestra ovalis
fpl	foramen perilymphatica
fpr	fenestra pseudorotunda
fr	floccular recess
hf	hypophyseal fossa
idp	interdental plate
ifb	interfenestral bar
ifc	interfenestral canal
inb	internarial bar
inn	internal naris (choana)
j	jugal
jpp	jugal process of palatine
lac	lacrimal
lb	lacrimal boss
lbd	labial margin of dentary
lcp	laterosphenoid contact of prootic
lsf	surface of contact with laterosphenoids
man	maxillary antrum
mg	maxillary groove
mpm	maxillary process of premaxilla
mpp	maxillary process of palatine
ms	metotic (prevagal) strut
mt	maxillary teeth
mx	maxilla
mxf	maxillary fenestra
n	nasal
nb	nasal boss
nc	nasal capsule
nlc	nasolacrimal canal
npm	nasal process of premaxilla
occ	occipital condyle
or	orbit
orm	orbital margin
os	osseous shaft buttressing cerebral carotid canals to rostral face of dorsum sellae
otc	otosphenoidal crest
pal	palatine
par	prearticular
pas	postantral strut
pb	parabasisphenoid
pbl	preorbital bar of lacrimal
pc	parasphenoid capsule
pfp	pneumatic foramen of palatine
pmx	premaxilla
po	postorbital
pop	paroccipital process
pp	parasphenoid process
pr	parasphenoid rostrum (= cultriform process)
prl	pneumatic recess of lacrimal
pro	prootic
prp	paroccipital ramus of prootic
prpa	pneumatic recess of palatine
psc	posterior semicircular canal
psm	palatal shelf of maxilla
pt	pterygoid
ptr	posterior tympanic recess
pvc	pneumatic fossa within acoustic recess
qf	surface for articulation with quadrate
rpp	rostral process of prootic
s	splenial
sa	surangular
sal	supraantorbital process of lacrimal
sf	surangular foramen
sol	supraorbital process of lacrimal
sp	supradentary
sqf	surface for articulation with squamosal
v	vomer
vcf	vestibulocochlear fossa
ve	vestibular eminence
vp	vestibular pyramid
vpp	vomeropterygoid process of palatine
vr	vomerine ridge
?	unknown or questionable

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