Cranial anatomy of *Stenonychosaurus inequalis* (Saurischia, Theropoda) and its bearing on the origin of birds

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The discovery in recent years of additional skull material of the rare carnivorous dinosaur *Stenonychosaurus inequalis* prompts the first thorough description of this animal. This species, known only from the Upper Cretaceous strata of North America, is closely related to, but distinct from, the two described species of *Saurornithoides* from Mongolia. A derived characteristic, an inflated parasphenoid capsule, is found in both the saurornithoidids and ornithomimids, strongly suggesting shared ancestry. The middle ear cavity is well defined and is connected to at least two systems of sinuses in the skull bones. Periotic sinuses like these have not been described in theropods, and their presumed absence has been used as evidence against theropod ancestry of birds. Although these and other cranial characteristics of *Stenonychosaurus* do not prove that birds descended from theropods, they strengthen the claim that small carnivorous dinosaurs are more plausible bird ancestors than either pseudosuchians or crocodiles.

La découverte au cours des années récentes de nouveaux morceaux de crâne du dinosaurien carnivore *Stenonychosaurus inequalis*, peu commun, a permis de décrire pour la première fois en détail cet animal. Cette espèce, trouvée seulement dans les strates du Crétacé supérieur de l'Amérique du Nord, est fortement apparentée à, mais demeure distincte des deux espèces de *Saurornithoides* décrites en Mongolie. Une capsule parasphénoïdale gonflée, considérée comme une particularité évolutive, commune aux saurornithoïdés et aux ornithomimidés, suggère fortement un même ancêtre. La cavité de l'oreille moyenne est bien définie, et elle est connectée à au moins deux systèmes de sinus dans les os du crâne. De tels sinus périotiques n'ont pas été décrits dans les théropodes, et cette absence présumée a servi de fondement pour nier la descendance des oiseaux à partir des théropodes. Même si ces particularités crâniennes, et autres, du *Stenonychosaurus* ne prouvent pas nécessairement que les oiseaux descendent des théropodes, elles militent en faveur de l'hypothèse que les dinosauriens carnivores sont des ancêtres plus plausibles des oiseaux que le sont les pseudosuchiens ou les crocodiles.

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Introduction

Stenonychosaurus inequalis was originally described on the basis of a partial skeleton; most of the elements were from the foot (Sternberg 1932). A second partial skeleton and a large number of isolated elements have been described since that time (Russell 1969; Carpenter 1982) from Campanian and Maastrichtian beds of western North America. Knowledge of the anatomy of this animal is limited by the lack of complete specimens, however, although much has been inferred by comparison with a closely related genus, *Saurornithoides*, from Mongolia (Osborn 1924; Barsbold 1974).

Some of the most commonly recovered elements of *Stenonychosaurus* are the roofing bones of the braincase—the frontals and parietals. It is evident from these specimens that this animal had a relatively large brain compared with the majority of dinosaurs and possibly even with many primitive birds and mammals (Hopson 1980; Russell and Séguin 1982). This has stimulated considerable speculation on the intelligence of this animal that has even sparked the imagination of the public (Hecht and Williams 1982).

Russell (1969) noted the similarities between *Stenonychosaurus* and *Saurornithoides* and suggested that these animals might turn out to be congeneric with *Troodon*. As no reasonably complete skeletons had been described for any of these genera, he was not willing to synonomize any of the three. Barsbold (1974) linked *Stenonychosaurus* and *Saurornithoides* into a new family, the Saurornithoididae, and demonstrated that *Troodon* was probably not closely related to these genera. Carpenter (1982) and Paul (1984) synonomized *Stenonychosaurus* and *Saurornithoides* but did not present any evidence for the synonomy, which was to be discussed in another paper

by Carpenter and Paul (in preparation).

The discovery of a nearly complete braincase of *Stenonychosaurus* in 1982 was significant because it represents the most complete cranial material ever recovered of this genus. More fragmentary skull elements were also discovered in recent years, making it possible to give a detailed description of the skull of *Stenonychosaurus* for the first time. The detailed anatomical information allows meaningful comparisons with *Saurornithoides* and forces a reinterpretation of the openings into the braincase. The saurornithoidid braincase has many derived characters that distinguish it from most other theropods and give it a surprisingly birdlike appearance.

Systematic paleontology

Class Reptilia
Subclass Archosauria
Order Saurischia
Suborder Theropoda
Family Saurornithoididae
Stenonychosaurus inequalis

Material studied

All of the following specimens were collected in the Judith River (Oldman) Formation in and around Dinosaur Provincial Park, northeast of Brooks, Alberta:[1] AMNH 6174 (NW 1/4, sec. 17, tp. 21, rge. 10, W 4th mer.; collected by C. H.

[1] Abbreviations: AMNH = American Museum of Natural History; NMC = National Museum of Canada; PU = Princeton University; TMP = Tyrrell Museum of Palaeontology; UA = University of Alberta.

Sternberg, 1917), frontals, parietals, laterosphenoid; NMC 12340 (E 1/2, sec. 28, tp. 21, rge. 10, W 4th mer.; I. Vanderloh, 1968), frontals, parietals, right postorbital, basioccipital; NMC 12392 (tp. 20 or 21, rge. 11, W 4th mer.; D. A. Russell, 1968), right maxilla, plus unidentified fragments; PU 23414 (tp. 21, rge. 11, W 4th mer.; J. Horner, 1965), parietals; TMP 79.8.1 (lsd 7, sec. 20, tp. 21, rge. 12, W 4th mer.; J. Acorn, 1979), frontals, parietals, right laterosphenoid; TMP 80.16.1473 (SE 1/4, sec. 34, tp. 21, rge. 12, W 4th mer.; D. A. Russell, 1980), parietals; TMP 80.16.1478 (SE 1/4, sec. 21, tp. 21, rge. 12, W 4th mer.; D. A. Russell, 1980), frontals, presphenoid; TMP 81.22.66 (lsd 12, sec. 32, tp. 26, rge. 11, W 4th mer.; Robin Digby, 1981); TMP 82.19.23 (lsd 2, sec. 31, tp. 20, rge. 11, W 4th mer.; L. Strong-Watson, 1982), left lacrimal, prefrontals, frontals, parietals, postorbitals, squamosals, parasphenoid—basisphenoid, orbitosphenoids, laterosphenoids, prootics, supraoccipital, exoccipital—opisthotics, basioccipital; TMP 82.16.124 (lsd 6, sec. 30, tp. 20, rge. 11, W 4th mer.; K. Aulenbach, 1982), frontals, parietals; and UA 5282 (lsd 14, sec. 35, tp. 20, rge. 12, W 4th mer.; J. Caldwell (Danis), 1968), right frontal.

Diagnosis

Medium-sized carnivorous dinosaur, closely related to *Saurornithoides* of Mongolia. It differs from both *Saurornithoides mongoliensis* Osborn 1924, and *Saurornithoides junior* Barsbold 1974 in that the anterior margin of maxillary fenestra is more rounded; sculpturing on surface of nasal process of maxilla does not extend as far posteriorly; the posttemporal region is longer relative to the height of the skull; the basioccipital tubers are much more pronounced; the lateral depression of the braincase is subdivided by a single vertical ridge rather than a pair of diverging ridges; the presphenoid is more anterior in relation to the laterosphenoid; there is no sulcus or trough on the ventral surface of the braincase posterior to the parasphenoid capsule; and the supraoccipital seems to be narrower.

Description

All known specimens of *Stenonychosaurus* were examined for this study. The following description is based primarily on TMP 82.19.23 (Fig. 1), the most complete skull of *Stenonychosaurus* collected to date. Although this specimen has been crushed and distorted somewhat, it is well preserved and shows many features that were only suspected for *Stenonychosaurus* until now. When discovered, the top of the skull was exposed, and both the sagittal and nuchal crests had been destroyed by erosion.

All specimens, with one exception, came from animals of approximately the same size and would have had an estimated skull length of 200–250 mm. Although badly fragmented, TMP 80.16.1478 came from a larger individual that was comparable in size with *Saurornithoides junior* (Barsbold 1974).

The orbits are enormous (Russell and Séguin 1982, Fig. 6), with an estimated diameter of 55 mm in TMP 82.19.23. The external naris is bounded by the premaxilla, nasal, and maxilla as in *Saurornithoides* and a few other theropods. There are two large antorbital fenestrae, the more anterior one being at least 15 mm in height and the other having a maximum height of 40 mm. Crushing in the temporal region makes it difficult to accurately reconstruct the temporal openings. The upper temporal fenestra is long (45 mm) and narrow (with an estimated width of about 20 mm). The upper temporal opening as reconstructed by Russell and Séguin (1982) appears to be too short

anterodorsally. In TMP 82.19.23, the length of the upper temporal opening is approximately 65% the anteroposterior diameter of the orbit, compared with 53% in the Russell and Séguin reconstruction. The lower temporal fenestra is a large rectangular opening, the maximum anteroposterior length of which is about half the diameter of the orbit. The height of the lateral temporal fenestra is unknown, but the length of its squared off dorsal outline is 23 mm and again suggests that the Russell and Séguin reconstruction is too short in the temporal region. In comparison, this opening is shorter in *Saurornithoides junior*, where its maximum length is only 40% the diameter of the orbit. The relative shortness of the temporal region is confirmed by comparing the length of the parietal with that of the frontal. In *Stenonychosaurus*, the parietal is 60% the length of the frontal, whereas in *Saurornithoides* it is only 45%.

Maxilla

An isolated right maxilla (NMC 12392, Fig. 2) described by Russell (1969) almost certainly belongs to *Stenonychosaurus*. The reservations about the assignment expressed in the original description were related strictly to comparative measurements of the alveoli, and these are certainly less reliable than the anatomical characteristics. The size and shape of the maxillary fenestra, the apparent size and shape of the teeth, and the fact that the premaxilla does not meet the nasal below the narial opening are all diagnostic, derived features of the Saurornithoididae (Barsbold 1974).

Only the anterior portion of NMC 12392 is preserved, but it includes the anterior rim of the maxillary fenestra (subsidiary antorbital foramen) and the suture for the nasal. The anterior alveolus is incomplete, therefore suggesting that the contact for the premaxilla is not preserved (as proposed by Russell 1969). The maxillary fenestra is large, as in *Saurornithoides* (Barsbold 1974), carnosaurs (Lambe 1917; Madsen 1976) and oviraptorids (Barsbold 1977), but not as in dromaeosaurids (Ostrom 1969; Colbert and Russell 1969; Sues 1977). The anterior margin is much rounder than that of either *Saurornithoides mongoliensis* or *S. junior* (Barsbold 1974). There are two distinct rows of foramina as in *Allosaurus* (Gilmore 1920) and *Chilantaisaurus* (Hu 1964) but not *Compsognathus* (Ostrom 1978), passing through the bone from the superior alveolar canal for branches of the supramaxillary artery and supramaxillary nerve. Foramina of the lower row pass vertrolaterally from the canal and emerge from the bone just above the curved ventral margin of the maxilla. There is approximately one large foramen per alveolus. The other row of foramina emerge dorsolateral to the canal. The external surface of the maxilla (Fig. 2a) is sculptured by a network of subdividing canals for the blood vessels and nerves that emerged from this dorsal row of foramina. The sculptured surface tapers posterodorsally and ends above the maxillary fenestra. The nasal process of the maxilla would have extended farther posterodorsally from this point to its narrow contact with the lacrimal but would not have been sculptured. In *Saurornithoides*, the sculptured surface extends posterodorsally beyond the maxillary fenestra (Barsbold 1974). The contact with the nasal is marked by a distinct groove in the dorsal surface of the nasal process of the maxilla. As pointed out by Russell (1969), the nasal suture ends at least 9 mm behind the maxillary—premaxillary contact. *Saurornithoides* (Barsbold 1974) is the only other small theropod known where the maxilla is not excluded from the posteroventral boundary of the external naris by the premaxilla—nasal contact. This is a derived character that is not seen in pseudo-

suchians (Ewer 1965; Romer 1972), small theropods (Ostrom 1969; Colbert and Russell 1969; Sues 1977), or most large theropods (Osborn 1912; Lambe 1917; Maleev 1974; Kurzanov 1976*b*) but appears to have developed independently in some large theropods, however (Russell 1970; Madsen 1976; Chatterjee 1978). The maxilla enters the nasal boundary in *Archaeopteryx* (Tarsitano and Hecht 1980).

Nine alveoli are preserved in whole or part, each measuring approximately 6 mm anteroposteriorly and 13 mm in dorsoventral depth. The lingual walls of the alveoli were evidently very thin bone. The mesial surface of the palatal shelf is preserved in two sections (Fig. 2*c*). Its smooth surface shows that the palatine suture lay posterior to the preserved section. The dorsal surface of the palatal shelf is pierced by foramina from the superior alveolar canal that would have carried blood and nerve endings to the nasal cartilages.

The maxillary sinus extends anteromedially from the maxillary fenestra into a single large chamber similar to that described for *Deinonychus* (Ostrom 1969), in contrast with the double chamber of *Allosaurus* (Madsen 1976). Broken processes anterodorsal and anteroventral to the maxillary fenestra clearly show that there would have been a thin pillar of bone in this region as in other theropods (Ostrom 1969; Madsen 1976). The maxillary sinus is connected anteriorly to the floor of the external narial opening by a relatively large foramen (diameter is at least 2.5 mm). There was a larger dorsal opening into the nasal cavity as in *Allosaurus*. The function of this chamber in theropods is presently unknown, although it may have served a function related to olfaction (Madsen 1976).

Lacrimal

The left lacrimal of TMP 82.19.23 (Fig. 1*b*) is virtually complete, lacking only the anterior tip. The upper portion of the lacrimal is widest at the anterior end of the orbit and tapers anteriorly into a long, slender process. The dorsal surface is convex in transverse section. Posterolaterally, it meets the prefrontal and frontal bones in a tongue and groove transverse suture. The medial edge overlaps the frontal as it curves anteromedially. It seems to meet the nasal in a simple butt joint. However, near the anterior limit of the frontal, there is a distinct groove along the edge of the dorsal surface where it is overlapped by the nasal.

The internal surface of the anterior process of the lacrimal (Fig. 1*d*) is divided into ventral and medial surfaces by a low longitudinal ridge. A groove on the medial surface halfway along the anterior process enters a duct that passes posterolaterally through the ridge and emerges from the bone on the outside of the anterodorsal corner of the preorbital bar. This is interpreted as the single lacrimal duct because no other foramina pierce the preorbital bar. It is in a more dorsal position than in *Deinonychus* (Ostrom 1969) or other theropods.

The preorbital bar is more strongly developed than that of dromaeosaurs (Ostrom 1969; Sues 1977). Unlike the case with dromaeosaurs, sculpturing does not extend from the dorsal surface onto the lateral aspect. The anterolateral edge of the shaft is strengthened by a ridge (Fig. 1*b*) and extends from the anterior limit of the overhanging process at the anterodorsal margin of the orbit to the jugal suture. The contact with the jugal has a longitudinal axis oriented at right angles to the long axis of skull. Most of the suture is horizontal, but a small, lateral, triangular facet is vertical. The rest of the shaft is flattened and twisted so that it lies medial to the lateral edge at the jugal suture and posteromedially for most of its length. The posterodorsal edge of the preorbital bar is strongly attached to

a triangular sutural surface on the ventral side of the frontal.

A shallow channel on the internal surface of the preorbital bar passes dorsoanteriorly and ends in a deep, blind pit in the corner between the lacrimal and frontal. This presumably marks the position of the lamina orbitonasalis.

Prefrontal

A relatively long, narrow bone excludes the frontal from approximately two thirds of the dorsal orbital rim. At its widest, it is only 20% of its own length. Until now, the existence of this bone has been missed entirely (Russell 1969; Russell and Séguin 1982). In most of the previously described specimens, it has separated from the frontal and been lost, although close examination reveals the sutural contact on the frontal. A fragment of the posterior end is preserved on the right side in AMNH 6174. This bone is present in NMC 12340, TMP 79.8.1, and TMP 82.19.23 but is fused to the frontal. Although the line of suture cannot be seen clearly in any one of these specimens, the presence of the bone can be detected by textural differences. The dorsal surface of this circumorbital bone is rugose, whereas the adjacent surface of the frontal is smoother and lined with small, shallow canals for blood vessels. A number of foramina pass vertically through the sutural contact.

It is possible that this slip of bone is a palpebral, although palpebrals have not been shown conclusively to be present in theropods. Ostrom (1978) reported a similarly shaped circumorbital bone in *Compsognathus* but suggested that it might be an anterior extension of the postorbital.

The position of the bone strongly suggests that it is a prefrontal. Primitively (Walker 1964; Ewer 1965; Romer 1971), the prefrontal is a relatively prominent bone that excludes the frontal from the anterodorsal portion of the orbital rim and contacts the frontal, lacrimal, and nasal bones. This relationship is maintained in most theropods, except in tyrannosaurids where the prefrontal is relatively small and does not reach the orbital rim (Osborn 1912; Russell 1970). Stovall and Langston (1950) suggested that the prefrontals probably completely obscured the frontals of *Acrocanthosaurus* in lateral aspect, but alternatively it could be interpreted that the lacrimal had expanded to exclude the frontal from the orbital rim as in tyrannosaurids.

The prefrontal of *Stenonychosaurus* contacts the lacrimal anteriorly but does not meet the nasal. Its posterior extent is similar to that seen in ornithomimids (Osmolska *et al.* 1972) and allosaurids (Madsen 1976). Reexamination of the type specimens of *Dromaeosaurus* (AMNH 5356) and *Saurornitholestes* (TMP 74.10.5) suggests that the prefrontal of dromaeosaurids may have been a long slender bone that excluded the frontal from most of the orbital rim, just as in *Stenonychosaurus*.

Frontal

The frontal (Figs. 1*a*, 3) is the most commonly identified skull element of *Stenonychosaurus*, probably because it is relatively large and distinctive. Each of the paired frontals approximates the shape of a right angle triangle, and together they separate the posterior ends of the paired nasals. The nasal overlaps the frontal extensively as in most reptiles, covering the tip completely anteriorly but diverging posterolaterally from the midline. The nasal sits in a longitudinal trough in the frontal (Fig. 1*h*), the surface of which is only lightly ridged. The lacrimal has a complex but strong contact with the frontal. The latter bone is overlapped by the posteromedial corner of the lacrimal, with the area of contact tapering anteriorly to a simple and relatively weak butt joint. The lacrimal suture twists
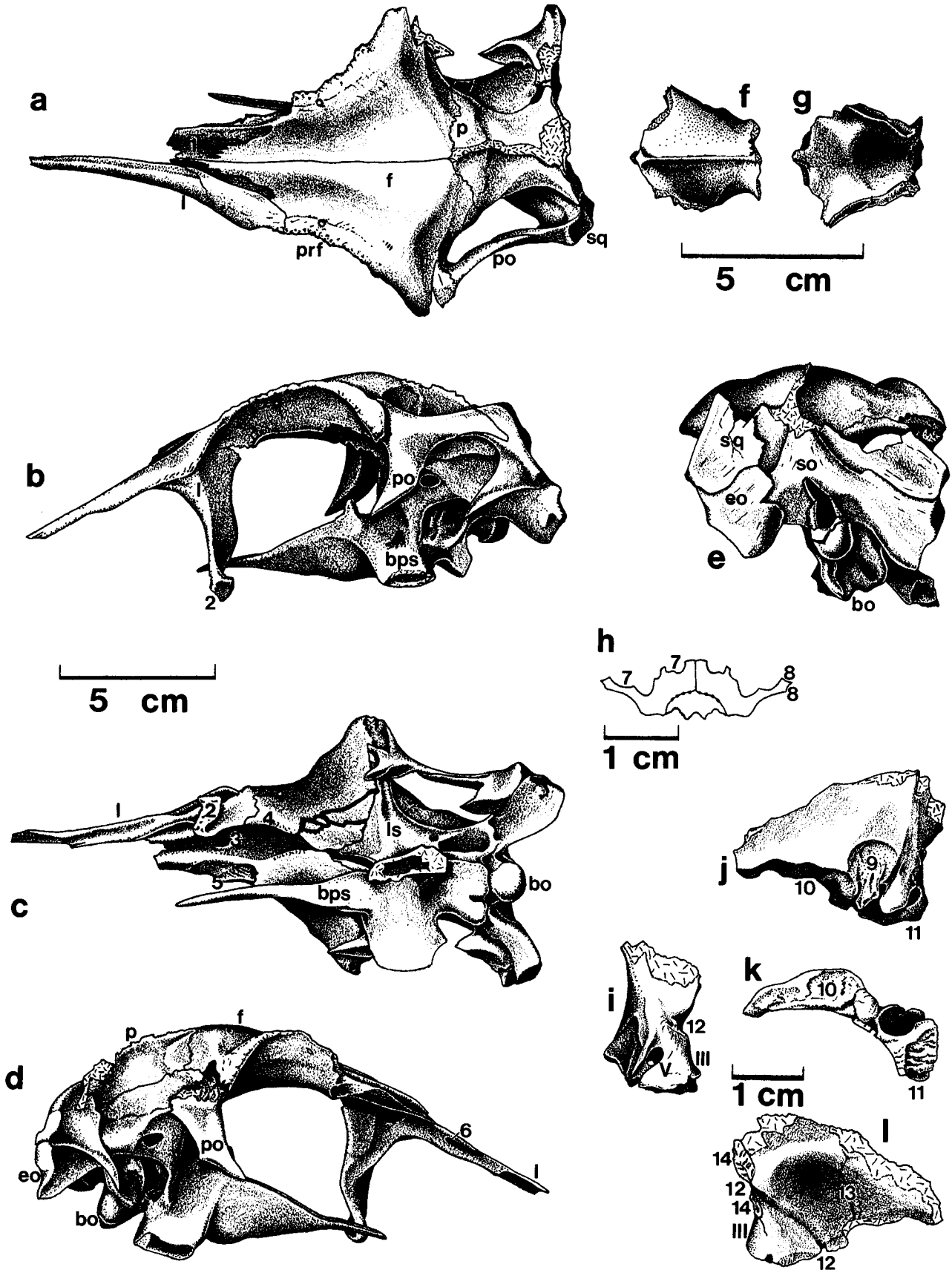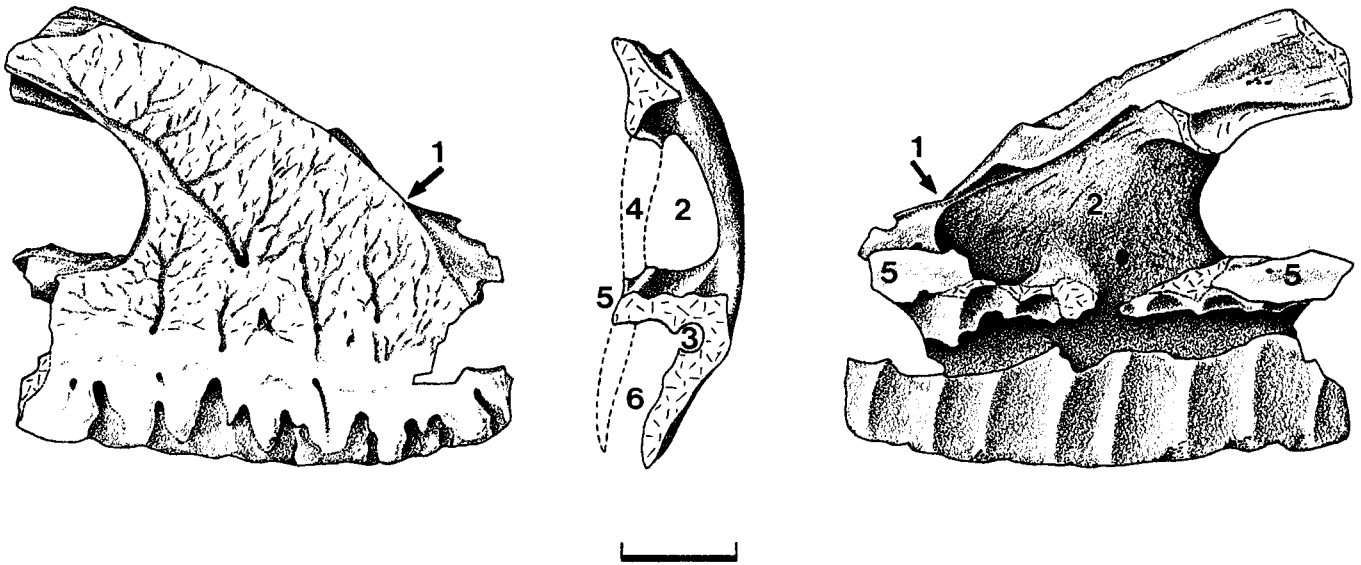
FIG. 2. *Stenonychosaurus inequalis*. Maxilla (NMC 12392) in (*a*) lateral, (*b*) posterior, and (*c*) medial aspects. (1) Anterior limit of nasal suture; (2) maxillary sinus; (3) superior alveolar canal; (4) position of pillar of bone; (5) original mesial surface of palatal shelf; (6) outline of alveolus. Scale = 1 cm.

around to the ventral surface, however, where the frontal overlaps the orbital rim of the lacrimal in a strong interdigitate contact.

The frontals meet in a straight line; the contact is strengthened by a pair of strong horizontal ridges and troughs in the interorbital region and by a series of vertical ridges and troughs more posteriorly (UA 5282). Posteriorly, the frontal is covered by the parietal at the midline but undercut by it more laterally. The postorbital suture on the frontal is divided into two distinct areas: a posterolateral facet that faces slightly ventrally and a dorsal facet that faces slightly posteriorly.

The groove in the posteroventral edge of the frontal cradles the lateral process of the laterosphenoid. The laterosphenoid suture curves anteromedially along the ventral edge of the interorbital ridge of the frontal.

The dorsal surface of the frontal is divided into dorsal and posterodorsal surfaces by a strong ridge running from the posteromedial corner of the frontal to the postorbital suture. This ridge marks the anterior limit of attachment of the temporal musculature. The position and prominence of the ridge are quite different from those of either *Dromaeosaurus* or *Saurornitholestes*, where the ridge curves sigmoidally anterolateral to the midline contact with the parietal (see Fig. 4 of Sues 1978). There is a longitudinal trough between the midline and the orbital rim, in contrast with *Saurornitholestes* (Sues 1978), and a circular depression anteromedial to the postorbital contact. The outer surface of the bone is generally smooth but is lightly sculptured where it takes part in the orbital rim.

Impressions of the olfactory bulbs and enlarged cerebral hemispheres are clearly preserved on the ventral surface of frontals. In relation to the size of the cerebral hemispheres, the olfactory bulbs are longer and narrower than in *Saurornitholestes* (TMP 74.10.5) or *Dromaeosaurus* (AMNH 5356).

A vertical plate of bone extends roughly 15 mm below the roof of the braincase to form the lateral wall of the olfactory tract and the anterolateral wall of the cerebral portion of the braincase. The ventral edge of this plate contacts the laterosphenoid for most of its length. Anteriorly, it thins to a sharp ridge with a rough edge that marks the attachment of the sphenethmoid cartilage. The sphenethmoid has not ossified as it did in many large theropods (Osborn 1912; Stovall and Langston 1950; Taquet and Welles 1977).

Next to the midline on the ventral surface of all specimens where this region is preserved (AMNH 6174, NMC 12340, TMP 82.19.23, TMP 80.16.1478), there is a shallow, longitudinal depression where the olfactory tract passed through its narrowest constriction. The roof of the tract is roughened here for attachment of the presphenoid. The depression is expanded posteriorly and tapers anteriorly, in the same manner as in *Dromaeosaurus* (AMNH 5356). However, in *Stenonychosaurus*, the presphenoid ends anterior to the olfactory bulbs, whereas in *Dromaeosaurus* the posterior extent of the presphenoid contact is at the back of the olfactory bulbs.

Parietal

Parietals are preserved in whole or in part in seven known specimens. The most distinctive features are the well developed sagittal and nuchal crests, reminiscent of much larger theropods with powerful jaw musculature. In all cases, the parietals are fused indistinguishably. It should be noted, how-

FIG. 1. *Stenonychosaurus inequalis* Sternberg. Partial skull (TMP 82.19.23) in (*a*) dorsal, (*b*) left lateral, (*c*) ventral, (*d*) right lateral, and (*e*) posterior views. Incomplete parietal (PU 23414) in (*f*) dorsal and (*h*) ventral aspects. Reconstructed cross section through the anterior region of the frontal and presphenoid, based on TMP 80.16.1478 (*h*). Portion of right laterosphenoid (TMP 79.8.1) in (*i*) anterior, (*j*) lateral, (*k*) ventral, and (*l*) medial views. (1) Overlapping nasal suture; (2) jugal suture; (3) midline slot in frontals for presphenoid; (4) rugose area for attachment of sphenethmoid; (5) ventral suture for lacrimal; (6) lacrimal duct; (7) slots for posterior processes of the nasal; (8) sutural areas for lacrimal; (9) impression of ganglia; (10) prootic suture; (11) basisphenoid suture; (12) ophthalmic artery impression; (13) impression of blood vessel; (14) orbitosphenoid suture. Roman numerals represent cranial nerves. Abbreviations: bo, basioccipital; bps, basisphenoid— parasphenoid complex; eo, exoccipital—opisthotic complex; f, frontal; l, lacrimal; ls, laterosphenoid; os, orbitosphenoid; p, parietal; po, postorbital; pr, prootic; prf, prefrontal; so, supraoccipital; sq, squamosal.
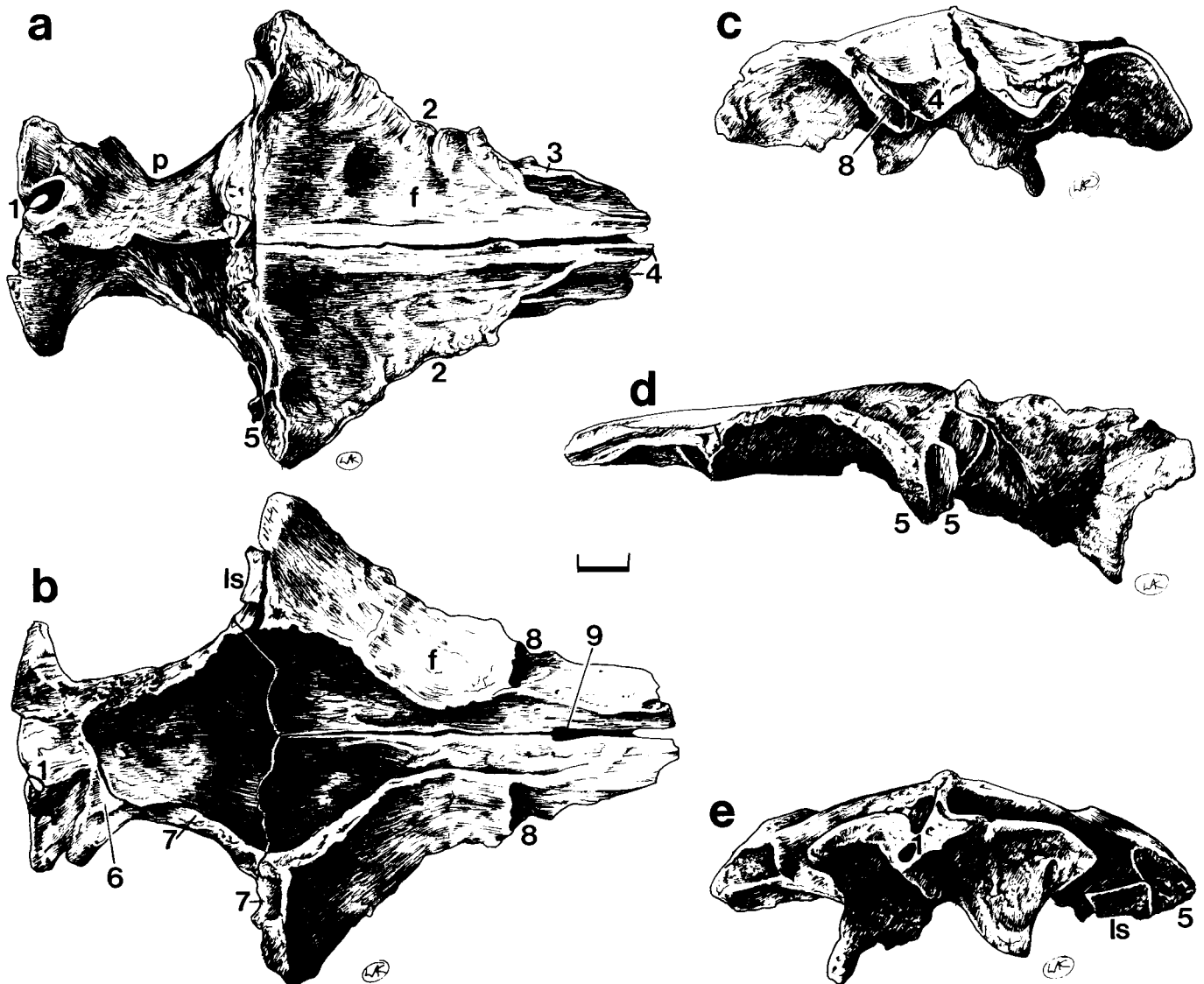
FIG. 3. *Stenonychosaurus inequalis*. Frontals, parietals, and laterosphenoid fragment (TMP 79.8.1) in (*a*) dorsal, (*b*) ventral, (*c*) lateral, (*d*) anterior, and (*e*) posterior aspects. (1) Pathological damage to bone; (2) prefrontal suture; (3) dorsal lacrimal suture; (4) nasal sutures; (5) postorbital suture; (6) suture for supraoccipital?; (7) laterosphenoid suture; (8) ventral lacrimal suture; (9) midline slot for presphenoid. Scale = 1 cm.

ever, that the smallest specimens (PU 23414, Fig. 1 *f* and *g*; TMP 80.16.1473) are only about 20% smaller than the largest. In TMP 82.16.124, the parietals and frontals also appear to have been coossified, although sutures are still discernable.

The parietal is virtually complete in TMP 79.8.1 (Fig. 3), where it is 49.5 mm in length to the back of the nuchal crest, 38.5 mm wide anteriorly, 26.0 mm across at its narrowest point, and about 53.0 mm across the nuchal crest.

The frontal suture is complex and consistent in all specimens in general pattern. The contact is nearly vertical on the centreline, but a shelf overlaps the frontal on either side (Fig. 1 *f* and *g*). Within 12 mm of the centreline, the anterior margin of the parietal curves sharply caudad, and the frontal overlaps a shelf on the parietal. Laterally, the parietal tapers into an anterolateral process that overlaps the frontal distally. From this process, the ventrolateral margin of the parietal curves gently posteromedially. In TMP 79.80.1, the bone narrows to 26.5 mm. The ventral margin of the lateral edge of the parietal bears a longitudinal groove for attachment to the latero-

sphenoid. The medial wall of the groove extends farther ventrally than the lateral wall, so that the laterosphenoid actually overlaps the lateral surface of the parietal. The groove and presumably the laterosphenoid contact end lateral to the constriction for the foramen magnum. Posterolateral to this, the parietal has a tapering posteroventral process, preserved on the right side of TMP 79.8.1 (Fig. 3 *b* and *e*). The distal end of the process overlaps the anteroventral edge of the supraoccipital slightly posteroventrally (AMNH 6174) and contacts the squamosal laterally. The nuchal crest curves dorsolaterally above this process, meeting the squamosal in a simple and relatively weak butt joint for most of its height.

The sagittal crest at its highest point in TMP 79.8.1 makes up almost 40% of the height of the bone. The supraoccipital (nuchal) crest is a high plate of bone inclined posterodorsally over the occipital region, and it expands to 53 mm, more than double the constricted width in the intertemporal region. In TMP 79.8.1 (Fig. 3 *a* and *e*) it is pierced on the left side, and the bone surrounding the hole is thickened and deformed.

This pathological condition may have been caused by a cyst. Posteroventrally, the nuchal crest of the parietal overlapped a broad plate of the supraoccipital. The dorsal margin and the dorsolateral tapering process of the nuchal crest contributed directly to the occipital plate.

Supraoccipital

Most of the supraoccipital is preserved in TMP 82.19.23, but it is so badly crushed and distorted that it provides little information. It is a plate of bone that resembles an inverted Y, with the fork forming the roof of the foramen magnum. The dorsal process narrows to a width of 9.8 mm in the preserved portion, with an anteroposterior thickness of 2 mm at the midline. The posterior surface of the occipital plate of the parietal of TMP 79.8.1 has dorsoventrally oriented, low ridges centrally, which presumably mark the sutural contact with the supraoccipital. The evidence in this specimen suggests that the supraoccipital expanded slightly dorsally but did not reach the top of the nuchal crest. The dorsal plate of the supraoccipital seems to be much broader in *Saurornithoides junior* (Barsbold 1974), but the crushed condition of all saurornithoidids in this region makes such comparisons uncertain.

The ventrolateral processes seem to fuse with the paroccipital processes distally, and the point of contact cannot be identified in TMP 82.19.23.

At the back of the parietal in AMNH 6174, a small slip of bone is preserved on each side. It appears that the supraoccipital had a pair of anterior processes that served to strengthen the contact with the parietal and may even have formed a minute portion of the dorsolateral walls of the braincase. This process was covered laterally by the laterosphenoid or prootic, which in turn was covered by the squamosal in this region.

Postorbital

A complete left postorbital is known for TMP 82.19.23 (Fig. 1 a and b), whereas incomplete postorbitals are preserved in the same specimen plus NMC 12340. The contact with the frontal and laterosphenoid is preserved in uncrushed condition in NMC 12340 (Russell 1969), where it is evident that the postorbital extended much farther laterally than the preorbital bar. This demonstrates that this animal probably had binocular vision (Russell and Séguin 1982).

The postorbital is a triradiate bone that forms portions of margins of both temporal fenestrae, and the orbit. The stout anterodorsal process is smoothly notched on the posteroventral surface for its contact with the laterosphenoid and meets the frontal in a complex but evidently strong suture. In contrast with that of dromaeosaurs (Ostrom 1969), this process does not twist to form a vertical lamina but remains horizontal. The intertemporal process curves posterodorsally, extending to the back of the lateral temporal fenestra. For most of its length, it overlaps the ventral prong of the squamosal's intertemporal process. As in most other reptiles, the ventral process of the postorbital meets the jugal in a twisting, oblique suture such that it is overlapped posterolaterally by the postorbital process of the jugal, in contrast with that of *Allosaurus* (Madsen 1976). As in *Deinonychus* (Ostrom 1969), the internal surface of the ventral process has a well defined ridge that marks the separation of the orbit and the lateral temporal fossa.

Squamosal

Both squamosals are known from TMP 82.19.23. As in other theropods, this is a complex bone that attached to at least four other bones. The outer surface of the bone is divided into posterodorsal and lateral portions by a strong ridge extending from the intertemporal bar to the lateral extent of the paroccipital process. In contrast with that of *Deinonychus*, the posterodorsal sheet is concave and is functionally part of the occipital surface. The ventromedial surface is also concave and delimits the posterolateral attachment of the temporal musculature. The tapering quadrate process of the squamosal is triangular in section and has a much broader and stronger articular surface for the shaft of the quadrate than that found in *Deinonychus* (Ostrom 1969), although it still is continuous with a distinct single articular cotylus for the dorsal head of the quadrate. It is possible that the quadratojugal also attached to the shaft of the quadrate process. The anterior process of the squamosal bifurcates dorsal and ventral to the tapering end of the postorbital, which also laterally overlaps the squamosal slightly. This is a primitive feature widespread in archosaurs (Ewer 1965; Gilmore 1946). The parietal process of the squamosal has been crushed on both sides of the specimen, although the butt suture can be interpreted from the parietal of TMP 79.8.1. The contact would have been covered posteriorly by the paroccipital process as in other theropods (Madsen 1976). The posterolateral process of the squamosal is relatively short and blunt, in contrast with that of *Deinonychus* (Ostrom 1969). The distal end is unfinished bone, continuous with a similar surface on the lateral surface of the paroccipital process, which strongly suggests that it was continued in cartilage and may have been longer in larger individuals. The suture with the paroccipital process is a butt joint, with the squamosal overlapping the paroccipital process slightly distally and being overlapped by it proximally.

Basisphenoid—parasphenoid

The parasphenoid is fused indistinguishably to the basisphenoid, so the two bones will be treated together. The shape of the parasphenoid portion is distinctive in that the cultriform process is expanded into a bulbous structure known as the parasphenoid capsule. This has been laterally crushed in TMP 82.19.23 (Fig. 1), so it is impossible to say if it had the same width as that of *Saurornithoides* (Barsbold 1974). The bulbous nature is certainly apparent in lateral view, however. Similar parasphenoid capsules have been noted in *Gallimimus* (Osmolska et al. 1972) and *Garudimimus* (Barsbold 1981). Barsbold (1974) felt that the structure developed independently in saurornithoidids and ornithomimids. However, other similarities suggest that this is synapomorphic. Anteriorly the cultriform process tapers into a delicate, vertical process. The hollow walls in this region are only 0.4 mm thick. There is a 2 mm wide trough along the dorsal surface of the cultriform process for the trabecular cartilages of the interorbital septum.

The suture between the basisphenoid and prootic passes along a vertical buttress above the anterior wall of a distinct lateral depression as in *Saurornithoides* (Barsbold 1974, 1983b). Anterodorsally, the basisphenoid meets the laterosphenoid and orbitosphenoid. Although it does not form the floor of the trigeminal foramen as in other theropods (Welles 1984), an anterior branch of the trigeminal does pass through the basisphenoid anterodorsally.

The stoutly built basipterygoid processes diverge ventrolaterally from the midline. At the base, each process is rectangular in section, about twice as long as high in its dimensions. The process ends distally in an elongate concave facet that faces laterally and in a smaller, more posterior facet with a posterolateral orientation. The process is hollow with a thick anterior wall and dorsal, ventral, and posterior walls of less

than 2 mm in thickness. The medial wall of the hollow space inside the basipterygoid process is pierced anteriorly by a large foramen entering the parasphenoid capsule and posteriorly by a smaller channel that passes posterodorsally into the lateral depression.

As in *Saurornithoides* (Barsbold 1974) and *Gallimimus* (Osmolska et al. 1972), there is a distinctive rectangular platform between the basipterygoid processes. In contrast with those of *Saurornithoides*, *Gallimimus*, and *Dromaeosaurus* (Colbert and Russell 1969), this platform is at a level higher than the basioccipital tubera. The platform is not separated from the parasphenoid capsule by a shallow sinus or furrow as it is in *Saurornithoides* (Barsbold 1974). Like *Saurornithoides* but unlike most other theropods (Colbert and Russell 1969; Osmolska et al. 1972; Madsen 1976; Taquet and Welles 1977; Welles 1984), there is no evidence of the remnants of the invagination forming Rathke's pouch. Presumably it was open during early stages of life as in most vertebrates.

There is a distinct pituitary fossa bounded anteriorly by distinct bony processes on the dorsal surface of the basisphenoid–parasphenoid complex. The processes appear to be a single, median ossification, because they were crushed together. They are equivalent to the parasphenoid processes of *Dromaeosaurus* (Colbert and Russell 1969). They presumably mark the posteroventral extent of the interorbital septum. Posterior to the paired processes, there is a shallow medial pit that was probably used by the rectus musculature of the eye. A foramen emerges from the bone at the left side of the retractor pit and may mark the passage of the anterior cerebral artery. However, because there is no evidence of a similar foramen on the right side of the pit, it could also represent an opening into the sinus system as in *Gallimimus* (Osmolska et al. 1972). The pituitary fossa is open posteriorly, and the internal carotid and abducens probably left the braincase here. The opening is bound dorsally by a bar from the paired orbitosphenoids.

Laterosphenoid

The laterosphenoid is preserved in whole or part in AMNH 6174, TMP 79.8.1 (Fig. 1 *i–l*) and TMP 82.19.23 (Fig. 1 *b–d*). The postorbital process has a smooth, slightly convex distal cotylus for contact with the postorbital. The frontal suture has strong ridges and deep grooves for firm attachment. Underlying the base of the postorbital process and adjacent to the lateral wall of the braincase, there is a 3 mm long cone on the sutural surface that inserted into a hole in the frontal of UA 5282 to further strengthen the contact. The postorbital process is supported by a ridge that is continuous ventrally with the corner of the anterior wall of the braincase. A longitudinal groove along the ridge was probably for the epipterygoid (Osmolska et al. 1972).

Anteriorly, a plate of the laterosphenoid tapers beneath the frontal to form part of the lateral margin of the braincase. It ends in a point in the mid-orbital region, just anterior to the cerebral expansion. Close to the anterodorsal margin, the laterosphenoid contacts the dorsal surface of the orbitosphenoid (Fig. 4a). A foramen passes between the two bones near the anterodorsal contact, probably for passage of the trochlear nerve. Ventrally, a second foramen is bounded by the laterosphenoid, orbitosphenoid, and basisphenoid and almost certainly was used by the oculomotor nerve. Two small foramina pass through the anterior face of the laterosphenoid posteroventral to the trochlear foramen. The upper (3 in Fig. 4) may have been for the anterior canal of the middle cerebral vein and the lower for the deep ophthalmic nerve (nasal and (or) frontal

branches) as in *Itemirus* (Kurzanov 1976a).

A well preserved fragment of bone (Fig. 1 *i–l*) was found lying against the right side of the skullcap of TMP 79.8.1. It is unquestionably the anteroventral corner of the right laterosphenoid. Although the dorsal portion of the fragment is broken and does not include the parietal suture, there can be little doubt that this fragment came from the same individual as the skullcap. It is almost identical to this region on TMP P82.19.23 but merits description because it is uncrushed and well preserved. The lateral wall of the laterosphenoid is a thin plate of bone (2.3 mm thick) with a concave mesial surface. Anteriorly it is strengthened by a vertical ridge of bone that is continuous dorsally with the postorbital process and is some 5 mm thick posterior to the base of the orbitosphenoid and 7.8 mm thick at the basisphenoid suture. The anterior margin of the vertical ridge curves posterolaterally and thins out at the contact with the orbitosphenoid. The orbitosphenoid contact is a simple butt joint on the anterior face of the laterosphenoid; the width of the contact is only 2 mm thick. The ophthalmic artery lay in a shallow trough (12 in Fig. 1 *i, k, l*) on the inner surface of the laterosphenoid and passed anterodorsally through the tapering ventral contact between orbitosphenoid and laterosphenoid. Below this point, a larger foramen for the oculomotor nerve is bounded by the laterosphenoid, orbitosphenoid, and basisphenoid. The basisphenoid suture is an interdigitating butt joint that must have been very strong. Posterior to this contact, the ventral margin of the laterosphenoid rises sharply for a short distance, and the prootic suture twists so that it has a slight lateral orientation (Fig. 1j). There is a large foramen for the first branch of the trigeminal nerve that passes through the body of the basisphenoid into the lower margin of the laterosphenoid, where it bifurcates. The large channel passes out of the anterior face of the laterosphenoid, and the smaller leaves the bone anterior to a distinct lateral impression (Fig. 1j) and enters a shallow trough dorsally. This is true in both specimens. The lateral impression presumably marks the position of the ganglia for the profundus branch of the trigeminal, the originating nerves passing primarily through the prootic and basisphenoid and into the laterosphenoid. The arrangement of nerve exits resembles that of large theropods (Osborn 1912; Russell 1970) and ornithomimids (Osmolska et al. 1972).

Posteriorly, the laterosphenoid tapers, extending to the end of the braincase, where it overlaps an anterior process of the supraoccipital and is in turn overlapped by the posteroventral process of the parietal, the squamosal, and possibly the prootic.

Dorsally, the laterosphenoid sits in a slot in the ventral edge of the parietal and overlaps the inner wall of this trough midway along its contact. The degree of overlap is variable and seems to be maximum in AMNH 6174. Near the posterior end of overlap on the right side of TMP 82.19.23, a small foramen passes between the laterosphenoid and parietal, possibly for the vena capitus dorsalis. Unfortunately, there is no evidence of this foramen on the ventral margins of any of the isolated parietals.

Orbitosphenoid

Both orbitosphenoids (sensu Madsen 1976) are preserved in TMP 82.19.23. The left orbitosphenoid is most clearly seen, as the right has shifted and slid underneath the laterosphenoid. In addition, the sutural contacts for the orbitosphenoid can be seen on the laterosphenoid fragment of TMP 79.8.1. The orbitosphenoids are thin plates of bone that thicken anteriorly and meet on the midline above and below the optic foramen. These contacts appear to have been coossified, as the bones have
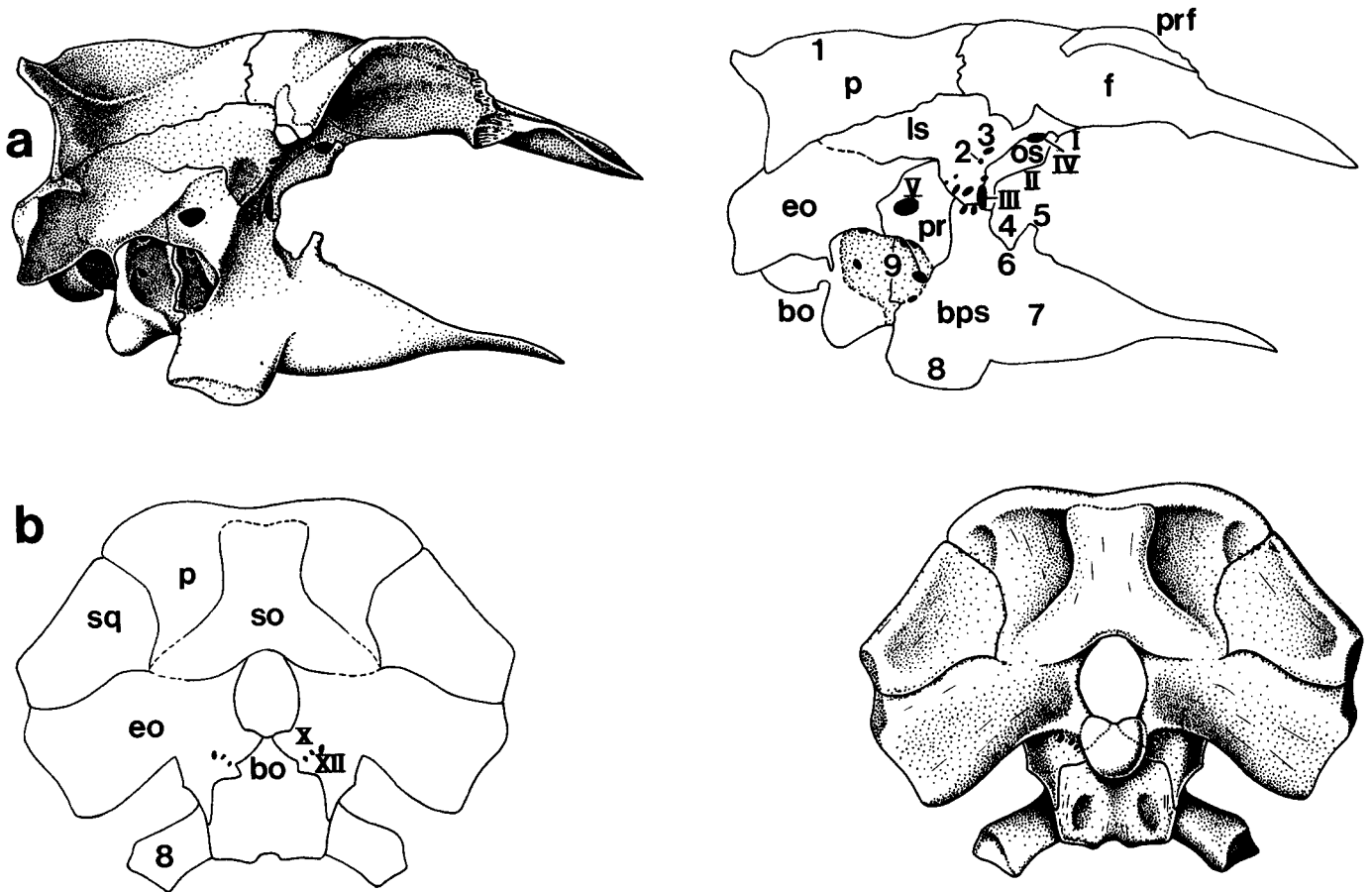
Fig. 4. *Stenonychosaurus inequalis*. Reconstruction of the braincase in (*a*) lateral and (*b*) posterior aspects. (1) Sagittal crest; (2) foramen for deep ophthalmic nerve; (3) anterior canal of middle cerebral vein; (4) pituitary fossa; (5) parasphenoid process; (6) origin of retractor muscles of the eye; (7) parasphenoid capsule; (8) basipterygoid processes; (9) lateral depression. Roman numerals represent cranial nerves.

remained together. Dorsally, each orbitosphenoid is separated from the frontal by a thin anterior projection of the laterosphenoid. A delicate ventral extension of the orbitosphenoid forms the anterior margin of the fenestra metoptica of the chondrocranium and contacts the parasphenoid–basisphenoid complex. A bar of bone joins the orbitosphenoids below the single optic foramen, in contrast with carnosaurs (Osborn 1912) where the fenestra optica has been divided into two by a vertical bar of bone. *Saurornithoides* also has a single opening, although this could be a factor of the age of specimens at the time of death. Barsbold (1983*a*) suggested that the orbitosphenoids were lost in *Saurornithoides*, but it is more likely that they had fused to the laterosphenoid in his specimens.

Orbitosphenoids are known in a variety of theropods (Stovall and Langston 1950; Hu 1964; Russell 1970; Taquet and Welles 1977; Perle 1979; Barsbold 1983*a*).

Presphenoid

A sphenethmoidal ossification is present in some of the large theropods (Osborn 1912; Stovall and Langston 1950; Taquet and Welles 1977) anterior to and coossified with the laterosphenoid and orbitosphenoid. Such an ossification is not found in *Stenonychosaurus*. However, the posterior end of the left side of a sphenethmoidal ossification, herein called the presphenoid, is preserved in TMP 80.16.1478. This medial ossification has coossified with the frontal. In section (Fig. 1*h*), however, the separation between the bones can still be made out, and when the right side of the presphenoid broke away, it

left no mark on the frontal. The posterior margin of the presphenoid is outlined by five minute foramina that passed longitudinally between the bones. The greatest posterior extent of the bone is along the midline. Here the bone is 4 mm high; the dorsal process sits in a notch between the paired frontals. The posterior margin is notched on either side of the midline. The olfactory tract passed anteriorly and slightly ventrally along the bottom of the presphenoid in a depression (Fig. 1*h*) that tapered anteriorly. The posterior end of a sphenethmoidal cartilage was observed in *Saurornithoides* (Barsbold 1974), but it is in a more posterior position, reaching the anterior limit of the laterosphenoid, whereas these bones are separated by at least 2 cm in TMP 82.19.23. A pronounced, but small (2 mm wide) pocket on the midline marking the posterior extent of this bone can be seen at the anterior end of the olfactory lobes in all the specimens where this region is preserved, including TMP 79.8.1 (Fig. 3*b*) and TMP 82.19.23 (Fig. 1*c*). The same mark is present on the midline between the paired frontals in *Dromaeosaurus* (AMNH 5356) but lies at the back of the olfactory lobes. A presphenoid was noted but not described or figured in *Gallimimus* (Osmólska *et al.* 1972).

Prootic

Anteroventrally the prootic is supported by the basisphenoid, and dorsally it supports the laterosphenoid. It forms the anterodorsal margin of the lateral depression but may not have participated in the medial wall as suggested by Barsbold (1974). Within the depression, it borders the fenestra ovalis
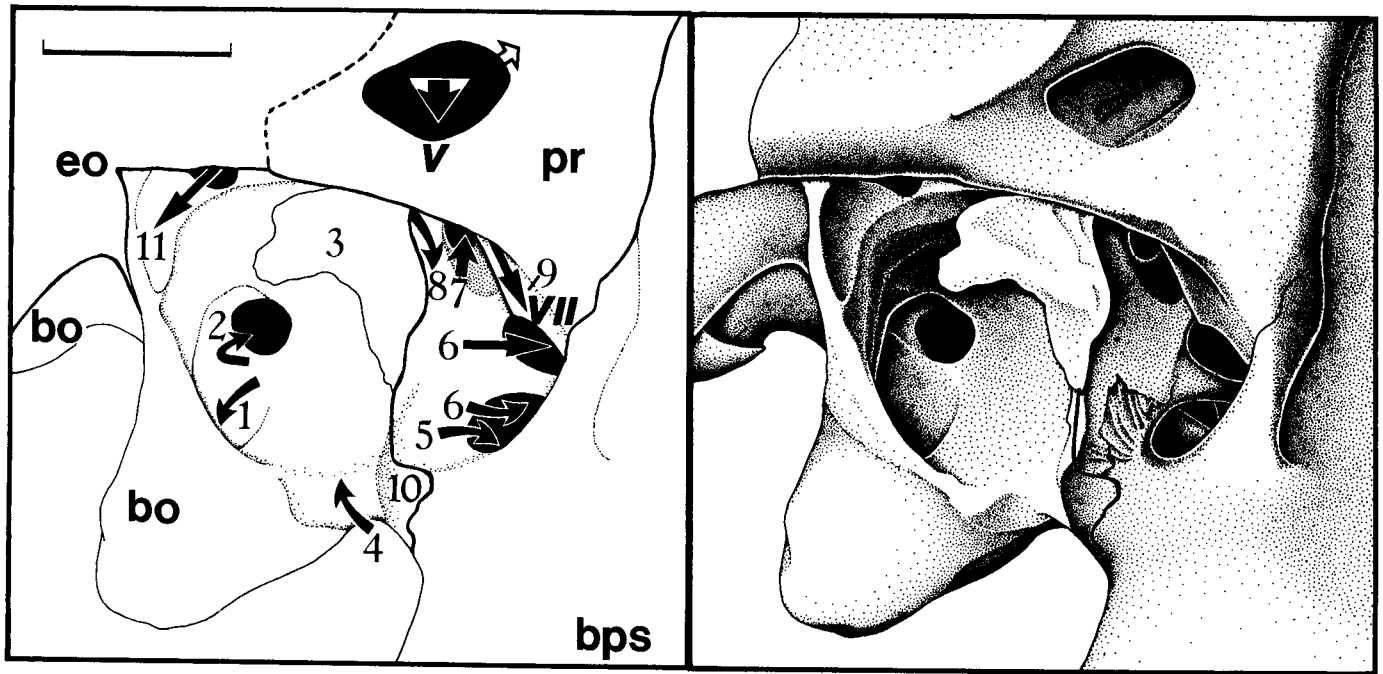
FIG. 5. *Stenonychosaurus inequalis*. Enlargement of lateral depression of the braincase (TMP 82.19.23). (1) Sinus opening into basioccipital tuber; (2) sinus openings into main body of basioccipital; (3) thin plate of bone covering part of lateral depression; (4) canal onto ventral surface of basioccipital for Eustachian tube; (5) sinus opening into basipterygoid process; (6) sinus openings into parasphenoid capsule; (7) fenestra ovalis; (8) fenestra pseudorotunda; (9) slip of bone from prootic within lateral depression; (10) groove for palatine artery and nerve; (11) pneumatic canal between lateral depression and floor of braincase. Scale = 1 cm.

anterolaterally and dorsally. A slip of bone (9 in Fig. 5) angles posteriorly, dorsally, and medially from the basisphenoid contact with the prootic on the anterior wall of the lateral depression. This slip divides the anterior wall into medial and lateral portions and seems to be made up entirely of the prootic. The slip also seems to have been present in the same position in *Saurornithoides* (Barsbold 1974, Fig. 1). A large foramen pierces the braincase dorsolateral to the slip in TMP 82.19.23 and probably marks the passage of nerve VII. In *Saurornithoides*, a foramen was interpreted as being for the seventh in the dorsal region of the lateral depression (Barsbold 1974). This foramen is more likely the fenestra pseudorotunda, given other similarities with *Stenonychosaurus*. The facial nerve is therefore bounded entirely by the prootic in the primitive manner also seen in *Archaeopteryx* (Whetstone 1983) but in contrast with *Piveteausaurus* (Taquet and Welles 1977), *Dilophosaurus* (Welles 1984), and other theropods, where it passes between the basisphenoid and prootic. A groove running down the external surface of the lappet of bone from the foramen for VII was almost certainly used by the palatine nerve. More distally this nerve may have joined the palatine artery in passing around the posterior edge of the basipterygoid process or simply continued forward across the dorsal surface of the process. The former condition is more likely, as it has been documented in other theropods (Barsbold 1983a).

The prootic–opisthotic suture has been obscured by fusion. The crista prootica, or otosphenoidal crest, inclined anterodorsally above the lateral depression and may mark the line of fusion. The most prominent feature in this region is a large foramen for the second and third branches of the trigeminal nerve. It seems to be enclosed superficially entirely by the prootic as in *Saurornithoides* (Barsbold 1983b) and *Piveteausaurus* (Taquet and Welles 1977) but in contrast with most other theropods (von Huene 1906; Osborn 1912; Gilmore 1920;

Osmolska *et al.* 1972; Welles 1984). This foramen is uncrushed on the left side of the specimen and passes laterally and somewhat posteroventrally out of the braincase. However, within the bone, which is almost 8 mm thick in this region, one or more foramina leave the main passage for the trigeminal and emerge as a pair of foramina between the prootic and laterosphenoid and through at least one foramen in the basisphenoid. A shallow groove between the crista prootica and the trigeminal foramen is probably for the stapedial artery as in *Stagonolepis* (A. D. Walker, personal communication, 1985). The posterodorsal margin of the prootic is not visible, and this bone may have extended far enough to contact the parietal as in less specialized theropods.

Exoccipital–opisthotic

The exoccipital coossified with the paroccipital process of the opisthotic, and there is nothing that can be clearly identified as a suture (Fig. 1e). The combined bones are often referred to as the otoccipital in birds and crocodiles.

The paired exoccipitals make up most of the upper portion of the occipital condyle but do not appear to meet on the midline. This characteristic is widespread in related genera (Ewer 1965; Gilmore 1920; Osmolska *et al.* 1972) and is therefore considered to be primitive. A distinct ridge rises vertically from each side of the condyle to form the lateral wall of the foramen magnum and is overlapped dorsally by the supraoccipital. The basioccipital–exoccipital suture is almost horizontal in lateral aspect on the head and neck of the condyle but turns sharply ventrad at the base of the condyle. As in *Allosaurus* (Gilmore 1920), the tapering ventrolateral process excludes the basioccipital from much of the posterior aspect of the skull. The exoccipital–opisthotic also overlaps posteriorly the posterior wall of the lateral depression as in *Saurornithoides* (Barsbold 1974).

Three foramina pierce the exoccipital lateral to the occipital

condyle, presumably for branches of nerves X and XII. There is no opening into the sinus system in this region as in ornithomimids (Osmolska *et al.* 1972) and tyrannosaurids (Russell 1970).

The paroccipital process is a large plate of bone that extends laterally and slightly ventrally from the foramen magnum (Fig. 4*b*). Distally the process is about 3 mm thick ventrally but expands dorsally to 7.5 mm on the right side and 9.5 mm on the left side of TMP 82.19.23. The distal surface of the bone is unfinished, suggesting that the process was capped in cartilage. This surface is continuous in position and texture with the distal end of the squamosal. The anterodorsal edge of the distal end of the right paroccipital process has a distinct depression supported ventrally by a process and presumably marks the position of the tympanum. The dorsal edge of the paroccipital process is overlapped posteriorly by the squamosal. Anteromedially, the paroccipital process overlaps a small triangular suture on the basioccipital posterodorsal to the lateral depression and forms part of the dorsal margin of the depression.

Anteriorly, the opisthotic does not contribute externally to the margin of the trigeminal foramen. However, the lateral wall of the braincase is almost 8 mm thick here, and it seems probable that much of that thickness is made up by the opisthotic. Similarly, a deep contact with the basisphenoid, within the lateral depression, is also probable.

Middle ear cavity

The lateral depression, a characteristic feature of saurornithoidids (Figs. 1 *b* and *d*, 4, 5) (Barsbold 1974, 1983*b*), is formed by the exoccipital–opisthotic, prootic, basioccipital, and basisphenoid. The depression is divided into anterior and posterior sections by a ridge. The posterior region is made up of the basioccipital and is described with that bone. The anterior section of the lateral depression forms the middle ear cavity. Sutures cannot be seen on the medial wall of the cavity, but it is possible that the wall was formed mainly by the prootic and an anteroventral slip of the opisthotic as in birds and crocodiles (A. D. Walker, personal communication, 1985). A rugose area in the lower part of the depression is suggestive of a sutural contact between one of these bones and the basisphenoid. At least five foramina pierce the medial wall in this region (Fig. 5). The lowest one (5, 6 in Fig. 5) is divided into two canals by a thin plate of bone; the lowermost branch passes ventrally into the body of the basipterygoid process, and the other branch probably enters the parasphenoid capsule. The internal carotid artery possibly would have passed through this foramen as well. A larger pneumatic foramen, equivalent to the foramen identified by Barsbold (1974) as being for the palatine artery, passes between this region and the prootic and enters the parasphenoid capsule as well. A shallow canal (10 in Fig. 5) enters the middle ear cavity behind the basipterygoid process and probably marks the passage of the palatine artery and nerve out of the middle ear cavity. Two more foramina pass dorsomedially through the dorsal region of the middle ear cavity. The more posterior one (8 in Fig. 5) is the fenestra pseudorotunda, which passes through the junction of the opisthotic with the basioccipital and prootic bones and enters the otic capsule. The more anterior foramen (7 in Fig. 5) opens anterodorsally into the braincase between the opisthotic and prootic. In *Saurornithoides*, a foramen in this position identified for the seventh cranial nerve (Barsbold 1974) is more likely the fenestra ovalis. The identification of these foramina is reinforced by the presence of a fragment of bone in this region on the left side of the skull, which seems to be a piece of the

stapes. The foramina identified by Barsbold (1974) as fenestra ovalis and fenestra rotunda in *Saurornithoides* are both in the basioccipital and almost certainly only enter the pneumatic system.

Basioccipital

The basioccipital is presently known in TMP 82.19.23 (Fig. 1), NMC 12340 (Fig. 6), and TMP 81.22.66 (Fig. 6). A small specimen (UCM 43218) described by Carpenter (1982) as a juvenile *Stenonychosaurus* is anatomically closer to a bird. The occipital condyle is not supported by a strong medial ridge, as it is in *Stenonychosaurus*, and the angle between the posterior and ventral surfaces is obtuse rather than acute. The angle is obtuse in *Saurornithoides junior*, however, and therefore this character is not a good one for distinguishing birds from saurornithoidids. Finally, the height of the dorsoventral contact with the basisphenoid is only 25% the height of the occipital condyle in UCM 43218, whereas in NMC 12340 the height is 175%.

The dorsal surface of the ventral body of the basioccipital rises very rapidly to a higher level to form the floor of the foramen magnum in both specimens of *Stenonychosaurus*.

The basioccipital makes up about 60% of the occipital condyle in TMP 82.19.23, where it has separated from the exoccipitals. In NMC 12340, these elements have fused indistinguishably. The occipital condyle is oval in outline, with a distinct canal on its dorsal surface.

The ventral portion of the basioccipital curves anteroventrally from the occipital condyle to form two tuberosities that are more pronounced than in *Saurornithoides* (Barsbold 1974) or *Dromaeosaurus* (Colbert and Russell 1969). The tuberosities have rugose surfaces for insertion of the M. longissimus capitis transversalis cervicus, and there is a characteristic depression on the posterior face of each analogous to the insertion of the M. rectus capiti anterior as in *Itemirus* (Kurzanov 1976*a*). In contrast with that of large theropods (Gilmore 1920; Madsen 1976), the basioccipital is relatively long between the back of the basioccipital processes and the basisphenoid suture (16.5 mm in TMP 82.19.23, 18.3 mm in TMP 81.22.66, and 17.8 mm in NMC 12340). The basisphenoid suture is a simple transverse contact ventrally, but the contact is very high dorsoventrally, amounting to almost 20 mm in NMC 12340.

The lateral surface of the ventral body of the basioccipital forms the posterior portion of the lateral depression and probably is equivalent to the paracondylar pocket of *Dilophosaurus* (Welles 1984). The depression is divided by a vertical ridge in *Stenonychosaurus* that coincides with the anterior edge of the basioccipital. In *Saurornithoides junior* (Barsbold 1974), the lateral depression is subdivided by two sloping ridges; the anterior one is equivalent to the single ridge in *Stenonychosaurus*. A thin wall of bone, arising from the ridge dividing the lateral depression, seems to have covered much of the basioccipital portion of the depression in TMP 82.19.23 (Fig. 5) but has been ruptured on both sides of the specimen. In TMP 81.22.66 it completely covered the lateral depression, including a pneumatic canal on the right side exposed by removal of part of the plate. This plate also appears to have been present in *Saurornithoides* (G. Paul, personal communication, 1983). Two large holes pierce the medial wall of this depression in the basioccipital of *Saurornithoides junior* (Barsbold 1974, 1983*b*) and on the right side of TMP 82.19.23. These were tentatively identified as fenestra ovalis and fenestra rotunda by Barsbold (1974). In the *Stenonychosaurus* specimen, the lower hole passes posteroventrally into the hollow interior of the basi-
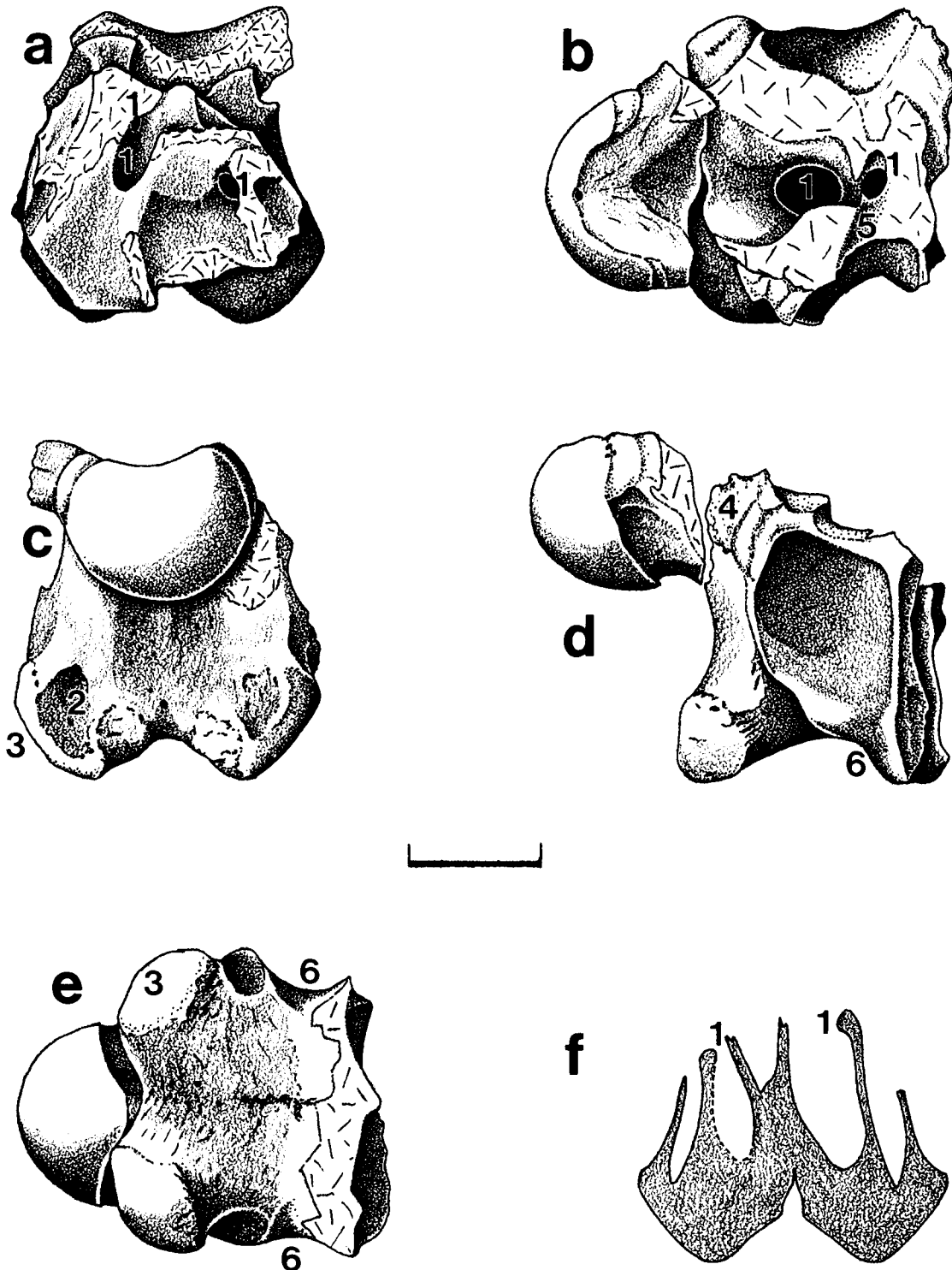
FIG. 6. *Stenonychosaurus inequalis*. Basioccipital (NMC 12340) in (*a*) anterior, (*b*) dorsal, (*c*) posterior, (*d*) lateral, and (*e*) ventral views. (*f*) Diagramatic cross section through basioccipital (TMP 81.22.6) showing asymmetry of pneumatic chambers. (1) Openings into sinus system; (2) insertion of M. rectus capiti anterior; (3) insertion of M. longissimus capitis transversalis cervicus; (4) exoccipital suture; (5) pneumatic canal between lateral depression and floor of braincase; (6) Eustachian canal. Scale = 1 cm.

occipital tuber and therefore could also be interpreted as an opening into the sinus systems. The identification of these foramina is clarified by NMC 12340 (Fig. 6), where the wall of the basioccipital portion of the lateral depression has *no* foramina. In TMP 81.22.66, the chamber ends blindly in the basioccipital tuber and does not loop back into the braincase. The anterior and dorsal surfaces of the ventral body are pene-

trated by a series of asymmetrical canals and sinuses as in large theropods (Russell 1970; Madsen 1976). These pneumatic chambers and passages would usually pierce the medial wall of the lateral depression. The lack of foramina in NMC 12340 and TMP 81.22.66 in contrast with TMP 82.19.23 *cannot be* attributed to preservational differences. The medial wall of the lateral depression of both specimens forms a smooth surface that

passes through a constriction anteroventrally to the ventral surface of the basioccipital (4 in Fig. 5; 6 in Fig. 6 *d* and *e*). A groove in the basisphenoid of *Dilophosaurus* (Welles 1984) is probably homologous. The presence of this constriction, which marks the entrance of the Eustachian tube (lateral pharyngotympanic canal of protosuchids and crocodiles, Busbey and Gow 1984), makes it easy to identify the medial wall of the depression. The specimens are well enough preserved to see that the medial wall has not been ruptured in TMP 82.19.23 and that the thin plate of bone lateral to the depression has not simply been crushed down in NMC 12340 to cover the foramina.

Another foramen pierces the braincase at the top of the lateral depression, passing between the basioccipital and the opisthotic (Fig. 5). The floor of the canal is preserved in NMC 12340 (Fig. 6 *b* and *d*), passing posterolaterally into the braincase, where it seems to joint the medial pneumatic system of the basioccipital.

The lateral depression of the basioccipital may not have been pierced in a consistent manner, but the depression itself is a persistent, well defined characteristic of both *Stenonychosaurus* and *Saurornithoides*. Ridges on the basioccipital define its limits posteriorly, dorsally, and posteroventrally.

Most of the interior of the basioccipital appears to have been hollowed out for pneumatic chambers. The arrangement of these chambers is asymmetrical and highly variable (Fig. 6 *a*, *b*, *f*). The lateral ones seem to connect to the middle ear and Eustachian tube by foramina in the medial wall of the lateral depression. Medial chambers open into the floor of the braincase (Fig. 6*b*). Two small foramina on the midline of the ventral surface of TMP 81.22.66 are symmetrical but do not seem to penetrate too deeply.

The posterior wall of the lateral depression is a sharp, well defined ridge of bone. A groove passing across the ridge about halfway up probably marks the course of the stapedial artery and the hyomandibular nerve.

Discussion

Barsbold (1974, 1983*a*) recognized two species of *Saurornithoides*. The type specimen of *Saurornithoides mongoliensis* (Osborn 1924) from the Djadokhta Formation is about 30% shorter than the type of *S. junior* from the Nemegt Formation. Other than differences in size and geological age, the only character cited by Barsbold (1974) as distinguishing the species is the greater number of maxillary teeth in *S. junior*. None of these features are particularly useful for separating palaeospecies, and once a range of specimens is known from each formation, the two species of *Saurornithoides* may turn out to be indistinguishable. Until such time that the species of *Saurornithoides* are shown to be conspecific, it is more reasonable to maintain *Stenonychosaurus* as a distinct genus because of significant differences between it and both species of *Saurornithoides*.

Saurornithoides junior seems to be approximately the same size as larger specimens of *Stenonychosaurus* and is not significantly different from the latter in degree of ossification. Differences observed between these animals are therefore unlikely to be attributable to ontogenetic variation. The postorbital region of *Stenonychosaurus* is longer than that of *Saurornithoides* in relation to both the height of the orbit and the length of the frontal. Russell (1969) also suggested that the skull of *Stenonychosaurus* was relatively broader in the postorbital region. However, the more recently described specimen of *Saurorni-*

thoides junior indicates that this probably was not the case. The more rounded anterior margin of the maxillary fenestra shows that this opening was relatively larger in *Stenonychosaurus* and suggests that the muzzle was higher than that of *Saurornithoides*. The most diagnostic cranial difference between these genera is the greater development of the basioccipital tubera in *Stenonychosaurus*. The tubera are not only larger, but they have shifted posteroventrally. Corresponding to this shift, the shape of the middle ear cavity has changed somewhat, along with the alignment of the foramina that pierce the braincase walls. The change also caused an increase in the length of the region between the parasphenoid capsule and the basioccipital tubera and loss of the sulcus or trough in this region. These changes seem to result in an increase in the size of the brain cavity, although this would be difficult to check because of the crushed condition of the specimen. The posterior limit of the presphenoid−frontal suture is more anterior in position in *Stenonychosaurus*, demonstrating that the olfactory tract was also more anterior in position, corresponding again to a possible increase in brain size. Regardless of whether the relative brain size of *Stenonychosaurus* is larger than that of *Saurornithoides* or not, most features of the braincase of the North American form seem to be more derived than those of the Asian genus.

The presence of canals for blood vessels on the mesial surface of the laterosphenoid suggests that the brain of *Stenonychosaurus* filled the relatively large brain cavity, in contrast with many reptiles.

The presence of an enlarged parasphenoid capsule in saurornithoidids, *Garudimimus*, and ornithomidids is considered here to be a synapomorphy. The possible function of the capsule will be discussed below.

The lateral depression of saurornithoidids is made up of the basisphenoid, basioccipital, prootic, and opisthotic−exoccipital complex. In *Stenonychosaurus*, and probably in *Saurornithoides* as well, the lateral depression is divided by a ridge along the anterior margin of the basioccipital. Two foramina generally pierce the medial wall of the posterior section of the lateral depression and enter the sinus system. A foramen passes through the dorsal edge of this part of the lateral depression and was probably also pneumatic. The anterior portion, the middle ear cavity, includes foramina that pass into the sinus system of the parasphenoid capsule and the basipterygoid process, foramina for the internal carotid artery and the facial nerve, the fenestra ovalis, and fenestra pseudorotunda. Assuming the identifications in *Stenonychosaurus* are correct, then Barsbold's (1974) identifications are incorrect in that his "fenestra ovalis" and "fenestra rotunda" are pneumatic openings, the "palatine" foramen is for the internal carotid, the "internal carotid foramen" is the fenestra ovalis, and "VII" is the fenestra pseudorotunda.

The lateral depression of saurornithoidids appears to be unique among the theropods. Barsbold and Perle (1980) described a similar depression in *Erlikosaurus*, but the position and shape are fundamentally different. Paul (1985) has also demonstrated that this animal is not theropod. All other theropods, including the ornithomimids (Osmólska *et al.* 1972), have not changed the fundamental arrangement of these foramina from that seen in thecodonts. The saurornithoidid lateral depression forms a well defined middle ear cavity, suggesting that these animals had an improved *sense of hearing over their* nearest relatives. The Eustachian tube entered the middle ear cavity along a groove in the basioccipital bone immediately

behind its contact with the basisphenoid, in the same relative position as in crocodilians (Iordansky 1973). Although a vertical ridge divides the lateral depression into anterior and posterior sections, it seems unlikely that the separation was complete because this ridge extends laterally only half the distance that the anterior, dorsal, and posterior edges of the lateral depression do in TMP 82.19.23. Air entering the lateral depression through the Eustachian tube would therefore have also entered the anterior part of the depression and through it the sinuses in the basipterygoid processes and the parasphenoid capsule. Pneumatization of the roof of the mouth was considered by Walker (1972) as one of the most significant features for showing the possible ancestral relationship of crocodiles to birds. The passage of the internal carotid through the middle ear cavity and anterodorsally into the braincase on its way to the pituitary fossa is similar to that of birds and crocodiles because of its association with the pneumatic system. The pneumatic foramina in the anterior portion of the lateral depression are similar in position and orientation to the precarotid and post-carotid recesses of *Sphenosuchus* (Walker 1972) and recent crocodiles and birds (Whetstone and Martin 1981). They are very similar in position and orientation to pneumatic foramina in *Archaeopteryx* (Walker, in press), although the palatine nerve seems to have passed anterolateral to these foramina in *Stenonychosaurus* and posterolateral in *Archaeopteryx*. Both situations are present in modern birds, however (A. D. Walker, personal communication, 1985).

Contrary to the statement of Whetstone and Martin (1981) that the lateral depression of saurornithoidids has no similarity to the periotic sinuses of birds and crocodiles, it is clear that the similarities are quite astonishing. In support of their argument, there is no evidence of a transverse canal joining the two middle ear cavities dorsally as is the case in crocodiles (Iordansky 1973) and birds (Whetstone and Martin 1979). However, there are at least two other systems of periotic pneumatic cavities and apparently two pneumatic cavities associated with the cerebral carotid. As pointed out by Whetstone and Martin (1979), enlargement of the periotic pneumatic cavities medial to the tympanic membrane produces a dampening effect of the air cushion for better detection of low-frequency sound. The enlargement of the parasphenoid into a "bulbous structure" may well be associated with this function, as the parasphenoid cavity is completely hollow and connected directly to the middle ear cavity. The inside of the parasphenoid capsule of ornithomimids is confluent with the sinus system (Osmolska *et al.* 1972), but the middle ear cavity is not as well defined, so it is difficult to know whether or not the two regions were connected directly. The enlargement of the basipterygoid processes into large, hollow structures in both saurornithoidids and crocodilomorphs like *Sphenosuchus* (Walker 1972) may also be a means of increasing the size of the air cushion associated with the middle ear. In many ways, the middle ear of *Stenonychosaurus* is closer in appearance to that of recent birds than either is to *Archaeopteryx*, the earliest known bird.

The presence of a foramen posterior to the fenestra ovalis suggests that *Stenonychosaurus* had a fenestra pseudorotunda. However, it would be difficult to prove this because of the large number of openings into the sinus system, because the foramen is largely obscured by an overhanging shelf of the prootic and because the internal course of the foramen is unknown. It does suggest that more specimens need to be studied before generalizations are made suggesting that theropods did not have a

fenestra pseudorotunda (Whetstone and Martin 1979, 1981).

As pointed out by Whetstone (1983), *Archaeopteryx* probably had a descending process of the squamosal, and the squamosal did not broadly overhang the otic region. Another characteristic, the presence of a quadrate cotyle at the anterior base of the parocciput rather than at its lateral terminus, was used to distinguish recent birds and crocodiles from theropods but does not apply to either *Stenonychosaurus* or *Deinonychus*. The arched configurations of the parietals and of the dorsal margin of the occipital plate, the reduction of the posttemporal fenestra to a small foramen, and the greater relative size of the foramen magnum would be expected in a theropod like *Stenonychosaurus* if it were the same small size at maturity as *Archaeopteryx*.

A depression in the lateral wall of the braincase of *Archaeopteryx* was interpreted as possibly the medial wall of the dorsal periotic sinus of recent birds. This is questionable because a depression is found in the same region in *Stenonychosaurus*, even though it appears to involve the laterosphenoid rather than the prootic. Although the prootic does not extend as far posteriorly in theropods as it does in birds and crocodiles (Walker 1972; Whetstone and Martin 1979; Whetstone 1983), it extends posteriorly beyond the opening for the second and third branches of the trigeminal in saurornithoidids and may have reached the parietal posteriorly.

In summary, the braincase of *Stenonychosaurus* shows a number of characteristics that have been considered as synapomorphic for birds and crocodiles, including periotic pneumatic cavities, pneumatic cavities associated with the cerebral carotid, a more medial position for the quadrate cotyle than that seen in the larger theropods, and a fenestra pseudorotunda. Restudy of the braincase of *Archaeopteryx* (Whetstone 1983) has shown that a number of other derived features of birds and crocodiles are due to convergence rather than common ancestry. Walker (in press) has shown that *Archaeopteryx* had a single-headed quadrate as in theropods. The posterior extent of the prootic and the tooth morphology are the only features listed by Whetstone and Martin (1981) that are presently unknown in theropod dinosaurs. Although *Stenonychosaurus* might have had a more extensive prootic than reconstructed here, the significance of the character by itself should not be overrated. Work in progress by the author suggests that tooth morphology in *Stenonychosaurus* is comparable with that of birds and crocodiles.

Considering the large number of similarities between small theropods and birds (Padian and Gauthier, in press), it is more reasonable to interpret the remaining similarities between birds and crocodiles as convergences rather than invoking an ancestor–descendent relationship.

The similarities between the middle ear regions of saurornithoidid theropods and birds are suggestive of relationship. On the other hand, the lack of some of these specializations in other theropods and *Archaeopteryx* may indicate that there has been convergent evolution in the braincase. Functionally, this could have occurred as a means to both lighten the skull and increase the capability of hearing low-frequency sound.

A third option is that periotic pneumatization may be a primitive characteristic shared by crocodiles, birds, and saurischians but modified in all but a few of the latter. The interrelationships of these three major lineages cannot be resolved on the basis of the braincase alone, and detailed analysis of other parts of the skeleton is essential.

Acknowledgments

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