A new troodontid (Dinosauria, Theropoda) braincase from the Dinosaur Park Formation (Campanian) of Alberta

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A new, well-preserved specimen of *Troodon formosus* is the first to reveal the internal anatomy of the lower part of the braincase. In addition to providing new information on the brain of this highly encephalized dinosaur, the uncrushed bones clear up anatomical details left obscure by earlier studies. Computerized tomography (CT) scans reveal the nature of the inner ear and the course of the pneumatic ducts diverging from the middle ear. Evidence is presented to show that four of the five periotic pneumatic systems found in bird skulls are present in *Troodon*. The anterior tympanic recess is the most elaborate system, and diverticula from each side extend anteriorly, dorsally and, posteriorly from the middle ear. The posterior tympanic recess is located within the paroccipital process and the basioccipital, but the pneumatopore posterolateral to the stapedial recess is secondarily closed. The dorsal periotic sinus is represented by a smooth-surfaced concavity on the lateral surface of the prootic. The position of a pneumatic recess in this region is demonstrated by the presence of a pneumatopore in the quadrate. Diverticula from the anterior and posterior tympanic recesses are connected within braincase bones, and a possible pneumatopore in the prootic may connect these to the dorsal tympanic recess. The pneumatic condition of the troodontid articular is unknown. Contralateral connections of the sinus systems have been used to argue for a close relationship between birds and crocodiles, but their presence in this specimen suggests that they appeared more than once in archosaurs or that they are plesiomorphic for crocodiles, dinosaurs, and birds. Cranial pneumaticity cannot be used by itself to resolve the interrelationships of crocodiles, theropods, and birds, but other characters suggest derivation of birds from theropods.

Un nouveau spécimen, bien préservé, de *Troodon formosus* est le premier à révéler l'anatomie interne de la partie inférieure de la boîte crânienne. En plus d'apporter de nouveaux enseignements sur le cerveau de ce dinosaure hautement encéphalique, les os complete divulguent clairement des détails anatomiques que les études antérieures n'avaient pas réussi à élucider. L'examen des balayages CT (tomographie assistée par ordinateur) divulgue la constitution de l'oreille interne, et indique en outre que le tracé des canaux pneumatiques diffère de celui de l'oreille moyenne. Les observations démontrent que quatre des cinq systèmes pneumatiques périotiques trouvés dans les crânes des oiseaux sont présents dans *Troodon*. C'est la cavité antérieure du tympan qui représente le système le plus sophistiqué, et les diverticules de chaque côté s'étendent vers l'avant, dorsalement et postérieurement en partant de l'oreille moyenne. La cavité postérieure du tympan est localisée à l'intérieur de l'apophyse paroccipitale et du basioccipital, mais la cavité entre le pneumatopore postérolatéral et stapédial est secondairement fermée. Le sinus périotique dorsal est représenté par une concavité à surface lisse creusée sur la surface latérale du prootique. La position de la cavité pneumatique dans la région est démontrée par la présence d'un pneumatopore dans le quadrate. Les diverticules des cavités antérieures et postérieures du tympan sont connectés par l'intérieur des os de la boîte crânienne, et il est possible qu'un pneumatopore dans le prootique puisse relier ces diverticules avec la cavité dorsale du tympan. La condition pneumatique de l'articulaire d'un troodontidé est inconnue. Les connections contralatérales des systèmes de sinus ont été utilisées pour plaider en faveur de l'existence d'une relation étroite entre les oiseaux et les crocodiles, mais leur présence dans ce spécimen suggère qu'elles sont apparues plus d'une fois dans les archosaures, alors que pour les crocodiles, dinosaures et oiseaux, elles sont plésiomorphiques. La pneumaticité crânienne n'est pas utilisable pour solutionner le problème des interrelations qui existent entre les crocodiles, les théropodes et les oiseaux, cependant d'autres critères suggèrent que les oiseaux sont dérivés des théropodes.

[Traduit par la rédaction]

一具新发现的 Troodon formosus 标本第一次揭示了该种脑颅下部的内部构造。它不仅提供了有关这种头颅非常发育的恐龙脑子的新信息，而且它没有变形的颅骨使以前无法深入研究的解剖学细节得到了澄清。CT 扫描揭示了内耳的特征以及从中耳外延的气腔管道的走向。本文提供的证据表明鸟类头骨所具备的五个围耳气腔系统有四个在 Troodon 中发育。前鼓窦（anterior tympanic recess）的气腔系统最为复杂，支气管道由中耳向前部、背部、和后部延伸。后鼓窦（posterior tympanic recess）位于副枕突和基枕骨之间，但位于蹬骨窦（stapedial recess）

后侧方的气腔已被次生封闭。背围耳窦（dorsal periotic sinus）由前耳骨侧面一表面光滑的凹所代表。方骨上一气腔的存在能够表明本处气窦的位置。从前、后鼓窦中外延的支气腔管道在颅骨中相连通，并且前耳骨中可能存在一气腔把这些气窦与背鼓窦连接起来。在似鸟龙类（troodontids）中，关节骨的气腔发育状况尚未可知。左右两侧血窦系统的连通一直被认为是鸟类和鳄鱼类亲密关系的证据，但是这种构造在新发现标本中的存在指出它在初龙类（archosaurs）中的出现似乎并不止一次，或者它对于鳄鱼类、恐龙类、和鸟类来说是近祖性的。脑颅气腔化这一性状本身不能用来揭示鳄鱼类、兽脚类、及鸟类的相互关系，但其它一些特征则说明鸟类起源于兽脚类恐龙。

[译文由杂志社提供]

Новый, хорошо сохранившийся экземпляр <u>Troodon</u> <u>formosus</u> впервые позволил узнать внутреннюю анатомию нижней части черепной крышки. Вдобавок к полученным новым сведениям об этом динозавре с сильно развитым мозгом, обследование неразрушенных костей прояснило те анатомические детали, которые остались неясными при предыдущих исследованиях. С помощью CT-анализа (CT-scan) была установлена природа внутреннего уха и направление пневматических каналов, расходящихся из среднего уха. Доказано, что четыре из пяти расположенных вокруг внутреннего уха пневматических систем, найденные в черепах птиц, присутствуют у <u>Troodon</u>. Передняя барабанная впадина представляет собой сложнейшую систему, а дивертикулы с каждой стороны идут вперед, дорсально и назад от среднего уха. Задняя барабанная впадина расположена внутри парооципитального и базиоципитального отростка, но пневматодор, постеролатеральный по отношению к стапедиальной (стремянной) впадине, вторично замкнут. Дорсальный синус, расположенный вокруг внутреннего уха, представлен гладкой вогнутостью на латеральной предушной поверхности. Расположение пневматической впадины в этом отделе подтверждается наличием пневматопора в квадратной кости. Дивертикулы из передней и задней барабанных впадин соединены внутри костей черепной крышки, а предполагаемый пневматопор, расположенный перед ухом, может соединять их с дорсальной барабанной впадиной. Пневматические условия суставов троодонтид неизвестны. Контралатеральные соединения синусных систем давно являются предметом дискуссий по поводу тесной связи между птицами и крокодилами, но их наличие у данного экземпляра свидетельствует о неоднократном их появлении у архозавров или об их плезиоморфности у крокодилов и птиц. Черепную пневматичность нельзя использовать как единственное доказательство взаимосвязей между крокодилами, тераподами и птицами, но другие характеристики свидетельствуют о происхождении птиц от терапод.

[Перевод выполнен для редакции Научно-Исследовательские Журналы]

Introduction

Troodontids were among the first dinosaurs described (Currie 1987a), and reasonably well-preserved specimens were discovered early this century (Osborn 1924; Sternberg 1932). However, the better specimens were not widely associated with *Troodon* until recently (Currie 1987a). Because of the widespread belief that theropods are ancestral to birds, the collection, preparation, and description of carnivorous dinosaurs has intensified. Troodontids are possibly the most birdlike theropods (Currie 1985, 1987a), but they are rare and fragmentary (Osmólska and Barsbold 1990). Fortunately, a number of better preserved specimens have now been collected (Currie and Peng 1993; Kurzanov and Osmólska 1991; Russell and Dong 1993; Varricchio and Currie 1991), and within the near future troodontids promise to become one of the best known families of small theropods.

In 1986, four scientists and technicians from the Institute of Vertebrate Palaeontology and Palaeoanthropology (Z.-M.

Dong, Z.L. Tang, C. Yu, and X.-J. Zhao) and a palaeontologist (R. Li) from the Inner Mongolia Museum (Hohhot) joined staff of the Royal Tyrrell Museum of Palaeontology at a field-camp in Dinosaur Provincial Park. This was the first collecting party of the Sino-Canadian Dinosaur Project (China — Canada — Alberta — Ex Terra). Late in July, Tang Zhilu discovered a theropod braincase in the heart of Dinosaur Provincial Park. The site of discovery (Leg. Subdiv. 1, Sec. 6, T. 21, R. 11, W4) has been marked in the field as Quarry 187. The anatomical significance of the specimen was immediately recognized, and preparation was initiated in the field. The identification as a troodontid is based on comparison with a more complete specimen (Currie 1985). At present only one troodontid, *Troodon formosus*, is recognized (Currie 1987a) from the Dinosaur Park Formation.

Systematic palaeontology

Reptilia Linnaeus, 1758
Archosauromorpha Huene, 1946
Dinosauria Owen, 1842
Saurischia Seeley, 1888
Theropoda Marsh, 1881
Troodontidae Gilmore, 1924
Troodon Leidy, 1856
Troodon formosus Leidy, 1856

Abbreviations

AMNH, American Museum of Natural History, New York; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MOR, Museum of the Rockies, Bozeman; PIM, Paleontological Institute of Mongolia, Ulan Bator; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller.

Description

RTMP 86.36.457 is a braincase lacking the roofing elements (frontals and parietals) and much of the basisphenoid—parasphenoid. Most of the previous description (Currie 1985) of the braincase of *Troodon*, based on RTMP 82.19.23, is still valid. Therefore, description of this specimen will be restricted to those regions not visible in the earlier discovered specimen, and correction of some inaccuracies. The latter category refers mostly to the region immediately around the otic cavity, which is collapsed in RTMP 82.19.23 and misidentified as a possible pneumatic canal by Currie (1985).

The size and degree of fusion clearly shows that RTMP 86.36.457 was a mature but not old individual. As previously noted (Currie 1985), most specimens of *Troodon formosus* recovered from Dinosaur Provincial Park are from animals of approximately the same size. There are numerous frontals (Currie 1987b) of individuals with estimated skull lengths of 200—250 mm, which suggests that this species may have had determinate growth. Histological work by Varricchio (1993) suggested that the maximum size for the species levelled off at a body weight of around 50 kg. This has been a great advantage in studying the braincase of *Troodon* because the fronto-parietal skull cap of a different specimen (RTMP 79.8.1) fits onto RTMP 86.36.457. The occipital condyle of RTMP 86.36.457 has a transverse diameter of 15.5 mm. The foramen magnum is subcircular with a maximum width of 15.0 mm. The distance between the back of the hypophysial fossa and the

posterior margin of the preserved portion of the occipital condyle is 45 mm.

RTMP 86.36.457 (Figs. 1, 2) includes the supraoccipital, the exoccipitals, the basioccipital, some of the basisphenoid—parasphenoid, both opisthotics, the laterosphenoids, and both prootics. Most of the sutures have been obscured by fusion, and references to individual bones in this paper actually refer to the corresponding regions of the braincase identified by comparison with other theropods in which the sutures are visible. It cannot be determined whether or not an epiotic arose from a separate centre of ossification. The presence of epiotics has long been suspected in theropods (Huene 1906), and they have been reported recently (McClelland, in press) in *Allosaurus*, so it is almost certain that they exist fused to the supraoccipitals of troodontids and other theropods. Although the epiotics arise as separate entities in birds, they also coossify completely with other braincase bones by maturity. The parasphenoid, which is a balloonlike bulbous structure in troodontids, was delicate enough to have been destroyed before burial and fossilization. The remaining skull bones had loose sutural contacts and had separated from the specimen during Cretaceous time.

The floor of the braincase, formed by the basioccipital and basisphenoid—parasphenoid complex, is remarkably deep in troodontids and tends to be highly pneumatized. The basisphenoidal depression (sometimes incorrectly referred to as Rathke's pouch), a widespread ventromedial pneumatic character in theropods and many other archosaurs, is lost in troodontids and is represented only by a shallow depression. The occipital plate is nearly vertical to the basal plate, whereas this angle is acute in dromaeosaurids (Colbert and Russell 1969) and most other theropods, and obtuse in most birds (Elzanowski and Galton 1991). Within the cranial cavity are well-defined tectal, auricular, and medullar fossae (Figs. 1b, 1e). The semicircular groove (sulcus semicircularis) is shallow (Fig. 3) and ends posteriorly above the arcuate eminence in a foramen for the posterior canal of the middle cerebral vein. The auricular fossa is large and has an oval outline, the longitudinal axis of which is vertical. The vestibular eminence, housing the vestibule, is clearly defined. The slitlike endolymphatic foramen opens posteromedially into the foramen magnum (Fig. 1d).

Supraoccipital — epiotic

The dorsal margin of the supraoccipital is complete on the left side and would not have extended to the top of the nuchal (supraoccipital) crest, which is formed mostly by the parietal. Laterally, a small venous foramen (Figs. 1b, 1d, 4b) passes anteroposteriorly through the suture between the supraoccipital and parietal. Most of this canal, which is 0.8 mm wide, is surrounded by the supraoccipital, although it is capped by the parietal posteriorly where it emerges from the skull. This was presumably the external opening of the posterior canal of the middle cerebral (= external occipital) vein, which was passing posterolaterally from the inside of the braincase (Fig. 1e). A small venous canal passes between the supraoccipital and parietal to join the middle cerebral vein as it passes out onto the occiput.

Above the foramen magnum and the posterior portion of the brain, the supraoccipital is hollow (Figs. 1b, 2b, 2e). Internally, a midline wall divides the hollow interior into left and right portions. The spaces within the supraoccipital are open
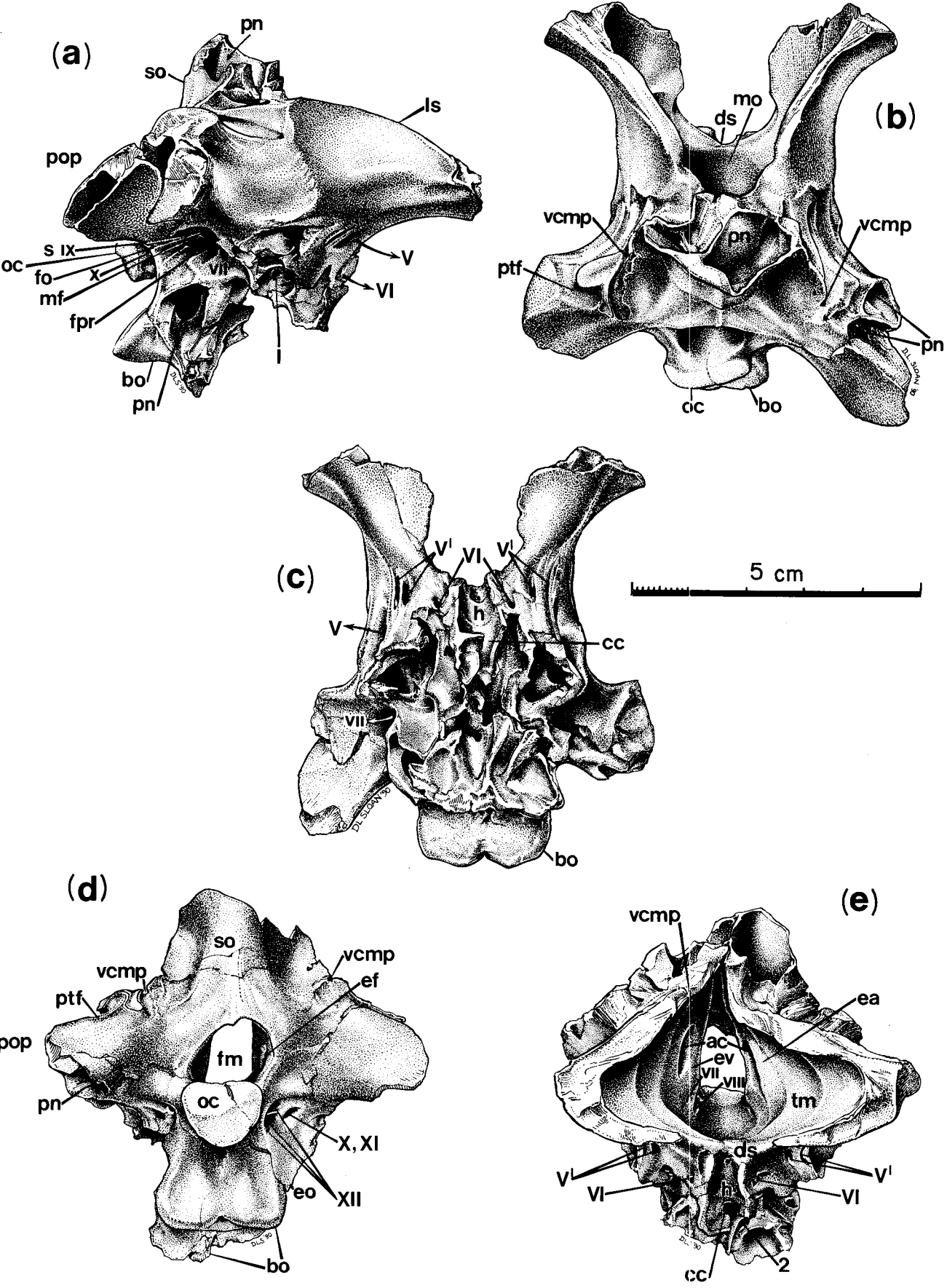
dorsally, but the nuchal (supraoccipital) crest of the parietals arches posterodorsally over the openings to close them from above like the lid of a box. On each side, a pneumatic duct in the prootic connects the supraoccipital sinus with the anterior (rostral) tympanic recess of the lateral depression. In *Dromaeosaurus* (AMNH 5356), the sutural contact between the supraoccipital and the parietal is similar to that of *Troodon* in shape and orientation above the otic capsule. However, a broken surface clearly shows that the supraoccipital was solid. Similarly, a break in *Itemirus* (PIN 327/699) demonstrates that the bone is anteroposteriorly thick beneath the parietal contact, but was apneumatic. This is also the case in *Tyrannosaurus* (Osborn 1912) and other theropods where the internal structure of the supraoccipital is exposed.

Squamosal

The squamosal is not present in RTMP 86.36.457, but its suture with the paroccipital process is exposed. The sutural contact is different than the kinds seen in *Deinonychus* (YPM 5210), *Dromaeosaurus* (AMNH 5356), and most other theropods, in which it is usually elongate and narrow. In *Troodon*, the squamosal–opisthotic suture is anteroposteriorly long (9.5 mm) between the posttemporal fenestra and the quadrate cotyle, but thins laterally and medially to about half of the length.

RTMP 79.8.1 shows that the dorsolateral margin of the nuchal crest of the parietal is very thin, suggesting that there was no contact with the squamosal. Therefore, there probably was a narrow slit on the occiput between the parietal and squamosal (Fig. 4*b*). The squamosal contacted the lower half of the lateral margin of the parietal's contribution to the supraoccipital crest.

Basisphenoid–parasphenoid

Much of the ventral portion of the basisphenoid was lost along with the parasphenoid.

Below the single medial opening for the optic nerves, the dorsal surface of the basisphenoid forms the posterior, lateral and ventral walls of the pituitary fossa (Figs. 1*c*, 1*e*, 2*g*). The pituitary fossa is divided by a horizontal ridge into two depressions (Fig. 2*d*). The lower portion of the fossa is penetrated by a single foramen (2 mm diameter) for the merged internal carotids. The internal carotid enters the basisphenoid–parasphenoid complex at the anterior margin of the lateral depression (Currie 1985) and passes through a large pneumatic sinus in the basisphenoid (Figs. 1*c*, 2*c*), as in *Itemirus* (Kurzanov 1976), before joining its mate and entering the pituitary fossa. The internal carotids entered the pituitary fossa through separate openings in *Dromaeosaurus* (AMNH 5356), but were also combined in *Itemirus* (PIN 327/699). Anterolateral to the dorsum sellae, the basisphenoid would have contacted the orbitosphenoid. Ventrolateral to the suture, the sixth cranial nerve emerges from the braincase through a single foramen 1.5 mm in diameter (Figs. 1*a*, 1*c*, 1*e*, 2*d*).

Only part of the medial wall of the basisphenoid portion of the lateral depression is preserved on RTMP 86.36.457. The depression is extended dorsally by pneumatic cavities that lead into other braincase bones. The pneumatic recess dorsomedial to the internal carotid opening and posterior to the hypophyseal fossa breaches the medial wall of the basisphenoid to connect with the lateral depression on the opposite side of the skull (Fig. 1*a*).

Laterosphenoid

The contact between the laterosphenoid and prootic is represented by a raised ridge on both sides of RTMP 86.36.457, and agrees with the arrangement seen in *Saurornithoides* (Barsbold 1974) and other theropods. It is clear that the laterosphenoid formed the anterior margin of the major, lateral opening of the trigeminal nerve and that this opening was not surrounded by the prootic as figured by Currie (1985). The anterior margin of the lateral trigeminal foramen is visible in a fragment of RTMP 79.8.1 (Figs. 1*j*, 1*k* of Currie 1985).

The distal condyle (for contact with the postorbital) was not preserved on either laterosphenoid. Medial to where the condyle would have been is a deeply rugose sutural surface, the lateral portion of which would have contacted the frontal. However, the laterosphenoid and frontal diverge here, and another bone must have closed the triangular gap. Sutures cannot be detected in this region in RTMP 82.19.23. Gilmore (1920) has argued in favour of an ethmoid in this position in *Allosaurus*, and Osborn (1912) identified the bone in this region of *Tyrannosaurus* as the orbitosphenoid (presphenoid). If this is correct, then the laterosphenoid did not form any part of the margin of the olfactory opening.

The internal surface of the laterosphenoid is divided into two concavities by a low anteroventral–posterodorsal ridge that marks the separation between the cerebral fossa anterodorsally and the optic fossa posteroventrally (Figs. 1*e*, 2*j*).

Ventromedially, the laterosphenoid has a small, fingerlike projection that crosses the top of the dorsum sellae to contact the laterosphenoid on the other side. Pneumatic diverticula apparently entered the laterosphenoid through the prootic (Figs. 2*d*, 2*i*).

Prootic

As in *Saurornithoides* (Barsbold 1974), the prootic forms the dorsal, posterior, and ventral margins of the trigeminal foramen, and the dorsal and part of the anterior margins of the lateral depression. A poorly developed crista prootica is continuous with the anterior margin of the lateral depression (alaparasphenoid). Unfortunately, even in this specimen, the prootic is indistinguishably fused to the opisthotic, and it is impossible to know how far it extended posterodorsally. In *Saurornithoides* it extended posterodorsally far enough to at least contact the parietal (Barsbold 1974).

The prootic would have contributed to most of the anterior boundary of fenestra ovalis (fenestra vestibularis). Posterodor-

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FIG. 1. *Troodon formosus*. Braincase (RTMP 86.36.457) in (*a*) right lateral, (*b*) dorsal, (*c*) ventral, (*d*) posterior, and (*e*) anterior views. Roman numerals represent cranial nerve openings. 1, contralateral pneumatic connection in basisphenoid; 2, pneumatopore connecting pneumatic systems within basisphenoid and basioccipital. ac, fossa auriculae cerebelli; bo, basioccipital; cc, ostium canalium caroticorum; ds, dorsum sellae; ea, arcuate eminence (eminentia arcuata); ef, endolymphatic foramen; eo, exoccipital–opisthotic complex; ev, vestibular eminence (eminentia vestibularis); fm, foramen magnum; fo, fenestra ovalis; fpr, fenestra pseudorotunda; h, fossa hypophysialis; ls, laterosphenoid; mf, metotic fissure; mo, medullar fossa (fossa medullae oblongatae); oc, occipital condyle; pn, pneumatic sinus or pneumatopore; pop, paroccipital process; ptf, posttemporal fenestra; s, suprarecessal compartment; so, supraoccipital; tm, tectal fossa (fossa tecti mesencephali); vcmp, posterior canal of middle cerebral vein.
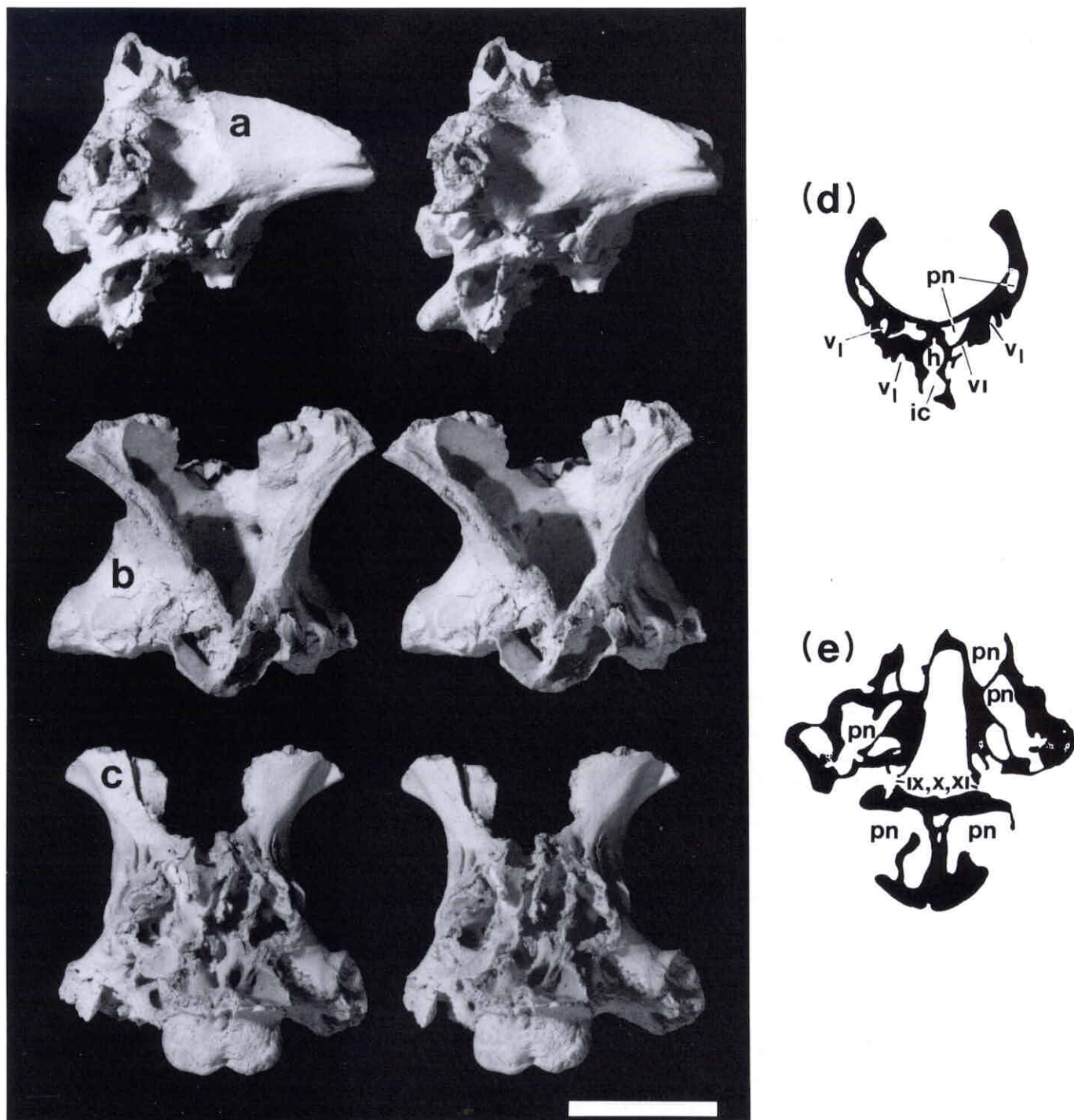
FIG. 2. *Troodon formosus*. Stereo photographs of RTMP 86.36.457 in (*a*) right lateral, (*b*) anterodorsal, (*c*) ventral, (*f* posterior, (*g*) anterior, and (*h*) left lateroventral views. Drawings from vertical CT scan sections through (*d*) hypophyseal fossa, and (*e*) region posterior to basioccipital−basisphenoid suture, and from horizontal CT scan sections through (*i*) mid-height of foramen magnum, (*j*) mid-height of occipital condyle, and (*k*) bottom of occipital condyle. Roman numerals represent cranial nerve openings. ac, fossa auriculae cerebelli; asc, anterior semicircular canal; c, cochlear; fm, foramen magnum; h, fossa hyupophysialis; ic, internal carotid; oc, occipital condyle; ot, otic cavity; pn, pneumatic sinus or pneumatopore; psc, posterior semicircular canal. Bar = 5 cm.

sal to the main body of the prootic, the outer surface of the braincase has a distinct, smooth surfaced concavity (Fig. 2*a*) anterior to the postemporal fenestra.

Exoccipital−opisthotic

In RTMP 86.36.457, the exoccipital−opisthotic complex forms most of the medial and ventral margins of the posttem-

poral fenestra (Figs. 1*b*, 1*d*, 2*f*, 4*b*). The canal is more than 3 mm wide and 10 mm long (anterior−posterior), and was probably partially occupied by the occipital artery (Walker 1985). In *Archaeopteryx* (Walker 1985) and theropods (Chatterjee 1991), the postemporal fenestra is generally located at the junction of the exoccipital−opisthotic complex with the squamosal and parietal. A second, more medial foramen is in
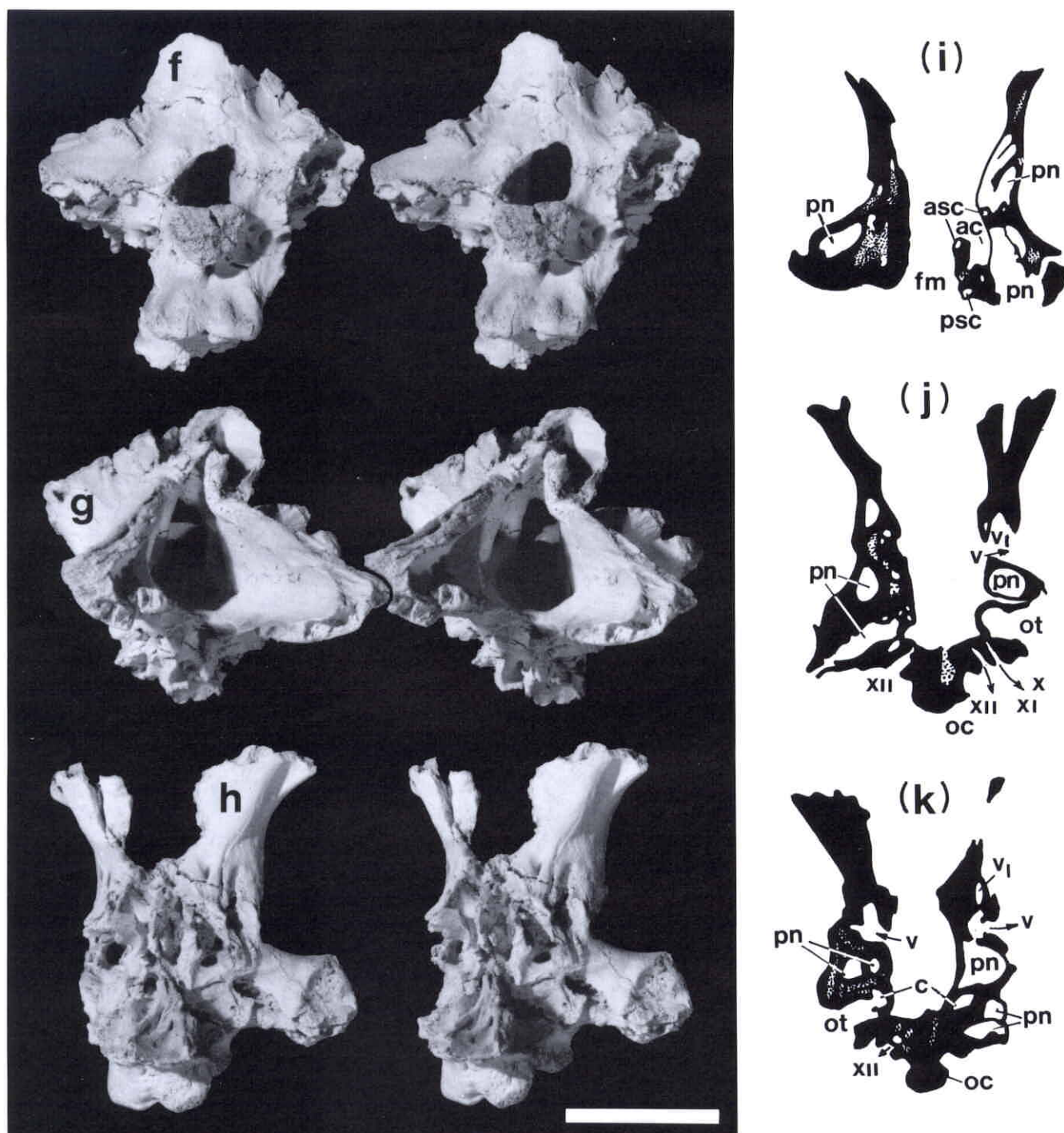
FIG. 2 (concluded)

this position in RTMP 86.36.457 (Figs. 1b, 1d, 4b), but is relatively smaller (1.3 mm wide), and was presumably used by the posterior canal of the middle cerebral vein as in *Itemirus* (Kurzanov 1976).

The sutural surface for the squamosal is ovoid medial to the posttemporal fenestra (Fig. 2b). Lateral to the fenestra, the squamosal contact is anteroposteriorly elongate (12 mm), although this tapers distally. Anterolateral to the thickest portion of the suture is a distinct facet 12 × 13.5 mm (Figs. 2c, 2h) facing anteriorly, ventrally, and laterally. This facet was damaged on both sides of RTMP 82.19.23 and was therefore

not observed in the earlier study. This is an extension from the squamosal of the articular facet for the head of the quadrate. Comparing this region with other theropods, the facet is near the prootic – opisthotic suture, but because of fusion it is difficult to say whether the facet is made up of one or both of these bones. The surface of the articulation for the quadrate is neither finished bone nor a rugose sutural surface, but is pitted with nutritive foramina, suggesting that it was covered by a cap of connective tissue. The existence of a facet on the braincase for articulation with the quadrate may have been widespread in other theropods, but cannot be seen in most
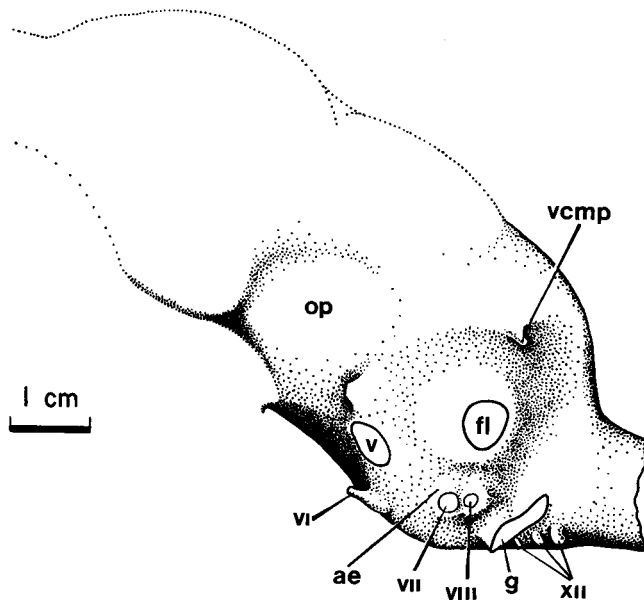
FIG. 3. Endocast of RTMP 86.36.457 (anterodorsal outline taken from endocast of RTMP 79.8.1) in left lateral view showing exits of the posterior cranial nerves. Roman numerals represent cranial nerve openings. ae, acoustic eminence; fl, flocculus; g, ganglii vagoglossopharyngealis; op, optic lobe; vcmp, posterior canal of middle cerebral vein.

specimens. The quadrates of ornithurine birds, on the other hand, do articulate with the squamosals and prootics, and often the opisthotics too.

A lateral recess in the base of the neck of the occipital condyle houses three major openings. The two, more medial openings (Figs. 1d, 2f) are for branches of the hypoglossal (XII) nerves, which originate on the floor of the braincase as three distinct foramina that increase in diameter posteriorly. The larger (maximum diameter is 2.4 mm) of the two occipital foramina is dorsal to the smaller one and originates from the most posterior of the three stems within the braincase. The ventral hypoglossal opening on the occiput is subdivided into a small (0.8 mm diameter) ventral branch and a larger (1.0 mm diameter), more dorsal branch. Lateral to the two hypoglossal exits is a larger foramen (2.6 mm in height) for the Xth (vagus) and XIth (spinal accessory) cranial nerves. The nerves came from a ganglia in a deep pit on the inside surface of the braincase as in birds and some theropods. The glossopharyngeal and posterior cerebral vein entered the same pit (fovea ganglii vagoglossopharyngealis) but exited laterally through a slitlike metotic foramen (see below).

The exoccipital tapers ventrally along the lateral margin of the basioccipital tuberosity (Figs. 1d, 4b) into the metotic strut (Witmer 1990), separating the exits of the IXth and Xth nerves and forming the posterior margin of the lateral depression. The metotic strut is separated from the paroccipital process in RTMP 86.36.457 by a pair of grooves (Figs. 1d, 2a, 4b) that leave the inner ear cavity from anteromedially. The more dorsal of the two grooves is deeper and wraps around onto the occipital surface. It probably marks the course of the posterior cerebral vein. The shallower ventral groove is oriented more laterally and shows the course of the glossopharyngeal (ninth) nerve.

The base of the crista interfenestralis is preserved on both sides in RTMP 86.36.457, but the bar itself was either broken

or not ossified. As in Archaeopteryx (Walker 1985), Protoavis (Chatterjee 1991), and all living archosaurs, the narrow crista interfenestralis would have been formed by the opisthotic.

Above the metotic strut, the paroccipital process extends posterolaterally. The ventral margin of the paroccipital process curves somewhat downward so that distally the ventral margin is at a slightly lower level than it is proximally (Figs. 1d, 4b). The downward turn in RTMP 82.19.23 (Currie 1985) appears to have been accentuated by crushing.

Basioccipital

The basioccipital of RTMP 86.36.457 has the same characteristics seen in other troodontid specimens. The occipital condyle, formed mostly by the basioccipital, is clearly smaller than the foramen magnum. This is expected in such a small animal, and it is only in larger theropods that the condyle is larger than the foramen magnum. Although it has been argued that the size ratio of the occipital condyle to the foramen magnum is a coelurosaur synapomorphy (Chatterjee 1991), in theropods the foramen magnum increases with negative allometry in relation to increase in skull length, whereas the diameter of the occipital condyle grows with positive allometry. The relationship between these two dimensions is therefore at least partially size related. The posterior face of the basioccipital (Fig. 2f), as in other specimens of *Troodon*, is smooth and concave below the neck of the occipital condyle and above the convex, rugose muscle attachments (Bakker et al. 1988). The smooth surface may mark the position of a pneumatic sac. There is an anterodorsally oriented pit at the base of the neck of the occipital condyle. This pit, which is to the right of the midline, may have held a pneumatic diverticulum. The position of these apparent pneumatic features is consistent with the situation found in tyrannosaurids, where pneumatic cavities clearly penetrate the posterior surface of the basioccipital ventrolateral to the occipital condyle. The pneumatic diverticula were probably anterior extensions of the pulmonary air sac system running along the cervical vertebrae. Some birds (Witmer 1990) have branches of the suborbital diverticulum of the antorbital sinus extending back onto the occiput, but these never pneumatize bone.

The pneumatic systems on the anterolateral surface of the basioccipital (in the lateral depression) are asymmetrical (Fig. 2e), but are well developed in RTMP 86.36.457. On the right side (Fig. 1a), a single opening invades the body of the right basioccipital tubera from the floor of the basioccipital portion of the lateral depression, whereas there were three pneumatic diverticula on the left side.

On the ventral surface is a foramen between the basioccipital tubera, as in RTMP 81.22.66 (Currie 1985). Because this foramen does not penetrate the body of the basioccipital in either of the specimens, and because the surface of the basioccipital around the opening is very rugose, it may mark the position for a ligament in the centre of the attachment of the iliocostalis cervicus et capitis (Bakker et al. 1988).

Endocast

The internal view of the braincase and an endocast of this region (Fig. 3) has confirmed previous identifications of most nerve foramina and provided new information on cranial nerves V to XII. No separate opening was identified for nerve XI (accessory).

As in pterosaurs and birds (Hopson 1977), the optic lobes were displaced laterally and ventrally (Fig. 3) by the enlarged cerebellum. This was also the case in dromaeosaurids (AMNH
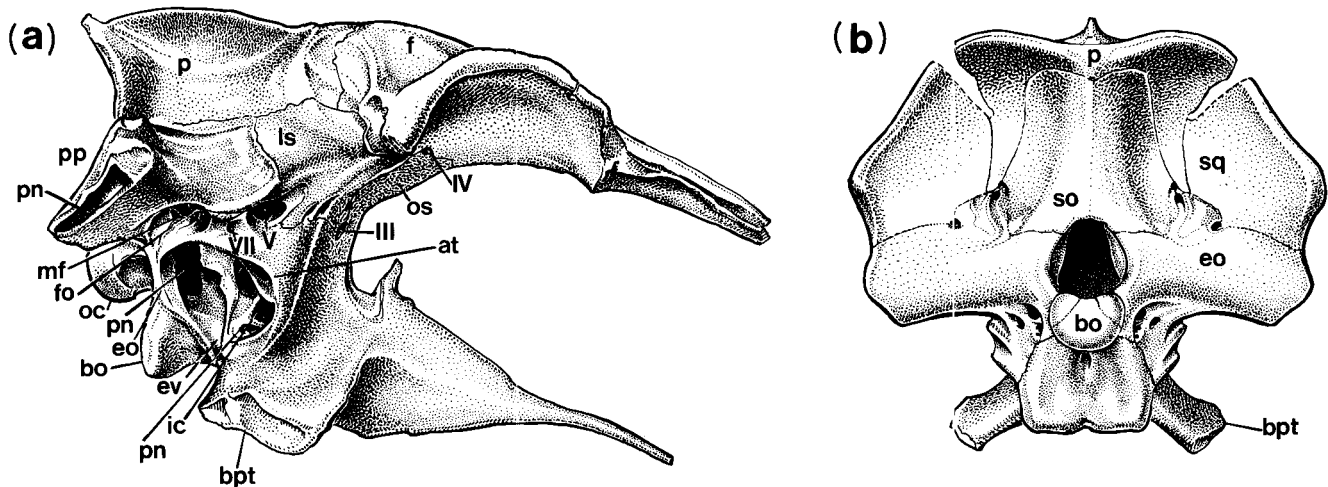
FIG. 4. *Troodon formosus*. Reconstruction of the braincase in (*a*) right lateral and (*b*) posterior views, based on RTMP 79.8.1 (frontals, parietals, laterosphenoid), RTMP 82.19.23 (braincase), RTMP 86.36.457 (braincase), and RTMP 86.49.90 (right frontal). Roman numerals represent cranial nerve openings. at, alaparasphenoid; bo, basioccipital; bpt, basipterygoid process; eo, exoccipital–opisthotic complex; ev, foramen magnum; f, frontal; fo, fenestra ovalis; ic, internal carotid; ls, laterosphenoid; mf, metotic fissure; oc, occipital condyle; os, orbitosphenoid; p, parietal; pp, paroccipital process; pn, pneumatis sinus or pneumatopore; so, supraoccipital; sq, squamosal.

5356), ornithomimids (CMN 12228), *Protoavis* (Chatterjee 1991), and avimimids, but not in large theropods like *Tyrannosaurus* (Osborn 1912). The fact that ventrolateral displacement of the optic lobe may also be characteristic of the primitive theropod *Syntarsus* (Raath 1977) suggests it may be a size-related feature.

There was a large floccular lobe (flocculus of the auriculae cerebelli) on each side of the brain, extending posterolaterally into the fossa auriculae cerebelli (Fig. 2*i*), which has a dorsoventral diameter of 3.5 mm. The size of this lobe may indicate that *Troodon* had a refined sense of balance as in pterosaurs, birds, and many small bipedal dinosaurs (Chatterjee 1991). Elzanowski and Galton (1991) point out that diving birds also have large auricular fossae, and Hopson (1979) showed that it is also prominent in *Allosaurus*, *Tyrannosaurus*, and possibly the ankylosaur *Euoplocephalus*.

As has been pointed out previously (Russell 1969; Hopson 1980), the relative brain size of *Troodon formosus* is large for a dinosaur and lies within the range found in living birds and mammals. An endocast made from RTMP 86.36.457 and RTMP 79.8.1 displaced 45 cm³ of water. This is conservative because the endocast did not account for the moderate crushing on the left side of the braincase, nor did it include the enlarged floccular lobes. If we assume that the specific gravity of the brain is 0.9, then the brain would have weighed about 41 g. This is higher than the 37 g estimate used by Hopson (1977, 1979, 1980), but lower than the 45 g estimate used by Russell (1969) and Russell and Séguin (1982). The encephalization quotient (conservatively calculated for an animal with a body weight of 45 kg) is 0.27 when compared with mammals (Jerison 1973) and 6.48 when compared with crocodilians (Hopson 1980). This does not differ significantly from the findings of either Hopson (1977, 1980) or Russell (1969), but confirms that the brains that they modeled for the calculations were relatively accurate.

Cranial nerves

The exits for the first four cranial nerves of *Troodon* have been described previously (Currie 1985), and nothing new can be added.

The main portion of the fifth cranial nerve (maxillary and mandibular branches of the trigeminal) exits laterally through a relatively large opening 5 mm × 4 mm (Figs. 1*a*, 2*a*). Close to the medial opening for the trigeminal, the ophthalmic branch (V₁, Figs. 2*d*, 2*j*, 2*k*) splits off and runs anteriorly to emerge on the anterior surface of the laterosphenoid (Figs. 1*a*, 1*c*, 4*b*). Although a separate opening for the ophthalmic is characteristic of some theropods and most birds, this character must be used with caution because it is also found in crocodylomorphs (Wu and Chatterjee 1993). Smaller branches of the nerve also appear to split off in this region, passing through the bone to emerge on the lateral surface of the laterosphenoid. One branch may pass through a narrow (0.25 mm) slit lateral to the opening for the ophthalmic branch (Fig. 1*e*), but a shallow channel leads to the posterior outlet from a groove on the outside of the braincase, suggesting that it may be an arterial canal. Posterolateral to the slitlike opening is a broad but shallow impression with at least three tiny foramina that originated from the trigeminal exit. The function of this depression is unknown (Currie 1985), although it may mark the position of a ganglion.

The sixth cervical nerve passes down and forward from the floor of the braincase medial to the posterior margin of the trigeminal opening (Fig. 3), through the basisphenoid, and out through the anterior surface (Figs. 1*e*, 2*d*) of the same bone. The anterior exit is lateral to the pituitary fossa and ventrolateral to the contact between the basisphenoid and orbitosphenoid.

The seventh cranial nerve leaves the braincase posterior to the trigeminal opening, anteroventral to the fossa auriculae cerebelli, and anterior to the eighth (Fig. 3). Foramina for the seventh and eighth cranial nerves both originate from a shallow depression (acoustic fossa) on the inside wall of the braincase and have the same basic arrangement as in *Dromaeosaurus* (AMNH 5356) and *Itemirus* (PIN 327/699). The seventh passes through the prootic at the front of the otic capsule above the lateral depression. In RTMP 86.36.457, there is a small opening connecting the canal within the prootic to the roof of the anterior tympanic recess. It is assumed that this opening was for a small branch of the facial nerve. The main
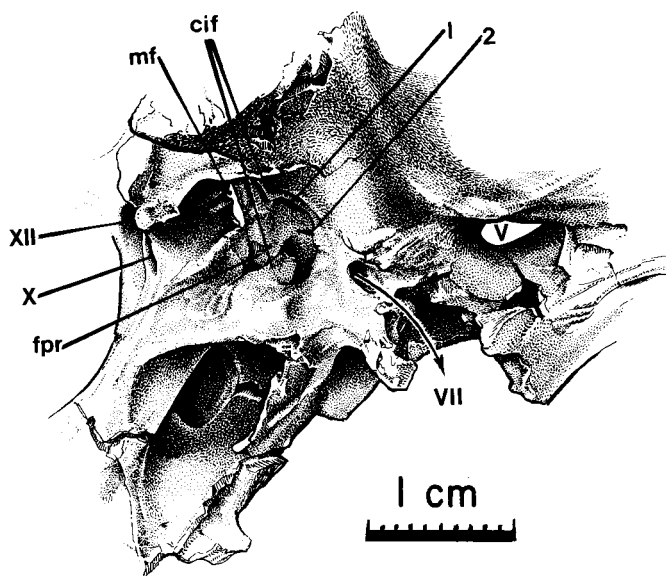
FIG. 5. *Troodon formosus*. Posteroventral view of RTMP 86.36.457 showing the middle ear region. Roman numerals represent cranial nerve openings. 1, utriculosaccular duct; 2, cochlear branch of cranial nerve VIII. cif, crista interfenestralis; fpr, fenestra pseudorotunda; mf, metotic fissure.

part of the seventh exits a foramen on the floor of a laterally open groove on the dorsal margin of the lateral depression (Fig. 1a). There it divides into an anterior palatine branch and a posterior hyomandibular. The groove for the nerve is shallow, and disappears posteriorly near the fenestra ovalis and anteriorly seems to run across the lateral margin of the main exit of the trigeminal.

The eighth cranial nerve (nervi vestibulocochlearis) splits into two branches shortly after exiting the acoustic fossa. The more dorsal vestibular branch runs posterolaterally to the vestibule. The more ventral cochlear branch entered the ossified cochlear duct (Fig. 5) through a foramen anteroventral to the utriculosaccular duct.

The IXth, Xth, and XIth cranial nerves enter the fovea ganglii vagoglossopharyngealis (metotic, jugular or vagus foramen) on the posteroventral margin of the otic capsule. The primitive exit of the nerves and the associated posterior cerebral vein has closed to a narrow slit at the back of the middle ear, and a new channel (1 mm wide × 2.6 mm high) carries the Xth and XIth nerves from the back of the metotic foramen to the occiput. The glossopharyngeal nerve, and probably the posterior cerebral vein, passed through two expansions of the metotic slit into the back of the recessus scalae tympani (Figs. 1a, 5). A pair of grooves proceed laterally along the anterior surface of the metotic strut, wrapping posterolaterally around its lateral edge.

The XIIth (hypoglossal) nerve has three distinct openings on the posterolateral region of the floor of the braincase, as in *Enaliornis* (Elzanowski and Galton 1991) and *Hesperornis* (Elzanowski 1991). The most anterior opening is minute, with a diameter less than 0.4 mm. In *Itemirus*, an opening of this size in this position was tentatively identified as being for the accessory nerve (Kurzanov 1976), but is more likely a branch of the XIIth. The middle opening is double the size, and the posterior opening is the largest (with a diameter of 1.2 mm). The posterior branch has the shortest osseous canal and

emerges through a foramen dorsal to the exit for the other two branches. The small anterior branch emerges on the occiput in the ventral portion of the rim of the exit of the middle branch.

Middle ear and periotic pneumatic systems

The middle ear would have been a relatively large sack lined by tympanic epithelium. It occupied the space between the lateral wall of the braincase, the tympanum, the quadrate, the quadrate process of the pterygoid, and various muscles (Wever 1978). The medial outline of the middle ear is well defined in troodontids as the lateral depression (Barsbold 1974; Currie 1985), which is formed by the prootic (anterodorsally), the opisthotic−exoccipital (posterodorsally and posteriorly), the basisphenoid−parasphenoid (anteriorly, anteroventrally, medially), and the basioccipital (posteroventrally, medially). Air entered the middle ear through the lateral eustachian tube, the course of which is marked by a troughlike depression on the anterolateral margin of the basioccipital (Currie 1985). The lateral eustachian tubes may have joined beneath the basioccipital and basisphenoid. From the middle ear air sac, pneumatic diverticula invaded most of the bones of the braincase and the quadrate. It is not known if a pneumatic diverticulum invaded the articular in troodontids as it does in tyrannosaurids (see Witmer 1990 for review of this character in theropods), *Protoavis* (Chatterjee 1991), and birds.

Although the stapes has not been recovered with any specimen of *Troodon*, it would have spanned the middle ear between the fenestra ovalis and the tympanum, which would have been attached to the anterolateral surface of the paroccipital process.

The lateral depression is subdivided into three distinct regions by osseous walls, none of which extend laterally as far as the outer margins of the depression. A large opening in the posterodorsal region of the middle ear is the entrance to the otic cavity (Fig. 1a, 2j). The opening would have been subdivided by a thin crista interfenestralis into the fenestra ovalis (fenestra vestibularis) and fenestra pseudorotunda (fenestra cochlearis) in the living animal. The crista interfenestralis is not preserved and may not have even been ossified. Its position is marked by small protuberances of bone on the upper and lower margins of the entrance to the inner ear (Fig. 5), especially on the left side of RTMP 86.36.457.

Pneumatic extensions of the tympanic cavity are consistent in modern birds, and avian terminology (following Witmer 1990) can be applied to theropods. The two lower regions of the lateral depression, separated by a bony ridge on the basioccipital−basisphenoid suture (Currie 1985), are both pneumatic. Topographically, they represent the anterior (rostral) tympanic recess and part of the posterior (caudal) tympanic recess of birds.

The most elaborate pneumatic diverticula originate in the anterior tympanic recess, which occupies the anterior portion of the lateral depression. As previously noted (Currie 1985), at least two openings associated with the internal carotid invade the interior of the bulbous parasphenoid capsule and the enlarged basipterygoid process. As in birds, but not crocodylomorphs (Wu and Chatterjee 1993), the anterior tympanic recess of *Troodon* is bound anterolaterally by the alaparasphenoid, dorsally by the prootic, and medially by the basisphenoid. The crocodylomorph *Dibothrosuchus* shows a similar degree of pneumatic invasion from the anterior tympanic recess (Wu and Chatterjee 1993). Within the bulbous capsule

(RTMP 82.19.23), there is no medial wall to separate air from the anterior tympanic recesses of either side. Because the parasphenoid and ventral portions of the basisphenoid were not preserved with RTMP 86.36.457, additional pneumatic openings are exposed for observation (Figs. 1c, 2h). Dorsomedially, a diverticulum extends anterodorsally to invade the basisphenoid beneath the sutural facet for the orbitosphenoid. The medial wall of bone separating the left and right anterior tympanic recesses is thin here, and is breached by a pneumatic opening (1.2 mm in diameter, Fig. 1a), thereby joining the two sides. Dorsolateral to the medial opening, a blind cavity invades the body of the alaparasphenoid. Posterolateral to the medial opening, another diverticulum passes posteroventrally into a large medial pneumatic chamber between the basisphenoid and basioccipital (Fig. 1e). This appears to have been confluent with the pneumatic chambers within the basal tubera.

Two cavities pass dorsally through the roof of the anterior tympanic recess (Figs. 2h, 2k). The smaller, anteromedial opening passes dorsally and somewhat posteriorly to open into the base of the dorsal chamber enclosed by the opisthotic—exoccipital and the supraoccipital—epiotic (Figs. 1b, 2b). The chamber would have been closed dorsally by the parietal. Because the dorsal margins of the supraoccipital are incomplete, it is not known whether the bilateral sinuses were connected by their diverticula above the braincase, although it seems likely that they were. Posterior to the suture between the prootic and laterosphenoid on the right side is a small (1 mm long) opening at the anterior margin of the concavity on the lateral surface of the prootic. This may represent a pneumatic connection between the anterior tympanic recess and the dorsal tympanic recess (see below). The bone in this region is damaged on the other side of the skull but there is an opening in the same region on the left side of RTMP 82.19.23.

The larger, posterolateral opening in the roof of the anterior tympanic recess (Figs. 1c, 2h) subdivides into anterior and posterior branches. The anterior branch opens into the body of the prootic above the trigeminal foramen. Computerized tomography (CT) scans show the diverticulum extended forward into the laterosphenoid. The posterodorsal branch follows the otosphenoidal ridge and enters the exoccipital—opisthotic complex, where it expands into a system of pneumatic chambers that hollow out the paroccipital process.

The posterior tympanic recess in modern birds, many theropods and Protoavis (Chatterjee 1991) is located posterolateral to the otic cavity. In birds and theropods this recess is in the opisthotic, whereas that of crocodylomorphs is positioned between the prootic and opisthotic (Wu and Chatterjee 1993). On the right side of RTMP 86.36.457, there is only a small foramen posterolateral to the otic cavity, probably for a blood vessel. A large hole enters the hollow paroccipital process on the left side, but damage to the specimen in this region suggests that it could be an artifact rather than a pneumatopore. The space in the paroccipital process is connected by pneumatic diverticula to the anterior tympanic recess in RTMP 86.36.457. CT scans suggest that it was also connected by internal passages to a pneumatopore in the basioccipital posteroventral to the fenestra ovalis.

The posteroventral portion of the lateral depression is an elaborate system of pneumatic diverticula that invade most of the interior of the ventral body of the basioccipital. Because the posterior tympanic recess extends ventrally to pneumatize

the basioccipital in many neornithines and Hesperornis (Witmer 1990), it is appropriate to consider the posteroventral cavity of the lateral depression of Troodon as part of the posterior tympanic recess.

A dorsal tympanic recess may have been present in Troodon. In Archaeopteryx (Walker 1985) and Protoavis (Chatterjee 1991), this recess is represented by a depression in the prootic anterodorsal to the quadrate capitulum, is bounded by the osseous labyrinths of the inner ear, and communicates with the occipital foramen. A shallow but distinct depression is also found in Gallimimus (Osmólska et al. 1972) and other theropods in the same region, and was previously noted in Troodon (Currie 1985). The presence of a deep, smooth-walled depression on the anteromedial surface of the quadrate process of the squamosal (RTMP 82.19.23) supports the suggestion that Troodon did have a dorsal tympanic recess that was bound posterodorsally by the squamosal. The strongest evidence is that one specimen of Troodon (MOR 430) has a pneumatopore in the anterior surface of the quadrate near the head, showing there was an air sac in this region. Furthermore, a dorsal tympanic recess, with a pneumatopore, is also present in the same region in Velociraptor (Norell et al. 1992).

Inner ear

The metotic foramen at the posteromedial margin of the middle ear cavity has closed to a narrow, vertical slit (Figs. 1a, 5), in contrast with the large round opening of Dromaeosaurus, Itemirus (PIN 327/699), and other theropods where this region is known. The metotic foramen opens laterally in the most primitive theropods, is subdivided by the metotic strut into a laterally oriented metotic foramen and a posteriorly directed vagus foramen in carnosaurs and ornithomimosaurs, and is closed off laterally in most birds (S. Chatterjee, personal communication, 1993). A slitlike metotic foramen similar to that of Troodon is still present in some birds. The fovea ganglii vagoglossopharyngealis and the recessus scalae tympani are separated by a thin plate of bone, with an elongate vertical concavity on the lateral side. The closure clearly shows that Troodon had developed an avian style inner ear, with an outward facing fenestra pseudorotunda. The metotic slit is constricted at mid-height, but is large enough above and below to have allowed passage of the glossopharyngeal nerve and the posterior cerebral vein. Two grooves pass posterolaterally from the middle ear cavity across the metotic strut. The upper one was probably occupied by the vein, and the lower probably follows the course of the glossopharyngeal nerve as in Archaeopteryx and modern birds (Walker 1985). The fenestra pseudorotunda opens anteroventrally into a deep pit (Fig. 2k), the cochlear recess, which appears to have been formed anteriorly, anterolaterally, and medially by the prootic, and posteriorly and posterolaterally by the exoccipital—opisthotic. In Archaeopteryx and carinate birds (Walker 1985), the metotic strut does not contribute to the cochlear recess as it does in ratites. The cochlear duct was elongate, roughly vertical, and curved slightly anteriorly distally. It is similar in position and orientation to one identified for Allosaurus (Hopson 1979). The saccule occupied part of the space medial to the fenestra ovalis and is joined to the utricle in the osseous labyrinth by a utriculosaccular duct (Fig. 5). Anteroventral to the foramen for this duct is the opening for the cochlear ramus of the eighth cranial nerve (Fig. 5). Posterodorsal to the utriculosaccular foramen is another foramen opening into the osseous labyrinth, presumably for the endo-

lymphatic duct. The ductus endolymphaticus ultimately left the inner ear chamber on the medial wall of the braincase posterodorsal to the fovea ganglii vagoglossopharyngealis.

The semicircular canals are completely contained within the otic capsule (Fig. 2), but were studied using a CT scan and external braincase landmarks. The osseous anterior vertical semicircular canal loops within the eminentia arcuata over the fossae auriculae cerebelli (Fig. 2i). The posterior vertical semicircular canal loops posterolaterally parallel to the alignment of the fossae auriculae cerebelli. The horizontal semicircular canal curves anterolaterally just beneath the floor of the auricular fossae, where it enters a large vestibular cavity. Overall, the osseous labyrinth is fundamentally the same as those of *Allosaurus* and *Itemirus* (Kurzanov 1976).

Discussion

Comparison with Saurornithoides

RTMP 86.36.457 has cleared up inconsistencies in the earlier interpretation of the braincase of *Troodon*. The lateral depression is more like that of *Saurornithoides* than the earlier reconstruction by Currie (1985) suggested. The lateral depression of *Troodon*, like that of *Saurornithoides* (Barsbold 1974), is subdivided into three distinct regions.

Like *Troodon*, the otic cavity is in the posterodorsal corner of the lateral depression of *Saurornithoides*. The margins are formed mostly by the prootic and opisthotic, but the basioccipital floors the cavity and forms the ridge separating it from a larger ventral concavity. The posteroventral region of the lateral depression is formed entirely by the basioccipital and is variably invaded by pneumatopores that open into an elaborate sinus system within the bone. The lateral depression has another subdividing ridge along the suture between the basioccipital and basisphenoid. The more anterior cavity is bound dorsally and anterodorsally by the prootic. The internal carotid passes through this region and enters a foramen anteriorly. Several additional foramina piercing the walls of this part of the depression are pneumatopores that led into the bulbous parasphenoid, the basipterygoid processes, and the interior of the prootic. Both Barsbold (1974) and Currie (1985) stated the seventh nerve exited through the lateral depression, but RTMP 86.36.457 shows that in troodontids it is located on the upper margin of the lateral depression and is completely surrounded by the prootic.

Comparison with Gallimimus

The braincase of the ornithomimid *Gallimimus*, well described by Osmólska et al. (1972), is highly pneumatic like that of *Troodon*. The greatest similarity is in the presence of a hollow, bulbous parasphenoid. In *Gallimimus*, however, the bulbous parasphenoid is pneumatized through a large, posteromedial opening that almost certainly represents the remnant of the basisphenoidal recess. It may also be invaded laterally by diverticula that pass through as many as three pneumatic openings in the side of the basisphenoid – parasphenoid. It is conceivable that the basisphenoid – parasphenoid complex of *Gallimimus* represents an intermediate stage in the development of the troodontid bulbous parasphenoid. The balloonlike structure may have initially been pneumatized by an anterior extension of the diverticulum in the basisphenoidal recess, which was being reduced posteriorly in *Gallimimus* from the condition seen in dromaeosaurids and most other theropods. As the basioccipital and basisphenoid deepened in troodontid ancestors, the medial opening would have closed up and more

emphasis would have been put on the lateral connections with the tympanic cavity.

Troodon and *Gallimimus* are similar in the degree of ossification around the optic fenestra. The paired optic nerves emerge from a large, single, medial foramen. There is an ossified orbitosphenoid (not identified separately from the laterosphenoid in Osmólska et al. 1972), and the laterosphenoids meet across the top of the dorsum sellae.

Other characteristics suggest that the ornithomimid braincase is intermediate between those of dromaeosaurids and troodontids. There is no pronounced lateral depression in *Gallimimus*, but pneumatic diverticula clearly invaded the parasphenoid – basisphenoid complex, the basioccipital, the exoccipital – opisthotic complex and the prootic as in *Troodon*. Like *Dromaeosaurus*, the internal carotids have separate openings into the pituitary fossa. The basal tubera are formed jointly by the basioccipital and the basisphenoid, a plesiomorphic character within Theropoda. Although the basipterygoid processes are not anteroposteriorly elongate as in *Troodon*, they are oriented more laterally than the primitive condition. Of the three exits identified for trigeminal branches by Osmólska et al. (1972), the most anterior is for the ophthalmic nerve, the second one is for the maxillo-mandibular trunk of the trigeminal, and the third, which is completely surrounded by the prootic, is undoubtedly for the seventh cranial nerve. The first two foramina are in close proximity (separate but close together on the left side of PIM 100/11, but confluent on the right side), suggesting that the ophthalmic branch of the trigeminal is in the process of separating from the maxillo-mandibular branches in *Gallimimus*. The hole in the opisthotic identified by Osmólska et al. (1972) as the fenestra pseudorotunda is more likely the posterior tympanic recess, passing into the paroccipital process as in *Archaeopteryx*, *Protoavis*, *Itemirus*, *Dromaeosaurus*, and *Velociraptor*. The universality of this opening in small theropods and primitive birds suggests that its absence in *Troodon* may be the result of a secondary closure.

Differences between troodontid and ornithomimid braincases are consistent with their evolutionary histories, which were diverging since at least the Early Cretaceous. In *Gallimimus*, the exoccipital takes a greater role in the formation of the occipital condyle, which is oriented more posteriorly than in troodontids and does not have a well-developed condylar neck. The vagus foramen is more primitive in ornithomimids, oriented anterolaterally instead of anteromedially (S. Chatterjee, personal communication, 1993). Pneumatic diverticula invade the occiput to a greater degree than they do in *Troodon*.

Comparison with dromaeosaurids

Troodontids and dromaeosaurids have long been linked together into the infraorder Deinonychosauria (Colbert and Russell 1969; Gauthier 1986; Ostrom 1969), a clade defined mostly by the presence of a specialized second pedal digit (Currie and Peng 1993). The association of these two families has been questioned by numerous authors (Barsbold 1983; Currie 1987a; Osmólska 1981, 1990; Osmólska and Barsbold 1990) because there are more derived characters shared by troodontids, ornithomimids, and elmisaurids than between dromaeosaurids and troodontids. Braincase morphology does not support the idea of a monophyletic Deinonychosauria. Although the paroccipital process encloses a hollow cavity in *Dromaeosaurus* (AMNH 5356), *Itemirus* (PIN 327/699), and *Velociraptor* (PIN 3143/8), the cavity opens into the back of

the middle ear cavity via a pneumatopore posterolateral to stapedial footplate, but not in *Troodon*. Posterior tympanic recesses similar to those of dromaeosaurids are also found in *Archaeopteryx* (Walker 1985), *Gallimimus* (Osmólska et al. 1972), and *Protoavis* (Chatterjee 1991), so this is probably a plesiomorphic character lost by *Troodon*. The basioccipitals of dromaeosaurids and troodontids are dorsoventrally deep bones, but that of the Troodontidae is anteroposteriorly elongate, excluding the basisphenoid from the basal tubera. The basipterygoid process of *Dromaeosaurus* is stout, but not elongate and not pneumatic like that of *Troodon* (Currie 1985). The basisphenoidal recess is present in dromaeosaurids, but not troodontids. *Dromaeosaurus* lacks all of the periotic pneumatic sinuses (AMNH 5356) found in *Troodon*. Velociraptorines may have a more pronounced dorsal tympanic recess (Norell et al. 1992), but lack the complicated system of anterior tympanic sinuses. The ophthalmic branch of the fifth nerve has a separate opening from the other branches of the trigeminal of *Troodon*, whereas in dromaeosaurids the nerve separates outside the braincase. The metotic foramen is open laterally in dromaeosaurids, but it is reduced to a slit in *Troodon*. If braincase characters are indeed conservative (Bakker et al. 1988; Kurzanov 1976), then the differences between dromaeosaurids and troodontids are significant enough to suggest they had long, independent evolutionary histories. Specialization of the second pedal digit in dromaeosaurids and troodontids would therefore be an example of convergent evolution.

Comparison with other theropods

Most theropods show some degree of cranial pneumatization associated with the middle ear sac, the basisphenoidal recess, and (or) the vertebral diverticula from the lungs. Cranial pneumaticity was reviewed by Molnar (1985) and Witmer (1990), and is a major consideration in assessing the interrelationships of Late Cretaceous species.

The braincase of *Syntarsus* represents the ancestral morphotype for both theropods and birds (Raath 1985). Although it lacks pneumatic specializations, there is a pneumatic recess between the pronounced crista prootica and the basisphenoid. This pneumatic recess, referred to as a lateral tympanic recess by Chatterjee (1991), is found in a wide range of archosaurs, including *Postosuchus*, and is a plesiomorphic character. Even though there is no pneumatopore invading the interior of the paroccipital process of *Syntarsus*, the position identified for the posterior tympanic recess (Raath 1985) is exactly where there is a pneumatic opening in *Archaeopteryx*, dromaeosaurids, *Itemirus*, *Gallimimus*, and *Protoavis*. A depression on the lateral surface of the braincase above the otosphenoidal ridge close to the occipital foramen may mark the position of the dorsal tympanic recess or it may simply be an attachment area for jaw musculature. The Xth and XIth cranial nerves exited the braincase laterally through the metotic foramen (Raath 1985). There is a single exit for all branches of the trigeminal in *Syntarsus*, and the ophthalmic followed a distinct groove anterodorsally from the foramen.

As in *Troodon*, there is a separate canal for the ophthalmic branch of the trigeminal in *Allosaurus* and tyrannosaurids (Hopson 1979). However, in most theropods, the ophthalmic splits off the main trigeminal trunk after the nerve exits the bone and then turns anteriorly where its course can be followed for a short distance because of a troughlike groove in the surface of the bone. The ophthalmic groove is supple-

mented in *Itemirus* (Kurzanov 1976) by two fine branches of the trigeminal (frontal branch of the deep ophthalmic, nasal branch), located in distinct sulci on the outside of the braincase. The emergence of the Xth and associated nerves on the occiput is generally considered to be an advanced characteristic. However, it appears likely that the Xth and XIth nerves did pass backwards between the metotic foramen and the occiput in *Dromaeosaurus* (AMNH 5356), *Itemirus* (PIN 327/699), and possibly *Allosaurus* (McClellan, in press). The significant change in *Troodon* is the partial closure of the metotic foramen, which nevertheless still allows the glossopharyngeal to pass laterally.

Comparison with *Protoavis*

A remarkable find from the Dockum Formation (Upper Triassic) of Texas has been identified by Chatterjee (1991) as an early bird. Although *Protoavis* has characteristics suggesting avian affinities, most of these are also found in theropods, which considerably weakens the claim that it is a bird. Chatterjee (1991) has already noted the strong similarity of the braincases of *Protoavis* and *Troodon*. There are some differences in interpretation that need to be addressed before comparing the two genera. RTMP 86.36.457 shows that the prootic is not reduced as stated by Chatterjee (1991) and Currie (1985). The depression identified by Chatterjee as the lateral tympanic recess of *Troodon* should be referred to as the anterior tympanic recess because, as in modern birds, it is associated with the internal carotid artery, the parasphenoid–basisphenoid, and the prootic. It is an elaborate system in *Troodon* with contralateral connections through the basisphenoid and within the cultriform sinus. The *Troodon* reconstruction by Chatterjee (1991) included an opening between the facial foramen and the lateral depression that was labeled as the posterior tympanic recess. This is not a natural opening in RTMP 86.36.457, but represents the collapsed lateral wall of an extension of the anterior tympanic recess. As the posterior tympanic recess of birds normally enters the opisthotic–exoccipital posterolateral to the fenestra ovalis and fenestra pseudorotunda, it is unlikely that the anteriorly placed opening that invades the prootic of *Troodon* is homologous, even though it does infiltrate the paroccipital process ultimately. As suggested by the comparison between *Troodon* and *Gallimimus*, the absence of an opening posterolateral to the stapedial footplate in *Troodon* may represent a secondary closure of a widespread plesiomorphic character. The fact that the paroccipital process is pneumatic and connects to the basioccipital sinuses of the posterior tympanic recess supports this conclusion. In many birds, diverticula of the different periotic sinuses are interconnected. This is clearly the case in *Troodon*, and the pneumatopore posterolateral to the otic cavity may no longer have been needed.

The lateral depression was referred to as a lateral tympanic recess by Chatterjee (1991), who equated it with the basisphenoidal recess of most other theropods. The lateral depression of troodontids (Barsbold 1974) is similar to a depression found in this area in many modern birds, although its distribution is erratic (A.D. Walker, personal communication, 1984), where it is an enlarged anterior tympanic recess. Furthermore, troodontids lack a ventrally open basisphenoidal recess, and it is highly unlikely that the lateral depressions ever had anything to do with this plesiomorphic, ventromedially positioned, ventrally oriented sinus.

Another aspect misinterpreted by Chatterjee (1991) deserves comment. The quadrate articulates mostly with the

squamosal in troodontids, although it appears to have also contacted the braincase. These contacts were clearly movable, and were neither sutured nor fused together. The heads of the quadrates of MOR 430 (*Troodon*) and IVPP 070888-4 (*Sinornithoides*) are well rounded, and the quadratojugal of the latter is no more robust than it is in other theropods. The quadrate was therefore as kinetic as those of other theropods where only anterior movement was prevented by the squamosal—quadratojugal bar.

Comparison between the braincases of *Troodon* and *Protoavis* does suggest that they are amazingly similar for animals separated by 160 Ma. The posttemporal fenestra is reduced to a small aperture that is continuous anteriorly with the dorsal tympanic recess. An anterior tympanic recess is defined dorsally by the prootic and anteriorly and medially by the basisphenoid—parasphenoid.

There appears to be contralateral communication of the anterior tympanic recesses of *Protoavis*, as there is in *Troodon*. *Protoavis* has retained a basisphenoidal sinus, but it is shallow and lacks the posterolateral extensions seen in typical theropod braincases like those of *Dromaeosaurus* and *Itemirus*. The basipterygoid process is not vertically deep. There is a well-developed alaparasphenoid, continuous dorsomedially with the dorsum sellae and pierced posteroventrally by the internal carotid. The vagus and spinal accessory nerves exit the skull on the occiput, diverted posteriorly by the metotic strut. There is a distinct notch in the metotic strut, interpreted either for the posterior cerebral vein (this paper) or for the internal carotid (Chatterjee 1991). The metotic strut forms the posterior wall of the recessus scalae tympani. The crista interfenestralis is present in *Protoavis* and *Troodon*, and was presumably formed by the opisthotic in both. The prootic is primitively pierced by the facial foramen for the seventh cranial nerve, forms the posterior borders of the exit for the trigeminal, and the anterior margin of the fenestra ovalis. The laterosphenoid contacts its mate anteroventrally, and extends dorsolaterally to meet the frontal and postorbital. The relatively large brains of *Troodon* and *Protoavis* have similar characteristics, with the optic lobe shifted ventrolaterally by expansion of the cerebellum, which has a large floccular lobe. In the inner ear, both have marked differentiation of the canalicular systems and the cochlear process. The vestibular region is relatively small and located in a ventral position to most of the anterior and posterior semicircular canals. The anterior semicircular canal is significantly longer than the others. The cochlear recess is a relatively long, vertically oriented tube. *Protoavis* seems to be less birdlike than *Troodon* in having only a single exit for the trigeminal.

The braincase of *Protoavis* is remarkably like that of a troodontid, and in our opinion has few unique avian characters. The latter would include the streptosylic quadrate and reduction in size of the olfactory lobes, but such characters are not robust enough to identify *Protoavis* as a bird.

Comparison with primitive birds

Known troodontids are all from strata deposited too late for any to have been directly ancestral to birds. Nevertheless, the Early Cretaceous forms (Barsbold et al. 1987; Russell and Dong 1993) have most or all of the specializations of the Late Cretaceous genera, suggesting that troodontids appeared in earliest Cretaceous or even Late Jurassic times. It is quite possible that these specialized theropods evolved around the same time as the earliest undisputed bird, *Archaeopteryx*.

The braincase of *Troodon* compares favourably in most respects with those of primitive birds (Witmer 1990) like *Archaeopteryx* (Walker 1985), *Enaliornis* (Elzanowski and Galton 1991), and *Hesperornis* (Elzanowski 1991). The basisphenoidal recess has been reduced or lost in both troodontids and birds. The trigeminal nerve subdivided within the prootic, and the ophthalmic branch passed through a tube in the laterosphenoid to emerge through a foramen on the anterior face of the alaparasphenoid. A second foramen lateral to this in *Troodon* and *Enaliornis* may be for a protractor nerve (Elzanowski and Galton 1991). There is a metotic strut, which has diverted the Xth and XIth nerves posteriorly onto the occiput. The glossopharyngeal splits from the fovea ganglii vagoglossopharyngealis and passes laterally through a slitlike metotic foramen into the back of the tympanic cavity. Extensive pneumatization of the cranial base can include contralateral connections (Witmer 1988). Basisphenoid—parasphenoid, prootic, basioccipital, opisthotic—exoccipital, supraoccipital—epiotic, quadrate, and possibly the articular are pneumatized directly or indirectly from the middle ear sac. The tympanic cavity is bounded anteriorly by the alaparasphenoid and posteriorly by the paroccipital process. There is no winglike development of the crista prootica. In most of these characteristics, *Troodon* is closer to birds than it is to other theropods. Nevertheless, there are some significant differences that are presently known only in troodontids. The increased length of the ventral margin of the basioccipital appears to be a troodontid autapomorphy. *Troodon* has an exceptionally large basipterygoid process, considerably larger than those found in any birds. Other dissimilarities can be attributable to differences in absolute size, such as the more inflated appearance of the bird braincase and the more prominent eminentia arcuata.

A more detailed comparison is possible with *Enaliornis* (Elzanowski and Galton 1991). The metotic strut is poorly developed in *Enaliornis*, whereas it is more sharply defined in *Troodon* than in any other theropod. Correlated with this feature, there are no grooves for the glossopharyngeal nerve and posterior cerebral vein in the bird, but there are in the dinosaur. *Troodon* has a strong sphenoccipital bridge (= jugamentum sphenooccipitale = otosphenoidal ridge), *Enaliornis* does not. Nevertheless, there are also some striking similarities between *Troodon* and *Enaliornis*. The paired parietals of the latter bear a narrow sagittal crest, such as is found only in troodontids, dromaeosaurids, oviraptorids, and tyrannosaurids amongst the Theropoda. Pneumatic spaces within the basisphenoid—parasphenoid complex are posteroventral to the pituitary fossa of *Enaliornis* (Witmer 1990) and *Troodon*. In both *Enaliornis* (Elzanowski and Galton 1991) and *Troodon*, the anterior margin of the tympanic recess is clearly defined by the alaparasphenoid. This is invaded by pneumatic diverticula from the anterior tympanic recess. The fifth cranial nerve divides before it emerges from the braincase, and the ophthalmic branch emerges anterolaterally through the bony plate close to a second foramen. The pituitary fossa lies anterior to the cranial cavity. Three hypoglossal foramina are present and decrease in size anteriorly. The angle measured from CT scans between the cranial base (a line drawn along the ventral midline of the basioccipital and basisphenoid) and the straight line connecting the top of the dorsum sellae with the occipital condyle is 32° in *Troodon*, which falls within the range for *Enaliornis*.

Cranial pneumaticity and the origin of birds

The significance of the nasal and tympanic pneumatic systems of birds and theropods has been discussed in an excellent review paper by Witmer (1990). Within that framework, the following discussion will focus on the new information provided by *Troodon*. As previously pointed out (Currie 1985), the extensive system of periotic pneumatic cavities would have extended the range of sounds that *Troodon* would have been capable of hearing. As in birds (Kühne and Lewis 1985 and references therein), enlargement of the middle ear cavities reduces the impedance of the middle ear at low frequencies and increases the ability of the animal to hear sounds with lower frequencies. Spacious middle ear cavities are found in birds with good or excellent hearing abilities, such as birds of prey, which suggests that *Troodon* also had an excellent sense of hearing. Contralateral connections between the periotic sinuses may have improved the animals ability to localize sound (Witmer 1988), although this is questionable in crocodylians (Wever 1978 and references therein). A second possible function of the pneumatic spaces in the bones surrounding the inner ear may be to protect the delicate structures within the inner ear (Smith 1985) by acting as shock absorbers.

Pneumatic invasion of bone is highly variable in both theropods and birds. Many species of theropods and diving birds have little or no evidence of cranial pneumaticity. In modern birds, there is tremendous variation in the distribution and appearance of the tympanic recesses (Witmer 1990). Within single individuals, pneumatic features are asymmetrical (Currie 1985; Osmólska et al. 1972), and the degree of pneumatic invasion can increase (B.B. Britt, personal communication, 1993) or decrease (L.M. Witmer, personal communication, 1993) with maturity. In mature individuals, diverticula can contact and merge within the braincase bones (Witmer 1990). All tetrapods have a middle ear sac lateral to the otic capsule, and extension of the air sac can lead to the pneumatic invasion of any and all bones in contact with it. In archosaurs, this includes basioccipital, basisphenoid, opisthotic, prootic, and quadrate. Pneumatic diverticula can pass through these bones and invade adjacent bones like the articular, epiotic, exoccipital, parasphenoid, and supraoccipital. Elaborate extension of the middle ear sac into the surrounding bones is characteristic of crocodylians (Wu and Chatterjee 1993), theropods, and birds. This has clearly evolved independently at least twice, and conceivably more than that. Theropods can have extensions of the middle ear sac that are in the same positions as avian anterior, posterior, and dorsal tympanic recesses, and diverticula invade the articulars and quadrates in birds and some theropods. Troodontids, like birds and crocodiles, have contralateral connections of the right and left middle ear sacs through the basisphenoid and across the top of the braincase. The similarities are striking, but because these characteristics have evolved more than once in archosaurs they cannot be used in isolation to prove relationships. The significance of the pneumatic braincase of *Troodon* is that it shows theropods have the elaborate middle ear cavities expected, but not necessary, for avian ancestry. In other words, theropods can not be eliminated from consideration as potential bird ancestors on the grounds that they lack the right kind of cranial pneumaticity (Whetstone and Martin 1979; Martin 1991).

Numerous cladistic analyses (Gauthier 1986; Paul 1984; Thulborn 1984; Witmer 1991) indicate birds evolved as a sub-
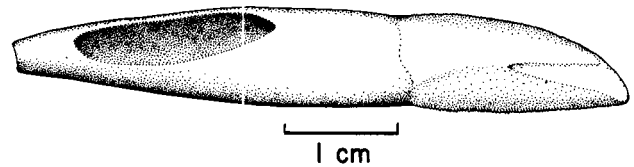

FIG. 6. Dromaeosaurid tooth (IVPP 270790-4) from the Iren Dabasu Formation near Erenhot, People's Republic of China, showing replacement pit on medial side of root.

set of the Theropoda. Martin (1991) continues to argue against this conclusion and has stated that he expects the avian ancestor to have 10 characters. He dismisses theropods from the ancestry of birds on the grounds that only four of these characters are found in these dinosaurs and show a scattered distribution suggesting independent derivation. However, seven of the 10 characters he listed appear to have been in troodontids, and the remaining three features (pneumatic articular, teeth with ventrally closed replacement pits, root cementum) are presently unknown. As tyrannosaurs have pneumatic articulars, it would not be surprising to discover this characteristic in troodontids. There is no special relationship between birds and crocodiles concerning the replacement pits in teeth. Resorption pits in all archosaur teeth start above the base of the tooth and progress proximally and distally until the tip is resorbed. Theropod teeth can show crocodilelike resorption pits (Fig. 6), but rarely do because the direction of replacement is at a higher angle in the relatively narrower jaws, and this stage of replacement is more transitory. The fact that *Archaeopteryx* teeth seem to have drifted out of the jaws readily does not support the statement (Martin 1991) that they are held in place by cementum.

Study of RTMP 86.36.457 has revealed other similarities between troodontids and birds that suggest these animals are more closely related to each other than either is to primitive theropods like *Syntarsus*. These include reduction of the basisphenoidal recess, separation of the exits of the glossopharyngeal and vagus nerves by a metotic strut, reduction of the crista prootica in favour of an alaparasphenoid, separation of the ophthalmic from the maxillo-mandibular branch of the trigeminal within the prootic, and physical separation of the two functional units of the inner ear.

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