Oviraptorosauria: Morphology, Phylogeny, and Endocranial Evolution

Amy M. Balanoff

Oviraptorosauria, an extinct lineage of coelurosaurian dinosaurs from the Cretaceous of Asia and North America, includes some of the most morphologically distinctive theropod taxa yet known. Their bizarre appearance and numerous skeletal similarities with extant birds instantly made oviraptorosaurs the subject of considerable interest when first discovered in the early 20th Century by the American Museum of Natural History Central Asiatic Expeditions. Subsequent discoveries have only increased the potential of the group for informing the origin of modern birds and characters that make birds distinctive among living vertebrates, including the origin of flight. The current list of shared similarities between oviraptorosaurs and modern birds includes such striking features as loss of teeth, extreme pneumatization and ornamentation of the skull, an unusual sliding jaw articulation, reduction of the tail vertebrae to form a pygostyle, feathers of modern aspect, and the behavior of brooding eggs in the same stereotypical posture.

Despite such an extended period of research and popular interest, some fundamental questions regarding oviraptorosaurs remain. First, what is the phylogenetic position of Oviraptorosauria within Coelurosauria? Recent analyses produce contentious results that disagree on whether oviraptorosaurs represent a clade of bird-like, non-avian coelurosaurians or whether they actually are nested within Avialae. Obviously, these disparate topologies pose disparate models of character evolution. For example, if oviraptorsaurs are avialans they
represent the first evolution of flightlessness within that clade. Second, what are the phylogenetic relationships of the taxa comprising Oviraptorosauria? And lastly, what insight would a resolved tree topology provide the study of morphological evolution, both within Oviraptorosauria specifically and more generally within Coelurosauria?

I analyzed 384 morphological characters and recovered two most parsimonious trees that resolve both the position of Oviraptorosauria within Coelurosauria as well as the interrelationships of species within Oviraptorosauria. Oviraptorosauria is found to have a sister group relationship with Therizinosauria, and this entire clade is positioned as the sister taxon to the clade formed by (Paraves + Alvarezsauridae). These findings support oviraptorosaurs as non-avian coelurosaurs and thus not avialans. The implication of this topology is that many of the avian-like characteristics expressed in the group are the product of homoplastic evolution between oviraptorids (a more exclusive clade within Oviraptorosauria) and avialans.

These phylogenetic hypotheses subsequently are used to elucidate the evolutionary history of endocranial morphology in Oviraptorosauria and more broadly within Coelurosauria near the origin of avian flight. Using the relatively newly employed technology of computed tomography (CT), this study provides descriptive morphology of five coelurosaurs endocasts (which approximate the shape of the brain in these taxa that effectively filled the endocranial space) and evaluates shared discreet morphological characters with respect to the aforementioned phylogeny. Diagnostic morphologies are found for Oviraptorosauria and the more exclusive clades, Maniraptora, Paraves, and crown birds.

This study also is the first to use CT technology to divide the endocranial casts into six neuroanatomical partitions that correspond closely to the olfactory bulbs, cerebrum, pituitary
space, optic lobes, cerebellum, and brain stem. These partitions are then used to evaluate how these different regions of the “brain” are evolving. The division of the endocranial cast into partitions is a novel approach to studying endocranial morphology. Previous analyses have been limited to surveying total endocranial volume and have not been able to distinguish between regions of the brain. Those earlier analyses established that crown birds possess a much larger endocranial space with respect to body size than more distantly related groups and that there is a general transition along the coelurosaur lineage towards an increased endocranial volume. This analysis distinguishes the expansion of the cerebrum as the primary driver of volumetric change within the entire endocranium and identifies three possible expansions of the cerebrum within the maniraptoran lineage. Unique volumetric morphologies are found for both Oviraptorosauria and Paraves. Most interestingly, the volumetric proportions of *Archaeopteryx lithographica* illustrate that this taxon shares a plesiomorphic morphology with other paravians, suggesting that non-avialan paravians such as *Microraptor zhaoianus* also possessed what has previously been referred to as a “flight-ready” brain that likely supported some type of volant activity.
# TABLE OF CONTENTS

CHAPTER ONE: INTRODUCTION ................................................................................................. 1
  Morphology and Phylogenetic History ............................................................................. 2
  Evolution of the Endocranial Space ................................................................................. 5

CHAPTER TWO: OSTEOLOGICAL MORPHOLOGY WITHIN OVIRAPTOROSAURIA .......................................................... 7
  Introduction ...................................................................................................................... 7
  *Incisivosaurus gauthieri* ............................................................................................... 11
  Materials and Methods ................................................................................................. 12
    Locality and Geological Setting .................................................................................. 12
    Scanning ...................................................................................................................... 14
  Cranial Description ........................................................................................................ 14
    Rostrum ...................................................................................................................... 21
    Premaxilla .................................................................................................................. 23
    Maxilla ........................................................................................................................ 25
    Vomer ........................................................................................................................ 27
    Palatine ....................................................................................................................... 27
    Pterygoid ..................................................................................................................... 31
    Ectopterygoid ............................................................................................................ 32
    Nasal ............................................................................................................................ 33
Lacrimal ................................................................. 34
Frontal ................................................................. 36
Parietal ................................................................. 37
Jugal ................................................................. 37
Postorbital ............................................................. 38
Squamosal ............................................................ 39
Quadratojugal ....................................................... 40
Quadrate ............................................................. 41
Lateral Surface of the Braincase ......................... 43
Occipital Surface of the Braincase ....................... 48
Ventral Surface of the Braincase ......................... 51
Endocranial Cavity, Inner Ear, and Tympanic Recesses  53
Mandible ............................................................. 54
  Dentary ............................................................. 55
Splenial ............................................................... 55
Angular and prearticular ....................................... 56
Surangular .......................................................... 56
Dentition ............................................................. 56
  Premaxillary teeth .............................................. 56
  Maxillary teeth ............................................... 57
  Dentary teeth .................................................. 58
Discussion ........................................................ 58
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cranial Pneumaticity</td>
<td>61</td>
</tr>
<tr>
<td>Conclusions</td>
<td>63</td>
</tr>
<tr>
<td><em>Khaan mckennai</em></td>
<td>64</td>
</tr>
<tr>
<td>Materials and Diagnosis of <em>Khaan mckennai</em></td>
<td>65</td>
</tr>
<tr>
<td>Geological Setting</td>
<td>72</td>
</tr>
<tr>
<td>CT scanning</td>
<td>73</td>
</tr>
<tr>
<td>Cranial Description</td>
<td>73</td>
</tr>
<tr>
<td>Premaxilla</td>
<td>80</td>
</tr>
<tr>
<td>Maxilla</td>
<td>83</td>
</tr>
<tr>
<td>Nasal</td>
<td>86</td>
</tr>
<tr>
<td>Frontal</td>
<td>89</td>
</tr>
<tr>
<td>Parietal</td>
<td>93</td>
</tr>
<tr>
<td>Lacrimal</td>
<td>94</td>
</tr>
<tr>
<td>Jugal</td>
<td>97</td>
</tr>
<tr>
<td>Postorbital</td>
<td>99</td>
</tr>
<tr>
<td>Squamosal</td>
<td>100</td>
</tr>
<tr>
<td>Supraoccipital</td>
<td>100</td>
</tr>
<tr>
<td>Exoccipital</td>
<td>101</td>
</tr>
<tr>
<td>Basioccipital</td>
<td>102</td>
</tr>
<tr>
<td>Parabasisphenoid</td>
<td>104</td>
</tr>
<tr>
<td>Quadratojugal</td>
<td>104</td>
</tr>
<tr>
<td>Quadrate</td>
<td>105</td>
</tr>
</tbody>
</table>
CHAPTER THREE: PHYLOGENETIC RELATIONSHIPS OF OVIRAPTOROSAURIA

Introduction .................................................................................................................. 186
Materials and Methods

Taxonomic Sampling

Character Sampling

Cladistic Analysis

Results

Tree Summary for Species Level Analysis
Zanabazar (=Saurornithoides) junior .................................................. 286
Incisivosaurus gauthieri (IVPP V 13326)............................................. 291
Conchoraptor gracilis (IGM 100/3006)................................................. 296
Citipati osmolskae (IGM 100/978)....................................................... 303
Khaan mckennai (IGM 100/973).......................................................... 309
Phylogenetically Variable Endocranial Morphology ....................... 315
  Absence of a pontine flexure in the hindbrain ................................. 315
  Retraction of the olfactory bulbs ................................................. 319
  Shape of cerebrum ....................................................................... 320
  Fronto-parietal suture ................................................................... 320
  Epiphyseal fossa ........................................................................... 322
  Ventrolateral displacement of optic bulbs .................................... 323
  Dorsal expansion of cerebellum and presence of a dorsal sagittal
  sinus ............................................................................................... 323
  Width of the cerebellum .............................................................. 325
Flocculus and size of the inner ear .................................................. 325

Position of the vagus foramen ......................................................... 327

Statistical Results ........................................................................... 327

Body Size and Endocranial Volume .................................................. 327

Total volume .................................................................................. 327

Cerebrum ....................................................................................... 329

Optic lobes .................................................................................... 329

Cerebellum .................................................................................... 330

Brain stem .................................................................................... 330

Olfactory bulbs .............................................................................. 331

Pituitary ......................................................................................... 340

Neuroanatomical Partitions: Proportional Volumetric Comparisons ...... 340

Cerebrum ....................................................................................... 340

Optic lobes .................................................................................... 342

Cerebellum .................................................................................... 342

Brainstem ...................................................................................... 343

Olfactory bulbs .............................................................................. 344

Pituitary ......................................................................................... 344

Principal Components Analysis ...................................................... 353

Discussion ...................................................................................... 359

Summary and Conclusions .............................................................. 368

CHAPTER FIVE: CONCLUSIONS .......................................................... 372
LIST OF FIGURES

Figure 2.1 Map of Liaoning Province (shaded gray). Beipiao City is marked by an asterisk.........................................................13

Figure 2.2 Oblique view of the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326)..................................................15

Figure 2.3 The skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) in A, right lateral and B, left lateral views. Abbreviations in Appendix 1....16

Figure 2.4 Skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) in A, dorsal and B, ventral views. Abbreviations in Appendix 1..............17

Figure 2.5 Skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) in A, anterior and B, posterior views. Abbreviations in Appendix 1...............18

Figure 2.6 Mandible of the holotype of *Incisivosaurus gauthieri* in A, anterior; B, right lateral; and C, left lateral views........................................19

Figure 2.7 Mandible of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) in A, ventral and B, dorsal views. View C shows magnified dorsal view of dentary teeth.................................................................20

Figure 2.8 Ventrolateral view of the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in Appendix 1...............................22

Figure 2.9 Horizontal CT slices through the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in Appendix 1......................28

Figure 2.10 Axial CT slices through the skull of the holotype of *Incisivosaurus*
gauthieri (IVPP V 13326) showing the pneumatic recesses within the facial region. Abbreviations in Appendix 1 .................................30

Figure 2.11 Sagittal CT slices through the skull of the holotype of Incisivosaurus gauthieri (IVPP V 13326). Abbreviations in Appendix 1 .........................42

Figure 2.12 Ventrolateral view of the left side of the braincase of the holotype of Incisivosaurus gauthieri (IVPP V 13326). Abbreviations in Appendix 1 ..........44

Figure 2.13 Sagittal cutaway of a virtual rendering of the skull of the holotype of Incisivosaurus gauthieri (IVPP V 13326) with the matrix rendered transparent. Abbreviation in Appendix 1 ........................................47

Figure 2.14 Khaan mckennai (IGM 100/1127, holotype) .................................................................66

Figure 2.15 Khaan mckennai (IGM 100/1002, referred specimen) ........................................67

Figure 2.16 Skull of Khaan mckennai (IGM 100/973, referred specimen).

A, dorsal; B, ventral; C, right lateral; D, left lateral; E, anterior;

F, posterior views .............................................................................................................................68

Figure 2.17 Proposed hypothesis for the relationships within Oviraptorosauria based on Norell et al. (2006) ........................................................................71

Figure 2.18 Skull of Khaan mckennai. A, right lateral view of holotype (IGM 100/1127); B, right lateral view of IGM 100/1002; C, right lateral view of IGM 100/1127. Abbreviations in Appendix 1 .....................76

Figure 2.19 Occipital surface of skull of Khaan mckennai (IGM 100/1002).

Abbreviations in Appendix 1 .........................................................................................................78

Figure 2.20 Detail of premaxilla of IGM 100/1127. Abbreviations in Appendix 1 .......81
Figure 2.21  Dorsal surface of skull of holotype of *Khaan mckennai* (IGM 100/1127). Abbreviations in Appendix 1 ......................87

Figure 2.22  CT images showing sagittal slices at various levels through IGM 100/973 (in mm). A, 13.33; B, 17.22; C, 22.09; D, 33.97; E, 41.67; F, 42.50. Abbreviations in Appendix 1 ......................91

Figure 2.23  CT images showing coronal slices at various levels through IGM 100/973 (in mm). A, 37.65; B, 50.75; C, 61.39; D, 69.57; E, 89.22; F, 103.95. Abbreviations in Appendix 1 ......................95

Figure 2.24  CT images showing horizontal slices at various levels through IGM 100/973 (in mm). A, 21.02; B, 21.70; C, 22.31; D, 22.85; E, 57.88. Abbreviations in Appendix 1 ......................108

Figure 2.25  Reconstruction using CT images of the inner ear of IGM 100/973.

A, lateral view; B, posterior view; C, anterior view; D, dorsal view.

Abbreviations in Appendix 1 .................................................................112

Figure 2.26  Cervical vertebrae. A, dorsal surface of cervical vertebral series in IGM 100/1127; B, lateral surface of cervical vertebral series in IGM 100/1002.........................................................122

Figure 2.27  Dorsal surface of axial vertebra in IGM 100/1002 .........................123

Figure 2.28  Dorsal vertebrae in IGM 100/1002. A, dorsal surface;

B, lateral surface..................................................................................128

Figure 2.29  Sacral vertebrae. A, anterior sacral vertebra in IGM 100/1002;

B, posterior sacral vertebra in IGM 100/1127........................................131
Figure 2.30  Caudal vertebrae in IGM 100/1127.................................133
Figure 2.31  Sternal plates. A, IGM 100/1127; B, IGM 100/1002............136
Figure 2.32  Scapulocoracoid. A, dorsal surface of right scapulocoracoid in
             IGM 100/1002; B, dorsal surface of right scapulocoracoid in
             IGM 100/1127...........................................................................139
Figure 2.33  Furcula. A, dorsal surface of furcula in IGM 100/1002; B, dorsal
             surface of furcula in IGM 100/1127........................................141
Figure 2.34  Humerus. A, lateral surface of right humerus in IGM 100/1002;
             B, posterior surface of right humerus in IGM 100/1127; C, Medial
             surface of right humerus of IGM 100/1127 showing deltopectoral
             crest...........................................................................................144
Figure 2.35  Radius and ulna. A, lateral surface of radius and ulna in IGM
             100/1002; B, lateral surface of radius and ulna in IGM 100/1127.......146
Figure 2.36  Manus. A, Right manus of IGM 100/1002; B, right manus of
             IGM 100/1127..............................................................................149
Figure 2.37  Ilium. A, Lateral surface of right ilium in IGM 100/1002; B,
             lateral surface of right ilium in IGM 100/1127.........................152
Figure 2.38  Ilium of IGM 100/973. A, lateral view of right ilium (top) and medial
             view of right ilium (bottom); B, lateral view of left ilium (top) and
             medial view of left ilium (bottom).................................................153
Figure 2.39  Lateral view of pubis in IGM 100/973.....................................156
Figure 2.40  Ischium. A, lateral view of right ischium in IGM 100/1002; B,
lateral view of right ischium in IGM 100/973 ........................................158

Figure 2.41 Right femur of IGM 100/973. A, anterior view; B, posterior view;
C, lateral view; D, medial view; E, distal view; F, proximal view .........160

Figure 2.42 Femur. A, posterior view of left femur in IGM 100/1127; B,
lateral view of right femur in IGM 100/1002 ......................................161

Figure 2.43 Tibiae and fibulae of IGM 100/973. A, anterior surface of left tibia
and fibula; B, posterior surface of right tibia; C, anterior surface of
right tibia; D, left lateral surface of right tibia; E, right lateral surface
of right tibia; F, detail of anterior surface of proximal end of right tibia
showing the astragalus and calcaneum; G, distal surface of right tibia...164

Figure 2.44 Tibia and fibula. A, posterior surface of right tibia and fibula in
IGM 100/1002; B, posterior surface of right tibia and fibula in
IGM 100/1127 ..................................................................................165

Figure 2.45 Feet of IGM 100/1002 ................................................................168

Figure 2.46 Feet of IGM 100/973. A, dorsal surface of left foot; B, palmer surface
of left foot; C, dorsal surface of right foot; D, palmer surface of
right foot .........................................................................................169

Figure 3.1 Phylogenetic hypotheses of Oviraptorosaur relationships. A, Maryanska
et al. (2002); B, Osmolska et al., (2004); C, Lu et al. (2004); D,
Lu (2005); E, modified from Turner et al. (2007); F, Zanno et al. (2009).
Note that trees A and B position oviraptorosaurs within Avialae, making
them secondarily flightless birds ......................................................188
Figure 3.2 The most parsimonious trees recovered from the present analysis.
Alternate positions of IGM 100/1253 are shown by dotted lines.
A, recovered relationships within Coelurosauria; B, recovered relationships within Oviraptorosauria

Figure 3.3 Examples of skulls from oviraptorosaur taxa. A, *Incisivosaurus gauthieri*; B, *Rinchenia mongoliensis*; C, *Conchoraptor gracilis*; D, IGM 100/42.

Modified from Osmolska et al. (2004) and Xu et al. (2002a)

Figure 3.4 Two possible reconstructions of oviraptorid relationships with the removal ZPAL MgD-I/106

Figure 3.5 Bremer support values for clades within A, Coelurosauria; and B, Oviraptorosauria

Figure 3.6 Maryanska et al. (2002) analysis including troodontids and alvarezsaurids

Figure 3.7 Maryanska et al. (2002) analysis including troodontids, alvarezsaurids, and *Incisivosaurus gauthieri*

Figure 3.8 Maryanska et al. (2002) analysis including troodontids, alvarezsaurids, *Incisivosaurus gauthieri* with *Allosaurus* as the outgroup rather than *Herrerasaurus*

Figure 3.9 Oviraptorosaur relationships obtained by a reanalysis of Maryanska et al. (2002) analysis including troodontids, alvarezsaurids, and *Incisivosaurus gauthieri* with *Allosaurus* as the outgroup rather than *Herrerasaurus*

Figure 3.10 Rostrum of A, *Incisivosaurus gauthieri*; B, *Khaan mckennai*; C,
Velociraptor mongoliensis; and, D, Anas platyrhynchos demonstrating the posterior position of the external naris (arrow) and reduction of the ascending (nasal) process of the maxilla.................................236

Figure 3.11 Skulls of A, Anas platyrhynchos; B, Tsaagan mangas; C, Khaan mckennai; and, D, Caudipteryx zoui demonstrating the morphology of the posterior margin of the jugal (arrow)........................................239

Figure 3.12 Skulls of A, Dromaius novaehollandiae; and B, Citipati osmolskae. Arrows indicate parasphenoid rostrum.................................................................241

Figure 3.13 Consensus tree (from 13 MPTs) recovered from a reanalysis of the Lu et al. (2004) data matrix.................................................................245

Figure 3.14 Consensus tree (from 2 MPTs) recovered from a reanalysis of the Lu (2005) data matrix.................................................................247

Figure 3.15 Perceived evolutionary history for the acquisition of a bony cranial crest.................................................................251

Figure 3.16 Alternate positions for the taxon Protarchaeopteryx robusta ..............254

Figure 4.1 Endocranial cast of the tropicbird, Phaethon rubricada, demonstrating the six neuroanatomical partitions distinguished in this analysis ..........267

Figure 4.2 Sagittally sectioned skull of Phaethon rubricada, with digitally created endocast. Osteological markers used to delineate the olfactory bulbs are indicated in the enlarged image below .........................269

Figure 4.3 Sagittally sectioned skull of Phaethon rubricada, with digitally created endocast. Osteological markers used to delineate the cerebrum
are indicated in the enlarged image below ........................................ 270

Figure 4.4  Two dimensional CT slice through braincase of *Phaethon rubricada*.
Arrows indicate osteological markers used to delineate posterior border of cerebrum ................................................................. 271

Figure 4.5  Sagittally sectioned endocast of *Phaethon rubricada* .................. 272

Figure 4.6  Sagittally sectioned skull of *Phaethon rubricada*, with digitally created endocast. Osteological markers used to delineate the pituitary are indicated in the enlarged image below ........................................ 273

Figure 4.7  Sagittally sectioned skull of *Phaethon rubricada*, with digitally created endocast. Osteological markers used to delineate the optic lobes are indicated in the enlarged image below ............................... 274

Figure 4.8  Sagittally sectioned skull of *Phaethon rubricada*, with digitally created endocast. Osteological markers used to delineate the cerebellum are indicated in the enlarged image below ........................................ 275

Figure 4.9  Sagittally sectioned skull of *Phaethon rubricada*, with digitally created endocast. Osteological markers used to delineate the brain stem are indicated in the enlarged image below .................................... 276

Figure 4.10  Endocranial cast of the ostrich, *Struthio camelus* ...................... 280

Figure 4.11  Endocranial cast of the common duck, *Anas platyrhynchos* ........ 281

Figure 4.12  Endocranial cast of *Zanabazar junior* .................................... 287

Figure 4.13  Endocranial cast of *Incisivosaurus gauthieri*. Cast of inner ear rendered in pink ................................................................. 292
Figure 4.14 Endocranial cast of *Conchoraptor gracilis* .............................................. 297

Figure 4.15 Endocranial cast of *Citipati osmolskae* .................................................... 304

Figure 4.16 Endocranial cast of *Khaan mckennai* ....................................................... 310

Figure 4.17 Endocranial morphological characters traced onto the maniraptoran tree.

Black dot indicates Oviraptorosauria ................................................................. 316

Figure 4.18 Endocast of *Incisivosaurus gauthieri* with skull rendered

semitransparent .................................................................................................. 321

Figure 4.19 Log transformed values of total endocranial volume and body mass

plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.1 ................................................................. 334

Figure 4.20 Log transformed values of total cerebral volume and body mass plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.1 ................................................................. 335

Figure 4.21 Log transformed values of total optic lobe volume and body mass
plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.1.

**Figure 4.22** Log transformed values of total cerebellar volume and body mass plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.1.

**Figure 4.23** Log transformed values of total volume of brain stem and body mass plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.1.

**Figure 4.24** Log transformed values of total olfactory bulb volume and body mass plotted against each other. Oviraptorosaurs are shown in red,
deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.1.

Figure 4.25 Log transformed values of total pituitary volume and body mass plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Dotted line represents best fit line for crown birds. Regression statistics can be found in Table 3.1.

Figure 4.26 Log transformed values of total cerebral volume and endocranial volume plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.2.

Figure 4.27 Log transformed values of total optic lobe volume and endcranial volume plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole
sample. Small dotted line represents best fit line for crown birds. Large
dotted line represents best fit line for non-avian theropods. Regression
statistics can be found in Table 4.2 ..........................................................348

Figure 4.28 Log transformed values of total cerebellar volume and endcranial
volume plotted against each other. Oviraptorosaurs are shown in red,
deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot,
and crown birds in blue. Solid line represents best fit line for whole
sample. Small dotted line represents best fit line for crown birds. Large
dotted line represents best fit line for non-avian theropods. Regression
statistics can be found in Table 4.2 ..........................................................349

Figure 4.29 Log transformed values of total brain stem volume and endcranial
volume plotted against each other. Oviraptorosaurs are shown in red,
deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot,
and crown birds in blue. Solid line represents best fit line for whole
sample. Small dotted line represents best fit line for crown birds. Large
dotted line represents best fit line for non-avian theropods. Regression
statistics can be found in Table 4.2 ..........................................................350

Figure 4.30 Log transformed values of total olfactory bulb volume and endcranial
volume plotted against each other. Oviraptorosaurs are shown in red,
deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot,
and crown birds in blue. Solid line represents best fit line for whole
sample. Small dotted line represents best fit line for crown birds. Large
dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.2

Figure 4.31  Log transformed values of total pituitary volume and endocranial volume plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.2

Figure 4.32  Plots of endocranial partition data on first and second principle component axes. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Dotted line drawn around paravians. Loadings given in Table 4.3

Figure 4.33  Plots of endocranial partition data on second and third principle component axes. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Dotted line drawn around paravians. Loadings given in Table 4.3

Figure 4.34  Inferred pattern of neuroanatomical expansion relative to body size. The alternative interpretation that the relative expansion of the optic lobes, cerebellum, and brain stem is a synapomorphy deep within Maniraptora
and that *Archaeopteryx* *lithographica* reflects an autapomorphically small derivation is hampered by similarly small values in some oviraptorosaurs (suggesting a homoplastic expansion within that clade). The possibility that the expansions expressed in *Zanabazar junior* and the crown reflect paravian synapomorphies, with secondary contraction in *Archaeopteryx* *lithographica* is ambiguous with the above interpretation. Cerebral expansion relative to body size is an unambiguous synapomorphy of the avian crown

Figure 4.35 Inferred pattern of neuroanatomical expansion relative to total endocranial volume. Possessing a cerebral volume over 50% of the total endocranial volume optimizes as a synapomorphy of Paraves. A subsequent cerebral expansion may also have taken place within crown birds
LIST OF TABLES

Table 2.1  Selected measurements (in mm) from the cranial skeleton of

Khaan mckennai........................................................................................................75

Table 2.2  Selected measurements (in mm) from the postcranial skeleton of

Khaan mckennai........................................................................................................143

Table 3.1  List of taxa included in phylogenetic analysis........................................193

Table 4.1  Regression statistics for body mass against volume of each region........327

Table 4.2  Regression statistics for total endocranial volume against each region...345

Table 4.3  Loadings obtained from a principal component analysis of the six

isolated brain regions ...............................................................................................354
ACKNOWLEDGMENTS

This undertaking is unlike anything that I have ever attempted before, and throughout the experience there have been so many people that have helped me along the way that I hesitate to mention anyone’s name lest I forget someone else. Protocol, however, must be followed, and I would like first to thank my defense committee. I am lucky enough to have a committee consisting of Mark Norell, John Flynn, Meng Jin, Matt Colbert and Dan Ksepka that surely is the envy of many graduate students. They have provided much needed feedback on the following thesis. My advisor, Mark Norell, has been an unending resource that has served to broaden my intellectual horizons with conversations about science, art, music and travel (among many other things).

I was lucky enough to have the opportunity to travel across the country and the globe to look at specimens and have conversations with colleagues in order to complete this dissertation. Those who have graciously allowed me into their collections include Rinchen Barsbold and Khishigjaw Tsogtbaatar (IGM), Magdalena Borsuk-Bialynicka (ZPAL), Dave Evans and Kevin Seymour (ROM), Randy Irmis (UMNH), Qingwei Tan (LH), and Jun Lui, Xu Xing, and Zhao Zhong-He (IVPP). This research was supported by an international travel grant from Columbia University and by an NSF dissertation improvement grant (DEB 0909970).

I must also acknowledge all of those graduate students that went through the program with me and whose conversations in class and elsewhere have helped refine much of this dissertation. Those that I began with included Jack Conrad (actually a postdoc), Andres Giallombardo, Dan Ksepka, Jun Lui, Sterling Nesbitt, Michelle Spaulding, and Alan Turner.
Those that I will finish with include Steve Brusatte, Jianye Chen, Shaena Montanari, Rei Pei, and my officemate Hongyu Yi.

A debt of gratitude is owed to all of the people throughout the American Museum of Natural History that have been incredibly kind during the years that I have been in residence there. Many have contributed to the completion of this thesis including Jason Brougham, Ana Balcarcel, Amy Davidson, Mick Ellison, Judy Galkin, Adam Kashuba, Dina Langis, Carl Mehling, Chris Norris, and Ruth O’Leary. Many also have contributed to the delay in completion of this thesis including Jason Brougham, Ana Balcarcel, Mick Ellison, Adam Kashuba, Dina Langis, Carl Mehling, and Chris Norris--not that I’m complaining. I am especially indebted to Mick Ellison for his amazing photographs of *Incisivosaurus gauthieri* and *Khaan mckennai* and Amy Davidson for her exceptional preparations. Thanks also to Mia Leo at Columbia University for helping me immensely through the past several years.

A very sincere thank you must also be extended to Mark Norell and Mike Novacek for providing me with the opportunity to spend my last five summers in Mongolia (four in the field and one in the collections). Very few people have the chance to travel to such exotic localities, and I count myself lucky to have been in one of the most remote spots in the world looking for some of the best fossils in world. These travels also allowed me to make many good friends and I want to thank Timor, Bayna, Bayra, Inday, Naba, Muggi, and Dr. Khand.

The research staff in the CT lab at The University of Texas at Austin is like a second family to me, and I know that I will always feel welcome in the basement of the geology building on that campus. Jessie Maisano and Matt Colbert have done much of the CT scanning and post processing for this project. Matt Colbert also has been the source of countless
conversations over the many years that I have know him that have done much to shape my subsequent years as a scientist. My master’s advisor Tim Rowe has graciously allowed me to use many of the CT scans that were completed for the DigiMorph website (digimorph.org) in this dissertation and has always supported my endeavors.

I would like especially to thank my family. I want to say thank you for being so understanding to my inlaws Steve and Johna Bever, as well as the whole Epp clan. My sister Emily and I are in the unique position of completing our dissertations at the same time. Through our bouts of sibling rivalry, she has been a source of support and companionship that I think only a sister can provide. My parents have never questioned anything that I have ever tried to do, but instead were always asking what they could do to help. It is hard for me to express exactly how much is owed to them, but needless to say that I would not be here without them.

Finally, my husband Gabe Bever has never doubted me despite my own periodic doubts about myself. He has in a way contributed as much to this dissertation as I have. His insights and edits have made the work as a whole a much more finished piece. I will always be grateful to him far beyond what words can express.
CHAPTER ONE
INTRODUCTION

The last twenty years has seen a flourishing of discoveries and novel studies of coelurosaur specimens from around the globe that have had a profound influence on our understanding of the origin of birds among non-avian theropods. One small morphologically unique group of extinct coelurosaurian theropods from the Early to Late Cretaceous of North America and Central Asia, Oviraptorosauria, remains poorly known and has the potential to play an important role in our understanding of the dinosaur crown (Osborn, 1924; Barsbold, 1976; Osmólska et al., 2004). Oviraptorosaurs include the small bodied forms such as *Incisivosaurus gauthieri* (Xu et al., 2002a), *Caudipteryx zoui* (Ji and Ji, 1997), *Avimimus portentosus* (Kurzanov, 1981), and *Microvenator celer* (Ostrom, 1969; Makovicky and Sues, 1998), all of which have been hypothesized by most existing phylogenetic analyses to lie at the base of the oviraptorosaur tree. Towards the more distal end of the oviraptorosaur lineage are the purported sister taxa Caenagnathidae and Oviraptoridae. Caenagnathids (Gilmore, 1924) have a distribution that ranges across North America and Central Asia, but unfortunately specimens assigned to this taxon typically are not well preserved--being represented for the most part by only a dentary or pes. *Chirostenotes per gracilis* (ROM 43250 and RTMP 79.20.1) is the one notable exception (see Russell and Currie, 1988; Sues, 1997; Varricchio, 2001). Oviraptoridae in contrast has a remarkable preservational record. Taxa within Oviraptoridae are found exclusively in Central Asia (namely China and Mongolia) and possess a range of body sizes from the small *Conchoraptor gracilis* (approximately 1.5m in length) (Barsbold, 1981) to the literally gigantic
**Gigantoraptor erlianensis** (approximately 8m in length) (Xu et al., 2007). These morphologically distinct taxa are the ones often compared with avialans, and they do share striking resemblances of cranial features such as the absence of teeth and the occasional presence of cranial casques.

**MORPHOLOGY AND PHYLOGENETIC HISTORY**

Despite almost one hundred years of study and intense popular interest (see Ostrom, 1924; Norell and Dingus, 1999), the evolutionary relationships among oviraptorosaurs (Makovicky and Sues, 1998; Maryánska et al., 2002; Osmólska et al., 2004; Lü et al., 2004; Lü, 2005; Turner et al., 2007) and the position of oviraptorosaurs within Coelurosauria remain contentious (Fig. 3; Sues, 1997; Makovicky and Sues, 1998; Lü, 2005; Maryánska et al., 2002; Osmólska et al., 2004; Turner et al., 2007). This lack of resolution makes it impossible to infer whether the shared characteristics between oviraptorosaurs and birds are apomorphic for a more inclusive clade that includes both groups, or whether these ‘avian-like’ features evolved independently. Resolution of this dilemma is crucial to understanding the phylogenetic relationships of derived coelurosaurans and the transformation of characters associated around the origin of flight. The primary goal of this study is to gain an understanding of the range of morphology present in Oviraptorosauria (including additional character systems such as endocranial morphology) and subsequently to reexamine the evolutionary relationships of Oviraptorosauria at a species level using cladistic methodologies.
The monophyly of Oviraptorosauria (Barsbold, 1976), has not been disputed (e.g., Gauthier, 1986; Maryánska et al., 2002; Senter, 2007; Turner et al., 2007), however, up to this time it is supported only by a handful of cranial characters, including ventrally curving pendant-shaped paroccipital processes, a thin coronoid ossification, and a slender retroarticular process of the mandible (Makovicky and Sues, 1998; Turner et al., 2007) and no postcranial characters. The determination of where oviraptorosaurs lie within Coelurosauria is critical in order to optimize characters within the clade, specifically to establish outgroup character states (Watrous and Wheeler, 1981). Some recent analyses have placed Oviraptorosauria in a much more derived position, within Avialae, a novel location that would make this clade the first example of flightlessness evolving within flighted birds (e.g., Maryánska et al., 2002 and Osmólska et al., 2004). Other recent analyses have positioned Oviraptorosauria alternatively as the sister taxon to Therizinosauria (among non-avialan theropods; e.g., Sues, 1997; Holtz, 1998; Makovicky and Sues, 1998; Turner et al., 2007) or Paraves (among non-avialan theropods; Senter, 2007; Zanno et al., 2009). Again taxon sampling, especially at the base of the oviraptorosaur clade (Huelsenbeck, 1991), likely has had a large influence on the position of the group within Coelurosauria.

There is a consensus that two identifiable clades lie within Oviraptorosauria, Oviraptoridae and Caenagnathidae (Sues, 1997; Makovicky and Sues, 1998; Maryánska et al., 2002; Osmólska et al., 2004; Turner et al., 2007); however this consensus does not extend to the taxa that compose these clades, the relationships within them, or the taxa that lie on the stem leading to these monophyletic groups. Lü (2005) postulates a traditional oviraptorid clade composed of *Nomingia gobiensis, Rinchenia mongoliensis, Ingenia yanshini, Citipati osmolskai*,
Nemegtia barsboldi, Heyuannia huangi, Oviraptor philoceratops, Conchoraptor gracilis, and Khaan mckennai and a Caenagnathidae composed of Chirostenotes pergracilis and an unnamed taxon. Maryánska et al. (2002) and Osmólska et al. (2004) retrieve similar results but have a sparser sampling of taxa. They do not include Incisivosaurus gauthieri, Citipati osmolskae, Nemegtia barsboldi, Heyuannia huangi, or Khaan mckennai in their analyses. Citipati osmolskae and Khaan mckennai represent some of the best-preserved material available and are invaluable specimens for understanding relationships within Oviraptorosauria (Clark et al., 2001).

Incisivosaurus gauthieri falls as the most basal taxon within the group in the Theropod Working Group (TWiG) analysis, and thus may be critical to resolving relationships within the larger group. TWiG (see Turner et al., 2007) includes an expanded taxon sampling that is slightly different from Lü (2005) and recovers two monophyletic clades similar to Lü (2005). Their results differ primarily in the position of Avimimus portentosus (a somewhat enigmatic taxon). The purpose of the TWiG matrix, however, is not explicitly to test the relationships among oviraptorosaurs but rather those of Coelurosauria; therefore, the relationships within these clades of interest remain unresolved. Again, taxon sampling would appear to be the largest factor affecting conflicting trees between analyses. Additional taxa are important for breaking up long branches. The analysis presented here benefits by including a comprehensive sampling of taxa including several previously undescribed specimens.

The phylogenetic hypothesis of coelurosaurian and oviraptorosaurian relationships generated by this study will additionally be used to interpret character transformations within Oviraptorosauria and reevaluate evolutionary trends among coelurosaurian dinosaurs as a whole. Whether Oviraptorosauria falls out as a basal member of Avialae (making it the first known clade
to become secondarily flightless; see Maryánska et al., 2002 and Osmólska et al., 2004) or as a non-avian theropod (see Hwang et al., 2004; Holtz, 1998; Turner et al., 2007), will have a large impact on the acquisition of characters leading to modern birds. Therefore, this study aims to address the following phylogenetic questions: 1) what are the evolutionary relationships within Oviraptorosauria; and, 2) what is the position of Oviraptorosauria within Coelurosauria? These phylogenetic hypotheses are then used to concentrate on the evolution of one specific character system, namely the evolution of the endocranial space.

EVOLUTION OF THE ENDOCRANIAL SPACE

The phylogeny generated by this analysis will be used to study the evolution of the endocranial space (i.e., endocast—the three-dimensional cast of the endocranial space provides a fairly accurate representation of the morphology of the brain in taxa who fill most of their cranial cavity as is the case in derived theropod dinosaurs; Hopson, 1979). Data generated for this analysis will yield insight into the evolution of the central nervous system (CNS) within this morphologically divergent group of dinosaurs. In addition to providing detailed anatomical descriptions of endocranial morphology using digital technologies and building a database of digital endocasts of extant and extinct species, this study aims to address the questions: what is the evolutionary history of endocranial morphology within Oviraptorosauria, and how does the position of this group affect the acquisition of ‘avian-like’ endocranial characters along the coelurosaur lineage? The evolution of endocranial morphology within Oviraptorosauria appears to demonstrate a larger amount of plasticity than previously documented and may be largely
affected by the uncertainty of relationships within the lineage (Balanoff et al., 2007; Kundrát, 2007).

Questions that will be vital to our understanding of oviraptorosaur endocranial anatomy include: how does increased understanding of endocranial anatomy in basal oviraptorosaurs affect perception of its evolution within the whole clade; what endocranial characters are diagnostic for oviraptorosaurs and successively nested clades; and finally, what transformations in endocranial morphology occur during oviraptorosaur evolution, and how do they affect our general perception of endocranial evolution in Coelurosauria as a whole? The morphology of the endocast may reveal general trends in cognitive abilities necessary for the acquisition of flight (Jerison, 1969; Hopson, 1979; Iwaniuk et al., 2005); therefore, this analysis also will address what these data can reveal about the sensory capabilities of coelurosaurian dinosaurs.
CHAPTER TWO
OSTEOLOGICAL MORPHOLOGY WITHIN OVIRAPTOROSAURIA

INTRODUCTION

Members of the coelurosaurian group Oviraptorosauria encompass a wide range of body shapes and sizes from the morphologically bizarre, toothed *Incisivosaurus gauthieri* to that of the medium-sized, crested oviraptorids like *Citipati osmolskae* and even the gigantic form *Gigantoraptor erlianensis* (approximately 8 m in length; Xu et al., 2007). Members of this clade have been known for nearly one hundred years, as reasonably complete specimens were first collected by the American Museum of Natural History’s Central Asiatic Expeditions in 1922 at the Late Cretaceous Bayn Dzak (Flaming Cliffs) locality (Osborn, 1924). The circumstances surrounding this find (the fact that it was lying on top of a nest of presumed *Protoceratops* eggs) was only the beginning of inquiry and controversy surrounding the phylogenetic relationships and paleobiology of the oviraptorosaur group (Norell et al., 1994, 1995; Dong and Currie, 1996; Clark et al., 1999). Although oviraptorosaurs have been able to capture the imagination of the public; well-illustrated, easily accessible descriptions of these taxa are conspicuously absent from the literature, except notably for Clark et al. (2002; *Citipati osmolskae* cranial elements), Balanoff et al. (2009; *Incisivosaurus gauthieri* cranial remains), Lu et al. (2004; *Nemegtia barsboldi* skeletal remains), Vickers-Rich et al. (2002; *Avimimus*)
portentosus well illustrated but no written description), and the multiple publications on *Caudipteryx zoui* (e.g., Ji et al., 1998; Zhou and Wang, 2000; Zhou et al., 2000).

The monophyly of Oviraptorosauria typically is so strongly supported as to be unquestioned in most literature (e.g., Holtz, 1998; Norell et al., 2006; Senter, 2007; Turner et al., 2007; Xu et al., 2007; Zanno et al., 2009). Generally their phylogenetic placement just outside of Paraves (defined as [[Dromaeosauridae+Troodontidae] +Avialae]; see Turner et al., 2007) is strongly supported. Controversial suggestions that oviraptorosaurs actually are derived from within Avialae (e.g., Osmolska et al., 2004) have been made contrary to the traditionally accepted arrangement. These results undoubtedly were influenced by restricted comparisons between advanced oviraptorosaurs and primitive avialans without incorporating basal oviraptorosaurs such as *Incisivosaurus gauthieri* and *Microvenator celer* into the analyses.

Despite the relative stability of the monophyly of the group as a whole, phylogenetic relationships among oviraptorosaurs remain unresolved (e.g., Holtz, 1998; Maryanska et al., 2002; Lu et al., 2004; Osmolska et al., 2004; Lu, 2005; Senter, 2007; Turner et al., 2007). Understanding the evolution within Oviraptorosauria will provide much needed insight into their many shared convergences with avians (*sensu* Gauthier, 1986) such as a loss of teeth, extreme pneumatization and ornamentation of the skull, and reduction of the tail vertebrae to form a pygostyle (see Osmólska et al., 2004; Barsbold et al., 2000). Oviraptorosaur specimens also have been collected that preserve the remarkable behavior of brooding nests of eggs in the stereotypical posture of modern birds (Norell et al., 1995; Dong and Currie, 1996; Clark et al., 1999). Examining the
acquisition of these characters within the oviraptorosaur lineage may shed light on the evolution of the same types of characters along the lineage leading to birds. Whether Oviraptorosauria falls out as a basal member of Avialae (making it the first known clade to become secondarily flightless; see Maryánska et al., 2002; Paul, 2002; Osmólska et al., 2004) or as a non-avian theropod (see Holtz, 1998; Rauhut, 2003; Senter, 2007; Turner et al., 2007) will have a large impact on the polarity of several characters in Avialae and their close nonavialan relatives.

As indicated above much of the uncertainty surrounding the phylogenetic position of Oviraptorosauria likely reflects the dearth of available morphological information for these taxa, which is especially surprising considering the large number of beautifully preserved specimens. Although many descriptions of oviraptorosaurs have been produced (e.g., Barsbold, 1981, 1983, 1986; Kurzanov, 1987), these historically have been published in journals that are not readily available to many scientists and lack detailed illustrations of the specimens they describe.

Our knowledge of primitive oviraptorosaurs has progressed extensively in the past several years (e.g., Ji et al., 1998; Xu et al., 2002a; Balanoff et al., 2009); however, descriptive morphology of the node-based group (Oviraptoridae + Caenagnathidae) has lagged behind. Oviraptoridae traditionally has been divided into two lineages, the crested Oviraptorinae (Barsbold, 1976) and the crestless Ingeniinae (Barsbold, 1981). Whether these represent monophyletic taxa or not, gaining a better understanding of the morphology of both groups will shed light on the evolution of the entire lineage. Clark et al. (2002) provided an important contribution to the morphology of the cranial
morphology of crested oviraptorids with their description of *Citipati osmolskae*. The remaining gap in our understanding of oviraptorids can be filled only by the further description of these taxa, especially with the addition of postcranial data. Once accomplished, such descriptions will present us with the opportunity to begin to make inferences about the evolution of morphological features in this group and allow direct comparison with other more completely described taxa like dromaeosaurids and basal avialans.

The goal of the first part of this study is to provide detailed osteological descriptions encompassing the breadth of oviraptorosaur morphology. To this end, descriptions including comprehensive illustrations and photographs are provided for the basal oviraptorosaur *Incisivosaurus gauthieri* (Xu et al., 2002a) and the derived oviraptorid *Khaan mckennai* (Clark et al., 2001). *Incisivosaurus gauthieri* consistently is found to occupy the basal position on the oviraptorosaur tree, making the documentation of its morphology imperative for the polarization of characters within the oviraptorosaur clade. *Khaan mckennai* is a derived, crestless oviraptorid from the Late Cretaceous Ukhaa Tolgod locality in the Gobi Desert of Mongolia. Several years of excavations at this locality have produced three specimens of this taxon in close proximity to each other, that represent some of the most completely known taxa of any fossil theropod known to date.

A list of anatomical abbreviations is given in Appendix 1. Institutional abbreviations are provided in Appendix 2.
Almost all aspects of oviraptorosaur paleobiology, from their relationships to their origins, have been poorly understood and highly controversial. This uncertainty stems primarily from their extremely apomorphic skeletons and the lack of fossilized material for the more primitive members of the group. This situation gradually has changed with the description of several newly discovered taxa representing various ontogenetic stages (e.g., Norell et al., 1994; Barsbold, 1997; Ji et al., 1998; Barsbold et al., 2000; Norell et al., 2001; Clark et al., 2001; Lü, 2002; Lü et al., 2004, Osmólska et al., 2004), the recent reassignment of previously known taxa to the group Oviraptorosauria (e.g., *Microvenator celer* [Makovicky and Sues, 1998], *Elmisaurus rarus* [Osmólska, 1981] and *Avimimus portentosus* [Kurzanov, 1987]), as well as the unique ‘preservation’ of behavior in the fossil record (i.e., nesting; Norell et al., 1995; Dong and Currie, 1996; Clark et al., 1999).

*Incisivosaurus gauthieri* certainly is one of the more bizarre theropods ever described (Xu et al., 2002a), and its inclusion within the equally bizarre Oviraptorosauria may not have been completely unexpected. This theropod was discovered in the Early Cretaceous rocks of northeastern China, which have produced numerous other amazing dinosaur specimens (see Xu and Norell, 2004; Norell and Ellison, 2005; Norell and Xu, 2005). Similar to many of the taxa recovered from the Jehol beds, *Incisivosaurus gauthieri* is known only from a single unique specimen (IVPP V 13326), although a synonymy with *Protarchaeopteryx robusta* (Ji and Ji, 1997) has been suggested (see Senter et al., 2004; Senter, 2007).
Aside from the familiar feathered dinosaurs, the Jehol beds (Zhou et al., 2003; Barrett and Hilton, 2006) also have produced myriad transitional forms. These dinosaurs (e.g., Liaoceratops [Xu et al., 2002b], the basal deinonychosaurs Microraptor [Xu et al., 2003] and Sinovenator [Xu et al., 2002c], the basal oviraptorosaur Caudipteryx [Ji et al., 1998], the transitional tyrannosaurid Dilong [Xu et al., 2004], the transitional therizinosaurs Beipiaosaurus [Xu et al., 1999], the basal toothed ornithomimosaur Shenzhousaurus [Ji et al., 2003], and the stem hadrosaurid Jinzhousaurus [Wang and Xu, 2001]) display many characteristics that place them at the base of established clades and therefore are crucial to the development of accurate phylogenetic trees. This generality holds true for Incisivosaurus gauthieri, which continually falls at the base of the oviraptorosaur tree (see Turner et al., 2007 and CHAPTER 2).

MATERIALS AND METHODS

Locality and geological setting

Locality: Lujiatun, Shangyuan, Beipiao City, Liaoning China (Fig. 2.1).

Geological occurrence: The specimen was collected from the lower part of the Yixian Formation. These beds are considered older than 128 million years old (Swisher et al. 1999, 2002).
Figure 2.1. Map of Liaoning Province (shaded gray). Beipiao City marked by an asterisk.
Scanning

The use of computed tomography (CT) provides a nondestructive means to view and study the internal structures of braincases (Carlson et al., 2003). In addition, CT allows the creation of digital endocasts of the endocranial cavity and its related structures of fossilized taxa. Computed tomography is used to augment both the description of the specimen and to extract a digital endocast from the endocranial cavity. IVPP V 13326 was scanned at Stony Brook University medical scanning facility. The specimen was scanned along the coronal axis for a total of 404 DICOM images at an image resolution of 512 x 512 pixels. The z-spacing (i.e., axial spacing) is 0.310 mm, and the x- and y-spacing (i.e., sagittal and horizontal spacing) is 0.188 mm. The original slice data and movies showing the endocranial cast are available at the DigiMorph website (www.digimorph.org/specimens/Incisivosaurus_gauthieri).

Cranial Description

IVPP V 13326 consists of a skull and anterior mandibles (Figs. 2.2–2.7). Although Xu et al. (2002a) reported a postdentary bone, it could not be located in IVPP collections at the time this paper was written. The skull is largely free from matrix, and removal of the remaining sediments would seriously endanger the specimen. Distinguishing sutures between some of the bones is difficult due to the degree of fusion between elements as in many other oviraptorosaurs specimens (e.g., Barsbold, 1981; Kurzanov, 1987; Sues, 1997; Clark et al., 2002). The cranium is well preserved and relatively undistorted,
Figure 2.2. Oblique view of the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326).
Figure 2.3. The skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) in **A**, right lateral and **B**, left lateral views. Abbreviations in Appendix 1.
Figure 2.4. Skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) in A, dorsal and B, ventral views. Abbreviations in Appendix 1.
Figure 2.5. Skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) in **A**, anterior and **B**, posterior views. Abbreviations in Appendix 1.
Figure 2.6. Mandible of the holotype of *Incisivosaurus gauthieri* in A, anterior; B, right lateral; and C, left lateral views.
Figure 2.7. Mandible of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) in **A**, ventral and **B**, dorsal views. View **C** shows magnified dorsal view of dentary teeth.
although the left side of the skull is displaced anteriorly relative to the right as is evidenced by the shape of the braincase and the more forward placement of the left preorbital bar (Figs. 2.3–2.5). The right side of the skull is more complete than the left, and the skull is laterally compressed. Compared to many oviraptorosaurs, the cranium is low in profile (see Osmólska et al., 2004:fig. 8.1) with a distinctly rounded roof. The nares are dorsally positioned on the skull and are displaced posteriorly lying dorsal to the antorbital fossa as in other oviraptorosaurs. The orbits are large and circular and the infratemporal fenestra is extensive and triangular (Fig. 2.3). The fragmentary anterior mandibles are fused at the dentary symphysis, as in other oviraptorosaurs (Figs. 2.5 and 2.6).

**Rostrum (Figs. 2.2–2.5, 2.8)**

The short rostrum is well preserved except for the slight deformations noted above. The short rostrum measured from the preorbital bar accounts for 44% of the total length of the skull. The nares are large and elliptical and displaced posteriorly from the anterior margin of the skull as in most other oviraptorosaurs (see Osmólska et al., 2004:fig. 8.1 and compare with Fig. 2.3). The orbits are large (making up 48% of the total skull length) and nearly circular, a condition found in other oviraptorosaurs. The infratemporal fenestra also is large and triangular with a larger ventral expanse.

Although much of the palate is distorted and many of the bones are tightly fused, which obscures most sutural connections, the majority of the palate is preserved (Fig. 2.4B). Compared to other oviraptorosaurs, the most distinctive features of the palate of
Figure 2.8. Ventrolateral view of the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in Appendix 1.
*Incisivosaurus gauthieri* are the antero-posterior elongation and lack of tapering of the skull posterior to the premaxillary-maxillary shelf. The slit-like choanae are remarkably different from the rounded choanae found in other oviraptorosaurs (see Clark et al., 2002:fig. 3). This morphology may be partially influenced by the overall compression of the skull; however, they are distinctly different in morphology from the rounded choanae in other oviraptorosaurs. The interpretation of these slit-like openings as choanae differs from Xu et al. (2002a), which suggested that the openings may represent confluent choanae and subsidiary palatine fenestrae. A subsidiary palatine fenestra is not known in other oviraptorosaurs (Currie, 1995; Elzanowski, 1999; Clark et al., 2002); therefore, the presence or absence of this structure remains ambiguous. The palatine fenestra is small but is much larger than in more derived oviraptorosaurs. Xu et al. (2002a) further describes a subsidiary ectopterygoid fenestra as a narrow opening lying in a depression on the right side of the skull between the ectopterygoid and palatine. CT imagery shows this fenestra opening into a pneumatic space within the ectopterygoid, thus indicating that this opening likely represents part of the ectopterygoid recess (Witmer, 1997).

**Premaxilla**

The premaxillae remain unfused along the anterodorsal external surface (Fig. 2.5A), unlike other oviraptorosaurs (however, fusion does not occur in *Conchoraptor gracilis*, *Khaan mckennai*, and *Caudipteryx zoui*). In lateral view the premaxilla forms the dorsal, anterior and ventral boundary of the elliptical naris. The posterior margin is made up of the contact between the maxillary process of the premaxilla and the nasal.
The maxillary processes are thick and massive similar to other oviraptorosaurs and have extensive exposure on the lateral surface of the skull (Fig. 2.3). In many oviraptorosaurs the maxillary process of the premaxilla extends posteriorly below the premaxillary process of the nasal to contact the lacrimal on the lateral surface of the skull. If this is the case in *Incisivosaurus gauthieri*, this contact is obscured by the overlaying nasal.

The nasal process of the premaxilla forms the internarial bar (Fig. 2.5A), which is thin and extends to meet the nasals posteriorly at the posterior margin of the narial aperture. This process is flat and strap-like, more typical of non-avian maniraptorans than other oviraptorosaurs (see Barsbold, 1981; Clark et al., 2002), in which the rounded internarial bar is thick and sometimes forms a crest with the nasals (with the exception of *Caudipteryx zoui*; Ji et al., 1998; Zhou et al., 2000).

The lateral surface of the premaxilla is medially depressed to form a shallow fossa anteroventral to the naris (Fig. 2.3) as is in oviraptorids, *Caudipteryx zoui*, and *Avimimus portentosus* (see Osmólska et al., 2004; Zhou et al., 2000; and Kurzanov, 1987). Several small foramina are scattered on the lateral surface of the bone, and a single larger foramen lies just ventral to the anterior corner of the naris. *Citipati osmolskae* and the unnamed Zamyn Khondt oviraptorosaur also have similar foramina scattered on the lateral surface of the premaxilla (see Clark et al., 2002; Osmólska et al., 2004). The ventral margin of the premaxilla is scalloped corresponding to the undulations of waves of teeth along a typical theropod tooth row. The suture between the premaxilla and the maxilla on the lateral surface of the skull contains a small subnarial foramen in the same position as in *Khaan mckennai* (Clark et al., 2001). The premaxilla-maxilla suture sweeps
posteriorly below the nares forming a small ridge that defines the anterior-most boundary of the antorbital fossa.

On the ventral surface, the premaxillae meet to form an extensive palatal surface typical of oviraptorosaurs (Fig. 2.4); however the palatal surface is smooth, lacking the longitudinal grooves apparent on the palate of oviraptorids. The premaxillae are tightly fused anteriorly as in other oviraptorosaurs to form a well-developed premaxillary shelf. They form a small longitudinal incisive crest at the point where they meet along the palate. The premaxilla meets the palatal shelf of the maxilla along a diagonal suture. Along the midline, the posterior end of the premaxilla overlies the anterior end of the vomer. Although the posteroverentral contact of the premaxilla with the maxilla and vomer is indistinct at the left vomer-premaxilla contact, there is a hint of the familiar “fleur de lis”-shaped contact present in other oviraptorosaurs (Elzanowski, 1999; Clark et al., 2002).

Maxilla

In contrast to most other maniraptorans, the maxilla contributes minimally to the lateral surface of the skull (Fig. 2.3). The maxilla contacts the jugal and lacrimal just ventral to the preorbital bar. The jugal ramus of the maxilla is thin and progressively overhangs the tooth row posteriorly. The nasal ramus of the maxilla is a small splint of bone that forms a ridge with the premaxilla and the nasal and defines the dorsal and anterior margins of the antorbital fossa.
The maxilla makes up a large part of both the osseous floor and interfenestral bar, which is located in the anterior portion of the antorbital fossa. The antorbital fossa is subtriangular and large, with a truncated anterior apex. The antorbital fenestra occupies approximately half of the entire fossa. The concave anterior margin of the interfenestral bar defines the antorbital fenestra within the fossa. Dorsally, a slightly concave lip of the maxilla overhangs the fossa. One small and one large foramen lie within the interfenestral bar (Fig. 2.3). The smaller of these foramina is positioned posteriorly just dorsal to the anterior extent of the jugal ramus. The larger foramen typically has been interpreted as the maxillary fenestra, a feature common to most theropods; yet, it lies at the anterior apex of the fossa, a position usually associated with the promaxillary fenestra. The ventral position of the smaller foramen is extremely unusual if it represents the maxillary fenestra, as this foramen usually lies topographically more dorsal relative to the promaxillary fenestra.

Although the paired maxillae are not exposed extensively on the palatal surface, they do contact the premaxillae anteriorly and the vomer anteriorly along the midline to form a secondary palate (Fig. 2.4B). In palatal view, the maxillae are separated along the midline by the vomer and taper posteriorly to terminate just posterior to the last tooth. The maxilla has at least five teeth set in a groove but lacks the tooth-like projection on the palatal surface that is present medially in more derived oviraptorosaurs (see Clark et al., 2002:fig. 3). The contact with the jugal can be seen along the lateral surface of the maxilla along this tapering edge. The vomerine process of the maxilla does not contact the vomer but, with the remaining medial margin of the palatine, forms most of the lateral
border of the choana (Figs. 2.4B and 2.8). The anteromedial edge of the maxilla comprises only the anterior-most lateral edge of the choana.

**Vomer**

The vomers are two vertically oriented sheets of bone that contact at the midline forming a septum that divides the choanae anteriorly (Fig. 2.4B). CT data reveal that the vomers remain unfused along most of their length and are fused only dorsally at the anterior end of the element (Figs. 2.9E and 2.10C). This arrangement contrasts with the typical condition seen in maniraptorans including oviraptorosaurs, in which a single stubby hourglass-shaped vomer separates the large rounded choanae along their entire length (see Elzanowski, 1999; Clark et al., 2002). The vomer contacts the maxilla anterolaterally, and together these elements form the anterior boundary of the choana. The vomer extends the length of the choana, forming the length of its lateral boundary. The stereotypical “fleur de lis” contact between the vomer(s) and premaxillae may be present, but is not distinct. Instead, the vomers contact the premaxilla anteriorly in a simple contact in which the vomer underlies the premaxilla. Posteriorly the vomer divides to form a notch that accepts the anterior vomerine process of the pterygoid. These elements form the posterior border of the choana.

**Palatine**

The palatines are extensively exposed on the palatal surface (Figs. 2.4B and 2.8). The element resembles that of other theropod dinosaurs in that it is divided into three
Figure 2.9. Horizontal CT slices through the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in Appendix 1.
Figure 2.9 (cont). Horizontal CT slices through the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in appendix 1.
Figure 2.10. Axial CT slices through the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) showing the pneumatic recesses within the facial region. Abbreviations in Appendix 1.
distinct rami: an anterior vomerine process, lateral maxillary process, and posterior pterygoid process. It is unclear if the maxilla contacts the vomer along the medial vomerine process as these elements contact on one side of the specimen but not the other; however, the palatine clearly abuts the maxilla along its lateral edge in a long diagonal process that terminates at the maxillary process. The maxillary process is small and contacts the maxilla at a level corresponding to the midpoint of the antorbital fenestra on the lateral surface of the skull. This contact sits dorsal to the ventral margin of the maxilla and defines the anterior boundary of the palatine fenestra (although see Xu et al., 2002a for a conflicting opinion). The medial border of the palatine fenestra is formed exclusively by the palatine (Fig. 2.4B). Posteriorly the palatine underlies the pterygoid just anterior to the ectopterygoid-pterigoid contact. The pterygoid process of the palatine expands slightly at this articulation.

**Pterygoid**

The pterygoid is a large bone that connects the anterior palatal elements with the braincase and suspensorium (Fig. 2.4B). Anteriorly it contacts the ectopterygoid dorsally and laterally, the palatine anteriorly, and the vomer mediolaterally. The pterygoid forms a small portion of the lateral border of the palatine fenestra. A small depression lies anterolaterally adjacent to the expanded bulbous region of the pterygoid that corresponds with the ectopterygoid articulation (Fig. 2.8). Along the anteromedial edge is a deep trough, which is an arc of flexure adjacent to a large ventrally projecting process termed the accessory ventral flange by Xu et al. (2002a). These processes on the right and left
pterygoids contact each other medially just anterior to the point of contact with the parabasisphenoid (Fig. 2.4B). The pterygoid forms a cup-like structure on its medial surface to accept the basipterygoid process of the basisphenoid. In many theropod dinosaurs this is an area where the pterygoid kinks, changes in elevation (i.e., becomes elevated anteriorly), thins, and diverges strongly laterally. The condition in *Incisivosaurus gauthieri*, in which the pterygoid is nearly equal in mediolateral dimension posteriorly and laterally, has anterior and posterior processes that lie on the same plane, and has no strong kinking or dramatic divergence is consistent with what is seen in a more extreme state within derived oviraptorosaurs like *Citipati osmolskae* (Clark et al., 2002). The pterygoid contacts an anterior process of the quadrate posteriorly, although this region is indistinct. Nevertheless it is apparent that the pterygoid, quadrate, and possibly the epipterygoid form the aforementioned extensive lateral flange that is preserved on the right side of the skull (Fig. 2.3A). This flange exhibits a deep pocket lateral to the braincase and, similar to the condition of more derived oviraptorosaurs, completely covers the lateral wall of the braincase.

**Ectopterygoid**

As in other theropods, the ectopterygoid is c-shaped and extends between the pterygoid and the jugal defining the posterior boundary of the palatine fenestra (Figs. 2.4B and 2.8). The jugal ramus of the ectopterygoid forms a concave surface, and has extensive contact with the jugal just posterior to the preorbital bar. The corresponding inflated surface on the opposite side of the ectopterygoid contacts the pterygoid and
palatine and lies within a small depression that is primarily contained on the dorsal surface of the pterygoid.

**Nasal**

The nasal is a complex element in *Incisivosaurus gauthieri* (Figs. 2.3–2.5) as in all oviraptorosaurs (Ji et al., 1998; Clark et al., 2002; Zhou et al., 2000), but not to the extent seen in derived oviraptorids (Osmólska et al., 2004). The nasals of *Incisivosaurus gauthieri* are paired and not fused, unlike oviraptorids but similar to the other basal oviraptorosaur *Caudipteryx zoui* (see Ji et al., 1998; Zhou et al., 2000). Anteriorly, the nasal process of the premaxilla overlies the paired nasal elements and extends midway through the naris, although the exact architecture of this region is obscured due to poor preservation (Figs. 2.4 and 2.5). Just posterior to the dorsal apex of the antorbital fenestra, the nasal contacts the lacrimal along a suture that continues onto the dorsal surface of the skull. The contact of the nasals with the frontals is short, transversely oriented, and blunt resulting in a fairly short overall appearance of the nasals (Fig. 2.4A). The blunt frontal-nasal contact differs from all other oviraptorosaurs and most maniraptorans, being more typical of more basally diverging theropods.

The concave anterior margin of the nasal (Fig. 2.3) forms the posterior margin of the narial opening. As in oviraptorids the subnarial process of the nasal is a large flat flange of bone that overlies the premaxilla as it descends, paralleling the anterodorsal border of the antorbital fossa. A slight ridge on the ventrolateral surface of the subnarial process is continuous with the premaxillary nasal ridge and with a corresponding ridge on
the maxilla, defining the anterodorsal margin of the antorbital fenestra. Just posterior to
the naris is a deep elongate opening, which is enclosed entirely by the nasal. CT data
show that this opening communicates with the sinus cavity that extends from the frontals
into the anterolateral portion of the frontal. A corresponding feature also is found in
Khaan mckennai, Citipati osmolskae, and possibly Oviraptor philoceratops.

Lacrimal

The lacrimal is large and well exposed on the lateral surface of the skull
(especially on the right side; Fig. 2.3); however, it is not broadly exposed on the dorsal
surface of the skull (Fig. 2.4A). In lateral view the lacrimal is “T” shaped (see Xu et al.,
2002a) as in other maniraptorans with a large ventral process forming the anterior wall of
the orbit (Gauthier, 1986). The anterior process, however, is not nearly as extensive as
that seen in paravians (see Norell et al., 2006:fig. 3C for comparison with the
dromaeosaurid condition). The ventrally projecting maxillary process of the lacrimal is
posteriorly concave, augmenting the circular shape of the orbit. This condition is similar
to that seen in Caudipteryx zoui and oviraptorids but differs from the relatively straight
preorbital bar apparent in other maniraptorans (see Currie, 1985; Norell et al., 2004;
Norell et al., 2006).

Anterodorsally, the lacrimal forms the dorsal-most corner and a portion of the
posterior margin of the antorbital fenestra (Fig. 2.3). Just anterior to this corner the
lacrimal contacts the ventral surface of the preorbital process of the maxilla and the
posteroventral surface of the nasal where it extends onto the skull roof. Although sutures
are indistinct on the skull roof, the lacrimal is somewhat exposed between the nasal and the frontal. The medial surface of the lacrimal contacts the frontal on the inside of the orbit along a posteriorly projecting diagonal suture. The posterior wall of the lacrimal is expanded to form a large anterior wall to the orbit. This surface is continuous with the frontal and is slightly concave giving the orbital margin a flared appearance.

The anterior surface of the lacrimal possesses a large lacrimal recess, lying posterodorsal to the antorbital fenestra (Fig. 2.2). This recess is found in most tetanurans (Witmer, 1990, 1997). In *Incisivosaurus gauthieri* the lacrimal recess opens into the lacrimal to pneumatize it and the anterolateral portion of the frontal. This opening also is present in the oviraptorids *Rinchenia mongoliensis* and *Citipati osmolskae*. Unlike *Citipati osmolskae* (Clark et al., 2002), however, the lacrimal recess appears to be undivided. A large lacrimal foramen perforates the posterior surface of the lacrimal. CT scans show that the corresponding canal is completely enclosed in bone and continues anterodorsally to open into the nasal passage (Fig. 2.9). The triangular lateral surface of the preorbital bar, which tapers ventrally may have housed an additional small pneumatic opening, similar to that seen in *Citipati osmolskae* (Clark et al., 2002), as is suggested by a small longitudinal depression on the right side (Fig. 2.3). The preorbital bar expands at its ventral-most extent especially anteriorly where it contacts the jugal and the jugal ramus of the maxilla. Anteroventrally it forms a large, recessed buttress in the antorbital fossa.
Frontal

The shape of the frontals is slightly distorted on the skull roof; however, the skull roof has a distinctly rounded shape (Fig. 2.3). The frontals are long relative to those of other oviraptorosaurs including *Caudipteryx zoui*, making up approximately 20% of the total skull length (Fig. 2.4A; Xu et al., 2002a). The left frontal is displaced slightly anteriorly in relation to the left element. The paired frontals contact each other by way of a simple straight suture that is not elevated. The anterior contact with the nasal is fairly blunt, differing from the long tapering nasal process present in other maniraptorans (e.g., Norell et al., 2000, 2006). Laterally, the anterior arm of the postorbital overlies the supraorbital surface of the frontal (Fig. 3). The frontal contacts the parietal posteriorly along a straight transverse suture; however, this contact is difficult to distinguish due to the distortion and high degree of fusion. CT slices show a slightly overlapping suture.

The dorsal surface of the frontal is elevated slightly above the orbit to form a pronounced supraorbital rim (Fig. 2.3). Posterolaterally, the frontal contacts the postorbital and has a descending process that buttresses the dorsal part of the postorbital bar. The posterior part of this bar forms the anterior corner of the supratemporal fossa. In comparison with other putatively more derived oviraptorosaurs such as *Citipati osmolskae, Oviraptor philoceratops*, and *Rinchenia mongoliensis*, the frontal lacks fenestrae or obvious pneumatic features (although CT imagery shows that the anterolateral portion of the frontal is pneumatized by the lacrimal recess [Figs. 2.9 and 2.10]).
**Parietal**

The parietals are poorly preserved and few features can be accurately determined (Figs. 2.4A and 2.5B). Nevertheless, it is apparent that the parietals were fused and contacted the frontal in a transverse suture near, or just posterior to the postorbital bar. CT imagery reveals that this contact is overlapping, with the frontal lying on the dorsal surface of the parietal. Further posteriorly a small sagittal crest develops and is confluent with a nuchal crest that defines the posterior boundaries of the supratemporal fossa (Fig. 2.4A), also present in *Ornitholestes hermanii* (Osborn, 1903) and other coelurosaurs (Turner et al., 2007).

**Jugal**

The jugal forms the ventral and posteroventral margin of the orbit and is only preserved on the right side of the skull (Fig. 2.3). The jugal is dorsoventrally broad and strap-like along its entire length, in contrast to the rod-like condition of the suborbital jugal seen in all more derived oviraptorosaurs for which material is available, with the exception of *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000).

The lateral surface of the jugal exhibits a longitudinal ridge that emanates from a point at the ventral margin just below the contact with the preorbital bar and terminates posteriorly at the level of the postorbital process in the middle of the element. Anteriorly the jugal receives the maxilla in a cup like contact where the maxilla inserts into a concave depression on the anterior surface. Just posterior to this contact a small ascending process extends along the posterior margin of the preorbital bar of the lacrimal.
The dorsal and ventral edges of the jugal are subparallel, and there is a dorsal expansion midway through the element to form the postorbital process. The postorbital process of the jugal is triangular and reaches only half the height of the orbit; the remainder of the postorbital process is made up of the postorbital, so that each element contributes equally to the structure (Norell et al., 2006). The posterior surface of the jugal forms the anteroventral border of the infratemporal fenestra. The jugal extends posteriorly from the postorbital bar toward the quadratojugal forming the entire ventral border of the infratemporal fenestra; however, the posterior process and other features of this region have been extensively restored disallowing any accurate description of morphological detail.

**Postorbital**

The postorbital is a “T-shaped” bone with posterior and anterior processes of subequal length. This element is preserved best on the right side of the skull (Fig. 2.3). The postorbital comprises most of the posterior margin of the orbit (approximately 2/3 of the entire length). Anteriorly, the postorbital overrides the dorsal surface of the frontal at the posterodorsal corner of the orbit to form an overlapping suture. The posterior process of the postorbital abuts the dorsal surface of the squamosal along an extensive longitudinal suture (Fig. 2.4A).

The anterior process extends anteriorly about 1/3 the length of the orbit to form a small posterior portion of the supraorbital rim. The anterior process is dorsally convex as it is in other maniraptorans (e.g., Currie, 1985; 1995; Norell et al., 2006) and
alvarezsaurids (Chiappe et al., 1998). The vertical jugal process tapers to meet the jugal, which it contacts along its posterior surface in an extensive diagonal suture. The postorbital does not extend as far ventrally as in *Citipati osmolskae*, in which it nearly reaches the suborbital bar (Clark et al., 2002:Fig. 2). Instead, it is similar to the condition in *Caudipteryx zoui* (Ji et al., 1998) or *Khaan mckennai* (Clark et al., 2001) and with the jugal makes up an equal portion of the postorbital process (Fig. 2.3). The posterior surface of the postorbital bar is straight, causing the anterior margin of the infratemporal fenestra to be rectangular in shape. The long posterior process of the postorbital forms the anterodorsal corner of the triangular infratemporal space. The lateral surface of the postorbital is excavated to form a shallow trough.

**Squamosal**

The squamosal is a tetraradiate bone that is exposed on the lateral surface of the skull posterodorsal to the infratemporal fenestra (Fig. 2.3A). The squamosal is preserved only on the right side of the skull, where it lies in articulation. Anteriorly, the thick postorbital process tapers to meet the postorbital to form a complete division between the supratemporal and infratemporal space. Posteriorly there is an extensive contact with the exoccipital, and a small ventrally directed paroccipital process extends posteriorly (Fig. 2.4A and 1.5B). This process has some lateral excursion forming a slight roof over the dorsal head of the quadrate. This condition however is not as extensive as the large squamosal hood that covers the quadrate head in dromaeosaurs like *Tsaagan maangas* (see Norell et al., 2006) and *Velociraptor mongoliensis* (Norell et al., 2004). A larger
posterior process also is present in other oviraptorosaurs such as *Citipati osmolskae* (see Clark et al., 2002:fig. 2). The ventral or quadratojugal process of the squamosal parallels the quadrate shaft, overlying the lateral surface of the quadrate. The quadratojugal process of the squamosal tapers to meet and underlie the ascending process of the quadratojugal at about the midpoint of the quadrate shaft. Thus, the ventral extent of the quadratojugal ramus of the squamosal cannot be determined (Fig. 2.3A).

**Quadratojugal**

The quadratojugal is preserved only on the right side (Fig. 2.3A). Unlike most other oviraptorosaurs, the quadratojugal of *Incisivosaurus gauthieri* has three distinct processes. The anterior jugal process is extensively reconstructed, and therefore its anterior extent cannot be determined. The squamosal and quadrate processes are vertical and situated at approximately a 90-degree angle to the jugal ramus. The squamosal process, described above, underlies the ventral process of the squamosal. The quadrate ramus is large and is fused to the lateral surface of the quadrate so that these two elements together form the articulation with the mandible. The jaw articulation lies well ventral to the level of the lower fenestral bar of the infratemporal fenestra. Although a ventrally placed mandibular articulation is common in oviraptorids, it is never expressed to the extreme degree that is seen in *Incisivosaurus gauthieri*. 
**Quadrate**

Only the right quadrate is present, and many features are not well preserved (Fig. 2.3A). Nevertheless, the quadrate is elongate and nearly vertical so that it is visible primarily in lateral view, posterior to the dorsal shaft of the quadratojugal ramus of the squamosal between the posterior process of the squamosal and the paroccipital. This configuration adjacent to the braincase makes it likely that the quadrate articulated both with the braincase and the squamosal as has been reported in other oviraptorosaurs (Maryańska and Osmólska, 1997; Maryańska et al., 2002; Kundrát and Janáček, 2007), alvarezsaurids (Chiappe et al., 1998), troodontids, and derived avialans (Baumel and Witmer, 1993). The posterior surface of the quadrate does not expand significantly ventrally at the mandibular articulation as in *Citipati osmolskae* or *Khaan mckennai*.

The posterior surface is unremarkable except for a small pneumatic foramen present about midway down the shaft. The quadrate contacts the quadratojugal via a dorsoventrally elongate straight suture, observable only in posterior view (Fig. 2.5B). There is no evidence of a quadrate foramen, although there is some breakage in this area. CT imagery, however, reveals that the quadrate is hollow and presumably pneumatic as is the condition in most other maniraptorans (Fig. 2.11; Witmer, 1990, 1995, 1997).

Anteriorly the quadrate with the pterygoid and possibly the epipterygoid forms a large flange, which hides the braincase from lateral view inside the infratemporal fenestra (Fig. 2.3). This feature is present in some other oviraptorosaurs, including oviraptorids but excluding *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000; Osmólska et al., 2004).
Figure 2.11. Sagittal CT slices through the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in Appendix 1.
Although the flange is well preserved on the right side of the skull, sutural boundaries cannot be determined. The flange as a whole is extensive and fills the ventral 2/3 of the visible area on the braincase wall. It is composed of very thin bone and the dorsal boundary forms a convex border increasing in height anteriorly. As can be determined from the right side, this structure terminates on the braincase just anterior to the trigeminal foramen (Fig. 2.3).

*Lateral surface of the braincase (Figs. 2.3 and 2.12)*

Little can be determined in the way of sutural boundaries on the braincase wall, therefore features of this area will be discussed in relation to the middle ear opening. The lateral wall of the braincase is obscured on the right side by the large wing made up of the pterygoid, quadrate, and epipterygoid, a feature that is shared by other oviraptorosaurs and therizinosaurs. The left braincase wall on IVPP V 13326 is completely exposed because the quadrate and quadratojugal are not preserved. The paroccipital process also is missing on the left side of the braincase. A large fracture runs obliquely through the middle of this portion of the skull further obscuring features of the braincase (Fig. 2.4 and 1.13). The exoccipital, opisthotic, prootic, parabasisphenoid, laterosphenoid, orbitosphenoid, and squamosal are all exposed on the lateral surface (Figs. 2.3 and 2.12). The braincase is divided by a horizontal ridge that extends from the paroccipital process to the inside of the supratemporal fossa just dorsal to the trigeminal foramen (CN V).

This ridge divides the braincase into laterally (ventral) and more dorsolaterally (dorsal)
Figure 2.12. Ventrolateral view of the left side of the braincase of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326). Abbreviations in Appendix 1.
directed surfaces. The crista continues ventrally onto the left basal tuber of the basioccipital.

The anterior-most extent of the braincase is formed by the ossified orbitosphenoids and laterosphenoids. The orbitosphenoids are poorly ossified and only visible in CT imagery (Fig. 2.10). These elements contact the frontals dorsally and the laterosphenoids posteriorly. The orbitosphenoids extend anteriorly as thin splints of bone that together form a ‘v’ (most easily seen in coronal cross section) and floor the space for the olfactory tracts (Fig. 2.10). The laterosphenoid, in contrast, is well ossified and best preserved on the left side of the specimen (Fig. 2.3). There is no trace of the pneumatization that is present in the laterosphenoid of oviraptorids (Osmólska et al., 2004). The laterosphenoid contacts the frontal dorsally, parietal posterodorsally, parabasisphenoid ventrally, orbitosphenoid anteriorly, and its posterior margin overlays the prootic. The external surface of the laterosphenoid is flat and relatively structureless. The entire extent of the internal surface is concave for the reception of the optic tectum. The laterosphenoid is notched approximately halfway up its posterior margin to form the anterior portion of the foramen for the trigeminal nerve (CN V); the remainder of the fenestra is formed by contributions of the prootic and parabasisphenoid (Fig. 2.12). A large unossified space is present along the midline between the two laterosphenoids. This single midline space for the exit of the optic nerve (CN II) opens anteroventrally.

Posterior to the laterosphenoid is the prootic, an irregularly shaped bone that contacts the laterosphenoid anteriorly, parietal dorsally, exoccipital posteriorly, and is overlain by the squamosal laterally (Figs. 2.3B and 2.12). The lateral surfaces of the
prootic and opisthotic form the majority of the middle ear, and this surface is marked by a distinct tympanic cavity. The middle ear opening is an elliptical opening at the base of the aforementioned crista that runs the length of the braincase (Fig. 2.12). The posterodorsal margin of the middle ear is formed by the paroccipital process, of which only the base remains on the left side. The middle ear cavity is divided into the anterior fenestra vestibuli and the posterior fenestra pseudorotundum by a crista interfenestralis, which is deeply recessed and oriented diagonally from anteroventral to posterodorsal. The recessed crista interfenestralis is not described in oviraptorosaurs but similar to the condition found in some dromaeosaurs and troodontids (e.g., Currie, 1985; Norell et al., 2004; Makovicky et al, 2003). In CT imagery the medial aperture of the adult remnant of the metotic fissure, the metotic foramen, is visible through the fenestra pseudorotundum (Fig. 2.9C). The metotic foramen is a small slit on the internal surface of the braincase (Fig. 2.13).

Dorsal to the middle ear and separated from it by a diagonal buttress is a shallow depression that forms the dorsal tympanic depression. Two small foramina pierce the dorsal border of this fossa and lead into the dorsal tympanic recess. These foramina are visible only in the CT imagery (Fig. 2.11). Anterior to the tympanic cavity is a wide pila otica that is pierced by the small opening for the facial nerve (CN VII; Fig. 2.12). The canal for the facial nerve can be traced in the CT images traveling a short distance medially and opening into the internal acoustic fossa on the internal surface of the prootic and opisthotic (Fig. 2.13). Anterior to the facial foramen on the external surface is a groove that runs anteroventrally and terminates ventral to the trigeminal fenestra (CN V;
Figure 2.13. Sagittal cutaway of a virtual rendering of the skull of the holotype of *Incisivosaurus gauthieri* (IVPP V 13326) with the matrix rendered transparent. Abbreviation in Appendix 1.
This groove likely transmitted the anterior ramus of the facial nerve. Ventral to this groove, situated between the tympanic cavity and the trigeminal foramen, is the well-developed dorsally convex otosphenoidal crest. The otosphenoidal crest runs from the facial foramen to halfway through the length of the trigeminal fenestra. A well-developed otosphenoidal crest is described in *Chirostenotes pergracilis* and troodontids (Sues, 1997; Osmólska et al., 2004; Norell et al., 2006) and marks the anterior extent of the middle ear cavity. Anterior to the facial foramen is the large, hourglass-shaped trigeminal fenestra. The prootic makes up by far the largest contribution to this partially divided fenestra.

**Occipital surface of the braincase (Figs. 2.5B and 2.12)**

Because the skull is distorted many of the features on the posterior region of the skull are difficult to decipher. The skull is broken at the base of the left paroccipital process, which is missing. In general view, the right paroccipital process drops below the level of the occipital condyle (Fig. 2.5B). This arrangement is a common feature of oviraptorids (Osmólska et al., 2004), yet how much this condition is influenced by crushing of the specimen is difficult to determine. The occiput is large (at least three times the size of the occipital condyle) and oval, with little of the anterodorsal slope that characterizes some oviraptorid braincases (e.g., *Citipati osmolskae*; Clark et al., 2002). Also because the bones are fused together, individual elements are difficult to discern. The parietals, supraoccipital, exoccipitals, and basioccipital are exposed on the external surface of the posterior braincase (Fig. 2.5B). The nuchal crest is present but only weakly
developed. The cerebellar prominence extends dorsoventrally from the nuchal crest ventrally to the foramen magnum. A large oval depression lies on either side of the cerebellar prominence. As in all oviraptorosaurs, the paroccipital processes are oriented ventrally and have a characteristic pendant shape (Turner et al., 2007). The foramen magnum is dorsoventrally elongate with a secondary circular depression at the base within the basioccipital, resulting in an opening that has a longer height than width. This shape of the foramen magnum is somewhat novel and differs from most coelurosaur except some troodontids and dromaeosaurs (Norell et al., 2006). The unusual shape may be due to a minor amount of mediolateral deformation.

The supraoccipital is roughly triangular in shape and forms the majority of the posterior braincase. The contacts of the supraoccipital are difficult to delineate because of the high degree of fusion. Lateral to the central keel are crescentic depressions that may correspond to the epiotic sutures. The element contributes a portion to the dorsal border of the foramen magnum. The entire cerebellar prominence lies within the supraoccipital. The internal surface of the supraoccipital is relatively featureless except for a groove traveling dorsoventrally along its lateral margin that housed the posterior-most extent of the anterior semicircular canal (Fig. 2.11B). The external occipital vein, which served to drain the lateral regions of the cerebellum, exits via a small fenestra between the supraoccipital and parietal at the level of the dorsal margin of the foramen magnum (Fig. 2.5B).

Lateral to the occiput (as preserved on the right side of the skull) is the exoccipital. The exoccipital contacts the supraoccipital dorsomedially, the basioccipital
ventrally, the opisthotic anteriorly, and the squamosal laterally (Figs. 2.5B and 2.12). The exoccipital comprises the majority of the paroccipital processes of *Incisivosaurus gauthieri* with contributions from the opisthotic and squamosal. These processes are highly pneumatic and a foramen can be seen penetrating the distal end through the boundary between the exoccipital and the opisthotic (Fig. 2.9). The paroccipital process extends laterally and ventrally tapering to a ventrally directed tip. The ventral border of the process is convexly rounded as is seen also in *Avimimus portentosus* (Kurzanov, 1987; Hwang et al., 2004; Norell et al., 2006). This condition differs from *Chirostenotes perigracilis* and *Citipati osmolskae* who possess slender, elongate dorsal and ventral edges (Sues, 1997; Hwang et al., 2004; Norell et al., 2006). A small ridge runs from the occiput onto the surface of the paroccipital process and continues onto the basioccipital (Fig. 2.12). The exoccipital forms the lateral borders of the foramen magnum and extends ventrally onto the stalk of the occipital condyle, but the element does not form any part of the articulating surface.

The ventrolateral region of the occipital surface between the basioccipital and exoccipital is deeply furrowed and a large fenestra is present in the dorsal region of this fossa (between the exoccipital and basioccipital; Fig. 2.5B) through which the jugular vein, glossopharyngeal (CN IX), vagus (CN X), and accessory (CN XI) cranial nerves likely exited, following the basal reptilian pattern (Goodrich, 1930; Romer, 1956). This condition differs from other oviraptorosaurs in which these foramina lie in the same plane as the surface of the exoccipital rather than in a depression (Hwang et al., 2004; Norell et
al., 2006). The corresponding canal leads into the adult remnant of the metotic fissure that comprises the space between the occipital bones and the otic capsule (adult otic bones).

The basioccipital is well preserved and forms the floor of the braincase, the ventral border of the occiput and the occipital condyle (Figs. 2.5B and 2.12). The basioccipital is bordered by the exoccipitals dorsolaterally, the parabasisphenoid anteriorly, and the prootic and optisthotic dorsolaterally. The basioccipital forms the majority of the occipital condyle (with a small contribution from the exoccipitals), which is mediolaterally elongate and has a kidney shape. The neck of the occipital condyle is short but not constricted, similar to the shape that is present in other coelurosaurs (Norell et al., 2006). Medial to the opening within the fossa at the base of the neck of the occipital condyle are two small foramina for the hypoglossal nerves (CN XII). These canals lie completely within the basioccipital and can be traced in the CT imagery traversing the short distance from the posterior surface to the floor of the braincase (Figs. 2.9D and 2.13). The ventral region of the aforementioned occipital furrow is penetrated by numerous foramina that lead into a pneumatic space within the basioccipital (Fig. 2.9E). The weakly developed basal tubera are located ventral to the occipital furrow and extend ventrolaterally. A shallow saddle separates the basal tubera (Figs. 2.4B, 2.5B, 2.12).

_Ventral surface of the braincase (Figs. 2.4B, 2.8, 2.12)_

The ventral surface of the braincase is obscured by the pterygoids, which extend posteriorly to the anterior border of the basioccipital; however, CT imagery aids in the
description of this region of the skull. The ventral surface is well preserved except for some slight deformation on the posterior left side. It is composed of the basioccipital, basisphenoid, and parasphenoid. Unlike other oviraptorosaurs, the basisphenoid and basioccipital are elongate making up approximately 20% of the entire skull length.

A shallow longitudinally oriented basisphenoid depression is the most prominent feature of the ventral braincase (Fig. 2.4B). It is bounded posteriorly by the basal tubera that are hollowed out into two “c-shaped” structures. A short septum runs along the midline and divides the posterior part of the depression into right and left chambers. Anteriorly, the septum disappears and the depression shallows. It is bounded laterally by low ridges, which also flatten anteriorly grading into the basipterygoid processes. The basipterygoid processes are short, but unlike other oviraptorosaurs they are displaced from the midline and oriented anterolaterally rather than strictly laterally.

Anterior to the basioccipital is the poorly ossified parabasisphenoid. The boundary between these two elements is not well defined due to the high degree of fusion of the braincase as well as a fracture that runs transversely through this region. The parabasisphenoid also contacts the laterosphenoid dorsolaterally and extends dorsally to form the floor of the braincase that houses the sella turcica (Fig. 2.9). The element slopes ventrally anterior to its contact with the laterosphenoid, as it does in all other oviraptorids (Norell et al., 2006). At the anterior-most extent of the element, the pneumatic, plate-like parasphenoid rostrum extends anterodorsally roughly two-thirds through the length of the orbit. Although pneumatic, the base of the parasphenoid rostrum is not expanded (as it is in ornithomimosaurus and some troodontids; Turner et al., 2007). At the contact with the
laterosphenoid, the parabasisphenoid forms a small portion of the ventral border of the trigeminal fenestra. The entrance of the carotid arteries cannot be determined on the ventral surface of the braincase; however, the canals can be seen in the CT imagery running through the parabasisphenoid and opening at the point of flexure of the parabasisphenoid (Fig. 2.9B). The cranial carotid canals anastomose within the parabasisphenoid and then separate again before exiting into the endocranial cavity. The basipterygoid processes are weakly developed and probably were not fully ossified within *Incisivosaurus gauthieri*, similar to therizinosaurus and other oviraptorosaurs (Norell et al., 2006). Accordingly, the basipterygoid recesses that are present in *Oviraptor philoceratops* and *Rinchenia mongoliensis* are not present in this specimen (IVPP V 13326).

*Endocranial Cavity, Inner Ear, and Tympanic Recesses (Figs. 2.9, 2.11, 2.13)*

On the internal surface of the braincase, the floccular recess is easily visible in CT imagery and three-dimensional reconstructions (Fig. 2.13). The large rectangular recess lies posterior to the opening for the trigeminal nerve at approximately the same horizontal level. The floccular recess is located wholly within the prootic/opisthotic (although sutures are not visible on the internal surface of the braincase), oriented posteroventrally, and bounded posteriorly by the horizontal semicircular canal. The entire fossa is outlined in the vertical plane by the inflated anterior semicircular canal (Fig. 2.11B). Inflation of the anterior semicircular canal is found in many paravians (Norell et al., 2004) but is not present in derived oviraptorosaurs like *Citipati osmolskae* (Clark et al., 2002).
The triangular internal acoustic fossa is located just ventral to the floccular recess and in life houses the geniculate ganglion. The anteroposteriorly wide fossa contains three foramina (Fig. 2.13). The dorsal-most foramen transmitted the facial nerve (CN VII). The corresponding canal exits directly laterally onto the lateral surface of the braincase (Fig. 2.9B; described above). The anteroventral foramen is only visible with CT imagery (Fig. 2.13), opens into the inner ear (vestibular space), and transmitted the anterior ramus of the vestibulocochlear nerve (CN VIII). The posterior-most foramen within this fossa pierces the internal wall of the braincase. This foramen leads into the inner ear (cochlear canal) and transmitted the posterior ramus of the vestibulocochlear nerve (CN VIII). Posterior to the floccular recess is the metotic foramen, a small slit-like opening that leads into the adult remnant of the metotic fissure. The opening is oriented posterodorsally and transmitted the glossopharyngeal (CN IX), vagus (CN X), and accessory nerves (CN XI). On the floor of the braincase, anterior and lateral to the foramen magnum are two small foramina for the hypoglossal nerves (CN XII).

*Mandible (Figs. 2.6 and 2.7)*

Although only the anterior parts are well preserved, the dentary rami are closer to being parallel than they are in other oviraptorosaurs including *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000). It lacks the high coronoid eminence of Oviraptoridae, the concave margin along the dorsal dentary border in *Chirostenotes pergracilis* (Sues, 1997), and the ventrally concave margin and depressed anterior end of Caudipterygidae (Ji et al., 1998; Zhou et al., 2000). The mandibular fenestra is large and anteroposteriorly
elongate (see Barsbold, 1981:Fig. 21; Sues, 1997) with no surangular spine entering the fenestra as in caenagnathids (Fig. 2.6).

*Dentary:* The dentary has an unusual morphology and is best preserved on the right (Fig. 6). This element is deep and, although distorted anteriorly, the borders converge at the symphysis giving it an anteriorly pointed appearance in lateral view. A row of small foramina on the lateral surface parallels the dorsal margin of the dentary for approximately 1/3 the length of the mandible. The anterior-most foramen is the largest, being about twice the diameter of the subsequent foramina. This area likely was covered with a keratinous beak during life.

Anteriorly the dentaries curve toward the midline to form the u-shaped symphysis as in other oviraptorosaurs, some troodontids, and some ornithomimosaurs. The symphysis is complex and somewhat distorted (Fig. 2.6A). In ventral view there is a large trough-like symphyseal shelf where the upper “rodentiform” teeth occluded (Fig. 2.7C). Posterior and ventral to this is a secondary symphyseal shelf that may have served to strengthen the symphysis.

*Splenial:* The right splenial, a large flat plate on the medial surface of the dentary, is well preserved (Fig. 2.7). It extends anteriorly to the level of the fourth tooth where it forms the dorsal, ventral, and posterior margins of the mandibular fenestra. It does not approach the symphysis as in oviraptorosaurs such as *Khaan mckennai* (Clark et al., 2001) and the unnamed Zamyn Khondt form (Barsbold, 1997). Posteriorly the splenial is
strap-like and overlies the dentary and the angular nearly to the level of the posterior terminus of the mandibular fenestra.

**Angular and Prearticular:** The angular cannot be distinctly differentiated from the dentary on the lateral surface of the mandible (Fig. 2.6). Presumably it articulates with the prearticular to form the bar that forms the ventral border of the mandibular fenestra and the ventral surface of the mandible.

**Surangular:** The surangular is much thicker than the angular and contacts the dentary at the anterior margin of the mandibular fenestra (Fig. 2.6). Just posterior to this contact is a small but distinct coronoid eminence. The surangular broadens transversely posterior to the coronoid eminence and dorsal to the mandibular fenestra.

**Dentition (Figs. 2.2–2.7)**

**Premaxillary teeth:** Four teeth are present in each premaxilla (Figs. 2.3–2.5). Undoubtedly the strangest thing about *Incisivosaurus gauthieri* is the anterior-most pair of large incisor-like premaxillary teeth. Teeth with this morphology are unknown in any other theropod dinosaur. In cross section they are subcircular at their bases. The posterior surface becomes flatter distally, and the anterior and posterior surfaces are delimited by carinae. More distally the posterior or interior surface of the tooth is modified by extensive flat wear surfaces that extend nearly half the length of the tooth. These wear facets expose the dentine on the interior of the tooth (Fig. 2.4B). Although the tips of the
teeth are broken, they apparently were convex and crescent shaped in anterior view, a
morphology that corresponds with the edentulous mandibular symphyseal shelf to which
they occluded.

One of the more vexing questions concerning *Incisivosaurus gauthieri* is the
nature of the large incisor-like premaxillary teeth. Xu et al. (2002a) compared these teeth
to the incisors found in rodent mammals, which display a similar morphology. Unlike
mammals, however, these teeth in *Incisivosaurus gauthieri* are not ever growing. Our CT
analysis offers definitive evidence showing the presence of a large replacement tooth just
behind the exposed tooth (Fig. 2.11C). Interestingly, this tooth is chisel shaped into the
same occlusal angle as the erupted tooth.

Posterior to the ‘incisor-like’ tooth in the premaxilla is a thin tooth with a very tall
(7 mm) crown. In cross section these teeth are oval and have labio-lingual surfaces
defined by very small carinae (Fig. 2.4B). These teeth end in a blunt chisel point formed
by the convergence of the labial and lingual surfaces. Posteriorly there appear to have
been another pair of similarly shaped teeth, which are represented only by their roots.

*Maxillary teeth:* There are nine maxillary teeth in each maxilla (Figs. 2.3 and
2.4B). The maxillary teeth are separated from the premaxillary teeth by a short symphysis
and lack serrations or denticles (Xu et al., 2002a). The teeth are smaller than the posterior
premaxillary teeth. The tooth crowns are slightly expanded above the bases and display
extensive wear facets on their lingual surfaces.
**Dentary teeth**: The dentary has positions for approximately nine small teeth (Figs. 2.6 and 2.7). Anteriorly, the teeth lie in distinct alveoli, while posteriorly they appear to lie in a common groove. The anterior-most right dentary tooth is just erupting and is labio-lingually compressed. The lingual surface is slightly concave, and strong carinae separate the labial from lingual tooth surfaces. It is slightly procumbent. There is no indication of serrations along the carinae at the base of the tooth. The next preserved tooth is in position 3. It is the best-preserved tooth on either dentary. It is much more bulbous than the first tooth and, although it is not well preserved, the labial and lingual surfaces are roughly symmetric and are separated by a faint carina. The more posterior teeth are visible only in cross-section at their bases because of breakage during preparation. These teeth resemble the third tooth, perhaps being slightly more labio-lingually compressed.

**DISCUSSION**

This study detailed description of the only known specimen of an extremely unusual and important specimen (IVPP V 13326), *Incisivosaurus gauthieri*, from the Early Cretaceous Jehol beds of northeastern China. This study expands on previous descriptions (i.e., Xu et al., 2002a; Osmólska et al., 2004) by providing further details and reinterpretations of previously described cranial material as well as describing previously unknown regions of the skull such as the internal morphology attained through the use of computed tomography.
Although the phylogenetic position of oviraptorosaurs at the base of the maniraptoran family tree has remained fairly stable (e.g., Gauthier, 1986; Holtz, 1998; Lü, 2005; Turner et al., 2007; Senter, 2007), the interrelationships within the clade have received only cursory attention (e.g., Maryańska et al., 2002; Lü et al., 2004; Lü, 2005). Not surprisingly, these interrelationships appear to have a large effect on the overall position of Oviraptorosauria within Maniraptora, including topologies in which it falls within Avialae based on a series of derived characters (Maryańska et al., 2002; Osmólska et al., 2004; Lü et al., 2004). Studies that include Oviraptorosauria within Avialae, however, suffer from taxon sampling issues (e.g., excluding the primitive oviraptorosaur Incisivosaurus gauthieri as well as the paravian group Troodontidae; Maryańska et al., 2002; Osmólska et al., 2004). Based on previous studies, the inclusion of Incisivosaurus gauthieri is able to break up the long branch leading to caenagnathids and oviraptorids and consequently to stabilize the overall position of this group within Maniraptora.

Not surprisingly considering its phylogenetic position, Incisivosaurus gauthieri presents a mosaic of derived oviraptorosaurian characters and morphologies typical of non-avian theropods that fall outside of Oviraptorosauria. Characters such as the ventrally displaced mandibular articulation and pendant-shaped ventrally curving paroccipital processes unambiguously support the placement of this specimen within Oviraptorosauria. IVPP V 13326 also shares derived features of the mandible with other oviraptorosaurs. For instance, an elongate retroarticular process and reduced splint-like coronoid help diagnose this specimen to Oviraptorosauria (Turner et al., 2007).
*Incisivosaurus gauthieri*, however, consistently falls at the base of this clade in phylogenetic analyses, lacking many of the more derived characteristics that diagnose oviraptorids and caenagnathids (Xu et al., 2002a; Lü, 2005; Norell et al., 2006; Turner et al., 2007). A rod-like jugal, crenulated palatal surface, tooth-like projections on the palatal surface of the maxilla, straight lateral border of the quadrate shaft, constricted ventral fossa on the ectopterygoid, and a large coronoid eminence on the mandible are present in caenagnathids and oviraptorids but missing in *Incisivosaurus gauthieri* (Figs. 2.3–2.6).

*Incisivosaurus gauthieri* also preserves many plesiomorphic characters that are not present in other oviraptorosaurs, most noticeable of which is the retention of teeth in the premaxilla, maxilla and dentary (see Xu et al., 2002a), although premaxillary teeth are found also in *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000). This study also offer an alternative interpretation to the original description of the palate (Fig. 2.4B) that is consistent with the condition found in non-avian theropods outside of Oviraptorosauria. The confluent choana and subsidiary palatine fenestra of Xu et al. (2002a) is alternatively identified as solely the choana. Although the choana differs from the rounded shape present in other oviraptorosaurs (Osmólska et al., 2004), its elongate morphology closely resembles that of most theropods outside of this clade (see Clark et al., 1994:fig. 4 for comparison with Fig. 2.4B). A subsidiary palatine fenestra is not present in other oviraptorosaurs; however, a fully isolated fenestra is present in closely related theropods (Clark et al., 1994). The morphology of the cranial pneumatic spaces as well as that of the endocranium is discussed in further detail below.
Cranial pneumaticity

There is little comparative material available to examine for cranial pneumaticity within oviraptorosaurs. No study has looked in depth at the pneumatic spaces within caenagnathids; however, several descriptions are available for comparison within Oviraptoridae (e.g., *Conchoraptor gracilis*, Kundrát & Janáček [2007]; *Citipati osmolskae* [Clark et al., 2002]) and theropods outside of Oviraptorosauria (e.g., Currie, 1985; Currie and Zhao, 1993; Witmer, 1997; Norell et al., 2004). The skulls of these derived oviraptorosaurs possess extremely complex pneumatic spaces. The pneumatic system in *Incisivosaurus gauthieri* corresponds more closely in complexity with that of theropods outside of Oviraptorosauria. The paranasal sinuses of *Incisivosaurus gauthieri* (Fig. 2.10) are more typical of non-avian theropods, and are associated with the promaxillary recess penetrating the maxilla, the nasal recess, and the lacrimal recess (Figs. 2.3 and 2.10) (Witmer, 1990, 1997). The only specimen of *Conchoraptor gracilis* examined by Kundrát and Janáček (2007) does not preserve the facial region of the skull; therefore, comparisons are based on unpublished data. *Citipati osmolskae* possesses the same sinuses described for *Incisivosaurus gauthieri*, but they are inflated to a more extreme degree (Clark et al., 2002). All oviraptorosaurs including *Incisivosaurus gauthieri* apparently lack a jugal recess (Witmer, 1997).

The anterior extension of the pneumatic cavity within the nasal appears to be present only in oviraptorosaurs, occurring in *Incisivosaurus gauthieri* (Fig. 2.10), *Citipati osmolskae* and *Conchoraptor gracilis* (Clark et al., 2002). The lacrimal recess of
Incisivosaurus gauthieri extends into the lacrimal and frontal but lacks the division found in Citipati osmolskae, which sends off various diverticulae (Figs. 2.2 and 2.3). Likewise, Incisivosaurus gauthieri lacks the enlarged sinus overlying the endocranial space that extends posteriorly from the circumnarial cavities to connect with the dorsal tympanic recess (Clark et al., 2002). This feature is present in Conchoraptor gracilis but is considerably less extensive.

The paratympanic recesses of Incisivosaurus gauthieri also most closely resemble those of other non-avian theropods rather than derived oviraptorosaurs. All three paratympanic recesses are present in Incisivosaurus gauthieri (three recesses occurring in almost all maniraptorans except some troodontids, which lack the posterior tympanic recess [see Xu and Norell, 2004]); however, the diverticulae that extend distally from the external openings lack the complexity observed in Conchoraptor gracilis and Citipati osmolskae (Kundrát and Janáček, 2007; Clark et al., 2002). The dorsal tympanic recess of Incisivosaurus gauthieri extends into the parietal (the condition found in most coelurosaurs [e.g., Witmer, 1990, 1997; Norell et al., 2006]), but lacks the extensive diverticulae present in Conchoraptor gracilis (Kundrát and Janáček, 2007). The posterior tympanic recess of Incisivosaurus gauthieri pneumatizes the entire paroccipital process and sends off small diverticulae along its posterior margin (Fig. 2.9C, D), a condition not observed in Conchoraptor gracilis and not widely assessed in other theropods. The pneumatization of the paroccipital process, however, is a common theropod feature. The anterior tympanic recess of Incisivosaurus gauthieri is more difficult to study (possibly
Owing to the only moderate amount of ossification in the parabasisphenoid, but appears to be simple and not diverging.

**Conclusions**

*Incisivosaurus gauthieri* represents a significant discovery from a locality that has produced some of the most unique fossils in recent years. Similar to many of the other fossils from the Jehol beds, *Incisivosaurus gauthieri* occupies a basal and thus phylogenetically important position. Within the oviraptorosaur lineage it is the basal-most member (see Norell et al., 2006; Turner et al., 2007); and therefore is able to break up the long branch leading to the extremely derived oviraptorids and caenagnathids. Although there are striking resemblances, primarily within the skull, between oviraptorosaurs and avialans (see Xu et al., 2002a; Osmólska et al., 2004), most phylogenetic analyses of maniraptoran relationships repeatedly recover a more basal position for this group well outside of Avialae (e.g., Lü, 2005; Norell et al., 2006; Turner et al., 2007; Senter, 2007). This long branch seems to be driving results from those analyses that exclude *Incisivosaurus gauthieri* and posit an avialan affinity for Oviraptorosauria. Therefore, the exclusion of *Incisivosaurus gauthieri* from any study analyzing the interrelationships of Oviraptorosauria or the relationship of this group with respect to other maniraptorans could have significant effects.
**KHAAN MCKENNAI**

*Khaan mckennai* is a crestless oviraptorid from the Late Cretaceous Ukhaa Tolgod locality in the Gobi Desert of Mongolia. In 1993 (the initial year of excavation at Ukhaa Tolgod) a single specimen (IGM 100/973) was collected. Two other specimens of this taxon were found in close proximity to each other in 1995 (IGM 100/1002 and 100/1127), and those represent two of the most completely known taxa of theropod to date. Interestingly, as the Ukhaa Tolgod assemblages have been shown to represent so-called “life assemblages” (where the animals were killed by the agents of their preservation—in this case liquefying sand dunes; Dingus et al., 2008) this pair of animals were undoubtedly behaviorally interacting in life. The primary goal here is to provide a detailed description of the crestless oviraptorid *Khaan mckennai* (Clark et al., 2001) including comprehensive illustrations of this taxon.

*Khaan mckennai* is placed into a phylogenetic framework by making explicit comparisons with the basal oviraptorosaurs *Incisivosaurus gauthieri* (cranial comparisons; Xu et al., 2002; Balanoff et al., 2009) and *Caudipteryx zoui* (postcranial comparisons; Ji et al., 1998) as well as the crested oviraptorids *Oviraptor philoceratops* (Osborn, 1924) and *Citipati osmolskae* (Clark et al., 2002). This framework will allow us to make preliminary inferences about the evolution of morphological features, especially those often allied with the acquisition of flight, along the oviraptorosaur lineage. These hypotheses can be tested further in future analyses that include an expanded taxon sampling.
MATERIALS AND DIAGNOSIS OF _KHAAN MCKENNAI_

Clark et al. (2001) named and provided a brief description of _Khaan mckennai_. The description provided here also is based on the three specimens referred to in that publication (Figs. 2.14-2.16). The holotype of _Khaan mckennai_ (Fig. 2.14; IGM [Geological Institute, Mongolian Academy of Sciences] 100/1127) is a complete, articulated specimen. IGM 100/1002 (Fig. 2.15; referred specimen) also is complete and articulated within a single block. The final specimen (Fig. 2.16; IGM 100/973; referred specimen), however, has been prepared completely out of its containing matrix, and therefore many of the three-dimensional observations of the skeleton are taken from this specimen. Because the skull of IGM 100/973 has been prepared out of the larger block, it was possible to scan it using high-resolution X-ray computed tomography (CT), enabling this study to access additional data on the internal anatomy of the cranium. Comparisons made with _Khaan mckennai_ are taken primarily from _Citipati osmolskae_ (Clark et al., 2002), _Incisivosaurus gauthier_ (Balanoff et al., 2009), _Oviraptor philoceratops_ (AMNH 6517; Osborn, 1924), or _Caudipteryx zoui_ (Ji et al., 1998).

The three specimens of _Khaan mckennai_ described here possess numerous derived features that diagnose them to the successively nested clades Oviraptorosauria, Oviraptoridae+Caenagnathidae, and finally Oviraptoridae (Fig. 2.17) using the most recent iteration of the Theropod Working Group (TWiG) analysis (Turner et al., 2007). These specimens are unambiguously assigned to Oviraptorosauria based on an extensively pneumatized narial region, ventrally curved (pendant-shaped) paroccipital
Figure 2.14. *Khaan mckennai* (IGM 100/1127, holotype).
Figure 2.15. *Khaan mckennai* (IGM 100/1002, referred specimen).
Figure 2.16. Skull of *Khaan mckennai* (IGM 100/973, referred specimen). 
A, dorsal; B, ventral; C, right lateral; D, left lateral; E, anterior; 
F, posterior views.
Figure 2.16 (cont). Skull of *Khaan mckennai* (IGM 100/973, referred specimen). **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, left lateral; **E**, anterior; **F**, posterior views.
Figure 2.16 (cont). Skull of *Khaan mckennai* (IGM 100/973, referred specimen). A, dorsal; B, ventral; C, right lateral; D, left lateral; E, anterior; F, posterior views.
Figure 2.17. Proposed hypothesis for the relationships within Oviraptorosauria based on Norell et al. (2006).
processes, a crenulate margin on the buccal edge of the premaxilla, an elongate dorsal
process of the dentary, an elongate and slender retroarticular process, and no distinct
transition point in the caudal vertebrae. An unambiguous diagnosis can be made to the
clade composed of Oviraptoridae and Caenagnathidae based on the following characters:
a palatal shelf with ventral ‘toothlike’ projections and an anteriorly concave pubic shaft.
Several unambiguous synapomorphies diagnose these specimens to Oviraptoridae. These
characters are an external mandibular fenestra that is subdivided by a spinous rostral
process of the surangular, an ectopterygoid fossa with a constricted opening (visible in
CT slices; using a DELTRAN optimization), and a mandibular articulation surface that is
at least twice as long as the quadrate surface. Rationale as to why these specimens are
referable to *Khaan mckennai* is provided by Clark et al., (2001).

**Geological setting**

The holotype of *Khaan mckennai* (IGM 100/1127) was found at Mark’s Second
Egg locality in Ukhaa Tolgod (Gurvan Tes Somon, Omnogov Aimak, Gobi Desert,
Mongolia; Clark et al., 2001). The specimen IGM 100/1002 was found adjacent (about 20
cm from and on the same bedding plane as) to IGM 100/1127. IGM 100/973 was
discovered about a kilometer away at the Granger’s Hill sublocality of Ukhaa Tolgod.
Further information concerning the geological provenance of these specimens can be
obtained from Dingus et al. (2008).
**CT scanning**

The cranium and attached mandible of IGM 100/973 were scanned at The University of Texas High-Resolution X-ray Computed Tomography Facility using the high-energy scanning source on 3 September 2009. The specimen was scanned along its coronal axis for a total of 913 slices. The specimen was too long to be accommodated by one pass in the high-energy system, which has a limit of 15 cm. It, therefore, was scanned in two passes, and the slices subsequently reassembled. The interslice spacing was equal to 0.1637 mm with a field of reconstruction of 78 mm. The resolution of the resulting images was 1024 x 1024 pixels. All image processing was done with the three-dimensional volumetric rendering program VG StudioMax 2.0.1. Any measurements taken from the CT images (indicated throughout the paper) are taken using this same software.

**Cranial Description**

IGM 100/973 consists of a complete skull, pelvic girdle, and hindlimb. This specimen is the only completely prepared skull of *Khaan mckennai* and allows examination in three dimensions of all surfaces. This specimen was originally designated *Ingenia yanshini* (Dingus et al., 1995) but was subsequently referred to *Khaan mckennai* by Clark et al. (2001). The skull includes the articulated cranium and mandible, which has been displaced posteriorly to give the appearance of a severe overbite (Fig. 2.16A, B). Preserved on the skull are the premaxilla, maxilla, part of the nasal, lacrimal, jugal,
postorbital, frontal, parietal, laterosphenoid, prootic, opisthotic, partial squamosal, supraoccipital, quadratojugal, quadrate, exoccipital, basioccipital, pterygoid, parasphenoid rostrum, and hyoid. The vomer, orbitosphenoid, epipterygoid, ectopterygoid and parabasisphenoid are not visible on the external surface of the skull; however, many of the palatal elements such as the ectopterygoid, vomer, palatine, and part of the parabasisphenoid can be observed by using CT images. The mandible is completely preserved, and CT imagery additionally allows access to the medial surface of this structure that otherwise would be unobservable.

Although preservation of the bone in IGM 100/973 is poor in places, it offers the best example of a fully three-dimensional skull of *Khaan mckennai*, and provides exposure of many otherwise unknown elements (Fig. 2.16). CT scans of the specimen likewise reveal internal structures that could not be observed in the other two specimens. Unlike the rounded cranium of the holotype IGM 100/1127 and 100/1002 (Fig. 2.18), which were preserved on their sides, the skull of IGM 100/973 is dorsoventrally compressed. This compression is most easily seen on the posterior surface of the skull, especially in the mediolaterally elongate foramen magnum (compare Fig. 2.16F with that of IGM 100/1002, Fig. 2.19). The rostrum accounts for approximately 42% of the skull length, which is 118.8 cm in IGM 100/973 (Table 2.1). This measurement is close to values obtained for the two other specimens, in which the preorbital region of the skull accounts for approximately 39% (IGM 100/1127) and 42% (IGM 100/1002) of the total skull length (Table 2.1). At least one poorly preserved cervical vertebra is attached to the skull of IGM 100/973.
Table 2.1. Selected measurements (in mm) from the cranial skeleton of *Khaan mckennai*.

<table>
<thead>
<tr>
<th></th>
<th>IGM 100/973</th>
<th>IGM 100/1127</th>
<th>IGM 100/1002</th>
</tr>
</thead>
<tbody>
<tr>
<td>Skull length*</td>
<td>118.8</td>
<td>~126.6</td>
<td>113.8</td>
</tr>
<tr>
<td>Preorbital skull length</td>
<td>50.1</td>
<td>48.8</td>
<td>47.7</td>
</tr>
<tr>
<td>Orbit length</td>
<td>37.2</td>
<td>35.4</td>
<td>-</td>
</tr>
<tr>
<td>Orbit height</td>
<td>27.0</td>
<td>33.4</td>
<td>-</td>
</tr>
<tr>
<td>Premaxilla length (palate)</td>
<td>14.6</td>
<td>20.4</td>
<td>20.0</td>
</tr>
<tr>
<td>Premaxilla height (below naris)</td>
<td>-</td>
<td>38.8</td>
<td>33.2</td>
</tr>
<tr>
<td>Maxilla length (palate)</td>
<td>31.7</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Frontal length</td>
<td>12.0</td>
<td>8.6</td>
<td>-</td>
</tr>
<tr>
<td>Parietal length</td>
<td>42.6</td>
<td>44.0</td>
<td>-</td>
</tr>
<tr>
<td>Infratemporal width</td>
<td>27.2</td>
<td>26.5</td>
<td>-</td>
</tr>
<tr>
<td>Infratemporal height</td>
<td>25.3</td>
<td>31.0</td>
<td>-</td>
</tr>
<tr>
<td>Supratemporal fenestra width</td>
<td>15.7</td>
<td>11.6</td>
<td>-</td>
</tr>
<tr>
<td>Supratemporal fenestra length</td>
<td>28.7</td>
<td>27.9</td>
<td>-</td>
</tr>
<tr>
<td>Mandible length</td>
<td>104.0</td>
<td>108.4</td>
<td>101.6</td>
</tr>
<tr>
<td>Mandible height</td>
<td>30.8</td>
<td>32.4</td>
<td>30.0</td>
</tr>
<tr>
<td>Mandibular fenestra length</td>
<td>26.7</td>
<td>29.2</td>
<td>26.1</td>
</tr>
<tr>
<td>Mandibular fenestra height</td>
<td>18.8</td>
<td>20.7</td>
<td>20.4</td>
</tr>
<tr>
<td>Foramen magnum width</td>
<td>14.8</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Foramen magnum height</td>
<td>7.5</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

*measured from the occipital condyle*
Figure 2.18. Skull of *Khaan mckennai*. **A**, right lateral view of holotype (IGM 100/1127); **B**, right lateral view of IGM 100/1002; **C**, right lateral view of IGM 100/1127. Abbreviations in Appendix 1.
Figure 2.18 (cont). Skull of *Khaan mckennai*. **A**, right lateral view of holotype (IGM 100/1127); **B**, right lateral view of IGM 100/1002; **C**, right lateral view of IGM 100/1127. Abbreviations in Appendix 1.
Figure 2.19. Occipital surface of skull of *Khaan mckennai* (IGM 100/1002). Abbreviations in Appendix 1.
The overall shape of the skull is obtained from the holotype and IGM 100/1002 (Fig. 2.18) due to of the dorsoventral distortion of IGM 100/973. The dorsal cranial surface is rounded and ends in a vertically oriented occiput, unlike the quadrangular skull and posterodorsally facing occipital surface of *Citipati osmolskae* and *Conchoraptor gracilis* (Clark et al., 2002). The nasal is extensively pneumatized but not dorsally enlarged to form a crest, like those morphologically diverse crests present on the skulls of *Citipati osmolskae, Oviraptor philoceratops, Nemegtia barsboldi, IGM 100/42 and Rinchenia mongoliensis*. The transitional area between the dorsal surface of the skull and the occipital surface lacks the distinct nuchal crest present in taxa such as *Incisivosaurus gauthieri* and *Conchoraptor gracilis* (Balanoff et al., 2009). The orbit is rounded in IGM 100/1002 and 100/1127 as it is in all coelurosaurs except advanced tyrannosaurids. The infratemporal fenestra is subrectangular in shape, closely approximating that of *Citipati osmolskae* (Clark et al., 2002). The quadrates extend below the ventral surface of the cranium (Fig. 2.16C, D), an arrangement present in all oviraptorosaurs. This condition, however, is not as pronounced in *Khaan mckennai* as it is in the basal taxon *Incisivosaurus gauthieri* (Fig. 2.2; Balanoff et al., 2009). The palatal surface for the most part is not visible, and only a small portion of the anterior palate including the premaxilla and maxilla can be observed in IGM 100/973 (Fig. 2.16B). A very small portion of the anterior end of the vomer and pterygoids is visible; however, little palatal morphology can be determined from IGM 100/973, and no part of the palate is visible in the other specimens. As in all other oviraptorids and caenagnathids, the skull is completely edentulous.
Premaxilla (Figs. 2.16, 2.18, 2.20)

The right and left premaxillae meet along the midline in a straight unfused suture (Fig. 2.16E), unlike the condition in *Citipati osmolskae* in which the premaxillae fuse completely to form a single element. The premaxillae also remain unfused in *Incisivosaurus gauthieri*. The premaxilla contacts the nasal posterodorsally, the maxilla and nasal posterolaterally, and the maxilla along its posterior margin on the palatal surface. The posterodorsal contact with the nasal is not preserved in IGM 100/973 but is visible in IGM 100/1127 and 100/1002 (Fig. 2.18). Together the premaxilla and nasal form the dorsal margin of the anteroposteriorly elongate, almost slitlike, external naris, which slants posterodorsally. The external naris in both *Incisivosaurus gauthieri* and *Citipati osmolskae* differs significantly in having a more circular appearance (see Fig. 2.2; Balanoff et al., 2009; Clark et al., 2002:fig. 2). The nasal process of the premaxilla has a straight anterior edge that slants posteroventrally. There is a slight bend near its posterior end where it contacts the nasal. The posterior slant to the premaxilla distinguishes *Khaan mckennai* from most other oviraptorosaurs such as *Citipati osmolskae, Rinchenia mongoliensis, or Conchoraptor gracilis* that have a more vertical orientation (see Osmolska et al., 2004:fig. 8.1).

The maxillary process of the premaxilla is a posteriorly tapering strap of bone that extends posterodorsally, and is overlain at its posterior end by a descending process of the nasal (Figs. 2.16C, D, 2.18). These two elements laterally overlie the premaxillary process of the maxilla. The premaxilla and nasal form a bar that separates the naris from
Figure 2.20. Detail of premaxilla of IGM 100/1127. Abbreviations in Appendix 1.
the antorbital fenestra and completely excludes the maxilla from the narial border (also excluding the maxilla from contacting the naris), a character that is shared among oviraptorosaurs (Osmolska et al., 2004) being present in *Caudipteryx zoui*, *Incisivosaurus gauthieri*, and *Citipati osmolskae*. The posterior tip of the maxillary process of the premaxilla also overlays a small portion of the anterior lacrimal. The premaxilla, maxilla, and lacrimal make up the anterior and dorsal borders of the antorbital fenestra, which is triangular in overall shape. The lateral surface of the maxillary process of the premaxilla is scarred by a shallow depression also seen in *Citipati osmolskae* (see Clark et al., 2002) but not *Incisivosaurus gauthieri*. The anterior and lateral surfaces of the premaxillary body are marked by numerous randomly distributed foramina (Figs. 2.16C, D, E, 2.18, 2.20), which presumably represent nervous colliculi that transported small divisions of the medial branch of the ophthalmic nerve (CN V) to innervate the ‘beak’, which may have been overlain by a keratinous sheath based on modern analogs such as turtles and birds (Bubien-Waluszewska, 1981) and at least one ornithomimid (Norell et al., 2001).

The palatal surface of the premaxilla possesses a distinct triturating surface as it does in all oviraptorosaurs and therizinosaurs (Clark et al., 1994; Clark et al., 2002); although, *Incisivosaurus gauthieri* and *Caudipteryx zoui* retain premaxillary teeth. The triturating surface of both *Khaan mckennai* and *Citipati osmolskae* and the corresponding surface in *Incisivosaurus gauthieri* and *Caudipteryx zoui* (although the latter two taxa retain teeth) each possesses a series of denticles. *Khaan mckennai* also possesses these structures, but they differ from those in other taxa in having only two large denticles similar to the morphology of *Rinchenia mongoliensis* (Fig. 2.20). Other oviraptorosaurs
have smaller more numerous denticles. These include *Citipati osmolskai* (five pairs; Clark et al., 2002:fig. 2), *Incisivosaurus gauthieri* (at least four pairs; Balanoff et al., 2009), *Caudipteryx zoui* (at least four pairs; Ji et al., 1998), and *Avimimus portentosus* (four pairs; Kurzanov, 1987). The ventral outline of the triturating surface of the premaxilla forms a distinct ‘u’ shape that is characteristic of therizinosaurus and oviraptorosaurs. The posterior margin of this surface slants dorsally, forming a parrot-like beak especially prominent in IGM 100/973 (Fig. 2.16C, D). The premaxilla has a larger exposure on the palate of *Khaan mckennai* than in *Citipati osmolskai* (Table 2.1) and expands at the palatal contact with the maxilla. The interdigitating suture between these elements has a chevron shape in both *Citipati osmolskai* and *Khaan mckennai*. This suture in *Incisivosaurus gauthieri* is distinctly v-shaped. The premaxilla of *Khaan mckennai* is edentulous, but two parasagittal rounded ridges mark the palatal surface of the element and extend to the posterior margin of the maxilla (Fig. 2.16B). Two additional ridges are present lateral to these structures on the maxilla. Premaxillary ridges are present in all oviraptorids, *Chirostenotes pergracilis*, and *Avimimus portentosus* (Barsbold, 1981, 1983, 1986; Kurzanov, 1981; Maryanska and Osmolska, 1997; Sues, 1997; Elzanowski, 1999; Clark et al., 2002), but absent in the more basal oviraptorosaur *Incisivosaurus gauthieri*.

**Maxilla (Figs. 2.16 and 2.18)**

The paired maxillae are edentulous and anteroposteriorly short when viewed laterally (Figs. 2.16C, D, 2.18), more in line with the morphology of *Citipati osmolskai*
than *Incisivosaurus gauthieri*, *Chirostenotes pergracilis* (Sues, 1997), or *Oviraptor philoceratops* (Clark et al., 2002). On the lateral surface of the skull, the maxilla contacts the premaxilla anterodorsally, lacrimal dorsally, and jugal posteriorly. On the palatal surface, the maxillary contact with the premaxilla is the only visible contact; the anterior portion of the vomer is not preserved. The maxilla makes up the ventral margin and floor of the antorbital fossa as well as the inset interfenestral bar similar to other oviraptorids (Figs. 2.16C, D, 2.20) and unlike the bar in *Incisivosaurus gauthieri*, which is confluent with the lateral surface of the rostrum. The interfenestral bar is badly damaged in IGM 100/973; however, this damage exposes many of the pneumatic fossae at the anterior end of the antorbital fossa where it typically is overlain by the premaxilla (Figs. 2.16C, 2.18C). These pockets presumably were pneumatized by the promaxillary fenestra. The posteriorly located antorbital fenestra is dorsoventrally elongate and occupies approximately 1/3 of the triangular-shaped antorbital fossa. Based on IGM 100/1127 and 100/1002, there are at least two accessory antorbital fenestrae, one large fenestra at the anterior margin of the fossa and a smaller more posterodorsal fenestra (Fig. 2.20). This arrangement is similar to what is observed in the basal taxon *Incisivosaurus gauthieri* (Fig. 2.2; Balanoff et al., 2009) as well as the oviraptorid *Citipati osmolskae* (Clark et al., 2002:fig. 2); therefore, homologies for this region are easily followed throughout Oviraptorosauria but difficult to correlate with other coelurosaurians (Witmer, 1997). The purported sister taxon to Oviraptorosauria in some analyses, Therizinosauria, possesses no accessory antorbital fenestrae (see *Erlicosaurus andrewsi*; Clark et al., 1994).
The maxilla underlies the jugal along its posterior (jugal) process (Figs. 2.16C, D, 2.18). The jugal process of the maxilla is thin and rod shaped. Approximately midway along the length of the maxilla, the maxilla and jugal extend dorsally to contact the preorbital process of the lacrimal to form the preorbital bar separating the antorbital fossa from the orbit.

The palatal surface is confluent with that of the premaxilla (Fig. 2.16B), and the aforementioned ridges that are present on the premaxilla extend along the entire length of the maxilla as well. Two additional ridges are added lateral to these premaxillary ridges and are present exclusively on the maxilla, as they are in *Citipati osmolskae* (Clark et al., 2002). Although present in all observed oviraptorids and caenagnathids, no ridges are present on the palatal surface of *Incisivosaurus gauthieri*. A small toothlike projection is located at the posterior end of each palatal ridge in *Khaan mckennai* (Fig. 2.16B, 1.18C). This structure is usually formed by the maxilla and vomer (Elzanowski, 1999; Clark et al., 2002), but the contact of these elements is not preserved in IGM 100/973; therefore, it cannot be determined what other elements contributed to these toothlike structures. The palatal ‘teeth’ present on the maxilla are present in all oviraptorids (see *Citipati osmolskae*; Clark et al., 2002; Osmolska et al., 2004) and are diagnostic of the group plus caenagnathids (see maxilla of *Chirostenotes pergracilis*; Sues, 1997). These structures may also be present in *Avimimus portentosus*; although, the damage to PIN 3907/1 makes it difficult to discern. Additional specimens recently collected in China may shed light on the presence of these structures (Currie et al., 2008). The triturating surface of the maxilla of *Khaan mckennai* lacks additional denticles. These structures are continued from the
premaxilla onto the maxilla in oviraptorids such as *Citipati osmolskae*, *Oviraptor philoceratops*, and the caenagnathid *Chirosenotes pergracilis* (Sues, 1997) but are completely absent in the more basal form, *Incisivosaurus gauthieri*.

**Nasal (Figs. 2.16, 2.18, 2.21)**

The nasals are paired and fully fused along the midline (Figs. 2.16A and 2.21), like all other oviraptorids but unlike *Incisivosaurus gauthieri*, therizinosaurs, or paravians (e.g., Clark et al., 1994; Norell et al., 2006; Balanoff et al., 2009). Much of the nasal of IGM 100/973 is damaged; therefore, many of the structures particularly on the anterior part of the dorsal surface are not easily distinguished. Most observations, as a consequence, are taken from IGM 100/1127. The nasal contacts the premaxilla anteriorly and laterally, the lacrimal posterolaterally, and the frontals posteriorly. The dorsal surface of the nasal is flared substantially posterior to the posterior edge of the naris (approximately four times the width of the premaxillary process). This morphology is similar to *Citipati osmolskae*, but substantially different from *Incisivosaurus gauthieri*, which similar to other theropods has nasals that are approximately subequal throughout their entire length (Fig. 2.3; Balanoff et al., 2009). The premaxillary process of the nasal in *Khaan mckennai* is extremely thin and extends anteriorly from the midline to meet the premaxilla. The posterior contact with the frontal is irregular but not fused. The dorsal surface of the nasal in this region is marked by numerous openings that through the use of CT data can be seen to extensively pneumatize the element. One large nasal recess dominates this area, and a small ridge along the midline is raised above the highly
Figure 2.21. Dorsal surface of skull of holotype of *Khaan mckennai* (IGM 100/1127). Abbreviations in Appendix 1.
pneumatic surface (Figs. 2.16A and 2.21). Numerous small fenestrae are distributed around the large opening and extend even onto the premaxillary process. A similar morphology is apparent in *Citipati osmolskae*, *Rinchenia mongoliensis*, and *Nemegtia barsboldi*—oviraptorids that possess a nasal crest (Clark et al., 2002)—but it does not appear to this same extent in those taxa that lack a crest such as *Conchoraptor gracilis* (Barsbold, 1986). *Incisivosaurus gauthieri* also possesses pneumatic foramina in this region of the skull but not to the extent seen in any of the oviraptorids.

The lateral descending process of the nasal slightly overlaps the maxillary process of the premaxilla and dorsal surface of the lacrimal (Fig. 2.18C). This process is abbreviated in comparison to the condition in *Citipati osmolskae* (compare Fig. 2.18C to Clark et al., 2002:fig. 2). The nasal and premaxilla together form the dorsal border of the naris (does not extend even half way along the length of the maxillary process of the premaxilla); however, only the descending process of the nasal forms the posterior border of the opening (Fig. 2.18C). The nasal opening (based on IGM 100/1127) is elongate with a slightly triangular shape (the apex being at the midpoint along the posteroverentral margin). The relative size of the external naris is larger than the antorbital fenestra yet comparable to that of the antorbital fossa (Fig. 2.18A, C). This is comparable to the arrangement in oviraptorids such as *Citipati osmolskae* and *Conchoraptor gracilis* (Osmolska et al., 2004), but the antorbital fenestra is larger than the external naris in *Incisivosaurus gauthieri* (Fig. 2.2; Balanoff et al., 2009) and *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000). The nasal of *Khaan mckennai* is excluded entirely from the border of the antorbital fossa by the lacrimal and premaxilla as it is in all oviraptorosaurs.
Frontal (Figs. 2.16, 2.18, 2.21)

The dorsal surface of the frontal is damaged in IGM 100/973 and not well exposed in IGM 100/1002; therefore, much of the description is based on 100/1127 (Fig. 2.21). The paired frontals are sutured together along their midline, but the interdigitating nature of the suture between the elements is still visible (Fig. 2.21). The anteroposterior length of the frontal is short, about one-quarter of the length of the parietal (Table 2.1), a feature in agreement with other oviraptorids (Osmolska et al., 2004). The frontal of the more basal *Incisivosaurus gauthieri*, however, is approximately the same length as the parietal (Fig. 2.3; Balanoff et al., 2009) and longer in *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000). The dorsal surface of the frontal is convex in IGM 100/1127 and 100/1002, but more flattened in IGM 100/973. This disparity in shape is likely due to diagenetic dorsoventral compression of IGM 100/973, although the morphology of this specimen does approach that of *Citipati osmolskai*. The anterior suture of the frontal with the nasal is extensive, complex, and not fused. This condition also is described for *Citipati osmolskai* (Clark et al., 2002). The posterior contact with the parietal on the dorsal surface is difficult to discern because of damage to the skull, but appears to be the typical condition with the frontal overlying the parietal. This contact is sinuous (saddle-shaped), which is similar to *Conchoraptor gracilis* but differs from the straight diagonal contact present in *Citipati osmolskai* (Clark et al., 2002). Although the frontal typically forms part of the supratemporal fossa, it is prohibited from contributing to this structure by the frontal arm of the postorbital (Fig. 2.21). The same arrangement is seen in
**Conchoraptor gracilis**, but absent in most other oviraptorosaurs (e.g., *Incisivosaurus gauthieri* and *Citipati osmolskae*). Broken portions of the dorsal surface of IGM 100/973 reveal that the frontal is pneumatized at least along its lateral margin. CT imagery also reveals that this lateral pneumatic pocket is connected to a large midline sinus that begins anteriorly in the frontal and extends posteriorly into the parietal where it connects with a pneumatic recess present in the parietal (Fig. 2.22). This sinus is similar to the frontal sinus described for *Citipati osmolskae* and *Conchoraptor gracilis* (Clark et al., 2002; Kundrat and Janacek, 2007). Unlike the initial description of *Citipati osmolskae*, the sinus has a median septum separating the paired structure, as is present in *Conchoraptor gracilis* (Kundrat and Janacek, 2007).

Laterally, the lacrimal contacts the anterior surface of the frontal for a short distance along a distinctive lacrimal process, and these two elements together form part of the supraorbital rim (Figs. 2.16 and 2.18). This contact with the lacrimal extends onto the orbital surface. The supraorbital rim lacks the pronounced everted lip present in *Incisivosaurus gauthieri* (Balanoff et al., 2009), but is more pronounced than the condition of *Citipati osmolskae*, in which a supracilliary rim essentially is absent. The ventral surface of the supraorbital rim lacks pneumatic pockets like those on the orbital surface in *Citipati osmolskae* (Clark et al., 2002). The orbit is round in IGM 100/1127 and 100/1002 but somewhat flattened into an ellipse in IGM 100/973 again due primarily to dorsoventral compression (Fig. 2.16C, D). The posterodorsal and posterior margins of the orbit are formed by the postorbital, which overlaps approximately the posterior one-third of the lateral edge of the frontal. The orbital surface of the frontal is oriented almost
Fig. 2.22. CT images showing sagittal slices at various levels through IGM 100/973 (in mm). Abbreviations in Appendix 1. A, 13.33; B, 17.22; C, 22.09; D, 33.97; E, 41.67; F, 42.50.
Fig. 2.22 (cont). CT images showing sagittal slices at various levels through IGM 100/973 (in mm). Abbreviations in Appendix 1. A, 13.33; B, 17.22; C, 22.09; D, 33.97; E, 41.67; F, 42.50.
horizontally, giving the element a somewhat flattened ‘L’ shape in cross section. A distinct fossa is present posteriorly on the orbital surface for the acceptance of the postorbital (capitate) process of the laterosphenoid.

*Parietal (Figs. 2.16, 2.18, 2.21)*

As with the other bones exposed on the dorsal surface of the skull, the parietals of IGM 100/973 and 100/1002 have incurred much damage. This surface in IGM 100/1127 is well preserved but only partially exposed (Fig. 2.21). The parietals are indistinguishably fused along the midline as in all oviraptorosaurs and form the majority of the skull roof, approximately one-third of the total length of the skull (Table 2.1; compare with *Citipati osmolskae*, Clark et al., 2002:fig. 5). The parietals make up a smaller portion of the skull roof in the basal oviraptorosaurs *Incisivosaurus gauthieri* and *Caudipteryx zoui*. The dorsal surface of the parietal in *Khaan mckennai* contacts the frontal anteriorly and the postorbital laterally along its anterior margin. Along the occipital surface the element contacts the supraoccipital ventrally and laterally, and the lateral surface contacts the laterosphenoid anteriorly and the prootic and squamosal posteriorly.

In IGM 100/1127 and 100/1002 the dorsal surface of the parietal (confluent with the frontal) is distinctly rounded (Fig. 2.18A). This shape is distinctive to *Khaan mckennai*, differing from the flattened parietals in both the basal *Incisivosaurus gauthieri* and the oviraptorids *Citipati osmolskae* and *Conchoraptor gracilis*, giving the top of the braincase a rounded profile. The parietal, which contacts the frontal at its widest point,
narrow slightly posteriorly. The posterior end of the element is slightly wider and forms a weakly developed nuchal crest. This condition differs from other maniraptorans (see *Tsaagan maangas*; Norell et al., 2006) as well as more closely related oviraptorids like *Conchoraptor gracilis*, which have a more pronounced nuchal crest. A small sagittal crest runs along the midline.

The lateral surface of the parietal extends ventrally to form the majority of the medial margin of the supratemporal fossa (Fig. 2.21), differing from *Citipati osmolskae*, whose parietal contributes only the posteromedial margin of the fossa, about one-quarter of the length (Clark et al., 2002). The parietal does not form a deep dorsal tympanic recess in *Khaan mckennai* as it does in *Citipati osmolskae* (Fig. 2.16C, D; Clark et al., 2002). The occipital surface of the parietal in IGM 100/973 and 100/1002 is not preserved, and the same surface remains unexposed in IGM 100/1127.

*Lacrimal (Figs. 2.16, 2.18, 2.21)*

The lacrimal is a tri-radiate element; however, the anterior nasal process is significantly shorter than that seen in deinonychosaurians (see Norell et al., 2006:fig. 3), more closely approximating that of *Incisivosaurus gauthieri* (Xu et al., 2002a; Balanoff et al., 2009). The lacrimal contacts the premaxilla and nasal anteriorly, the frontal posteriorly, and the jugal and maxilla ventrally along its preorbital process.

The concave posterior surface of the descending process of the lacrimal forms nearly the entire preorbital bar. This surface is marked by a large opening that penetrates through to the anterior surface and opens into a recess (Fig. 2.23B). This foramen likely
Figure. 2.23. CT images showing coronal slices at various levels through IGM 100/973 (in mm). A, 37.65; B, 50.75; C, 61.39; D, 69.57; E, 89.22; F, 103.95. Abbreviations in Appendix 1.
Figure 2.23 (cont). CT images showing coronal slices at various levels through IGM 100/973 (in mm). A, 37.65; B, 50.75; C, 61.39; D, 69.57; E, 89.22; F, 103.95. Abbreviations in Appendix 1.
transported the nasopharyngeal duct while the recess housed the laterally exposed nasopharyngeal canal (see Clark et al., 2002 and Witmer, 1997). Another opening directly anterior to this foramen leads into the nasopharyngeal cavity (Fig. 2.22). The anterior (nasal) process of the lacrimal extends a short distance over the dorsal edge of the antorbital fossa, underlying the maxillary process of the premaxilla and the nasal. This process of the lacrimal is marked by a deep pneumatic recess on its lateral surface directly dorsal to the nasopharyngeal canal (Fig. 2.23B; a feature found in both *Incisivosaurus gauthieri* and *Citipati gauthieri*). CT slices also show that the lacrimal is highly pneumatic. These pneumatic spaces join with the larger sagittal and lateral sinuses of the frontal (Fig. 2.23C, D), as they do in *Incisivosaurus gauthieri* and *Citipati osmolskae*; however, Kundrat and Janacek (2007) were not able to establish this connection in *Conchoraptor gracilis*. The jugal process of the lacrimal, with the jugal, forms the preorbital bar separating the antorbital fossa from the orbit. The posterior (frontal) process of the lacrimal is short and extends only the anterior quarter of the length of the orbit. The medial border of the frontal process in *Khaan mckennai* abuts the frontal in a straight contact. The lacrimal is not exposed to a significant degree on the skull roof along its medial contact with the frontal; instead, only a narrow portion of the element is visible, which tapers posteriorly (Fig. 2.21).

**Jugal (Figs. 2.16 and 2.18)**

The jugal is elongate and slender, differing from the straplike appearance of the jugal in the basal oviraptorosaur *Incisivosaurus gauthieri* (compare Fig. 2.18A, C with
Fig. 2.3). The rodlike shape of the jugal has been used as a diagnostic character of oviraptorids (Turner et al., 2007); however, this element in *Conchoraptor gracilis* also has a distinctly straplike appearance more closely resembling the morphology in *Incisivosaurus gauthieri*.

The jugal contacts the maxilla anteriorly in a simple overlapping contact, the postorbital dorsally along the dorsal (postorbital) process, and the quadratojugal posteriorly (although this contact is not well preserved in any of the specimens). The maxillary process of the jugal forms the ventral margin of the orbit. Similar to *Citipati osmolskae* and *Conchoraptor gracilis*, this process turns slightly ventrally anterior to the margin of the orbit to make a slight contribution to the posteroventral corner of the antorbital fossa (Fig. 2.18A, C). The jugal in *Incisivosaurus gauthieri* does not contribute to the fossa; however, the process does extend to this length in *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000).

The posterior margin of the orbit is comprised of the postorbital and postorbital process of the jugal. The postorbital process of the jugal extends posterodorsally for at least two-thirds of the height of the orbit, somewhat less than in *Citipati osmolskae* (Clark et al., 2002) and *Conchoraptor gracilis* (Osmolska et al., 2004). The posterior flexion of the postorbital process of the jugal differs in the three specimens of *Khaan mckennai* observed here (Figs. 2.16C, D and 2.18). Flexion in IGM 100/973 is much more pronounced than it is in either IGM 100/1127 or 100/1002. Both specimens have a postorbital process that is almost vertical (the condition present in *Incisivosaurus gauthieri* and *Citipati osmolskae*). Posteriorly the quadratojugal process lies lateral to the
quadratojugal, and these two elements are sutured but not fused. The quadratojugal process of the jugal extends at least two-thirds the length of the infratemporal fenestra, further than in *Citipati osmolskae*. The medial surface of the jugal is not visible.

**Postorbital (Figs. 2.16 and 2.18)**

The triradiate postorbital is best preserved on the right side of IGM 100/973 and in IGM 100/1127 (Figs. 2.16C and 2.18A, C). The postorbital contacts the frontal anteriorly along the frontal process, the squamosal posteriorly along the posteriorly projecting squamosal process, and the jugal ventrally. The medial surface of the frontal process of the postorbital has a short contact with the laterosphenoid within the orbit. The postorbital forms, with the jugal, the postorbital bar completely separating the orbit from the infratemporal fenestra. The anterior margin of the jugal process of the postorbital is concave and forms the posterior margin of the circular orbit. The infratemporal fenestra is subrectangular in shape (although the squamosal is damaged and its shape cannot be assessed confidently on IGM 100/973, it is better preserved in IGM 100/1127 [Fig. 2.18C], and almost all other oviraptorosaurs have a subrectangular fenestra). The infratemporal fenestra is bordered by the postorbital and jugal anteriorly, jugal ventrally, quadratojugal posteroventrally, quadratojugal and squamosal posteriorly, and squamosal and postorbital dorsally. The distal end of the frontal process of the postorbital turns dorsally and expands slightly at the terminus. Although similar to most oviraptorids such as *Citipati osmolskae* and *Conchoraptor gracilis*, this morphology differs substantially from *Incisivosaurus gauthieri*, which has a frontal process that curves slightly ventrally
following the shape of the orbit (Fig. 2.3; Balanoff et al., 2009). The posterior squamosal process is damaged on the right side of IGM 100/973, but well preserved in IGM 100/1127. This process extends only one-half of the length of the infratemporal fenestra, differing from the elongate process of *Citipati osmolskae* and *Conchoraptor gracilis*, which extends almost the entire length of the this fenestra (Osmolska et al., 2004). The jugal process of the postorbital extends ventrally approximately two-thirds the length of the infratemporal fenestra (based on IGM 100/1127), unlike the process in *Citipati osmolskae* that extends the entire length of the fenestra (Clark et al., 2002). On the dorsal surface the postorbital, with the squamosal, forms the lateral border of the supratemporal fenestra.

*Squamosal (Figs. 2.16 and 2.18)*

The squamosal is too damaged in all three of the specimens to make any confident statements concerning its morphology. The quadrate process does overlap the quadrate to form the immobile joint that is present in other oviraptorids (Fig. 2.16C; see Clark et al., 2002). The contact with the postorbital is also visible in IGM 100/1127 and, as described above, the postorbital lies anteriorly and laterally to the squamosal.

*Supraoccipital (Figs. 2.16 and 2.19)*

The supraoccipital is not exposed in IGM 100/1127 and is severely damaged in IGM 100/1002 (Fig. 2.19). In IGM 100/973 the supraoccipital is wide and triangular but damaged along its dorsal border where it presumably contacted the parietal (Fig. 2.16F).
The only other contact that can be discerned is the long diagonal contact with the exoccipital along the ventral edge of the supraoccipital. The majority of the foramen magnum is bordered by the paired exoccipitals; however, the ventral margin of the supraoccipital provides a very small contribution to this structure along its dorsal border (Figs. 2.16F and 2.19; the supraoccipital may be excluded from foramen magnum in *Citipati osmolskae* and *Conchoraptor gracilis*—see Clark et al., 2002). The supraoccipital makes a broad contribution to the foramen magnum in *Incisivosaurus gauthieri* (Fig. 2.5; Balanoff et al., 2009). A pronounced vertical nuchal prominence is present on the external surface of the supraoccipital (Fig. 2.21).

**Exoccipital (Figs. 2.16 and 2.19)**

The paired exoccipitals are damaged in all of the specimens, yet several aspects of their morphology can still be discerned (Figs. 2.16F and 2.19). These elements form the lateral and most of the dorsal margins of the foramen magnum; however, as indicated above the supraoccipital may contribute a small portion to the dorsal midline and the basioccipital forms the ventral border of this structure. The foramen magnum is mediolaterally elongate. This shape may due to the dorsoventral compression in IGM 100/973 (Fig. 2.16F); however, a similar shape also is present in IGM 100/1002 (Fig. 2.19), which if deformed is compressed along the mediolateral axis. Dorsally, the exoccipital contacts the supraoccipital (described above). A small opening is present on the border between the two elements; however, it is difficult to ascertain whether this is real or a result of breakage. The opening is bilaterally symmetrical and likely represents
the foramen for the external occipital vein (Fig. 2.16F), also present in most other theropods. The only other contact visible on IGM 100/973 is the ventral contact with the basioccipital. The exoccipital sits on the dorsal surface of the basioccipital and forms part of the neck to the occipital condyle. This element, however, does not appear to contribute to the condyle itself, as is the case in *Citipati osmolskae*. One small opening is visible on the ventral surface of the exoccipital of IGM 100/973. This foramen is likely for the exit of the hypoglossal (CN XII) (Fig. 2.16F). The paroccipital processes are preserved and visible only in IGM 100/1002 (Fig. 2.19). These structures possess the characteristic ventrolaterally curved, pendant orientation of all oviraptorosaurs (including the basal form, *Incisivosaurus gauthieri*). Although the shape of the paroccipital processes corresponds closely with *Citipati osmolskae*, the dorsoventral depth is much more slender in *Khaan mckennai* (compare Fig. 2.19 with Clark et al., 2002:fig. 6). The neck of the paroccipital processes is slightly pinched towards the proximal end.

*Basioccipital (Figs. 2.16B, F, 2.19)*

The basioccipital forms the entire occipital condyle and the ventral margin of the foramen magnum. The occipital and ventral surfaces of the basioccipital are preserved in IGM 100/973. In IGM 100/1002 only the occipital surface is visible, but it lacks the distortion that is seen in IGM 100/973 (compare Figs. 2.16F and 2.19). The occipital condyle of *Khaan mckennai* lacks a distinct neck that extends beyond the occipital surface of the skull and does not possess the unique, pronounced morphology of *Citipati osmolskae* (Clark et al., 2002). The neck of the occipital condyle is similar to other
oviraptorosaurs such as *Conchoraptor gracilis*, *Incisivosaurus gauthieri*, and *Caudipteryx zoui* (Ji et al., 1998; Osmolska et al., 2004; Balanoff et al., 2009) in being short and not constricted (in contrast *Chirostenotes pergracilis* possesses a ventrally constricted neck; Sues, 1997). The occipital condyle is rounded with no central depression (differing significantly from the flat morphology with a central depression seen in *Citipati osmolskae*) and is distinctly narrower than the foramen magnum similar to other oviraptorosaurs including *Chirostenotes pergracilis* (Sues, 1997). This condition cannot be assessed in *Incisivosaurus gauthieri* due to distortion of the skull.

On the ventral surface of the skull the basal tubera are reduced relative to those in *Incisivosaurus gautieri* (Fig. 2.4b; Xu et al., 2002; Balanoff et al., 2009). The basal tubera of *Khaan mckennai*, however, are relatively larger than those in *Citipati osmolskae*. Despite the differences in size, the basal tubera of *Khaan mckennai* and *Citipati osmolskae* both have a small circular depression along the midline. These structures in IGM 100/973 have a distinct anterior orientation differing drastically from the vertical orientation present in *Conchoraptor gracilis*. No pneumatic openings (subcondylar recesses) are visible opening into the basioccipital on the lateral surface of the basal tubera like in *Citipati osmolskae* and *Conchoraptor gracilis* (Clark et al., 2002). The anterior contact with the parabasisphenoid is not preserved in any of the specimens. CT imagery of IGM 100/973 reveals that this region of the skull is poorly ossified, as it is in all oviraptorosaurs including *Incisivosaurus gauthieri*, and therefore probably not preserved.
Parabasisphenoid (Fig. 2.16)

This element is not wholly preserved in any of the specimens, but a small portion of the mediolaterally compressed parabasisphenoid rostrum is visible through the orbit of IGM 100/973 (Fig. 2.16D). CT data shows that the parasphenoid rostrum has a slight anterodorsal slant from its base (Fig. 2.22).

Quadratojugal (Figs. 2.16 and 2.18)

The quadratojugal is an ‘L’ shaped element with a short, rounded posterior process that is abbreviated compared to the same process of *Citipati osmolskae*, *Rinchenia mongoliensis*, or IGM 100/42 (Zamyn Khondt oviraptorid in Osmolska et al. [2004]) (Figs. 2.16C, D, 2.18; Clark et al., 2002; Osmolska et al., 2004). In IGM 100/1127 and 100/973 the quadratojugal is present but damaged; in IGM 100/1002, the element is not articulated with the skull yet is preserved in its entirety (Fig. 2.18). The quadratojugal contacts the jugal anteriorly, the squamosal dorsally, and the quadrate dorsally and ventrally along its medial surface. It forms the posterior and ventral margins of the infratemporal fenestra. The anterior (jugal) process of the quadratojugal extends just over half of the length of the infratemporal fenestra and contacts the jugal along its lateral surface. An elongate posterior process extends from the posterovertral surface of the quadratojugal. This extension is approximately half of the length of the jugal process, shorter than that of *Citipati osmolskae*. The cross section of the element underlying the infratemporal fenestra is similar to the jugal in that it is extremely gracile and circular in cross section—the same morphology present in *Citipati osmolskae* and *Caudipteryx zoui*.
(Ji et al., 1998; Zhou et al., 2000). The extent of the dorsal (squamosal) process cannot be determined in any of the three specimens; however, the medial contact of this process with the quadrate is preserved in IGM 100/973. A large quadrate foramen is present along this contact between the quadratojugal and quadrate, visible in posterior view (Fig. 2.16F; see also Clark et al., 2002).

*Quadrate (Figs. 2.16, 2.18, 2.19)*

The quadrate is difficult to observe due to overlying bones; however, the overall structure of this element can be pieced together using a composite of all three specimens as well as CT imagery (Figs. 2.16C, D, F, 2.18). The quadrate is oriented obliquely, the same orientation seen in other oviraptorosaurs. Visible contacts include the pterygoid anteriorly (IGM 100/1002) and medially (IGM 100/973), the quadratojugal dorsally and ventrally on the lateral surface (IGM 100/973), and the squamosal dorsally on the lateral surface of the optic wing (IGM 100/973 and 100/1002). Although established in other oviraptorosaurs (Maryanska and Osmolska, 1997) such as *Incisivosaurus gauthieri*, *Citipati osmolskae*, and *Conchoraptor gracilis* (Kundrat and Janacek, 2007), the contact with the braincase is not visible externally on any of the specimens of *Khaan mckennai*. CT images also fail to show an extensive contact between the quadrate and exoccipital/opisthotic of *Khaan mckennai* (Fig. 2.23F).

The overall size of the quadrate is large due to an extremely expanded optic wing that forms the medial wall of the infratemporal fenestra and with the dorsal expansion of the pterygoid covers much of the lateral wall of the braincase (Figs. 2.16C and 2.18). This
unusual arrangement is present in other oviraptorosaurs including the basal-most
*Incisivosaurus gauthieri*, but in no theropod taxa outside of this group (Xu et al., 2002; Balanoff et al., 2009). The optic wing of the quadrate contacts the pterygoid ventrally so that this entire structure is made up of at least the quadrate and pterygoid and extends anteriorly to just posterior to the trigeminal foramen. The contact of the optic wing with the pterygoid is best observed in IGM 100/1002 (although also present in IGM 100/973). The distal end of the optic wing is rounded and lateral to the pterygoid wing (Fig. 2.18B) as is the morphology of *Citipati osmolskae*. The quadrate of *Incisivosaurus gauthieri* also possesses this same basic construction.

The articulation of the quadrate with the squamosal is not visible in IGM 100/973; however, IGM 100/1002 shows the squamosal overlying the optic wing of the quadrate in a non-moveable joint, as is present in all oviraptorids but not *Incisivosaurus gauthieri*. The squamosal is badly damaged in IGM 100/1002, but the articulation remains. The posterior surface of the dorsal process of the quadrate as seen in IGM 100/973 is flat with no pneumatic foramen (Fig. 2.16F); however, this absence may be due to the foramen being obscured by other bones or matrix. CT data, nonetheless, does reveal a hollow quadrate (Figs. 2.22B and 2.23E). The lateral edge of the dorsal process bears a thin lip likely for the articulation with the quadratojugal. Because the mandible is still articulated with the skull in all specimens of *Khaan mckennai*, the mandibular surface of the quadrate is not visible, but CT imagery shows a sliding articulation as is present in known oviraptorids (see Barsbold, 1983; 1986; Clark et al., 2002; Osmolska et al., 2004).
*Avimimus portentosus*, however, does not exhibit this same sliding articulation (Kurzanov, 1987; Vickers-Rich et al., 2002).

**Laterosphenoid (Figs. 2.16 and 2.18)**

The laterosphenoid of IGM 100/973 is well preserved on the right side of the skull (Fig. 2.16C). IGM 100/1002 does not preserve the laterosphenoid, and only the orbital surface is partially preserved in IGM 100/1127. The description, therefore, is based almost entirely on IGM 100/973. The element has a similar morphology to other oviraptorids (see Clark et al., 2002) in that it is an anteroposteriorly-compressed element oriented almost horizontally with a thin elongate postorbital process (capitate process of Clark et al., 2002). The laterosphenoid contacts its opposite medially, the frontal, parietal, and postorbital along the lateral postorbital process, and the prootic posteriorly. A depression on the anterior surface lateral to the optic foramen in IGM 100/973 implies that the epipterygoid also contacted the laterosphenoid, as it does in *Citipati osmolskae* (Clark et al., 2002:fig. 2). A small, fused orbitosphenoid can be seen in CT images contacting the laterosphenoid along its medial edge (Fig. 2.24A).

A small ridge runs vertically posterior to the postorbital process of the laterosphenoid dividing the main body of the element into two surfaces, an anterior orbital surface and a posterior lateral surface (Fig. 2.16C). This arrangement is also present in *Citipati osmolskae* and *Conchoraptor gracilis*. On the anterior (orbital) surface of the laterosphenoid, a notch is present approximately halfway along the medial margin forming (along with the other laterosphenoid) a single opening for the exit of the optic
Figure 2.24. CT images showing horizontal slices at various levels through IGM 100/973 (in mm). Abbreviations in Appendix 1. A, 21.02; B, 21.70; C, 22.31; D, 22.85; E, 57.88.
Figure 2.24 (cont). CT images showing horizontal slices at various levels through IGM 100/973 (in mm). Abbreviations in Appendix 1. A, 21.02; B, 21.70; C, 22.31; D, 22.85; E, 57.88.
nerve (CN II). All oviraptorids possess only single opening for the optic nerve; however, all specimens of *Khaan mckennai* lack the ventral midline process that underlies this foramen in *Citipati osmolskae*, *Rinchenia mongoliensis*, and *Nemegtia barsboldi* (Clark et al., 2002:fig. 2; Lu et al., 2004). The morphology of the anterior surface of the laterosphenoid is not visible in basal oviraptorosaurs including *Incisivosaurus gauthieri*. The postorbital process of *Khaan mckennai* sits in an impression that spans the posterior orbital surface of the frontal and the anteroventral portion of the postorbital.

The lateral surface of the laterosphenoid contacts the prootic posteriorly and these two elements form the single trigeminal opening (CN V; Fig. 2.16C). The trigeminal foramen is approximately one-half the size of the opening for the optic nerve. This single opening is small in the oviraptorids *Citipati osmolskae* and *Conchoraptor gracilis* (see prootic description), but relatively large in the basal oviraptorosaur *Incisivosaurus gauthieri* (Fig. 2.3B; Xu et al., 2002; Balanoff et al., 2009) as well as *Chirostenotes pergracilis* (Sues, 1997:fig. 3b). The prootic and laterosphenoid are not fused in *Khaan mckennai* or *Conchoraptor gracilis* as they are in *Citipati osmolskae*.

**Prootic (Fig. 2.16D)**

The lateral braincase elements are difficult to distinguish in all specimens of *Khaan mckennai* because of the overlying bones (Figs. 2.16D and 2.18). The only contacts of the prootic that can be differentiated are the dorsal contact with the parietal and the anterior contact with the laterosphenoid. A small arm extends anteriorly beneath the laterosphenoid to contribute to the trigeminal fenestra (CN V). A relatively deep
impression that corresponds to the dorsal tympanic recess lies dorsally on the lateral surface (Norell and Makovicky, 1997, 1999; Witmer, 1997), although no foramina can be seen penetrating the recess as is seen in *Conchoraptor gracilis*, *Citipati osmolskae*, and *Incisivosaurus gauthieri*. As in *Citipati osmolskae*, a distinct horizontal swelling forms the ventrolateral border of the fossa. The foramen for the facial nerve (CN VII) is not visible on the external surface of any of the *Khaan mckennai* specimens, but can be identified in the CT imagery piercing the prootic directly anterior to the vestibule of the ear (Fig. 2.24). The ear region also is completely obscured on the external surface by the extensive quadrate/pterygoid wing.

**Inner ear (Fig. 2.25)**

The size of the inner ear canals is difficult to determine because of mineral deposits within the canals (especially the lateral canal; Fig. 2.24A–D), and the cochlear canal is not discernable in the CT data. These hindrances not withstanding, the internal ear structure was digitally reconstructed using CT imagery for IGM 100/973 (Fig. 2.25). The overall structure of the internal ear is roughly triangular in lateral view, similar to all other theropods (Witmer and Ridgely, 2009); however, it lacks the elongate morphology of many coelurosaurs. Instead, the morphology is slightly compressed, which undoubtedly is influenced to some degree by the dorsoventral compression of the skull as a whole. The inner ear, otherwise, closely resembles the typical coelurosaur ear. The posterior semicircular canal is bowed dorsally so as to twist at the common crus. The anterior and posterior semicircular canals have a very thin appearance; however, the
Figure 2.25. Reconstruction using CT images of the inner ear of IGM 100/973. Abbreviations in Appendix 1. A, lateral view; B, posterior view; C, anterior view; D, dorsal view.
lateral canal appears more robust than in typical coelurosaur ears, even basal taxa such as tyrannosaurids (Witmer and Ridgely, 2009; Brusatte et al., 2009).

The anterior semicircular canal does expand anteriorly and posteriorly, but does not bend posteriorly past the common crus as it does in the basal oviraptorosaur *Incisivosaurus gauthieri* (Balanoff et al., 2009) and paravians (Dominguez Alonso, 2004). The canal, therefore, lacks the extreme kidney shape that is characteristic of most coelurosaurs (Norell et al., 2006). The lateral canal has a distinct arc shape. The posterior and lateral canals join posteriorly (and the posterior canal extends ventrally beyond the level of the lateral canal) so that they cannot be distinguished from one another at this point. The vestibule resembles other theropods in that it does not extend dorsally above the dorsal margin of the lateral semicircular canal (Witmer and Ridgely, 2009). The endolymphatic duct is not visible in the reconstruction or the CT slices.

The bony division (crista interfenestralis) between the vestibular portion of the ear and the pseudorotundum is not visible externally (covered by bony quadrate/pterygoid flange) or in the CT imagery. This division likely is present, as it is present in the basal taxon, *Incisivosaurus gauthieri* (Balanoff et al., 2009), as well as *Citipati osmolskae* (Clark et al., 2002). Although not visible externally on the skull, the vestibular foramen is discernable in the CT imagery (Fig. 2.25) set into a depression as it is in all maniraptorans. The stapes is not preserved.
MANDIBLE

The lateral surface of the mandible of *Khaan mckennai* is exceptionally preserved in all three specimens. The best example, however, is IGM 100/1127, and most of this description is based on that specimen. IGM 100/973 exhibits good preservation, and IGM 100/1002 is disarticulated slightly at its posterior end (Figs. 2.16C, B, 2.18B). The mandible of *Khaan mckennai* preserves the unusual morphology present in all other oviraptorids being shortened anteroposteriorly so that it lacks the elongation of caenagnathids and basal oviraptorosaurs such as *Incisivosaurus gauthieri* and *Caudipteryx zoui* (Sternberg, 1940; Barsbold, 1981; Currie et al., 1993; Sues, 1997; Ji et al., 1998; Zhou et al., 2000; Balanoff et al., 2009). Other features that it shares with all oviraptorids include a dorsoventrally high coronoid eminence, a surangular spine that extends into (but does not divide) the enlarged heart-shaped mandibular fenestra, an edentulous dentary, a u-shaped dentary symphysis that is slightly downturned, and an elongate slender retroarticular process. Although the coronoid likely is absent or reduced as in *Citipati osmolskae* (Clark et al., 2002), the medial surface of the mandible is not visible, and CT images do not indicate the presence of a coronoid.

Dentary (Figs. 2.16 and 2.18)

The dentaries of IGM 100/973 are sutured but not fully fused and have a distinct u-shape in dorsal view, as do all oviraptorosaurs and therizinosaurs. CT data also indicate a highly pneumatic internal structure to the dentary (Fig. 2.23A). The overall morphology
of the dentary in oviraptorids is very distinctive, and *Khaan mckennai* does not differ in any substantial way from this morphology. The dentary contacts its opposite anteriorly along its medial surface, the surangular posteriorly by way of the dorsal process, and the surangular and angular posteriorly along the ventral process (Fig. 2.18). The dentary is edentulous and has a small downturn of the dentary at the anteriormost edge to form, with the premaxilla, a parrot-like ‘beak’. An expanded ventrally sloping shelf is present on the labial surface of the dentary forming a sharp triturating surface dorsally.

The lateral surface of the dentary bifurcates into dorsal and ventral processes posteriorly. These processes enclose a central space forming the enlarged mandibular fenestra. The dorsal process spans approximately two-thirds of the length of the entire fenestra and is overlain by the surangular laterally. This process is curved dorsally forming a large coronoid prominence like that present in all known oviraptorids (Figs. 2.16C and 2.18; Osmolska et al., 2004) and possibly *Microvenator celer* (Makovicky and Sues, 1998:Fig. 2). Caenagnathids and basal oviraptorosaurs like *Incisivosaurus gauthieri* and *Caudipteryx zoui* lack the coronoid prominence (Sues, 1997; Ji et al., 1998; Balanoff et al., 2009). The ventral process of the dentary spans the entire length of the mandibular fenestra but tapers posteriorly and sits underneath the angular at its posterior end. All oviraptorosaurs, including the basal *Incisivosaurus gauthieri*, have elongate dorsal and ventral dentary processes. The external surface of the dentary is covered in neurovascular foramina, which are concentrated towards the anterior symphyseal region (Figs. 2.16C, E, 2.18). These foramina suggest that the dentary was covered by a keratinous rhamphotheca in life similar to what is seen in modern birds and turtles (Bubien-
Waluszewska, 1981). The medial surface of the dentary is not readily visible in any of the three specimens (except a small anterior portion in IGM 100/973, although no morphology can be assessed); however CT imagery shows a medial contact with the straplike splenial along the posteroventral process (Fig. 2.24E). The straplike morphology is also found in caenagnathids and other oviraptorids but not in basal forms like *Incisivosaurus gauthieri* and *Caudipteryx zoui*, which have a more triangular morphology to their splenial.

**Surangular (Figs. 2.16 and 2.18)**

The surangular makes up the majority of the lateral surface of the posterior body of the mandible, continuing from its anterior articulations with the dentary posteriorly near the mandibular articulation with the cranium. The surangular articulates with the dorsal process of the dentary anterodorsally, angular along its ventral margin, and articular posteriorly. CT imagery shows the medial contact of the surangular with the prearticular (Fig. 2.24E). The surangular sits within a fossa on the prearticular. The anterior end of the surangular and the dentary make up the majority of the mandibular fenestra as they do in all oviraptorosaurs. As is characteristic of oviraptorids (but not caenagnathids or basal oviraptorosaurs), the enlarged surangular spine projects into the mandibular fenestra. In *Khaan mckennai*, however, the spine extends less than halfway across the length of the opening. This distance is far less than the three-quarters length of the mandibular fenestra that the surangular spine extends in *Citipati osmolskae* and other large oviraptorids (see Zamyn Khondt oviraptorid, IGM 100/42; Osmolska et al., 2004)
and does not appear to be a result of breakage (Fig. 2.16C, 1.18). The posterior end of the surangular tapers along the articulation with the articular, ending just under the mandibular articulation surface with the cranium. The surangular does not contribute to the mandibular articulation and is not fused into a surangular/articular/coronoid complex as it is in caenagnathids (Currie et al., 1993). The posterior region of the lateral surface of the surangular has a shallow fossa that is longitudinally oriented, probably for the attachment of the adductor muscles. Just posterior to the adductor fossa a small foramen pierces the lateral surface of the surangular (Fig. 2.16C, 1.18). A small foramen also is present in Citipati osmolskae in this same position.

Angular (Fig. 2.22)

The angular is difficult to see in any of the specimens, but can be observed in the CT images (Fig. 2.22A). The splintlike element extends approximately two-thirds of the length of the mandibular fenestra underlying the dentary and reaches posteriorly to the mandibular articulation. The posterior end tapers and does not reach the level of the retroarticular process as it does in Citipati osmolskae.

Prearticular (Fig. 2.24E)

Most of the prearticular is located on the medial (labial surface) of the mandible and therefore is partially obscured by matrix. Externally, the ventral surface of the prearticular is visible adhering to the ventral surface of the articular along this element’s midline. CT imagery shows the prearticular articulating with the surangular medially, the
angular ventrally, and the articular posteromedially (Figs. 2.22, 2.23, 2.24E). The element is shallow along its entire length and extends to the posterior end of the retroarticular process as it does in all oviraptorosaurs.

Articular (Fig. 2.16C)

The entire articular is visible only in IGM 100/973 (Fig. 2.16C). The articular makes up all of the dorsal surface of the mandibular articulation with the cranium as well as the dorsal surface of the retroarticular process, which lies immediately posterior to the articulation. The articular contacts the prearticular anteriorly along the midline of its ventral surface and surangular along its lateral surface. CT images show that the articular surface of the articular is entirely convex (Fig. 2.22A), as in all other oviraptorids and caenagnathids. *Avimimus portentosus* and therizinosaurs differ from this morphology and instead possesses a cotyle (Kurzanov, 1981, 1987; Clark et al., 1994). *Caudipteryx zoui* appears to possess a cotyle rather than the sliding articular joint characteristic of oviraptorids and caenagnathids (contra Ji et al., 1998). The dorsal surface of the mandibular articulation of the articular flares laterally beyond the margins of the mandibular ramus. The slender and elongate retroarticular process is a distinctive characteristic of oviraptorids (Maryanska et al., 2002; Lu et al., 2004; Lu 2005; Turner et al., 2007). This process in *Khaan mckennai* makes up approximately one-fifth of the entire length of the mandible (Table 2.1).
**Splenial (Fig. 2.16B)**

The splenial is exposed only in IGM 100/973 along the medioventral surface of the mandible (Fig. 2.16B, D). From what can be gleaned from such limited exposure, the splenial lies along the medial surface and extends from the anterior region of the dentary posteriorly to just beyond the mandibular foramen (at about the midpoint of the adductor fossa). This arrangement corresponds well with that in *Citipati osmolskae* but differs from *Incisivosaurus gauthieri*, in which the splenial expands dorsally at its anterior end (Xu et al., 2002). CT imagery shows that, similar to the condition in all other oviraptorosaurs, the splenial is elongate and straplike (Figs. 2.22B and 2.24E) (Sternberg, 1940; Maryanska et al., 2002).

**HYOID (Fig. 2.16B)**

A pair of hyoid elements is preserved in specimen IGM 100/973 of *Khaan mckennai* (Fig. 2.16B). These likely are the ceratohyals and closely resemble those of *Citipati osmolskae* (compare Fig. 2.16B with Clark et al., 2002:Fig. 20). The ceratohyals are small and rodlike and approximately one-half of the length of the mandible. They do not, however, curve medially as they do in *Citipati osmolskae*; instead, the ceratohyals approach being completely straight. These elements bend only slightly laterally at their posterior ends. The anterior and posterior extremities are expanded and somewhat compressed mediolaterally as in *Citipati osmolskae*. The hyoid elements are preserved parallel to the mandibular rami.
POSTCRANIAL DESCRIPTION

*Khaan mckennai* provides a unique opportunity to observe both articulated and disarticulated postcranial skeletons. Same as the skull, the postcranium of IGM 100/973 has been disarticulated and includes the pelvis and hindlimbs. No forelimb for IGM 100/973 is preserved. IGM 100/1127 and IGM 100/1002 remain in articulation with both fore- and hindlimbs (Figs. 2.14 and 2.15). The description of the forelimbs, therefore, comes exclusively from these specimens. The holotype (IGM 100/1127) is the best preserved of all the skeletal elements except for a few dorsal vertebrae, which are disarticulated and dispersed. Some appear to be missing but likely underlie the skeleton. IGM 100/1002 also preserves the postcranial skeleton almost in its entirety except for an incomplete caudal series. Only the seven proximal caudal vertebrae are present in IGM 100/1002, as the remainder of the tail was lost to erosion. Because the descriptions of the forelimbs and vertebral column are based on the two specimens still encased in blocks, not all of the surfaces can be described.

The postcranial skeleton of *Khaan mckennai* is gracile when compared to the much larger and more robust skeleton of *Citipati osmolskae*. It possesses a morphology that more closely resembles the crestless small oviraptorid *Conchoraptor gracilis*. *Ingenia yanshini*, though considered a small oviraptorid, is larger than *Khaan mckennai*. As stated above, a complete vertebral column does not exist for any of the specimens of *Khaan mckennai*; yet, using a composite of the two articulated specimens (IGM 100/1127 and IGM 100/1002) a rough estimate of the total number of vertebrae can be attained at
approximately 57. This number is consistent with other oviraptorid taxa (see Barsbold, 1997; Osmolska et al., 2004). Oviraptorosaurs such as *Caudipteryx zoui* and *Nomingia gobiensis* are exceptional in having a reduction in the number of caudal vertebrae (Ji et al., 1998; Barsbold et al., 2000).

*Cervical vertebrae (Figs. 2.26 and 2.27)*

The cervical series in oviraptorosaurs typically is composed of 12–13 vertebrae (Osmolska et al., 2004), with *Citipati osmolskae* and *Caudipteryx zoui* each having 12 cervical vertebrae (Ji et al. [1998] gives the vertebral count as ten, but personal observation revises this number to at least 12—this earlier count might not have included the atlas and axis). Both articulated specimens of *Khaan mckennai* have 13 cervical vertebrae including the atlas, axis, and cervicodorsal vertebra. A long neck is a characteristic of oviraptorosaurs in general; whereas, other theropods typically possess fewer than 10 cervical vertebrae (e.g., Wellnhofer, 1992; Norell and Makovicky, 1997; 1999; Novas, 1997). Although, the atlas is not visible in any of the specimens, the best example of an axis is seen in IGM 100/1002 (Fig. 2.27). Only the dorsal, lateral, and part of the anterior surfaces of the axis are exposed in this specimen. The overall morphology of the axis closely approximates that of other small oviraptorids such as *Conchoraptor gracilis* and *Ingenia yanshini* (Barsbold, 1981; Osmolska et al., 2004). A small odontoid process is visible on the anterior articular surface just ventral to the neural canal. The dorsal surface of the neural arch bears a subtriangular spine oriented posteriorly similar to other oviraptorid taxa. The spine is minimally taller than the succeeding cervical vertebra.
Figure 2.26. Cervical vertebrae. A, dorsal surface of cervical vertebral series in IGM 100/1127; B, lateral surface of cervical vertebral series in IGM 100/1002.
Figure 2.27. Dorsal surface of axial vertebra in IGM 100/1002.
A small oval pleurocoel is present on the axis (Fig. 2.27). This opening also is present in *Citipati osmolskae*, but is much larger (as are pleurocoels in all subsequent cervical vertebrae as well). In *Citipati osmolskae* the posterior surface of the neural spine of the axis is pneumatized; however, this surface is not exposed in *Khaan mckennai*.

The postaxial cervical vertebrae are best seen in dorsal view in IGM 100/1127. IGM 100/1002 provides a detailed view of the lateral surface of this series (Fig. 2.26B). The anterior (approximately three to five) postaxial vertebrae are distinctive from the more posterior ones in having a rectangular neural arch in dorsal view, being relatively shorter and fatter than the elongate cervical vertebrae of *Citipati osmolskae*. This rectangular morphology of *Khaan osmolskae* is a result of a lamina of bone extending between the zygapophyses and transverse processes as well as the zygapophyses being oriented almost parallel to each other (Fig. 2.26A). The zygapophyses of the first preserved cervical vertebra in *Oviraptor philoceratops* (AMNH 6517) also are oriented parallel to each other. The zygapophyses in both *Khaan* and *Oviraptor* tend to spread more laterally in the more posterior cervical vertebrae. The ‘webs’ of bone between the transverse processes and postzygapophyses become more excavated towards the posterior end of the cervical column in addition to the lateral spreading of the zygapophyses; thus, producing the distinctive x-shape of oviraptorosaur cervical vertebrae (Fig. 2.26A) (Makovicky and Sues, 1998). The neural spine on all postaxial vertebrae is low, rectangular and centered on the neural arch (at the intersection of the ‘x’). The neural spine becomes longer in more posterior vertebrae (this morphology is shared by *Oviraptor philoceratops*, but appears to be the opposite of the arrangement in *Citipati*
osmolskae, where the neural spine becomes shorter and more triangular). The base of the postzygapophyses, beginning with the third postaxial vertebra, has a posterolaterally facing fossa with an associated pneumatic foramen. At the base of the anterior and posterior surfaces of the neural spine of all the postaxial cervical vertebrae there are large fossae and pneumatic foramina; therefore, both the centra and neural arches are pneumatized. In Citipati osmolskae and Conchoraptor gracilis, the ventral surface of the base of the transverse processes also possesses a pneumatic fossa with associated foramina. It is likely that this structure also is present in Khaan mckennai, but the surface is not exposed.

The centra of the cervical vertebrae are not extensively exposed in either of the specimens; nonetheless, they are best seen in IGM 100/1002. The centra are more easily visible in the posterior cervical vertebrae (Fig. 2.26B). The cross-sectional shape of the centra appears to be rectangular (wider than tall), although shape is difficult to determine because of lack of exposure. All cervical vertebrae possess a single pleurocoel on the lateral surface of the centra, as is the arrangement in all oviraptorosaurs and most theropods in general except Microvenator celer, which has two pleurocoels on each cervical vertebra (Makovicky and Sues, 1998). The pleurocoels in Khaan mckennai are placed anteriorly on the anterior centra and gradually move towards the center of the lateral face proceeding towards the posterior end of the column. The articular faces of the centra are not visible, the posterior articular faces of the anterior cervical vertebrae (through the fourth cervical) appear to be directed posterodorsally with the succeeding anterior face corresponding to the posterior face (directed anteroventrally). The extreme
slant of the articular faces is present in all oviraptorids and possibly caenagnathids (i.e., *Chirostenotes pergracilis*; Sues, 1997), but does not appear to be present in more basal forms such as *Caudipteryx zoui* (Ji et al., 1998) or *Avimimus portentosus* (Kurzanov, 1987). This condition gradually changes proceeding posteriorly along the cervical series as the articular faces become more vertical in orientation. The cervical ribs are tightly fused to the vertebrae in *Khaan mckennai*; however, the third and fourth cervical ribs appear to be unfused (Fig. 2.26B). This is also the case in *Citipati osmolskae* with the anterior cervical ribs remaining unfused. Fused cervical ribs also are found in *Avimimus portentosus*, *Oviraptor philoceratops*, and *Conchoraptor gracilis* among oviraptorosaurs (Kurzanov, 1987; Osmolska et al., 2004) but not in *Caudipteryx zoui* (Ji et al., 1998; Zhou et al., 2000). In the anterior cervical vertebrae the cervical ribs do not extend past the associated centrum; however, the cervical ribs extend well past the margin of the associated centra in more posterior cervical vertebrae, a condition also found in *Citipati osmolskae*. The cervicodorsal vertebra lies at a transitional point between the cervical and dorsal vertebrae (Osmolska et al., 2004), and is marked by expanded transverse processes that are oriented laterally and horizontally (Fig. 2.26B). *Oviraptor philoceratops* shares a similar morphology of the flared transverse processes; however, this vertebra is not as distinctively shaped in *Citipati osmolskae*.

**Dorsal vertebrae (Fig. 2.28)**

There are approximately ten dorsal vertebrae present in *Khaan mckennai*. This number is considerably larger than that of *Citipati osmolskae* (IGM 100/978) and
Caudipteryx zoui, which only have seven (Ji et al., 1998; Zhou et al., 2000). The dorsal vertebral column of IGM 100/1127 is not articulated and not all dorsal vertebrae are preserved; therefore, the description of this region is based primarily on IGM 100/1002 (Fig. 2.28), except when features are visible only in the disarticulated series (i.e., articular surfaces of the centra). The dorsal and lateral surfaces of the vertebrae are exposed in IGM 100/1002. The dorsal surface of the neural arches in this region, like the cervical vertebrae, has a centrally placed neural spine. The neural spine in the anterior part of the series is rectangular as it is in Oviraptor philoceratops and Citipati osmolskae, but in Khaan mckennai the neural spine is shorter than that of the cervical series. This condition changes proceeding posteriorly along the dorsal vertebral column, as the spine becomes slightly longer and more robust. In Oviraptor philoceratops the neural spine is longer than that found in its cervical vertebrae, and the neural spine of Citipati osmolskae is long throughout the entire series but becomes progressively taller proceeding posteriorly. This is also the arrangement found in the more basal Caudipteryx zoui. The pre- and postzygapophysis of Khaan mckennai are oriented almost parallel to the midline. The transverse processes of the anterior dorsal vertebrae are expanded beyond the prezygapophyses and have rounded distal ends that are oriented almost horizontally, similar to the processes present in the anterior dorsal vertebrae of Oviraptor philoceratops. The transverse processes towards the posterior end of the dorsal column become shorter with rectangular distal ends. Again, this differs from Citipati osmolskae, which has short transverse processes throughout the dorsal series. The excavations of fossae within the neural arch are the same in dorsal vertebrae as in cervical vertebrae.
Figure 2.28. Dorsal vertebrae in IGM 100/1002. A, dorsal surface; B, lateral surface.
These fossae, however, are more extensive than in the cervical series, and a bony strut now divides the ones at the base of the neural arches, a condition shared with *Citipati osmolskae*.

The centra of the dorsal series are spool shaped as they are in most maniraptorans (Fig. 2.28). The circular articular surfaces are flat to minimally concave towards the posterior end of the series; this feature cannot be assessed in *Citipati osmolskae* due to damage to the articular surfaces of the centra. All dorsal vertebrae have an anteroposteriorly elongate pleurocoel (much larger than is present in the cervical series) that is centered on the lateral surface of the centrum. The pleurocoel gets larger in the dorsal vertebrae towards the posterior end of the column, a feature that also occurs in *Citipati osmolskae*. The pleurocoels present in *Citipati osmolskae*, however, are significantly larger, relatively and absolutely. Although only the anteriormost dorsal vertebrae can be seen in *Oviraptor philoceratops* (AMNH 6517), the pleurocoels share the same basic morphology as those in *Khaan mckennai*. Among oviraptorosaurs only *Avinimus portentosus* and *Caudipteryx zoui* lack dorsal pleurocoels (Ji et al., 1998; Osmolska et al., 2004). Along the ventral edge of the centrum (in lateral view) on the first three to four dorsal vertebrae is an extremely expanded hypapophysis. This structure is anteriorly placed but extends almost the entire length of the vertebra. A hypapophysis is present in most oviraptorosaurs, including *Oviraptor philoceratops*, *Citipati osmolskae* (only present on the first two dorsal vertebrae) and *Chirostenotes pergracilis* (Sues, 1997), although the morphology differs among taxa. In *Khaan mckennai*, the hypapophysis extends the anteroposterior length of each centrum and has a rectangular
distal end. The process is relatively short (not being longer than the centrum is tall). The hypapophysis present in *Citipati osmolskae* also extends from the anterior end of the ventral centrum as it does in *Khaan mckennai*; however, the shape is more elongate, curving anteriorly with a rounded distal end. The full extent of the shape of the hypapophyses cannot be assessed in *Oviraptor philoceratops*. Dorsal to the hypapophysis in IGM 100/1002 is a circular parapophysis on the lateral surface of the centrum just ventral to the level of the pleurocoel. The dorsal ribs of *Khaan mckennai* are relatively thin in comparison to *Citipati osmolskae* and *Oviraptor philoceratops*, but otherwise closely resemble those taxa.

**Sacrum (Fig. 2.29)**

The sacral vertebrae for the most part are not visible. Two anterior sacral vertebrae (IGM 100/1127) and one posterior sacral vertebra (IGM 100/1002) are the only ones that can be observed (Fig. 2.29). The remainder of the series is obscured by the ilium. The posterior sacral vertebra that is visible is distinguished by its greatly expanded, fused sacral ribs. The ribs extend approximately four times the width of the vertebral centrum and have a large pleurocoel on the dorsal surface at their base. The distal end of each sacral rib expands where it contacts the ilium. The neural spines are not fused together (at least at the posterior end of the series); however, they are knoblike and extend posteriorly. A small fossa is visible on the posterior surface of the neural spine. The postzygapophyses are small and extend posterolaterally.
Figure 2.29. Sacral vertebrae. A, anterior sacral vertebra in IGM 100/1002; B, posterior sacral vertebra in IGM 100/1127.
Caudal vertebrae (Fig. 2.30)

A nearly complete series of caudal vertebrae is present in IGM 100/1127 (Fig. 2.30); only one or two of the very distalmost caudal vertebrae may be missing. The first seven caudal vertebrae are the only ones preserved in IGM 100/1002. Approximately 28 vertebrae are present in the caudal series, which is less than the 32 vertebrae present in *Citipati osmolskae*. Caudal vertebral numbers for oviraptorosaurs in general are reduced, which is also the condition in the putative sister group to Oviraptorosauria, Therizinosauria (27 caudal vertebrae in *Alxasaurus*, Russell and Dong, 1993).

*Caudipteryx zoui* has a more extreme reduction of the tail, having only 22 caudal vertebrae. The proximal caudal vertebrae in *Khaan mckennai* are visible in dorsal view in both specimens. They possess narrow but long transverse processes that are oriented posterolaterally and are slightly curved (Fig. 2.30), similar to the morphology of *Citipati osmolskae*. The distal end of the transverse processes are rounded in more anterior caudal vertebrae but become rectangular and expanded at the distal end as one proceeds posteriorly (also in *Citipati osmolskae*). The transverse processes towards the posterior end of the tail become shorter; however, their width remains the same giving them a short but comparatively robust appearance in the posterior region. Thus, as the size of the vertebrae decreases more abruptly at the distally, the transverse processes eventually disappear (the exact number cannot be assessed; however this disappearance occurs in the final four vertebrae of *Citipati osmolskae*). As is the case in all oviraptorosaurs, *Khaan mckennai* lacks a distinct transition point in the tail (Osmolska et al., 2004). A neural spine is present in all of the caudal vertebrae that are preserved and has a morphology
Figure 2.30. Caudal vertebrae in IGM 100/1127.
that is low and posteriorly inclined along the entire length of the caudal series. The spine is located more posteriorly on the neural arch than it is in either the cervical or dorsal vertebrae. The anterior and posterior surfaces of the base of the neural spine bear fossae as they do in the rest of the vertebral column. The prezygapophyses are spread wider than the postzygapophyses. Overall, the length of the zygapophyses is short, extending less than half the length of the adjoining vertebra unlike the distinctive elongate zygapophyses that are present in dromaeosaurids. As in *Citipati osmolskae*, the pneumaticity in the neural arches of the caudal vertebrae of *Khaan mckennai* becomes increasingly reduced towards the distal end of the tail.

The centra of the proximal caudal vertebrae are not observable. For most of the length of the caudal series only the dorsal surface is exposed, but the tail of IGM 100/1127 twists laterally at its distal end exposing the lateral surface of the vertebrae in this region (approximately the last five vertebrae). These distal caudal vertebrae lack a pleurocoel on their lateral surface. It cannot be determined where this absence first occurs in *Khaan mckennai*; however, in *Citipati osmolskae* the 27th caudal vertebra is the first to completely lack a pleurocoel. The distal caudal centra are concave along their ventral surface when viewed laterally, which agrees with the morphology of *Citipati osmolskae*. The anterior and posterior surfaces of the centra are not visible. There does not appear to have been a pygostyle (fused caudal vertebrae) like what is described for *Nomingia gobiensis* (Barsbold et al., 2000) and *Caudipteryx zoui* (Ji et al., 1998).
Chevrons (Fig. 2.30)

Several chevrons are visible articulating with the proximal four vertebrae of the tail in IGM 100/1127 (Fig. 2.30). Although they are not visible along the entire length of the tail, it is likely that chevrons were present as they are in *Citipati osmolskae* (IGM 100/978), *Conchoraptor gracilis*, *Nomingia gobiensis*, and *Caudipteryx zoui* (Ji et al., 1998; Barsbold et al., 2000; Zhou et al., 2000). In *Khaan mckennai*, the chevrons are dorsoventrally elongate and flattened mediolaterally. There is a slight curvature along the shaft such that the posterior border is concave unlike *Nomingia* or *Ingenia*. The chevrons are slenderer than the same elements in *Nomingia gobiensis* (Barsbold et al., 2000) but have a similar morphology to those from the same region of the tail in *Citipati osmolskae* and *Caudipteryx zoui* (Ji et al., 1998; Zhou et al. 2000). As in most other maniraptorans, the chevrons become shallower and more dorsoventrally elongate towards the distal end of the tail.

Sternum (Fig. 2.31)

Paired sternal plates are preserved in many oviraptorosaurs including *Caudipteryx zoui* and *Citipati osmolskae*; although, these elements are fused into a single sternum in *Ingenia yanshini*. The sternum of IGM 100/1127 is preserved in articulation, but overlying ribs, gastralia, and one of the humeri obscure the ventral surface (Fig. 2.31A). The general shape can be gathered from IGM 100/1002, which is not preserved in articulation but whose dorsal surface is completely exposed (Fig. 2.31B). The paired
Figure 2.31. Sternal plates. **A**, IGM 100/1127; **B**, IGM 100/1002.
ossified sterna are thin plates of bone with no obvious articular surfaces for either the
coracoid or sternal ribs. This absence does not preclude these articulations from having
occurred in life as they are easily seen in *Citipati osmolskae* (IGM 100/978). In *Khaam
mckennai*, the anterior edge of the sternum is straight and slants slightly posterolaterally.
The medial margin is straight, and the sterna appear to have contacted each other along
this edge (Fig. 2.31A). The posterior margin of the element slants towards the anterior
margin (anterolaterally). The lateral margin is the only part of the sternum that preserves
any structures. This border has a deep notch that probably bore articulations with the
sternal ribs, as is the case in *Caudipteryx zoui* and *Citipati osmolskae* (IGM 100/979) (Ji
et al., 1998; Clark et al., 1999). This notch is bordered by two processes, one anteriorly
and one posteriorly. The homologies of these processes are not completely understood;
however, it is likely that they correspond to the anterolateral (anterior) and the xiphoid
(posterior) processes that are present in other oviraptorosaurs (Clark et al., 1999;
Osmolska et al., 2004). The xiphoid processes are found also in paravians including
modern avians (Hwang et al., 2002).

*Scapulocoracoid (Fig. 2.32)*

The scapula and coracoid of *Khaan mckennai* are fused into a single element with
no trace of a suture except inside the glenoid fossa (Fig. 2.32). A fused scapulocoracoid is
present in most oviraptorids in which these elements are found (e.g. *Citipati osmolskae*
and *Ingenia yanshini*), but not the more basal taxa (e.g., *Caudipteryx zoui* and
*Microvenator celer*; Ostrom, 1970; Currie and Russell, 1988; Ji et al., 1998; Makovicky
and Sues, 1998). An unfused scapulocoracoid, however, is also found in *Conchoraptor*. The glenoid fossa faces posteroventrally in *Khaan mckennai*; although, it is directed laterally in the oviraptorids *Citipati osmolskai* and *Chirostenotes pergracilis* (Turner et al., 2007). The scapulocoracoid overall is bowed as it is in *Oviraptor philoceratops*, with an angle between the two elements being approximately 150–160 degrees (Osmolska et al., 2004), thus lacking the distinctive ‘L’-shape of dromaeosaurs (Norell and Makovicky, 1999). The scapular blade is elongate and straplike (making up two-thirds of the entire element—including the coracoid), as it is in oviraptorids. This blade expands slightly distally and has a blunt end similar to other oviraptorosaurs but differing from the pointed scapular blade present in paravians (Fig. 2.32). The scapula possesses a large acromion process along its dorsal edge that is inflected anterolaterally providing a large dorsal surface for articulation of the furcula. This orientation also is observed in other oviraptorids such as *Oviraptor philoceratops*, *Citipati osmolskai*, and *Conchoraptor gracilis* (Omsolska et al., 2004). Most coelurosaurians (excluding paravians) as well as the basal oviraptorosaur, *Caudipteryx zoui*, possess a more dorsally oriented acromion process (Lu, 2005). *Ingenia yanshini*, however, has a more pronounced acromion process than that of *Khaan mckennai*.

The coracoid of *Khaan mckennai* is similar to all oviraptorosaurs being quadrangular in shape and having a large distally tapering caudoventral process that extends just past the glenoid (Fig. 2.32). On the anterolateral surface of the coracoid is an extensive process that corresponds to the coracoid tubercle. This same process was described as the ‘biceps tubercle’ in Osmolska et al. (2004), but see Makovicky and
Figure 2.32. Scapulocoracoid. A, dorsal surface of right scapulocoracoid in IGM 100/1002; B, dorsal surface of right scapulocoracoid in IGM 100/1127.
Norell (1999) for discussion. The large tubercle is present in other oviraptorosaurs including basal forms such as *Caudipteryx zoui* as well as the more derived *Citipati osmolskae*, *Conchoraptor gracilis*, and *Oviraptor philoceratops* (although shape cannot be determined in *Oviraptor philoceratops* because of damage to this surface in AMNH 6517). The coracoid foramen is so small as to be hardly noticeable in *Khaan mckennai*, much smaller than the foramen that is present in the more basal *Caudipteryx zoui* and other derived oviraptorids such as *Oviraptor philoceratops* (see Osmolska et al., 2004:fig. 8.2G). The small oval-shaped foramen in *Khaan mckennai* is positioned just below the coracoid tubercle on its posterior side. IGM 100/1127 lacks a subglenoid fossa on the posterolateral surface, distinguishing the coracoid from that of paravians (Makovicky and Norell, 2004).

**Furcula (Fig. 2.33)**

The furcula is not unlike that of other maniraptoran furculae (Nesbitt et al., 2009). It has an interclavicular angle (~90°) that corresponds closely with *Oviraptor philoceratops* and *Heyuannia huangi* (Nesbitt et al., 2009) and overall possesses a dorsoventrally flattened morphology (Fig. 2.33). The suture along the midline symphysis is not easily visible. The lateral process expands approximately midway along its length and tapers distally after this point. The tapered distal edge, epicleidium, contacts the pectoral girdle (Fig. 2.33). Along the midline of the furcula, a large hypocleidium protrudes ventrally as it does in all oviraptorosaurs except *Caudipteryx zoui* (Nesbitt et al., 2009). The length of the hypocleidium cannot be determined because the ventral
Figure 2.33. Furcula. A, dorsal surface of furcula in IGM 100/1002; B, dorsal surface of furcula in IGM 100/1127.
portion of this structure is not exposed in either specimen, but it does not appear to be as
elongate as that of either *Oviraptor philoceratops* or *Citipati osmolskae.*

**Humerus (Fig. 2.34)**

Humeri in both IGM 100/1127 and 100/1002 are preserved. IGM 100/1127
preserves the humerus in medial and anterior views; whereas, IGM 100/1002 preserves
the humerus in lateral view (Fig. 2.34). The humerus of *Khaan mckennai* is
approximately 31% of the entire forelimb length including the manus and 80% of the
forearm length without the hand (Table 2.2, measurements taken from the holotype, IGM
100/1127), not unlike the proportions found in other maniraptorans (Ostrom, 1969; Norell
and Makovicky, 2004). Overall the shaft is straight with slight torsion at midshaft
(Osmolska et al., 2004). The deltopectoral crest is expanded, stretches for over one-third
of the length of the element (Table 2.2), and has an angular apex towards the distal end of
the crest. This same morphology is found in other derived oviraptorids like *Citipati
osmolskae, Ingenia yanshini,* and *Oviraptor philoceratops* but differs from more basal
oviraptorosaurs such as *Avimimus portentosus* (Kurzanov, 1987) and *Microvenator celer*
(Makovicky and Sues, 1998), and the bizarre oviraptorid *Gigantoraptor erlianensis* (Xu
et al., 2007). All of these taxa have rounded deltopectoral crests. Therizinosauria possess a
deltopectoral crest morphology similar to that found in derived oviraptorids (Zanno,
2006). The articular head of the humerus is not well developed in *Khaan mckennai.* A
small transversely elongate articular surface is present on the anterior surface of the
proximal end of the humerus (best seen in IGM 100/1127, Fig. 2.34B, C). The distal
Table 2.2. Selected measurements (in mm) from the postcranial skeleton of *Khaan mckennai*.

<table>
<thead>
<tr>
<th></th>
<th>IGM 100/973</th>
<th>IGM 100/1127</th>
<th>IGM 100/1002</th>
</tr>
</thead>
<tbody>
<tr>
<td>left humerus length</td>
<td>-</td>
<td>110.5</td>
<td>-</td>
</tr>
<tr>
<td>right scapulocoracoid length</td>
<td>-</td>
<td>154.1</td>
<td>167.0</td>
</tr>
<tr>
<td>right scapula length</td>
<td>-</td>
<td>124.7</td>
<td>138.6</td>
</tr>
<tr>
<td>(from glenoid to distal end)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>right humerus length</td>
<td>-</td>
<td>108.6</td>
<td>117.5</td>
</tr>
<tr>
<td>right radius length</td>
<td>-</td>
<td>~102.0</td>
<td>95.3</td>
</tr>
<tr>
<td>right ulna length</td>
<td>-</td>
<td>96.5</td>
<td>~101.6</td>
</tr>
<tr>
<td>right metacarpal I length</td>
<td>-</td>
<td>-</td>
<td>24.7</td>
</tr>
<tr>
<td>right metacarpal II length</td>
<td>-</td>
<td>47.3</td>
<td>50.4</td>
</tr>
<tr>
<td>right metacarpal III length</td>
<td>-</td>
<td>44.4</td>
<td>47.6</td>
</tr>
<tr>
<td>right digit I length</td>
<td>-</td>
<td>-</td>
<td>99.4</td>
</tr>
<tr>
<td>right digit II length</td>
<td>-</td>
<td>138.1</td>
<td>135.8</td>
</tr>
<tr>
<td>right digit III length</td>
<td>-</td>
<td>125.1</td>
<td>122.4</td>
</tr>
<tr>
<td>sternum length</td>
<td>-</td>
<td>58.8</td>
<td>55.1</td>
</tr>
<tr>
<td>sternum width (widest point)</td>
<td>-</td>
<td>43.9</td>
<td>50.7</td>
</tr>
<tr>
<td>left ilium length</td>
<td>193.5</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>left ischium length</td>
<td>133.1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>left pubis length</td>
<td>156.8</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>left femur length</td>
<td>188.8</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>left tibia length</td>
<td>221.4</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>left fibula length</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>left metatarsal I length</td>
<td>26.7</td>
<td>-</td>
<td>23.3</td>
</tr>
<tr>
<td>left metatarsal II length</td>
<td>82.8</td>
<td>-</td>
<td>91.2</td>
</tr>
<tr>
<td>left metatarsal III length</td>
<td>97.7</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>left metatarsal IV length</td>
<td>87.3</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>right ilium length</td>
<td>187.5</td>
<td>182.0</td>
<td>186.0</td>
</tr>
<tr>
<td>right femur length</td>
<td>199.0</td>
<td>185.0</td>
<td>196.0</td>
</tr>
<tr>
<td>right tibia length</td>
<td>224.0</td>
<td>212.0</td>
<td>232.0</td>
</tr>
<tr>
<td>right fibula length</td>
<td>-</td>
<td>201.0</td>
<td>214.0</td>
</tr>
<tr>
<td>right metatarsal I length</td>
<td>~23.0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>right metatarsal II length</td>
<td>89.9</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>right metatarsal III length</td>
<td>98.8</td>
<td>-</td>
<td>105.6</td>
</tr>
<tr>
<td>right metatarsal IV length</td>
<td>93.9</td>
<td>~95.0</td>
<td>98.3</td>
</tr>
<tr>
<td>right metatarsal V length</td>
<td>35.8</td>
<td>-</td>
<td>35.9</td>
</tr>
</tbody>
</table>
Figure 2.34. Humerus. A, lateral surface of right humerus in IGM 100/1002; B, posterior surface of right humerus in IGM 100/1127; C, Medial surface of right humerus of IGM 100/1127 showing deltopectoral crest.
condyles are not exposed in their entirety in any of the specimens. All that can be said is that they are rounded, and the medial condyle extends further ventrally than the lateral condyle, similar to oviraptorids such as *Conchoraptor gracilis* and *Citipati osmolskae*.

**Ulna (Fig. 2.35)**

The ulna is exposed only in lateral view in both specimens (Fig. 2.35). It is short, approximately 28% of the entire length of the forelimb including the manus (Table 2.2). The relative length of the ulna is approximately the same in *Khaan mckennai* than *Oviraptor philoceratops*, 89% and 88% the length of the humerus respectively. The shaft of the element is bowed posteriorly as it is in maniraptorans (Norell and Makovicky, 1999) but differing from the oviraptorid *Ingenia yanshini* and *Rinchenia mongoliensis*, which have a straight ulna (Osmolska et al., 2004). The shaft tapers distally and a shallow depression is present on the lateral surface of the ulna. This structure likely served as an articulation point for the triceps tendon. The proximal end of the ulna has a subtriangular articular face that is angled anterodorsally (visible in IGM 100/1002; Fig. 2.35A) for articulation with the humerus and radius. The olecranon process is not well developed, typical of all oviraptorosaurs including the basal *Caudipteryx zoui* as well as oviraptorids such as *Conchoraptor gracilis* and *Citipati osmolskae* (Osmolska et al., 2004). The distal articular surface is not exposed in either specimen; therefore, it cannot be determined if this surface expands as it does in *Citipati osmolskae* and *Oviraptor philoceratops*.
Figure 2.35. Radius and ulna. **A**, lateral surface of radius and ulna in IGM 100/1002; **B**, lateral surface of radius and ulna in IGM 100/1127.
**Radius (Fig. 2.35)**

The radius is preserved in both articulated specimens of *Khaan mckennai* and, as with the ulna, is exposed only in lateral view (Fig. 2.35). The proximal and distal ends are most easily visible in IGM 100/1002. The radius is approximately the same length as the ulna (Table 2.2). Overall the element is similar to *Oviraptor philoceratops* and possesses a straight, mediolaterally-compressed shaft. The radial shaft in *Citipati osmolskae* is curved anteriorly; however, the lack of a curvature in the radius of *Khaan mckennai* may be a result of its orientation. A small oval divot is present on the lateral surface about one-third of the length from the distal end of the element. The radial shaft is the same width along its length, somewhat narrower than the ulna, and expands at the extremities. The distal end of the radius extends beyond the distal end of the ulna as it does in *Oviraptor philoceratops*. The articular surfaces are not visible.

**Manus (Fig. 2.36)**

Beautifully preserved hands are present in both articulated specimens of *Khaan mckennai*, including carpals, metacarpals and phalanges (Fig. 2.36). The best example of a complete hand is found in IGM 100/1002. Although little can be discerned about the morphology of the wrist bones, there are at least three separate elements present, as are present in other maniraptorans (Fig. 2.36A). *Avimimus portentosus* possesses a distinct morphology of the hand in having a marked reduction in the number of phalanges in digit III (i.e., Kurzanov, 1987; Osmolska et al., 2004). *Khaan mckennai*, however, has a
typical theropod phalangeal formula of 2-3-4, as do *Citipati osmolskae*, *Ingenia yanshini*, *Oviraptor philoceratops*, and *Caudipteryx zoui*. Digit II in *Khaan mckennai* is the longest, followed by digit III and finally digit I. The metacarpals remain unfused along their length; *Avimimus portentosus* and *Oviraptor philoceratops* being the only reported oviraptorosaurs in which the metacarpals are fused proximally (Osborn, 1924; Kurzanov, 1987; Osmolska et al., 2004). The length of the metacarpals in *Khaan mckennai* reflects that of the digits as a whole, with MC II being the longest followed by MC III, and finally MC I.

Metacarpal I is robust and the shortest of any of the metacarpals, about half of the length of MC II (Table 2.2). The entire lateral surface of MC I is adhered to the posteromedial surface of MC II. The distal articular surface of MC I is strongly concave in dorsal view (Fig. 2.36A), and the proximal surface appears to have a straight contact with the carpals. This straight contact differs from most observed oviraptorids, including *Oviraptor philoceratops*, *Conchoraptor gracilis*, and *Citipati osmolskae*. These taxa have an articular surface of MC I that slants proximally towards MC II in dorsal view. *Caudipteryx zoui*, however, has a morphology similar to that of *Khaan*. Metacarpal II is approximately twice the length of MC I (Table 2.2), similar to all other oviraptorosaurs. This element is straight and the proximal articulation surface is ventrolaterally slanted in dorsal view. The proximal articulation surfaces of metacarpals I and II are at the same level. Metacarpal II also has a concave distal articulation surface. Metacarpal III is long and narrower than the other two metacarpals. Its proximal articulation surface lies slightly ventral to that of MC I and II, and it likely did not contact the distal carpals (Fig.
Figure 2.36. Manus. **A**, Right manus of IGM 100/1002; **B**, right manus of IGM 100/1127.
Oviraptorids in general seem to differ from this condition in possessing a contact with the distal carpals in taxa in which this region is visible (Oviraptor philoceratops and Citipati osmolskae [Clark et al., 1999]). The distal articulation surface, however, lies in the same plane as that of MC II and has a convex-shaped surface (Fig. 2.36A). The medial and lateral surfaces of the metacarpals cannot be seen.

Digit I is by far the most robust of the three digits. Phalanx I-1 is long, almost twice the length of MC I, and curves slightly dorsally. The dorsal curvature is much more pronounced than in Citipati osmolskae (Clark et al., 1999) or Oviraptor philoceratops, which has a straight phalanx I-1. A deep ligament pit is located on the distal trochlea near the dorsal surface. The ungual phalanx associated with digit I is the largest of any on the hand and, like the penultimate phalanx, the most extensively curved. This disparity in curvature is more pronounced in Khaan than in either Citipati osmolskae or Oviraptor philoceratops. Unlike the ungual phalanges of manual digital II and III, there is no dorsal lip on the articular surface (Fig. 2.36). The dorsal lip also is reduced on the ungual of digit I in Citipati osmolskae (Clark et al., 1999:fig. 5), present in Oviraptor philoceratops, and absent in all digits in Caudipteryx zoui. The phalanges of digit II in Khaan mckennai are more slender than those of digit I. The two proximal phalanges are approximately the same length, which is slightly shorter than phalanx I-1. A distinct ligament pit can be seen on the lateral side of phalanx II-2 in IGM 100/1002. The ungual phalanx for digit II is approximately the same length as the ungual phalanx in digit I but lacks the extreme curvature, differing from Oviraptor philoceratops, whose ungual
phalanx I is shorter than that of digit II. The ungual phalanx of digit II in *Khaan mckennai* is also narrower dorsoventrally than is that of digit I. The phalanges of digit III are shorter than those of the other two digits. Phalanges III-1 and III-2 are approximately the same length (Table 2.2), and their additive length is longer than that of digit III, a distinctly oviraptorosaur feature (Maryanska et al., 2002). Ligament pits are visible on the lateral surfaces of the phalanges of digit III; however, these are much shallower than those present on the phalanges of digits I and II, similar to the depth apparent in both *Citipati osmolskae* and *Oviraptor philoceratops*. The ungual phalanx of digit III in *Khaan mckennai* is shorter than that of digit II and also possesses the dorsal lip above the proximal articular surface.

*Ilium (Figs. 2.37 and 2.38)*

The ilium, ischium, and pubis are not fused; therefore, each element is described individually. The ilium is well preserved in all three specimens of *Khaan mckennai* (Figs. 2.37 and 2.38). The ilia are not fused, and it is impossible to infer whether they contacted each other medially along the dorsal edge. A contact between these elements is unlikely as the mediodorsal surface of each ilium shows no indication of a contact point with its pair. They do, however, appear to diverge from each other posteriorly as suggested by the lateral flexure of the dorsal margin, a feature also present in other maniraptorans (Norell and Makovicky, 1997). The pre- and postacetabular portions of the ilium are approximately the same length, the morphology apparent in most oviraptorids (although the preacetabular portion is longer in the oviraptorids *Rinchenia mongoliensis* and
Figure 2.37. Ilium. **A**, Lateral surface of right ilium in IGM 100/1002; **B**, lateral surface of right ilium in IGM 100/1127.
Figure 2.38. Ilium of IGM 100/973. A, lateral view of right ilium (top) and medial view of right ilium (bottom); B, lateral view of left ilium (top) and medial view of left ilium (bottom).
*Nomingia gobiensis*, and the caenagnathid *Chiros tenotes pergracilis*, but shorter in *Avimimus portentosus* [Osmolska et al., 2004]). The dorsoventral height of the ilium is approximately the same along the length of the element except for a ventrally expanded preacetabular process. This rounded process extends anterodorsally from the anteriormost region of the ilium (as do all oviraptorosaurs except *Avimimus portentosus*; Figs. 2.37 and 2.38), but does not reach as far ventrally as in *Caudipteryx zoui* where it extends beyond the ventral margin of the pubic peduncle (Ji et al., 1998). The preacetabular process borders a weakly developed cuppedicus fossa anterolaterally (preacetabular fossa of Hutchison [2001]) on the ventral edge of the element. The cuppedicus fossa is more or less a flat shelf on the ventral surface of the preacetabular process similar to the morphology of other oviraptorosaurs except *Caudipteryx*, which has a well-developed cuppedicus fossa (Ji et al., 1998; Zhou et al., 2000; Osmolska et al., 2004). The dorsal margin of the ilium has a flat profile from the anterior end to the level of the ischiadic peduncle. The flat dorsal margin is similar to most oviraptorosaurs but differs from the apomorphic, curved ilium of *Rinchenia mongoliensis* (Barsbold, 1986; Osmolska et al., 2004), *Nomingia gobiensis* (Barsbold et al., 2000), and *Caudipteryx zoui* (Ji et al., 1998; Zhou and Wang, 2000; Zhou et al., 2000). Posterior to the acetabulum, the dorsal edge is slightly rounded as it tapers to a blunt posterior margin (Figs. 2.37 and 2.38). The supracetabular rim is not well developed so that there is little overhang. An antitrochantor is present but not pronounced, being almost confluent with the supracetabular rim. This condition is apparent in almost all oviraptorosaurs except *Avimimus portentosus*, which has a strongly pronounced antitrochantor (PIN 3907; Kurzanov,
1987). On the medial surface of the ilium an expanded crista curves from the posterior end of the ilium anteriorly to about halfway along the length of the postacetabular process. The ridge then turns and extends straight anteroventrally to the ischiadic peduncle. The space between the crista and the ventral surface of the ilium forms the small ventromedially facing brevis fossa. The pubic peduncle exceeds the length of the ischiadic peduncle ventrally. The ischiadic peduncle extends straight ventrally; however, the pubic peduncle is medially inflected.

Pubis (Fig. 2.39)

The distal end of the pubis is not visible in either IGM 100/1127 or 100/1002; therefore, most of the description of this element is based on the disarticulated specimen, IGM 100/973 (Fig. 2.39). Only the left pubis is preserved in IGM 100/973. Hence, it can be assumed that the pubic elements were not fused distally as they are in *Citipati osmolskae* and *Nomingia gobiensis*. The pubis of *Khaan mckennai* is extremely delicate, as are all of the pelvic elements (especially true in IGM 100/973). The shaft of the element is strongly concave anteriorly—a character tying together all oviraptorosaurs (except *Avimimus portentosus*, which has an almost straight morphology; Kurzanov, 1987). The pubic boot is expanded both anteriorly and posteriorly, with the anterior process being much more developed than the posterior process (A pubic boot is present in all oviraptorosaur taxa; however, the extent to which the pubic boot projects both anteriorly and posteriorly varies among taxa. Osmolska et al., 2004). Although the morphology is probably correctly reflected, the distal end of the shaft is damaged in IGM
Figure 2.39. Lateral view of pubis in IGM 100/973.
100/973. The shaft is mediolaterally compressed distally and becomes more rounded towards the proximal end. A pubic apron extends medially from the proximal end of the shaft to about halfway along its length. The pubic apron of *Citipati osmolskae* is located more distally on the shaft. The proximal end of the pubic apron in *Khaan mckennai* is located along the anterior edge of the shaft, but it ends (distally) along the midline of the shaft. The apron is poorly developed but clearly visible.

*Ischium (Fig. 2.40)*

The ischium is present in all specimens of *Khaan mckennai*, but the morphology is somewhat divergent between them (Fig. 2.40). The convergent morphology in all specimens is typical of oviraptorosaurs in general in that the ischium is short and concave laterally (although *Chirostenotes pergracilis* has a more flattened lateral surface of the ischium, Sues, 1997). The shaft is mediolaterally compressed. The differences between the specimens in the ischial morphology is seen best in the morphology of the obturator process and the associated distal edge. In IGM 100/973 the obturator process is located distally along the shaft and is rounded. In IGM 100/1002 the obturator process has the same placement but is much more pronounced than in the other specimen, tapering to almost a point with a rounded distal end (Fig. 2.40A). The distal surface of the ischium from the obturator process to the distal end in this specimen is concave; whereas, it is straight in IGM 100/973, *Citipati osmolskae, Ingenia yanshini, Nomingia gobiensis*, and *Caudipteryx zoui* (Fig. 2.40B; although see IGM 100/978). The distal surface of the ischium is smooth in IGM 100/1002 but roughened in IGM 100/973. IGM 100/973 may
Figure 2.40. Ischium. **A**, lateral view of right ischium in IGM 100/1002; **B**, lateral view of right ischium in IGM 100/973.
represent an ontogenetically immature specimen. It cannot be assessed if the ischia contact or even approach each other medially as they do in *Avimimus portentosus*, *Conchoraptor gracilis*, *Chirostenotes gracilis*, and *Ingenia yanshini* (Barsbold et al., 1990; Osmolska et al., 2004).

**Femur (Figs. 2.41 and 2.42)**

The femur of *Khaan mckennai* is relatively gracile. IGM 100/973 preserves both femora, and parts of this element also are exposed in both articulated specimens (Figs. 2.41 and 2.42). Neither femur of IGM 100/973 preserves a complete trochanteric crest. The matrix has been prepared to reflect the shape of a crest, yet this shape should not be taken as a real feature (Fig. 2.41). The trochanteric crest is preserved in IGM 100/1002 but only the posterolateral surface is exposed. It does show, however, that the femur has a relatively low greater trochanteric crest similar to what is displayed in other oviraptorids (Fig. 2.42B); but, the lesser trochanter is not exposed in this specimen. The entire lateral surface of the trochanteric crest is visible in IGM 100/1127 and displays morphology similar to what has been described for other oviraptorosaurs including *Caudipteryx zoui* (Fig. 2.42A) (Osmolska et al., 2004). The distinct greater trochanteric crest is broad. The lesser trochanteric crest is at the same level as the greater trochanter, not displaced ventrally in relationship to it as in dromaeosaurs (Ostrom, 1990; Norell and Makovicky, 2004). The trochanteric crests are separated from each other by a deep groove, but are still pressed firmly together (Fig. 2.42A). This differs from the single crest (fused greater and lesser trochanters) that is present in *Citipati osmolskae* (IGM 100/978 and IGM
Figure 2.41. Right femur of IGM 100/973. A, anterior view; B, posterior view; C, lateral view; D, medial view; E, distal view; F, proximal view.
Figure 2.42. Femur. **A**, posterior view of left femur in IGM 100/1127; **B**, lateral view of right femur in IGM 100/1002.
100/1004; Turner et al., 2007) or the deep notch in *Microvenator celer* (Ostrom, 1970; Makovicky and Sues, 1998); thus, more variation exists in this character in oviraptorids than was previously acknowledged. A large foramen (likely a nutrient foramen) is found on the medial surface of the trochanteric crest in *Khaan mckennai* (also in *Citipati osmolskae*). The greater and lesser trochanters in *Khaan mckennai* are separated from the spherical femoral head by a slightly constricted femoral neck. Again differing substantially from *Citipati osmolskae* in which no neck is present, instead there is a confluent surface from the trochanter to the femoral head. No fourth trochanter could be distinguished on any of the specimens of *Khaan mckennai*; this structure also is lacking in other oviraptorids (Osmolska et al., 2004), troodontids (Currie and Dong, 2001), and some dromaeosaurs (Norell and Makovicky, 1999); however, a fourth trochanter is present in therizinosaurians (Clark et al., 2004). In *Khaan mckennai*, a muscular scar is present along the shaft in the region where a fourth trochanter would be expected to reside (Fig. 2.41). This roughened surface also is present in *Citipati osmolskae*. No ventral vascular foramen could be found in this area on *Khaan mckennai*, although present in other theropods including *Citipati osmolskae* (Norell and Makovicky, 1999). *Khaan mckennai* also lacks an accessory crest like that present in *Caudipteryx zoui*, *Microvenator celer*, and *Nomingia gobiensis*.

The femoral shaft is subtriangular in cross section caused by a rounded ridge running on the anterior surface from the lesser trochanter across to the medial condyle. This same crest is also present in *Citipati osmolskae* though not as pronounced, and it does not influence the shape of the femoral shaft. The distal region of the femur is poorly
preserved on both sides of IGM 100/973, but IGM 100/1002 provides a good example of
the posterior surface of this area (Fig. 2.42B). The distal condyles are separated from
each other, and as in other oviraptorosaurs, the lateral (fibular) condyle extends further
distally than the medial condyle (Osmolska et al., 2004). The tibiofibular crest is very
distinct in oviraptorids, and this taxon also possesses an extensive crest that projects
posteriorly beyond the level of the medial condyle (Fig. 2.42B). The extent of the
tibiofibular crest is much more pronounced in *Khaan mckennai* than in *Citipati
osmolskae*. A distinct but relatively shallow popliteal fossa is present between the two
distal condyles. There also is a small ectepicondyle (not present in *Citipati osmolskae*); however, the entepicondyle is not pronounced.

*Tibia (Figs. 2.43 and 2.44)*

The right tibia of IGM 100/973 is extremely well preserved in three dimensions.
The tibia is elongate (approximately 113% of the length of the femur; Table 2.2) with a
pronounced cnemial crest that is inflected only slightly laterally (Fig. 2.43; Osmolska et
al., 2004). The cnemial crest of *Khaan mckennai* is more gracile, does not project as far,
and lacks the distinct boss that is present on the distal end of the crest in *Citipati
osmolskae* and *Nomingia gobiensis*. The extension of the cnemial crest onto the tibial
shaft in IGM 100/973 is limited to about the proximal one-fifth of the element; it ends at
the proximal extent of the fibular crest. The fibular crest is preserved on the lateral
surface of the tibia in a proximal position and is more pronounced than the one in *Citipati
osmolskae*. Directly posterior to the fibular crest is a small foramen, likely a nutrient
Figure 2.43. Tibiae and fibulae of IGM 100/973. A, anterior surface of left tibia and fibula; B, posterior surface of right tibia; C, anterior surface of right tibia; D, left lateral surface of right tibia; E, right lateral surface of right tibia; F, detail of anterior surface of proximal end of right tibia showing the astragalus and calcaneum; G, distal surface of right tibia.
Figure 2.44. Tibia and fibula. **A**, posterior surface of right tibia and fibula in IGM 100/1002; **B**, posterior surface of right tibia and fibula in IGM 100/1127.
foramen, with a short dorsal groove associated with it. This foramen and groove are not present on the tibiae in all specimens of *Khaan mckennai*, nor is it present in *Citipati osmolskae*. Thus, the foramen appears to be intraspecifically variable. The tibia becomes more anteroposteriorly flattened distally. The astragalus (described below) is preserved in articulation, so that the anterior surface of the distal end of the tibia is not visible in any of the specimens. The posterior surface of the distal tibia bears a shallow fossa between the condyles of the astragalus, and a distinct tubercle for the attachment of a branch of the fibularis muscle is present on the lateral surface of the distal end.

*Fibula* (Figs. 2.43 and 2.44)

The fibula is preserved in all three specimens and extends from the proximal head of the tibia to contact the distal lateral condyle of the calcaneum (Figs. 2.43 and 2.44). The proximal head of the fibula is expanded anteroposteriorly as in *Citipati osmolskae*, but lacks the mediolateral flattening present in that taxon. The proximal shaft of the fibula of *Khaan mckennai*, instead, is triangular in cross section. Approximately one-third down the length of the shaft is a rounded, anteriorly inflected iliofibularis tubercle. The shaft then tapers as it continues distally to contact the calcaneum.

*Astragalus and calcaneum* (Fig. 2.43)

The astragalus and calcaneum of IGM 100/973 are well preserved and articulated to the right tibia (Fig. 2.43). Neither of these elements is fused to each other or the tibia. The astragalus spans the width of the distal end of the tibia. The two condyles on the
articular surface are separated by a wide shallow depression. The ascending process of the astragalus spans the entire width at the distal condyles but tapers proximally on the antero-distal surface of the tibia. The height of the ascending process is greater than the width across the widest point as it is in all oviraptorosaurs (Table 2.2), differing from the morphology of therizinosaurs. The lateral condyle is more fully developed than the medial condyle; although, the medial condyle extends further anteriorly (also present in Citipati osmolskae). The lateral condyle has a distinct lateral depression in which the calcaneum sits. The calcaneum is preserved in articulation on this same specimen. As would be expected, the calcaneum is similar to other maniraptorans morphologically and is preserved only as a small tab of bone (Fig. 2.43).

Pes (Figs. 2.45 and 2.46)

The distal tarsals are not easily visible in any of the three specimens of Khaan mckennai, but they do not appear to be fused with the metatarsals as in the therizinosaur Elmisaurus rarus (Currie and Russell, 1988) or the basal oviraptorosaur Avimimus portentosus (Kurzanov, 1987). The tarsals of Citipati osmolskae also are partially fused to the metatarsus; therefore, this character may vary among oviraptorosaurs or may be ontogenetically correlated. Only one indistinct central tarsal is present on the left foot of IGM 100/973 (Fig. 2.46A, C). A small sliver of bone that is most likely a distal tarsal can be seen on the proximal end of MT IV on the right foot of IGM 100/1002 (Fig. 2.45). The distal tarsals; therefore, are interpreted as not being fused to the metatarsals in this specimen as well.
Figure 2.45. Feet of IGM 100/1002.
Figure 2.46. Feet of IGM 100/973. A, dorsal surface of left foot; B, palmer surface of left foot; C, dorsal surface of right foot; D, palmer surface of right foot.
**Khaan mckennai** preserves extraordinary examples of articulated feet in all three specimens (Fig. 2.46). The foot as a whole occupies approximately 32% of the entire length of the hindlimb (Table 2.2). Digits I–V are present in this taxon in all three specimens. The metatarsals are not fused at all along their length as they are in *Elmisaurus rarus* and *Avimimus portentosus* (Currie and Russell, 1988; Kurzanov, 1987); and the third metatarsal, although narrowing somewhat towards the proximal end, is exposed along its entire length. This condition is found in most oviraptorids; although, MT III is much more tightly constricted in *Caudipteryx zoui* and even *Citipati osmolskae* (Ji et al., 1998 and Clark et al., 1999, respectively). *Avimimus portentosus* and *Chirostenotes pergracilis* are the only oviraptorosaurs to have a true arctometatarsalian condition in which the proximal end of MT III is not exposed in anterior view (Kurzanov, 1987; Currie and Russell, 1988). None of the proximal articular surfaces of any of the metatarsals of *Khaan* are preserved. Only a roughened surface is present. MT I is highly reduced and represented by a small splint of bone on the distal end of the medial surface of MT II. MT I closely resembles the same element in other maniraptora taxa (see Norell and Makovicky, 1997). It is crescent shaped and possesses a subtle ligament pit (Fig. 2.46). The distal end of this metatarsal has a rounded articular surface that is visible medially. The entirety of digit V is reduced to a small splint along the proximal end of the lateral surface of MT IV and extends a little over one-third of the length of the metatarsus. MT III is the longest metatarsal; metatarsals II and IV are approximately the same length. Distal articular surfaces are not visible on the metatarsals. The medial and lateral surfaces appear to possess deep ligament foveae.
The phalangeal formula for *Khaan mckennai* is 2-3-4-5, which is the same as the traditional theropod formula. Digit III extends the furthest distally. The articular surfaces again are not visible, but all phalanges possess a deep ligament fovea on the lateral and medial surfaces. These pits are approximately circular in shape. A shallow pit is seen on the dorsal surface of the phalanges for the flexor muscles of the foot. These are pronounced in the proximal phalanges and gradually fade in the more distal ones. The phalangeal joints are symmetrical but are not ginglymoid. The ungual phalanges are slightly curved (distinct from the purported oviraptorosaur sister taxon therizinosaurs) with a shallow groove running along the medial and lateral surfaces that becomes deeper as it approaches the distal end of the phalanges.

**DISCUSSION**

The primary goal of this study is to put forth a relatively comprehensive osteological description for the oviraptorid coelurosaur, *Khaan mckennai*. To fully understand the morphology it is essential to put these observations within an evolutionary context. This study, therefore, looks at several specific characters within a phylogenetic framework based on the hypothesized relationships of taxa within Oviraptorosauria (Turner et al., 2007) to establish preliminary hypotheses of evolutionary transformations. Their optimization within oviraptorosaurs may in turn shed light on their larger pattern within Maniraptora.
Pneumaticity of the narial region (Figs. 2.16 and 2.18)

The most obvious distinction between oviraptorid taxa is the presence (e.g., *Citipati osmolskae*) or absence (e.g., *Khaan mckennai*) of a bony crest. This one character is likely correlated with a series of other characters such as the pneumatization of the fronto-nasal region and the presence or absence of a dorsal sinus. The development of a highly complex pneumatic and porous dorsal surface to the fronto-nasal region, however, is apparent in both *Khaan mckennai* and *Citipati osmolskae* (Fig. 2.16) and is considered to be characteristic of oviraptorids in general (Osmolska et al., 2004; Witmer, 1997; Turner et al., 2007). The morphology of the fronto-nasal pneumatic structures in *Citipati osmolskae* is more exaggerated than that of *Khaan mckennai*, and there is a definite distinction in the size of the dorsal nasal openings. The shape and dispersal of these pneumatic recesses on the dorsal surface of the nasal, however, are closely correlated between the two taxa. One large opening (nasal recess) resides directly dorsal to the antorbital fenestra almost in the center of the main body of the nasal, and several smaller accessory foramina are scattered around this one central opening. The large recess is raised above the level of the naris in *Citipati osmolskae* but is in the same horizontal plane in *Khaan mckennai*. The pattern of the accessory pneumatic openings, however, does not correlate exactly between these two taxa. The openings on the dorsal surface of the frontal, unlike the nasal, are limited to small circular foramina at the anteriormost margin of the element in both taxa. A bony strut running along the midline of the nasal separates the paired pneumatic structures.
Pneumatic recesses also appear in the nasal of the basal taxon *Incisivosaurus gauthieri* (Balanoff et al., 2009). Although pneumaticity is not as extensive in *Incisivosaurus gauthieri* as it is in either *Khaan mckennai* or *Citipati osmolskae*, its presence indicates that this facial feature is found in the entire oviraptorosaur lineage. Based on a tree of Oviraptorosauria (Fig. 2.17), one would predict that these structures are present in caenagnathids as well; however, known specimens do not include this region of the skull (Triebold and Russell, 1997; Sues, 1997; Triebold et al., 2000). Overlapping morphology in the fronto-nasal region of *Khaan mckennai*, *Citipati osmolskae*, and *Incisivosaurus gauthieri* includes the presence of a pair of pneumatic recesses (may be covered by extremely thin bone in *Incisivosaurus gauthieri*; Balanoff et al., 2009) on the dorsal surface of the nasal (Fig. 2.3A). The accessory foramina that appear in this region in both *Khaan mckennai* and *Citipati osmolskae*, however, are not present in *Incisivosaurus gauthieri*. The absence of these structures indicates that, although pneumaticity is present at the base of the lineage, it becomes much more extensive within the oviraptorid group (possibly Oviraptoridae + Caenagnathidae), finally culminating in the extreme morphology that is observable in crested taxa like *Citipati osmolskae* (Clark et al., 2002), *Oviraptor philoceratops* (Osborn, 1924; Smith, 1993; Clark et al., 2002), and *Rinchenia mongoliensis*. The presence of pneumatic recesses in both *Incisivosaurus gauthieri* and *Khaan mckennai* (crestless forms) also shows that this pneumaticity is not correlated strictly with the presence or absence of a bony casque in the narial region of the skull.
Dorsal sinus (Fig. 2.23)

Computed tomographic imagery reveals that both *Khaan mckennai* (IGM 100/973) and *Citipati osmolskae* (IGM 100/978) have a dorsal sinus that extends from the aforementioned fronto-nasal pneumatic openings posteriorly to join the dorsal tympanic sinuses (Fig. 2.23 and Clark et al. [2002]:fig. 7). This sinus not only extends almost the entire length of the skull, but also lies completely dorsal to the endocranial cavity. This feature, first described by Clark et al. (2002) in *Citipati* and later by Kundrat and Janacek (2007) in *Conchoraptor gracilis*, is found only among oviraptorosaurs and does not correlate with the presence or absence of a bony crest. The original description of this feature in *Citipati osmolskae* was not able to determine with certainty if bony struts were present subdividing this cavity. CT scans for *Khaan mckennai* (this study) and *Conchoraptor gracilis* (Kundrat and Janacek, 2007), however, clearly show a medial partition within the cavity indicating a paired structure (Fig. 2.23B, C). Based only on these two specimens the optimization of this division within Oviraptoridae cannot be clearly determined.

Although pneumatic recesses also are present in this region of the basal oviraptorosaur *Incisivosaurus gauthieri* (see Balanoff et al., 2009), these structures are not as extensive nor do they reach as far posteriorly over the endocranial cavity as those in oviraptorids. These sinuses in *Incisivosaurus gauthieri* extend posteriorly only into the anteirormost region of the frontal. Absence of these sinuses in taxa outside Oviraptorosauria (e.g., *Zanabazar junior*, Norell et al., 2009 and *Tsaagan mangas*, Norell et al., 2006) demonstrates that they are a unique feature in this group. The evolutionary
progression of this dorsal sinus in oviraptorosaurs appears to be an invasion of the frontal by a paired sinus early in their evolutionary history. Following an initial excavation of the frontal, the dorsal narial sinus progresses posteriorly to join the dorsal tympanic recess (Fig. 2.23). The bony division of the cavity may be lost in *Citipati osmolskae* (Clark et al., 2002) or may simply not be apparent in the CT imagery. The addition of caenagnathid taxa obviously would be useful in documenting the posterior progression of the sinuses along this lineage.

*Accessory antorbital fenestrae (Fig. 2.16, 1.18)*

The accessory antorbital fenestrae in the interfenestral bar of the maxilla are problematic in oviraptorosaurs, and few authors have attempted to work out their homologies with those of other coelurosaur (see Witmer, 1997 and Balanoff et al., 2009). The typical condition within Coelurosauria is the presence of at least one large accessory foramen (maxillary foramen) anterior to the antorbital fenestra and a smaller promaxillary fenestra that pneumatizes the maxilla and premaxilla anterior to the maxillary foramen (Witmer, 1997). The pattern present in oviraptorids (i.e., *Khaan mckennai* and *Citipati osmolskae*) departs from this model and surprisingly appears to correspond most closely to that described for the allosauroid *Sinraptor dongi* (Fig. 2.18) (Currie and Zhao, 1993b; Witmer, 1997). This arrangement includes a large promaxillary foramen anterior to the antorbital fenestra and a smaller maxillary fenestra immediately posterior and somewhat dorsal to the promaxillary foramen (Fig. 2.18). Although this may seem to be an unusual morphology within Coelurosauria, the identification is the
simplest based merely on their spatial distribution (although see contradictory labels on Conchoraptor gracilis in Osmolska et al., 2004:fig. 8.1G). One additional accessory foramen is present in the antorbital fossa of both Khaan mckennai and Citipati osmolskae. This accessory antorbital foramen is in the portion of the maxilla that forms the floor of the fossa. The foramen is anteroposteriorly elongate and extends ventrally to the promaxillary fenestra; although, Citipati osmolskae exhibits individual variation in that two foramina are present on the right side of the skull and only one on the left side. This opening does not correspond to any other observed coelurosaurs and appears to be an oviraptorosaur neomorph. In Khaan mckennai, at least two smaller foramina are positioned posterior to the promaxillary fenestra in a ventral location (Fig. 2.18).

The arrangement of the accessory antorbital fenestrae within Incisivosaurus gauthieri also is unique compared to most other coelurosaurs. Similar to Khaan mckennai and Citipati osmolskae, it shares a large promaxillary foramen and a small posterodorsally placed maxillary fenestra (Figs. 2.2 and 2.18). Incisivosaurus, however, does not possess a ventral fenestra that extends beneath the promaxillary foramen. It does have a small, circular foramen located immediately posteroventral to the margin of the promaxillary foramen (Figs. 2.2 and 2.18). All three taxa examined, accordingly, have the overlapping pattern of one large anteriorly placed foramen and at least one smaller foramen between this anterior foramen and the antorbital fenestra. This pattern suggests that the unique arrangement of antorbital accessory foramina (promaxillary and maxillary) evolved somewhere along the lineage leading to oviraptorosaurs. Unfortunately, the typically recovered sister taxon to Oviraptorosauria, Therizinosauria
(although see Zanno et al., 2009), does not possess accessory antorbital fenestrae (see *Erlikosaurus andrewsi*, Clark et al., 1994). This makes it difficult to optimize exactly where along the stem of this lineage the transformation occurred (Currie and Dong, 1993). The ventrally placed opening beneath the promaxillary fenestra appears first in oviraptorids, as there are no accessory openings in the antorbital fossa in known caenagnathids (i.e., *Chirotrognosaurus pergracilis*; Sues, 1997).

**Trigeminal foramen (Fig. 2.16)**

The trigeminal foramen (CN V) in *Khaan mckennai* and *Citipati osmolskae* is a small, single opening between the prootic and laterosphenoid (compare Fig. 2.16 with Clark et al., 2002:fig. 2 [mislabeled foramen ovalis, “foo”]). This differs from the condition in Therizinosauria (Clark et al., 1994) and tyrannosaurids (Witmer and Ridgely, 2009; Brusatte et al., 2009), in which there are two distinct openings for the separate branches (ophthalmic and maxillomandibular) of the trigeminal nerve. Crown avians also have two openings for the trigeminal branches (Baumel and Witmer, 1993). Deinonychosaurus and basal avialans, however, possess only a single trigeminal opening (Walker, 1985; Currie and Zhao, 1993a; Currie, 1997; Dominguez Alonso et al., 2004; Norell and Makovicky, 2004a; 2004b). A single opening is thought typically to correlate with a branching of the gasserian ganglion outside of the braincase, and two foramina with a branching of the ganglion within the braincase (Goodrich, 1930). The one opening in oviraptorids would suggest that this group had an external branching point of the trigeminal nerve. The morphology of *Incisivosaurus gauthieri*, however, indicates that
this interpretation might be incorrect. *Incisivosaurus gauthieri* possesses a single trigeminal foramen; however, this foramen is severely pinched at its midpoint (Fig. 2.12; Balanoff et al., 2009). It can be inferred from this morphology that *Incisivosaurus gauthieri*, and its outgroups (e.g., *Erlikosaurus andrewsi*; Clark et al., 1994), had a gasserian ganglion lying within the braincase that branched internally, but whose bony strut between the two openings did not fully ossify. If this scenario were correct, then an internal branching pattern would be the most parsimonious reconstruction for *Khaan mckennai* and *Citipati osmolskae*. Perhaps a secondary loss of the ossified strut between the foramina occurred early in oviraptorosaur history, making this morphology plesiomorphic for oviraptorids. *Chirostenotes pergracilis* has a morphological pattern very similar to that of *Incisivosaurus gauthieri* (Sues, 1997), indicating that a single, large trigeminal foramen is an oviraptorid characteristic. *Chirostenotes pergracilis*, like *Incisivosaurus gauthieri*, also possesses a pinched trigeminal foramen, but additionally has a fossa located directly behind the opening, suggesting that the gasserian ganglion sat in this fossa (Sues, 1997).

**Maxillary length (Fig. 2.16, 1.18)**

Clark et al. (2002) first noted that significant variances are present in the anterior-posterior length of the maxilla between oviraptorid taxa. The length of the maxilla intuitively would correlate with the shortening of the facial region as a whole. *Khaan mckennai* and *Citipati osmolskae* both possess shortened maxillae in lateral view relative to the overall length of the preorbital region (~63% and 75% of preorbital region length,
respectively; Table 2.1); however, the presence of a ‘long’ maxilla in both *Oviraptor philoceratops* (AMNH 6517) and *Chirostenotes pergracilis* (Sues, 1997) suggests that the shortening of the maxilla is not completely tied to the shortening of the facial region (Clark et al., 2004). Not surprisingly, *Incisivosaurus gauthieri* possesses a more elongate maxilla than either of the oviraptorids discussed above; however, because the facial region is not shortened in *Incisivosaurus* the elongate maxillary morphology is not reflected in the given ratio (~78%; Fig. 2.3). These data do suggest that a ‘short’ maxilla evolved within Oviraptoridae and may be diagnostic of a subclade containing both *Khaan mckennai* and *Citipati osmolskae*.

*Postcranium (Figs. 2.14 and 2.15)*

As is the case with other regions of the postcranial skeleton, the vertebral column of Oviraptoridae is heavily pneumatized. Both *Khaan mckennai* and *Citipati osmolskae* possess pleurocoels throughout the entire column with only the exception of the distalmost tail vertebrae (Figs. 2.14 and 2.15). Variation within the vertebral column appears to occur primarily in the extent of pneumatization in the cervical vertebrae. *Citipati osmolskae* possesses pleurocoels in the anteriormost cervicals that take the shape of large fossae, which pierce the entire centra so that one can see through to the opposite side of the vertebra. *Khaan mckennai* however lacks this dramatic feature, and instead possesses the more typical morphology of foramen-like pleurocoels that are present in other theropods (Fig. 2.26). More basal oviraptorosaurs such as *Caudipteryx zoui* also possess a nearly completely pneumatized vertebral column (Ji et al., 1998). The
pleurocoels of the cervical centra of *Khaan mckennai* are more similar to those present in *Caudipteryx zoui*. The extreme pneumatization appears, therefore, to have evolved at some point within the group Oviraptoridae and is possibly an autapomorphy of *Citipati*.

Similarly, the pneumatic features of the axial vertebra are much the same in *Khaan mckennai* and *Citipati osmolskae* as they are in the remainder of the cervical series. The axial vertebra of *Khaan mckennai* has a small foramen in the anterior/middle region of the lateral surface of the centrum (Fig. 2.27); whereas, that of *Citipati osmolskae* is a large fossa that pierces through the element. To complicate the pattern, *Conchoraptor gracilis* differs from both these specimens by not having any trace of a pleurocoel in the axial centrum. As it is not apparent whether *Caudipteryx zoui* possesses a pleurocoel in its axis or not, polarization of this character within Oviraptoridae is difficult.

A shortened tail has long been cited as a characteristic of all oviraptorosaurs for which relatively complete postcranial material is available (Osmolska et al., 2004). There are approximately 28 caudal vertebrae in *Khaan mckennai* and 32 vertebrae present in *Citipati osmolskae*. Maniraptorans in general typically have around 44 or fewer caudal vertebrae (Farlow et al., 2000); therefore, a reduction in the number of caudal vertebrae has definitely taken place within oviraptorids. *Caudipteryx zoui* and *Nomingia gobiensis*, however, take this reduction to a more extreme degree having no more than 20 and 22 caudal vertebrae, respectively (Ji et al., 1998; Barsbold et al., 2000). The predisposition for reduction of the number of tail vertebrae, therefore, took place early in the history of Oviraptorosauria. The reduction of caudal vertebrae has been cited as a potential
synapomorphy of an avialan and oviraptorosaur clade (e.g., Maryanska et al., 2002; Osmolska et al., 2004). Although these two clades do share a reduction in tail vertebrae, this similarity appears to be a convergent feature as there is no reduction in this region in deinonychosaurus, nor is there and indication of a pygostyle in deinonychosaurus or basal paravians. More data, however, are needed to properly map this feature on the coelurosaur tree.

In the pectoral girdle, the coracoid of Khaan mckennai has a morphology that overall is similar to other coelurosaurs except in the size of the coracoid foramen (Fig. 2.32). This foramen is extremely small in Khaan mckennai. Citipati osmolskae also possesses a reduced coracoid foramen (see Clark et al., 1999). The coracoid foramen in Caudipteryx zoui is relatively larger than that in oviraptorids and bears a morphology similar to that present in the purported sister taxon of Oviraptorosauria, Therizinosauria (see Falcarius utahensis; Zanno, 2006) as well as other maniraptorans (Currie and Dong, 2001). The presence of a large coracoid foramen in Caudipteryx zoui (Ji et al., 1998; Zhou et al., 2000) and Chirostenotes pergracilis (Currie and Russell, 1988) suggests that this structure is reduced somewhere at the base of Oviraptoridae.

Variation also is present in the shape of the trochanteric crest of the femur in oviraptorids (Fig. 2.30). This crest in Khaan mckennai is not unlike what has been previously described for oviraptorids (Osmolska et al., 2004). The morphology is made up of a lesser and greater trochanteric crest, each of which are approximately at the same level and separated only by a small groove (these structures are appressed tightly against one another). This arrangement differs significantly from the trochanteric crest of Citipati
Citipati osmolskae in which there is no indication of a groove separating the greater and lesser trochanters. These processes instead are fused in Citipati osmolskae forming a single arching trochanteric crest. The morphology of Caudipteryx zoui more closely resembles that of Khaan mckennai in that it also possesses a groove separating these two crests, which are at approximately the same level (Ji et al., 1998). The distribution of this character indicates that the morphology observed in Citipati osmolskae is derived for a more exclusive group within Oviraptoridae.

The degree of exposure of metatarsal III along the length of the metatarsus has been used extensively in coelurosaur systematics (see Holtz, 1996, 1998, 2001), and there indeed is some variation in this feature within Oviraptorosauria. Khaan mckennai has a MT III that remains visible along the length of the element with only a slight constriction near the proximal end (Fig. 2.46). Citipati has a MT III that looks much the same as that of Khaan mckennai but is slightly more constricted proximally (Clark et al., 1999:fig. 6). Although this overall morphology is similar to the condition in Caudipteryx zoui, that taxon has the most extreme constriction of the three taxa, maintaining visibility throughout the length but almost completely disappearing near its proximal end (Ji et al., 1998). Other oviraptorosaurs also have this extremely pinched morphology (e.g., the proximal end of MT III in Avimimus portentosus is not retained [Kurzanov, 1987]; see also Chirostenotes pergracilis [Currie and Russell, 1988; Sues, 1997]). The apparent evolutionary history of this feature, therefore, is the presence of an ‘arctometatarsalian’ condition in the basalmost taxa, followed by a loss of the condition within Oviraptoridae.
Although perhaps not useful as a phylogenetic character because it most likely encompasses changes of many features, the evolution of body size in Oviraptorosauria demonstrates an interesting evolutionary pattern. The taxa hypothesized to fall at the base of the oviraptorosaur tree all exhibit small body sizes (e.g., *Caudipteryx zoui* [Ji et al., 1998; Zhou and Wang, 2000; Zhou et al., 2000], *Avimimus portentosus* [Kurzanov, 1987], *Microvenator celer* [Ostrom, 1970; Makovicky and Sues, 1999]). The more derived caenagnathids and oviraptorids are the taxa that begin to develop larger body sizes culminating in the extraordinarily large *Gigantoraptor erlianensis* (Xu et al., 2007). This pattern corresponds to that suggested by Turner et al. (2007), in which taxa at the base of maniraptoran clades are small in size but may exhibit size increase within their individual clades. Overall, small body size at the base of these clades suggests that ‘miniaturization’ occurred early along the lineage leading to Avialae (Turner et al., 2007). The presence of small body size at the base of Oviraptorosauria may help push this transformation further down the maniraptoran tree.

**CONCLUSIONS**

*Khaan mckennai* is a crestless oviraptorid from the Late Cretaceous of Central Asia, which is known from very well preserved specimens. This study presents the most comprehensive description of a member of this group to date, using three specimens both disarticulated and articulated. Few accessible descriptive studies of oviraptorosaurs are available; therefore, I provide an important piece to understanding the morphological transformations within this bizarre group of dinosaurs. By making comparisons with
crested oviraptorids (i.e., *Citipati osmolskae*) and more basal oviraptorosaurs (i.e., *Incisivosaurus gauthieri* and *Caudipteryx zoui*) we provide a framework for setting up hypotheses that then can be tested by a more comprehensive phylogenetic analysis.

The unusual morphology of oviraptorosaurs has led several recent analyses (e.g., Maryanska et al., 2002; Lu et al., 2002, 2004; Osmolska et al., 2004) to recover a close relationship between Oviraptorosauria and Avialae. Characters such as a shortened tail and the loss of teeth are recovered as unambiguously supporting ties between Oviraptorosauria, *Archaeopteryx lithographica* and *Confuciusornis sanctus* (Maryanska et al., 2002). Other more inclusive analyses (e.g., TWiG [see Turner et al., 2007]; Holtz, 1998; Lu, 2005; Senter, 2006) consistently have recovered a phylogenetic position for Oviraptorosauria much further down the theropod tree, residing among non-avian coelurosaurs. Although its position within Coelurosauria is not constant among analyses (e.g., Holtz, 1998; Sereno, 1999; Turner et al. 2007; Zanno et al., 2009), Oviraptorosauria continues to fall outside of Avialae.

Not surprisingly, the majority of the characters that have been used to link Oviraptorosauria with Avialae are from the cranium. Very few postcranial characters are cited as being synapomorphic for these two groups. A lack of postcranial characters may be affecting the results of these analyses because many of the ‘avian’ characters are centered around the loss of teeth (Maryanska et al., 2002; Osmolska et al., 2004). Descriptions such as the one presented here are instrumental in presenting new data, including endocranial as well as postcranial morphology, to researchers. These analyses can then hopefully be used to help elucidate the acquisition of characters along the
oviraptorosaurian lineage. Working out the transformations within Oviraptorosauria not only clarifies the evolutionary changes within this group, but also within the broader spectrum of Coelurosauria.
CHAPTER THREE
PHYLOGENETIC RELATIONSHIPS OF OVIRAPTOROSAURIA

INTRODUCTION

The phylogenetic debate concerning the relationships within Oviraptorosauria is a recent one, just becoming prominent in the past decade (Maryańska et al., 2002; Osmólska et al., 2004; Lü et al., 2004; Lü, 2005). This surge of interest largely reflects the growth of available specimens. Oviraptorosaurs long were known only by a handful of specimens, most notably *Oviraptor philoceratops*, which was collected by R.C. Andrews and Walter Granger on the initial American Museum of Natural History expeditions into the Gobi Desert of Mongolia in the 1920s--described in the same iconic paper that introduced *Velociraptor mongoliensis* and *Saurornithoides mongoliensis*; Osborn [1924]). The more recent discovery of rich paleontological sites such as the Late Cretaceous Ukhaa Tolgod in the Nemegt Basin of Mongolia (Dashzeveg et al., 1995; Dingus et al., 2008) and the taxonomic reassignment of previously known specimens (e.g., *Microvenator celer*, a North American specimen from the Early Cretaceous Cloverly Formation originally described by Ostrom [1970] as a “coelurid” [see Makovicky and Sues 1998]) are the most notable factors driving recognized diversification within the group. Although many oviraptorosaur specimens are well preserved (especially those from central Asia), a consensus regarding phylogenetic relationships within the group has yet to emerge.
The majority of published analyses that consider Oviraptorosauria are aimed at the broader relationships within Coelurosauria (e.g., Gauthier, 1986; Holtz, 1998; Sereno, 1999; TWiG analyses [e.g., Hwang et al., 2004; Norell et al., 2006; Turner et al., 2007]; Rauhut, 2003; Senter, 2007; Zanno et al., 2009). These studies consistently recover a monophyletic Oviraptorosauria (Barsbold, 1976) diagnosed by a ventrally curving, pendant-shaped paroccipital processes, a thin or absent coronoid ossification, and a slender retroarticular process of the mandible. Less clear is the sister taxon of Oviraptorosauria within Coelurosauria. Most studies, including those most recently published, conclude that Oviraptorosauria does not have a privileged relationship with avialans, but rather is one of several clades of non-avian coelurosaurs (Fig. 3.1). As non-avialan coelurosaurs, oviraptorosaurs have been recovered as the sister taxon to Therizinosauria (Sues, 1997; Holtz, 1998; Makovicky and Sues, 1998; Hwang et al., 2002; Turner et al., 2007) or as the sister to Paraves (Sereno, 1999; Rauhut, 2003; Senter, 2007; Zanno et al., 2009). Alternatively, Oviraptorosauria has been recovered in a position even closer to the origin of crown birds, as the sister taxon of *Confuciusornis sanctus* within Avialae (Paul, 2002; Lü et al., 2002; Maryánska et al., 2002; Osmólska et al., 2004; Fig. 3.1). The matrix of Maryánska et al. (2002) is especially noteworthy as it forms the basis for most subsequent analyses including all of the relatively few studies directed specifically at the relationships within Oviraptorosauria (i.e., Lü, 2002; Maryánska et al., 2002; Lü et al., 2004; Osmólska et al., 2004; Lü, 2005).

Since its inception as a recognized taxon, Oviraptorosauria was conceived to include two primary subclades, Oviraptoridae and Caenagnathidae (Barsbold, 1976, 1981; Sues, 1997; Makovicky and Sues, 1998; Maryánska et al., 2002; Osmólska et al.,
Figure 3.1. Phylogenetic hypotheses of Oviraptorosaur relationships. 

A, Maryanska et al. (2002); B, Osmolska et al., (2004); C, Lu et al. (2004); D, Lu (2005); E, modified from Turner et al. (2007); F, Zanno et al. (2009).

Note that trees A and B position oviraptorosaurs within Avialae, making them secondarily flightless birds. Oviraptorosauria indicated by black dot.
Figure 3.1 (cont). Phylogenetic hypotheses of Oviraptorosaur relationships. 
A, Maryanska et al. (2002); B, Osmolska et al., (2004); C, Lu et al. (2004); D, Lu (2005); E, modified from Turner et al. (2007); F, Zanno et al. (2009). Note that trees A and B position oviraptorosaurs within Avialae, making them secondarily flightless birds. Oviraptorosauria indicated by black dot.
Figure 3.1 (cont). Phylogenetic hypotheses of Oviraptorosaur relationships. 
A, Maryanska et al. (2002); B, Osmolska et al., (2004); C, Lu et al. (2004); D, Lu (2005); E, modified from Turner et al. (2007); F, Zanno et al. (2009). 
Note that trees A and B position oviraptorosaurs within Avialae, making them secondarily flightless birds. Oviraptorosauria indicated by black dot.
2004; Turner et al., 2007; Fig. 3.1). In contrast, little consensus exists for what taxa comprise these clades, the topology of their intraclade relationships, and the taxonomic composition of their mutual stem (the stem of the Caenagnathidae + Oviraptoridae clade) (Fig. 3.1). It is likely these inconsistencies largely reflect a lack of consistency in the terminal taxa considered. For example, Maryańska et al. (2002) and Osmólska et al. (2004) (Fig. 3.1.A, B) both recover an Oviraptoridae composed of *Ingenia yanshini*, *Conchoraptor gracilis*, *Oviraptor philoceratops* (based on specimen IGM 100/42), and *‘Oviraptor’ mongoliensis* (also known as *Rinchenia mongoliensis*; Barsbold, 1997), a Caenagnathidae composed of *Chirostenotes pergracilis* and *Nomingia gobiensis*, and a mutual stem that includes *Caudipteryx zoui* and *Avimimus portentosus* (successively more basal; Fig. 3.1A, B). Neither of these studies considered *Microvenator celer* and *Incisivosaurus gauthieri*, both of which are likely basal within Oviraptorosauria and therefore likely to influence the arrangement of the remaining forms. In addition, taxon sampling, especially at the base of the clade, has considerable potential for influencing the topology of more inclusive clades (Huelsenbeck, 1991) and for breaking long branches that often separate larger groups (e.g., Gauthier et al. 1988). Inconsistent sampling of taxa likely to form the base of the oviraptorosaur radiation therefore presents a problem in need of resolution. This issue is especially pressing considering the potential of outgroup selection to influence the optimization of character evolution within the in-group (Watrous and Wheeler, 1981). Considering the possibility that oviraptorosaurs lie within Avialae, detailed analysis of their phylogenetic history is essential for understanding the acquisition characters along the ancestral lineage of crown birds. The avian-like morphology so apparent in Oviraptorosauria, and which was recognized at
their initial discovery (Sternberg 1940) may reflect unique features inherited from a common ancestor with birds (oviraptorosaurs as avialans), features independently evolved (convergence), or a deeper evolutionary history for these “avian” features than previously appreciated.

The primary objectives of this chapter is a species-level analysis of the phylogenetic relationships within Oviraptorosauria and a reanalysis of the position of Oviraptorosauria within Coelurosauria. These analysis are the most taxonomically comprehensive and character rich to date (within Oviraptorosauria) and provide the opportunity to address important questions of character evolution along the avian stem.

MATERIALS AND METHODS

TAXONOMIC SAMPLING

Because previous analyses of oviraptorosaur relationships differ foremost in the range of taxa that are included (Fig. 3.1), this study comprises a species-level analysis that uses attempts all oviraptorosaur taxa for which relatively complete specimens are available (Table 3.1). This analysis incorporates a more refined outgroup than previously studies by omitting taxa that have been shown to be far removed from the ingroup, such as *Herrerasaurus ischigualastensis* and *Coelophysis bauri* (see Maryańska et al., 2002; Osmólska et al., 2004; Lü, 2005), and expanding the number of relevant taxa (i.e., includes troodontids, alvarezsaurids, *Incisivosaurus gauthieri*, and *Microvenator celer* which were excluded from Maryańska et al., 2002 and Osmólska et al., 2004).
Table 3.1. List of taxa included in phylogenetic analysis.

<table>
<thead>
<tr>
<th>Oviraptorosauria</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Incisivosaurus gauthieri</em> Xu et al. 2002</td>
</tr>
<tr>
<td>IVPP V 13326 (skull and mandible)</td>
</tr>
<tr>
<td><em>Caudipteryx zoui</em> Ji et al., 1998</td>
</tr>
<tr>
<td>NGMC 97-4-A (holotype)</td>
</tr>
<tr>
<td>NGMC 97-9-A</td>
</tr>
<tr>
<td>IVPP V 12430</td>
</tr>
<tr>
<td>IVPP V 12344</td>
</tr>
<tr>
<td><em>Similcaudipteryx</em> He et al. 2008</td>
</tr>
<tr>
<td>IVPP V 12556</td>
</tr>
<tr>
<td><em>Avimimus portentosus</em> Kurzanov 1981</td>
</tr>
<tr>
<td>PIN 3907/1 (holotype)</td>
</tr>
<tr>
<td>IGM unnumbered</td>
</tr>
<tr>
<td><em>Protarchaeopteryx robusta</em> Ji and Ji, 1997</td>
</tr>
<tr>
<td>NGMC 2125</td>
</tr>
<tr>
<td>NGMC 97-9-A</td>
</tr>
<tr>
<td><em>Chirostenotes pergracilis</em> Gilmore 1924</td>
</tr>
<tr>
<td>CMN 2367 (holotype)</td>
</tr>
<tr>
<td>CMN 8538 (=<em>Macrophalangia canadensis</em>)</td>
</tr>
<tr>
<td>CMN 8776 (=<em>Caenagnathus collinsi</em>)</td>
</tr>
<tr>
<td>RTMP 79.20.1</td>
</tr>
<tr>
<td>ROM 43250</td>
</tr>
<tr>
<td><em>Microvenator celer</em> Ostrom 1970</td>
</tr>
<tr>
<td>AMNH 3041 (holotype)</td>
</tr>
<tr>
<td><em>Elmisaurus rarus</em> Osmólska 1981</td>
</tr>
<tr>
<td>ZPAL MgD-I/98 (postcranium)</td>
</tr>
<tr>
<td><em>Nomingia gobiensis</em> Barsbold et al., 2000</td>
</tr>
<tr>
<td>IGM 1/119 (holotype)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Oviraptoridae</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nemegtia barsboldi</em> Lü et al., 2004</td>
</tr>
<tr>
<td>IGM 100/2112 (holotype)</td>
</tr>
<tr>
<td><em>Oviraptor philoceratops</em> Osborn, 1924</td>
</tr>
<tr>
<td>AMNH 6517 (holotype; skull and postcranium)</td>
</tr>
<tr>
<td>IGM 100/791</td>
</tr>
<tr>
<td><em>Rinchenia mongoliensis</em> Barsbold 1986</td>
</tr>
<tr>
<td>IGM 100/32 (=<em>Oviraptor mongoliensis</em>)</td>
</tr>
<tr>
<td><em>Citipati osmolskae</em> Clark et al. 2001</td>
</tr>
<tr>
<td>IGM 100/978 (holotype)</td>
</tr>
<tr>
<td>IGM 100/979</td>
</tr>
<tr>
<td>IGM 100/1004</td>
</tr>
<tr>
<td><em>Heyuannia huangi</em> Lü 2002</td>
</tr>
<tr>
<td>HYMV1</td>
</tr>
<tr>
<td><em>Ingenia yanshini</em> Barsbold, 1981</td>
</tr>
<tr>
<td>IGM 100/30 (holotype; lower jaw and postcranial skeleton)</td>
</tr>
<tr>
<td>IGM 100/31</td>
</tr>
<tr>
<td>IGM 100/33</td>
</tr>
<tr>
<td><em>Conchoraptor gracilis</em> Barsbold 1986</td>
</tr>
<tr>
<td>IGM 100/20 (holotype)</td>
</tr>
<tr>
<td>IGM 100/19</td>
</tr>
<tr>
<td>IGM 100/1203</td>
</tr>
</tbody>
</table>
Khaan mckennai Clark et al. 2001
IGM 100/1127 (holotype)
IGM 100/1002
IGM 100/973

Gigantoraptor erlianensis Xu et al., 2007
LH V 0011 (holotype)
IGM 100/42
IGM 100/1253 (skull)
MgD-I/106 (partial skull, disarticulated postcranium)

Outgroups:
Allosauroidea
   Allosaurus fragilis
Tyrannosauridae
   Tyrannosaurus rex
Struthiomimidae
   Struthiomimus altus
   Garudimimus brevipes
Compsognathidae
   Huaxiagnathus orientalis
Dromaeosauridae
   Velociraptor mongoliensis
   Dromaeosaurus albertensis
   Tsaagan mangas
Troodontidae
   Saurornithoides mongoliensis
   Zanabazar junior
   Byronosaurus jaffei
   Troodon formosus
Alvarezsauridae
   Shuvuuia deserti
Therizinosauria
   Elikosaurus andrewsi
   Segnosaurus galbinensis
   Alxasaurus elesitaiensis
Avialae
   Archaeopteryx lithographica
   Apsaravis ukhaana
   Confuciusornis sanctus

Aves
   Gallus gallus
   Anas platyrhynchos
In addition to specimens that already have been scored in previous analyses, oviraptorosaurs from museums in Mongolia, China, Canada, Poland, Russia, and the United States are included in this phylogenetic study. The primary analysis is conducted at a species level and includes 44 operational taxonomic units (OTUs). A total of 19 of these represent the ingroup, Oviraptorosauria, and the remaining 25 taxa lie outside of the group of interest (Table 3.1). The ingroup is a collection of oviraptorosaur specimens from North America and Central Asia (China and Mongolia). All well represented oviraptorosaur species are included in this analysis as well as new specimens from Mongolia that were described in Chapter 2 of this dissertation. More comprehensive scorings of both Citipati osmolskae and Khaan mckennai are possible for this analysis. Lü (2005) is the only other phylogenetic study to include Khaan mckennai, and they did so only for cranial characters. Some specimens (marked NXMV and BPM-112), however, that were scored in Lü (2005) have been eliminated from this study because first hand observation was not possible and no illustration or description of these specimens are available at the present time.

Although oviraptorosaurs have been reported from South America, the United Kingdom, and Australia (Frankfurt and Chiappe, 1999; Naish and Martill, 2002; Currie et al., 1996, respectively), none of these specimens were included in the phylogenetic analysis because of their fragmentary nature (e.g., being represented by half of a vertebra; Naish and Martill, 2002) and questionable assignment (see Makovicky and Sues, 1998; Agnolin and Martinelli, 2007).

Taxon sampling within Oviraptorosauria is built on previous studies of their relationships, specifically those of Maryańska et al. (2002), Lü (2005), and the most
recently published iteration of the Theropod Working Group (TWiG; Turner et al., 2007). The selected taxa that fall outside of the group Oviraptorosauria were chosen based on the hypothesis of evolutionary relationships of coelurosaurian theropods presented in that publication by TWiG (Turner et al., 2007:fig. S1). The current study attempts to use at least two representatives of each major clade within Coelurosauria to bracket these often large, diverse groups (Table 3.1). For situations in which there is not as much known diversity, such as alvarezsaurids or compsognathids, at least one member of the group is represented. The sampling among avialans follows that of Maryańska et al. (2002) with the addition of crown avians (i.e., Gallus gallus, and Anas platyrhynchos) and the stem taxon Apsaravis ukhaana (Clarke and Norell, 2002).

CHARACTER SAMPLING

The character sampling for this current analysis again is compiled primarily from past oviraptorosaur phylogenetic studies of Maryańska et al. (2002), Lü (2005), and the most recently published version of the TWiG dataset (Turner et al., 2007). The characters from these studies were compiled and then reviewed to ensure that there was no redundancy, violation of independence, or weak homology statements. Several characters from the Maryańska et al. (2002) and Lü (2005) analyses were rephrased to omit arbitrary cutoffs within continuous characters that had been broken up into discreet states. Several characters from these analyses were scored differently in the current study to comply with first hand observations. Several new characters were added and aimed specifically at refining the resolution within Oviraptoridae because this remains the area of most conflict between analyses. Combining previously published and new characters resulted in a total
of 409 characters (Appendix 3). Although not used in the analysis, rejected characters from Lü (2005) are retained in the character list, and reasons for redefinition or rejection is provided therein. The final number of characters, without those that were rejected, totals 384. Cranial characters have proven to be most effective in resolving the relationships among oviraptorosaur taxa, and this remains the case in the present analysis. An effort, however, has been made to incorporate a larger number of postcranial characters. The breakdown of characters by anatomical region is as follows: cranial (40%), mandibular (10%), and postcranial (50%).

CLADISTIC ANALYSIS

All phylogenetic relationships are analyzed using standard cladistic methodology (Farris 1988; Swofford 2001). A total of 384 morphological features were coded into binary and multistate characters (Appendix 4) and analyzed using current versions of the phylogenetic software TNT (Goloboff et al., 2003), Mesquite 2.74 (Maddison and Maddison, 2010), and MacClade 4 (Maddison and Maddison, 2000). All phylogenetic analyses are evaluated in the manner of recent publications of the TWiG (Norell et al., 2006; Turner et al., 2007) by performing a heuristic tree search utilizing the software TNT v. 1.0 (Goloboff et al., 2003). One thousand replicates of Wagner trees were performed, holding 10 trees per replicate. The best trees were then subjected to a final round of TBR branch swapping. Zero length branches were collapsed if they lacked support under any of the most parsimonious reconstructions. Consensus trees were reconstructed by using a strict consensus methodology.
The Bremer support values (Bremer, 1994) were calculated by saving trees that were up to 15 steps longer than the MPTs. The tree search strategy employed to conduct this analysis consisted of 1,000 replicates of random addition sequences each followed by a round of TBR branch swapping holding only one tree in memory per replicate. The resulting set of trees were subjected to a round of TBR branch swapping saving a total 2377 trees. The Bremer support values are displayed on a strict consensus tree of the MPTs (Fig. 3.5).

RESULTS

TREE SUMMARY FOR SPECIES LEVEL ANALYSIS

The initial goal of the species-level analysis performed here is to discern the position of Oviraptorosauria within Coelurosauria. This analysis resulted in two most parsimonious trees (MPT; Fig. 3.2) each with a length of 1149 steps, with a total of different 96,569,461 rearrangements reviewed. Although the is support is not high within the derived oviraptorosaur group, Oviraptoridae, most regions of the tree are reasonably well supported. Oviraptorosauria is revealed as a strongly supported monophyletic group, the position of which consistently is recovered among non-avian theropods. Oviraptorosaurs are positioned as the sister taxon to therizinosauras as opposed to being nested well within Avialae (these results are contra Paul, 2002; Maryańska et al., 2002; Osmólska et al., 2004; Lü, 2002) (Fig. 3.1A, B). The recovered topology, therefore, reaffirms the position of Oviraptorosauria as discerned in several other recent phylogenetic analyses of coelurosaur relationships (e.g., Hwang et al., 2004; Lü, 2005;
Figure 3.2. The most parsimonious trees recovered from the present analysis. Alternate positions of IGM 100/1253 are shown by dotted lines. A, recovered relationships within Coelurosauria; B, recovered relationships within Oviraptorosauria. Letters refer to clades that are explained in the text.
Figure 3.2 (cont). The most parsimonious trees recovered from the present analysis. Alternate positions of IGM 100/1253 are shown by dotted lines. A, recovered relationships within Coelurosauria; B, recovered relationships within Oviraptorosauria. Black dot indicates Oviraptorosauria. Letters refer to clades that are explained in the text.
Turner et al., 2007; Holtz, 1998; Senter, 2007) (Fig. 3.1B–F). This topology differs from that obtained by TWiG only in the position of Alvarezsauridae as the sister taxon to Paraves. This unusual position may be the result of only one alvarezsaurid being scored for the analysis, the derived *Shuvuuia deserti*, which in conjunction with the addition of a large number of “birdlike” characters, have helped reposition this clade as sister to Paraves (Fig. 3.2A).

Within Oviraptorosauria, the relationships at the base of the clade are strongly supported and mostly consistent with alternative phylogenetic analyses of this group (Figs. 3.1 and 3.2). The resultant topology includes *Incisivosaurus gauthieri* as the basal-most taxon among oviraptorosaurs. This result is not surprising given that all previous analyses that have included *Incisivosaurus gauthieri* (e.g., Lü, 2005; Senter, 2007; Turner et al., 2007) have recovered it as the basal-most taxon within the clade. Also recovered are the positions of *Caudipteryx zoui*, *Avimimus portentosus*, *Similcaudipteryx yixianensis*, *Microvenator celer*, *Chirostenotes pergracilis*, and *Nomingia gobiensis*, each being successively closer to Oviraptoridae (Fig. 3.2). This topology differs from recent iterations of the TWiG analysis, which have recovered a Caenagnathidae that consists of *Microvenator celer*, *Chirostenotes pergracilis*, and *Avimimus portentosus* (Norell et al., 2006). The present analysis recovers these taxa as being a paraphyletic assemblage along the stem leading to the oviraptorid clade (Fig. 3.2B).

The monophyly of the derived oviraptorosaur group, Oviraptoridae, is strongly supported. A few sister-group relationships within this group do bear relatively good support in the preferred tree (Fig. 3.2B). These regions include the sister-group relationship of *Oviraptor philoceratops* and ‘Rinchenia’ mongoliensis as well as the close
relationship between the cranially crested forms of IGM 100/42 with *Gigantoraptor erlianensis* and *Citipati osmolskae*. Interestingly, *Oviraptor philoceratops* and *Rinchenia mongoliensis* have at one time or another both been allied with the genus *Oviraptor*.

*Oviraptor philoceratops* (AMNH 6517) is the holotype specimen for the genus, and ‘*Rinchenia’ mongoliensis’ was initially described as a separate species of *Oviraptor*, subsequently taken out of that genus by Barsbold (1997) because of what were perceived to be significant morphological differences between these taxa. This clade repeatedly is found to be the sister taxon to *Nemegtia barsboldi* (Fig. 3.2B), another taxon possessing a large, extensive midline crest along the entire dorsal surface of its skull. The sister-group relationship between *Gigantoraptor erlianensis* and *Citipati osmolskae* is a novel finding in this analysis. Xu et al. (2007), the only other study to include *Gigantoraptor erlianensis*, recovered a much more basal position for the taxon. Features such as a trochanteric crest and a weak adductor fossa and associate anteromedial crest on the femur help tie these species together.

**Oviraptorosauria Barsbold, 1976 (Fig. 3.2B)**

Definition--A stem-based clade that is defined as *Oviraptor philoceratops* (Osborn, 1924) and all coelurosaurs more closely related to it than both *Erlikosaurus andrewsi* (Perle, 1981) and *Passer domesticus* (Linnaeus, 1758).

Oviraptorosauria is a well-supported clade whose monophyly has not been questioned in any phylogenetic analysis. The only question that has been raised concerning this taxon is its position within Coelurosauria (see Discussion). It is often placed among avialans by the distinctly avian-like morphology of its more derived
members, but taxa along the stem have strong morphological affinities with non-avian theropods, and therefore lack derived avian features.

This analysis positions Oviraptorosauria as the sister taxon to Therizinosauria. Although this result is often recovered (see Hwang et al., 2004; Norell et al., 2006; Turner et al., 2007) some recent evaluations of coelurosaur relationships have failed to produce the sister group relationship between these taxa (e.g., Sereno, 1999; Senter, 2007; Zanno et al., 2009). This relationship between the two groups is supported by 19 synapomorphies, four of which are unique (under a DELTRAN optimization; Farris, 1982). Unique characters supporting the position of Oviraptorosauria as the sister taxon to Therizinosauria include a pterygoid that has a quadrate wing that overlaps the braincase wall—expanding dorsally (57.0); the suborbital (ectopterygoid-palatine) fenestra on the palate is closed or reduced (68.1); the preacetabular process at the anterior edge of the ilium is expanded ventrally below the level of the dorsal margin of the acetabulum (153.1); and, the cranioventral process of the ilium also is shaped into a hooklike process (155.2).

A number of synapomorphic supporting the sister group relationship of Oviraptorosauria and Therizinosauria are also found to be present in other more distantly related lineages. The clade of oviraptors and therizinosaurs shares with some taxa within crown Aves basipterygoid processes that are either abbreviated or absent (50.1), a vomer that is approaching or in contact with the parasphenoid rostrum (67.1), and a symphyseal region that is strongly recurved towards the midline (203.2). A symphyseal region of the dentary that is downturned slightly (74.1) and that is u-shaped in ventral view (75.1) is shared only among (Oviraptorosauria + Therizinosauria), Gallus gallus, and
Garudimimus brevipes. The absence of a surangular foramen is found only in this clade, Shuvuuia deserti, and Archaeopteryx lithographica (225.0).

Oviraptorosauria is strongly supported in this analysis, as it is in other published studies (e.g., Holtz, 1998; Senter, 2007; Turner et al., 2007). Under the DELTRAN optimization of character evolution, this node has no synapomorphic characters from the postcranium because Incisivosaurus gauthieri, which occupies the basal-most position in the clade is represented only by a single specimen with no postcranium. Obviously, as more specimens are collected this situation will be remedied. Under this optimization, 24 total synapomorphies and eight unambiguous synapomorphies are diagnostic of Oviraptorosauria. The pneumatization of the entire narial region including the dorsal and lateral surfaces unambiguously diagnoses this clade (18.1 and 27.1). As discussed in the Khaan mckennai description of Chapter 1, all oviraptorosaurs share extreme pneumatization in this region of the skull regardless of whether they are crested or uncrested. This pneumatization may be taken to an extreme degree in the crested forms (Figs. 2.14–2.16 and 3.3). The paroccipital processes of oviraptorosaurs possess an unusual morphology in which the distal end curves ventrally and has a pendant shape (45.2). On the palate, the ectopterygoid of oviraptorosaurs occupies a more rostral position than it does in other coelurosaur taxa (59.1). The ectopterygoid in Incisivosaurus gauthieri and other oviraptorosaurs in which it is visible articulates with the rostral margin of the pterygoid rather than along its lateral edge. The ectopterygoid also has a lateral contact with both the jugal and the maxilla (60.1), rather than an exclusive contact with the jugal. The margin of the premaxilla (tomial surface) has a crenulate surface (229.1) rather than the even surface that is seen in other coelurosaur taxa. Another
Figure 3.3. Examples of skulls from oviraptorosaur taxa. A, *Incisivosaurus gauthieri*; B, *Rinchenia mongoliensis*; C, *Conchoraptor gracilis*; D, IGM 100/42. Modified from Osmolska et al. (2004).
uniquely oviraptorosaur character is the covering of the lateral face of the braincase by a large flange composed of the quadrate, pterygoid, and epipterygoid (257.1).

Oviraptorosaurs possess a rather unique morphology of the mandible; however, it is not as extremely divergent from the typical coelurosaur morphology as that seen in the more exclusive group, Oviraptoridae. A mandibular articular surface that is at least twice as long as the quadrate mandibular surface to allow for anteroposterior movement of the mandible is an unambiguous synapomorphy of this group (204.1). A few characters are shared by Oviraptorosauria and the distantly removed Allosaurus fragilis, including a pterygo-palatine fenestra that is either extremely reduced or absent (69.0).

Clade A (Fig. 3.2B)

Clade A consists of the monophyletic group of Caudipteryx zoui and all other oviraptorosaurs excluding Incisivosaurus gauthieri. The position of Caudipteryx zoui is extremely labile between different studies of this group (see Maryańska et al., 2002; Lü et al., 2004; Osmólska et al., 2004; Lü, 2005; Norell et al., 2006). This position on the tree is alternately most typically occupied by either Avimimus portentosus or Caudipteryx zoui. Caudipteryx zoui is represented by a fairly large number of well preserved but flattened specimens including some that preserve feather impressions (Ji et al., 1998; Zhou and Wang, 2000; Zhou et al., 2000). All of the known specimens were collected from the Early Cretaceous Yixian Formation of China. Another species, Caudipteryx dongi, was described by Zhou and Wang (2000) based on a single specimen that lacks any distinctive autapomorphies, and which is therefore treated as a member of Caudipteryx zoui in this analysis.
This node is well supported by a large number of synapomorphies under a DELTRAN optimization criterion. Twenty three characters are diagnostic for this clade, of which only five are unambiguous. These unambiguous characters include an ascending (squamosal) process of the quadratojugal that is slender and borders approximately two-thirds of the posterior margin of the infratemporal fenestra (37.2). The external mandibular fenestra is more than one-fourth of the length of the entire mandible (79.1). These taxa all possess a mandibular adductor fossa on the surangular that is large and extends dorsally and anteriorly (93.1). A constriction between the articulated premaxilla and maxilla is also diagnostic for this clade (214.1). This clade shares with only Gallus gallus a maxilla that is only one-third or less than the length of the entire skull (222.1). Clade A shares with only Confuciusornis sanctus a humerus that has an ectepicondyle that is more pronounced than the entepicondyle (133.1). This clade shares with crown Aves and ornithomimids the absence of maxillary teeth (205.1).

**Clade B (Fig. 3.2B)**

Avimimus portentosus (Kurzanov, 1981; 1987) and all other oviraptorosaurs (excluding Incisivosaurus gauthieri and Caudipteryx zoui) are included in this clade. Most analyses have recovered a position for this taxon that is somewhere near the base of the tree; however, Lü et al. (2004) recovers Avimimus portentosus as being the sister taxon to oviraptorids (Fig. 3.1). This derived position is not found in any other oviraptorosaur analyses. All known specimens of Avimimus portentosus are from the Late Cretaceous of China and Mongolia, but the taxon is known most completely from a specimen that is housed in the Paleontological Institute in Moscow (PIN 3907/1;
This specimen is from the Nemegt Basin in the Gobi Desert of Mongolia. There is some confusion as to the specific formation from which the specimen was collected (Watabe et al., 2000). Another specimen housed in the Paleontological Institute in Ulaan Baatar also was included in this analysis (IGM unnumbered; Watabe et al., 2000). This specimen lacks a skull and part of the forelimb. Recently reported is an extensive bone bed in China preserving several specimens of *Avimimus* (Currie et al., 2008). The specimens from this locality are not yet available for general study.

Clade B is diagnosed by a total of 14 synapomorphies under a DELTRAN optimization, only one of which is an unambiguous character. The one unambiguous character is a parasphenoid rostrum (cultriform process) that is directed anteroventrally rather than horizontally or rostroventrally (52.1). Although Maryańska et al. (2002) used this character as an unambiguous synapomorphy of an Avialae that included oviraptorosaurs, the parasphenoid rostrum of *Archaeopteryx lithographica* and other avialans including crown birds does not project ventrally but rather in a horizontal direction.

A number of characters are shared only by Clade B and one other taxon. These include medially extended pterygoids that meet each other along the midline, shared with *Garudimimus brevipes* (56.1); a fronto-parietal contact that is sinuous instead of angular shared with *Shuvuuia deserti* (253.0); a broad, immovable joint between the squamosal and optic wing of the quadrate is shared with *Erlikosaurus andrewsi* (260.0); and an elongate and slender retroarticular process on the mandible shared with modern birds.
In the postcranial skeleton, a tibiofibular crest on the lateral condyle of the femur is present only in this clade and *Confuciusornis sanctus* (52.1).

**Clade C (Fig. 3.2B)**

This clade consists of *Similcaudipteryx yixianensis* (He et al., 2008) and the clade formed by *Microvenator celer, Chirostenotes pergracilis, Nomingia gobiensis*, and Oviraptoridae (Barsbold, 1976). This is the first time that *Similcaudipteryx yixianensis*, an Early Cretaceous form from the Jiufotang Formation of western Liaoning, China, has been included in a phylogenetic analysis, and the position of the taxon near the base of the tree is not surprising (He et al., 2008). This species has been postulated to be closely related to *Caudipteryx zoui* (hence the derivation of the name, meaning similar to *Caudipteryx*) and may indeed fall out as its sister taxon once more material is discovered. The only specimen that was available for inclusion within this analysis (IVPP V 12556) lacked a skull. At this time, these two taxa are distinguished primarily by size.

Unnamed Clade C is weakly supported by only eight synapomorphies, and just two unambiguous synapomorphies. The clade is diagnosed by the characteristic morphology of their vertebral column. Clade C possesses two horizontally arranged pleurocoels on the cervical centra (99.1), a character that is subsequently reversed later within the group. In addition, the entire presacral vertebral column is pneumatized, unlike other coelurosaurians (321.1). Clade C also is diagnosed by a number of characters that show up in just one other clade. These include a cranioventral process on the preacetabular part of the ilium that is rounded in morphology (155.1). Troodontids and
Clade C share short, wide, and slightly inclined transverse processes on the anterior dorsal vertebrae (322.1).

**Clade D (Fig. 3.2B)**

Clade D is comprised of *Microvenator celer* and the clade including *Chirostenotes pergracilis, Nomingia gobiensis*, and Oviraptoridae. *Microvenator celer*, found in the Lower Cretaceous beds of the Cloverly Formation, is one of the few North American forms of oviraptorosaur. It was first described by Ostrom (1970) as a ‘coelurid’ dinosaur, but remained enigmatic until the detailed description by Makovicky and Sues (1998), which documented its affinities with Oviraptorosauria. These common characteristics include an edentulous dentary, cervical neural spines that give an x-shaped outline in dorsal view, short and wide transverse process on the dorsal vertebrae, and an anteriorly concave pubic shaft (Makovicky and Sues, 1998).

This clade is supported by six synapomorphies, with only one unambiguous synapomorphy. This character is a lesser trochanter that possesses a cylindrical shape (357.3), a character derived from the TWiG analyses. Ambiguous character support of this clade includes an extended symphyseal shelf at the mandibular symphysis (73.1) that is also present in (*Confuciusornis sanctus* + modern birds) and *Incisivosaurus gauthieri*. Clade C, *Allosaurus fragilis*, and *Velociraptor mongoliensis* have an internal tuberosity on the humerus that is subtriangular and distinctly extended medially (130.2). Several groups including Clade C, therizinosaurs, *Confuciusornis*, compsognathids, and *Tyrannosaurus rex* all have a supractabular crest that is either reduced or absent (157.1). Clade C and *Caudipteryx zoui* have a poorly developed antitrochanter posterior to the
acetabulum (163.0). Clade C, *Erlikosaurus andrewsi*, and *Tyrannosaurus rex* have cervical pleurocoels that are developed as deep depressions (218.0).

*Clade E (Fig. 3.2B)*

The taxa that comprise clade E include *Chirostenotes pergracilis*, *Nomingia gobiensis*, and Oviraptoridae. *Chirostenotes pergracilis* has been closely allied with several other taxa to form the group Caenagnathidae. Unfortunately, much of this material is too fragmentary to be included in this phylogenetic analysis (e.g., the foot representing *Elmisaurus rarus*; Osmólska, 1981). Sues (1997) gives a comprehensive review of this fragmentary material as well as the taxonomic history of the group. In that review, much of the fragmentary material that had been named as different taxa are condensed into *Chirostenotes pergracilis*. It is the taxonomy of Sues (1997) that is followed here in this study. *Chirostenotes pergracilis* typically is considered a member of the group Caenagnathidae (Sternberg, 1940). Caenagnathidae was defined by Sues (1997) as the most recent common ancestor of *Chirostenotes pergracilis*, *Chirostenotes elegans*, an unnamed large taxon from North and South Dakota (Triebold and Russell, 1995), *Caenagnathasia martinosoni*, *Elmisaurus rarus*, and all of its descendants. Only *Chirostenotes pergracilis* was used in this analysis because it is the best preserved of these taxa, most of which are represented only by a pes and/or jaw. The unnamed caenagnathids (Triebold and Russell, 1995), in contrast, are extremely well preserved. These specimens are currently the subject of a student thesis at the Carnegie Museum and are not presently available for inclusion in this analysis.
Unnamed Clade E is well supported by 19 synapomorphies, seven of which are unambiguous. One additional synapomorphy, the presence of foramina or fossae on all sacral vertebrae (175.2) is present exclusively in Clade E and the mallard duck (*Anas platyrhynchos*). The dentary in both *Apsaravis ukhaana* and Clade C has an elongate dorsal process that extends over the length of the external mandibular fenestra (51.2). Present only in Clade C and *Garudimimus brevipes* is the extension of the anterior cervical centra posteriorly beyond the neural arch of that vertebra (102.1).

Unambiguous synapomorphies include a maxilla that bears paired “tooth-like” projections on the palate surface near the contact with the vomer (12.1). Most of the remainder of the unambiguous synapomorphies concern the morphology of the mandible. The midpoint of the mandibular rami are bowed laterally when viewed dorsally (81.1). The rostrodorsal margin of the dentary is deeply excavated and therefore has a concave shape (82.1). The rostral part of the prearticular is shallow and strap-like. It does not come near to reaching the dorsal margin of the mandible (91.1). The splenial of Clade C is shallow and strap-like, opposed to the subtriangular morphology of other coelurosaurians (92.1). One postcranial character diagnoses this clade. The anterior articular facets in the postaxial cervical centra are strongly inclined (101.1).

**Clade F (Fig. 3.2B)**

Clade F is a monophyletic group composed of *Nomingia gobiensis* (Barsbold et al., 2000) and Oviraptoridae. *Nomingia gobiensis*, from the Late Cretaceous sediments of Bugin Tsav in Mongolia, is known from only one specimen. It is one of the few non-avian coelurosaurians, and the only oviraptorosaur, that has a distinct pygostyle formed by
the fusion of several caudal vertebrae at the distal end of the tail. A pygostyle is a characteristically avian feature; therefore, it can be deduced that this character is most likely an autapomorphy for *Nomingia gobiensis*. A pygostyle also was reported in *Similcaudipteryx yixianensis* (He et al., 2008), but this present study was not able to confirm that report after personal observation of the specimen.

*Nomingia gobiensis* is known from a single specimen that lacks both a skull and forelimb; therefore, all unambiguous synapomorphies for this clade that are derived from a DELTRAN optimization criterion are from the postcranial skeleton. There are a total of seven synapomorphies diagnosing Clade F in this analysis. Two of these synapomorphies are considered unambiguous with two more being found in Clade F and distant outgroups. The unambiguous synapomorphies include having pleurocoels in at least the proximal region of the caudal vertebral series (115.1) and having only 11 or 12 dorsal vertebrae (196.1). One diagnostic character is present only in Clade F as well as tyrannosaurids and allosaurids: having 15 or more caudal vertebrae with transverse processes (228.0). Character 263 is shared by Clade F, *Zanabazar junior* and modern birds, all of which have sacral centra that decrease in width posteriorly (263.1).

**Oviraptoridae Barsbold 1976**

Definition--A node-based monophyletic group that is composed of the most recent common ancestor of *Oviraptor philoceratops* Osborn 1924 and *Citipati osmolskae* Clark et al., 2001 and all of its descendants.

The above definition is emended from that given by Maryańska et al. (2002). The previous definition was stem-based and therefore would be less stable if the position of
*Chirostenotes pergracilis* were to shift in subsequent analyses. The monophyly of Oviraptoridae has never been called into question, most likely because of the extremely unique morphology exhibited by the taxa that comprise the most diverse clade among oviraptorosaurs (see Osmólska et al., 2004). It is purely central Asian in geographic extent and contains some of the most well-known dinosaur specimens, including the “nesting” specimens collected by the Mongolian Expeditions of the American Museum of Natural History in the early Twentieth Century (Osborn, 1924) as well as those of more recent expeditions in the 1990s and 2000s (see Norell et al., 1995; Clark et al., 2001).

Not surprisingly given this clade's incredibly bizarre morphology, oviraptorids are supported by a large number of synapomorphies, a total of 49. Fifteen of these synapomorphies are unambiguous. Elements of rostrum of the skull of oviraptorids can be considered to be displaced posteriorly so that several of the features of this region, such as the external nares, lie posterior to their position in the ‘typical’ theropod condition; accordingly, several characters are products of this telescoping. The preorbital region of the skull is approximately equal to the length of the postorbital region (16.1). This differs from the condition found in other coelurosaurids that have a rostrum that is much longer than the postorbital region of the skull. Also because of the same posterior displacement, the maxillary process of the premaxilla extends posteriorly to separate the maxilla from the nasal posterior to the naris (17.1). The caudal margin of the naris broadly overlaps most of the antorbital fossa (19.2). The ventral margin of the external naris lies dorsal to the body of the maxilla (20.1). The rostrum width to length ratio is 0.5 or more (64.2). In lateral view the dorsal border of the antorbital fenestra is formed by the premaxilla, maxilla, and lacrimal (238.2). Oviraptorids have a unique palatal morphology
(Maryańska and Osmólska, 1997). They possess an ectopterygoid fossa that has a constricted opening (201.1). The palatal surface of the premaxilla and maxilla has a series of four ridges and troughs (250.1). Also on the palate, the articular surface for the pterygoid on the quadrate extends to the articular surface of the medial mandibular condyle (258.0). In taxa outside of oviraptorids the articular surface for the pterygoid is more anteriorly placed on the quadrate. The frontals in all oviraptorids are highly pneumatic and have several small openings at the anterior margin of this element (254.0).

Oviraptorids possess a mandibular morphology that is not found in any other coelurosaurs. This morphology consists of a large, circular external mandibular fenestra that is subdivided by a spinous process of the surangular (78.1 and 87.1, respectively), a mandible with a large coronoid prominence (86.0), a mandibular articulation formed exclusively of the articular (88.1), and a mandibular articular facet that is convex in lateral view (89.1).

Several characters are shared only by oviraptorids and modern birds. These similarities may be what initially led (in the absence of more basal taxa) to the notion that oviraptorosaurs belong within the group Avialae. Oviraptorids and birds share a ratio of preorbital skull length to basal skull length that is 0.5 or less (1.1). Both groups have a maxilla that is inset medially ventral to the antorbital fossa (10.1). Avians and oviraptorids both possess a parietal that is anteroposteriorly longer than the frontal (26.1). The pterygoid basal process for contact with the basisphenoid is found only in oviraptorids and avians (58.1). Snout width to length ratio is approximately 0.5 or more in oviraptorids, avians, and tyrannosaurids. Only oviraptorids and avians share an
external narial opening that is larger than the antorbital fenestra (262.1). Both groups also have a distinct hypocleidium on their furcula (165.1).

**Clade G (Fig. 3.2B)**

Clade G is formed by the monophyletic clade (*Citipati osmolskae*, *Gigantoraptor erlianensis*, and IGM 100/42; see following section) and those taxa that traditionally have made up the Ingeniinae (Barsbold, 1976). These ‘ingeniine’ taxa include *Heyuanxia huangi* (Lü, 2002), *Ingenia yanshini*, *Conchoraptor gracilis*, and *Khaan mckennai*. *Heyuanxia huangi* is one of the only oviraptorid species that has been collected from outside of the Gobi Desert. This taxon is found in the Late Cretaceous sediments in Guangdong Province in southern China (Lü, 2002; 2005). It is a fairly fragmentary specimen, but preserves most of the postcranium and part of the cranium and mandible.

This clade is supported by a large number of synapomorphies, a total of thirteen. None of these characters is unambiguous. In only Clade G and avialans is the proximal end of metacarpal III not in contact with the distal carpals (199.1).

**Clade H (Fig. 3.2B)**

Clade H is made up of the unnamed taxon (ZPAL MgD-I/106) and the remainder of the oviraptorids (*Ingenia gracilis*, *Conchoraptor gracilis*, *Khaan mckennai*, IGM 100/42, *Gigantoraptor erlianensis*, and *Citipati osmolskae*). This clade is weakly supported by only four characters. One of these characters is unambiguously diagnostic for Clade H. This unambiguous character is the presence of at least one accessory antorbital fenestra on the floor of the antorbital fossa (272.1).
ZPAL MgD-I/106 occupies an important position within the oviraptorid clade and the removal of this specimen has a large impact on the base of the oviraptorid tree. It is a fairly complete undescribed specimen collected by the Polish-Mongolian expeditions to the Gobi Desert. The specimen is represented by a partial skull, mandible, and postcranium. When this taxon is removed from the analysis, the \((Nemegtia barsboldi + (Oviraptor philoceratops + Rinchenia mongoliensis))\) clade is disassembled (Fig. 3.4). Although the remainder of the oviraptorid clade is stable with the removal of this specimen, \(Nemegtia barsboldi\) varies in position from its original placement to being the sister taxon to \(Heyuannia huangi\).

**Clade I (Fig. 3.2B)**

Clade I is composed of \(Ingenia yanshini\) and the remainder of the taxa forming Oviraptoridae (\(Conchoraptor gracilis, Khann mckennai, IGM 100/42, Gigantoraptor erlianensis, and Citipati osmolskae\)). \(Ingenia yanshini\) is a crestless oviraptorid that is known by an almost complete skull and postcranium. Several specimens of this taxon are known and often confused with \(Conchoraptor gracilis\); although \(Conchoraptor gracilis\) is more gracile and somewhat smaller than \(Ingenia yanshini\). The confusion of these taxa is due to the circumstance that almost all crestless specimens found for a number of years were included within \(Ingenia yanshini\). \(Ingenia yanshini\) also possesses a unique morphology of the forelimb, having shorter proportions relative to the hindlimb than any of the other oviraptorids (Osmólska et al., 2004). This clade is supported by eight synapomorphic characters, none of which is unambiguous. Only this group and ornithomimids possess large openings at the base of the neural arches of the anterior
Figure 3.4. Two possible reconstructions of oviraptorid relationships with the removal ZPAL MgD-I/106.
caudal vertebrae (212.1). A pronounced, transverse nuchal crest is lacking only within this clade, derived avialans, and Garudimimus brevipes (224.1).

**Clade J (Fig. 3.2B)**

The taxa that form Clade J include Conchoraptor gracilis, Khaan mckennai, IGM 100/42, Gigantoraptor erlianensis, and Citipati osmolskae. Conchoraptor gracilis is another crestless oviraptorid that is known from several well preserved specimens (Table 3.1). Again, all known specimens of this taxon are from the Late Cretaceous sediments of the Gobi Desert. Included within Conchoraptor gracilis are two new specimens (IGM 100/3006 and IGM 100/1203) collected from the Djadokhta formation at the Ukhaa Tolgod locality that were not included in previous analyses. Nine characters diagnose this clade, only one of which is unambiguously diagnostic. All oviraptorosaurs possess denticles or crenulations on the premaxilla; however the presence of five denticles is found only in Clade J. Although not unambiguous, the ratio of the length of the premaxilla to the overall length of the skull is more than 0.15 exclusive to modern birds and Clade J.

**Clade K (Fig. 3.2B)**

Clade K is formed by the taxa Khaan mckennai, IGM 100/42, Gigantoraptor erlianensis, and Citipati osmolskae. Khaan mckennai is a small-bodied crestless form of oviraptorid that is known from two of the most pristinely preserved specimens of any theropod taxon (IGM 100/1127 [holotype] and IGM 100/1002). There also is a fairly complete disarticulated specimen that is missing the axial skeleton and forelimb (IGM
100/973; Clark et al., 2001; see Chapter 1). IGM 100/1253 most likely is another representative specimen of *Khaan mckennai* that is known only from a partial skull. *Khaan mckennai* can be distinguished from other crestless oviraptorid taxa by a unique hand morphology in which the first metacarpal is not expanded and the third metacarpal does not reach the distal carpals (Clark et al., 2001). There are a total of eight synapomorphies for Clade K, all of which are ambiguously diagnostic. The constriction of the dorsal part of the infratemporal fenestra by the descending process of the squamosal, however, is present only in Clade K, *Allosaurus fragilis*, and *Tyrannosaurus rex* (31.0).

**Clade L**

The crested oviraptorids are not recovered as a monophyletic group in this analysis. IGM 100/42, *Citipati osmolskae*, and *Gigantoraptor erlianensis* form Clade L, but *Oviraptor philoceratops*, *Rinchenia mongoliensis*, and *Nemegtia barsboldi* lie in a more basal position on the oviraptorid tree (see Oviraptorinae). IGM 100/42 has not been provided with a proper name. Although initially described and included within *Oviraptor philoceratops* (Barsbold, 1981), it was later shown to have much stronger affinities with *Citipati osmolskae* as opposed to *Oviraptor philoceratops* based in part on the maxillary morphology as well as the nasal crest (Clark et al., 2002). The Clark et al. (2002) hypothesis is supported by this current analysis as well (Fig. 3.2). Clade L is supported by ten synapomorphies, one of which is unambiguously diagnostic for the clade. Clade L is the only group to have a nasal/premaxillary crest with accessory openings on the anterior surface (Fig. 3.3).
Clade M (Fig. 3.2B)

The sister taxon relationship between *Citipati osmolskae* (Clark et al., 2002) and *Gigantoraptor erlianensis* (Xu et al., 2007) is a novel finding of this analysis. *Citipati osmolskae* is a crested form (with an anteriorly placed crest on its nasals and premaxillae) and is one of the most completely known oviraptorids, being represented by at least three incredibly preserved specimens (Clark et al., 1999; 2002; Erickson et al., 2007). Two of these specimens (IGM 100/979 and IGM 100/1004) were found to be brooding nests of eggs (Clark et al., 1999), one of the few examples of behavior preserved in the fossil record. The other specimen (IGM 100/978) is complete and disarticulated, providing an amazing opportunity to fully analyze the morphology of this taxon.

*Gigantoraptor erlianensis* is the largest known oviraptorosaur and possesses a number of autapomorphic features (Xu et al., 2007). Although some of these are correlated to its extremely large size, others do not conform to patterns normally observed in gigantism (Schmidt-Nielsen, 1999). These autapomorphies include an unusual morphology of the humerus and distinct hindlimb proportions (Xu et al., 2007). Only the postcranium and mandible are preserved for this specimen.

This clade has weak character support. Three characters are diagnostic for the sister group relationship between *Citipati osmolskae* and *Gigantoraptor erlianensis*. Two of these characters, however, are shared only with distantly related taxa outside of Oviraptorosauria. These taxa have a lesser and greater trochanter of the femur that is completely fused, forming a trochanteric crest (176.2). This characteristic also is found in *Shuvuuia deserti* and derived avialans. Likewise, only ornithomimids, *Tyrannosaurus rex*,
and Clade M possess anterior, postaxial cervical vertebrae that are highly excavated between the pre- and postzygapophyses, so that they are x-shaped in dorsal view rather than more rectangular (103.1).

**Clade N (Fig. 3.2B) --Oviraptorinae Barsbold 1976**

Definition--Oviraptorinae is a stem based clade that is defined as the monophyletic group that includes all taxa that are more closely related to *Oviraptor philoceratops* than *Khaan mckennai*. Oviraptorinae initially was used by Barsbold (1976) as a “sub-family” name for crested oviraptorids. This feature still may be used as a distinguishing character for the group; however, not all crested oviraptorids are included within this group.

*Oviraptor philoceratops* (Osborn, 1924), *Rinchenia mongoliensis* (Barsbold, 1986) and *Nemegtia barsboldi* (Lü et al., 2004) have not been placed together as a clade in previous analyses. All of the mentioned taxa are fairly large bodied forms having a bony crest. *Oviraptor philoceratops* was the first oviraptorosaur to be discovered and described (Osborn, 1924). This specimen (AMNH 6517) was the one found by the American-Mongolian expeditions in the early 20th Century. It consists of a badly damaged skull and fragmentary postcranium (the anterior vertebral column and forelimb; Osborn, 1924).

When initially described, *Rinchenia mongoliensis* was included in *Oviraptor*. The fragmentary nature of the holotype of *Oviraptor* most likely led to its inclusion within this taxon. These taxa are considered morphologically distinct based on, among other things, the anterior-posterior extent of the cranial crest as well as the relative length of the
maxilla (and associated telescoping of the skull). The present analysis, however, does position these two taxa as sister taxa (Fig. 3.2B). Outside of *Oviraptor philoceratops* + *Rinchenia mongoliensis* is the taxon *Nemegtia barsboldi* (Lü et al., 2004). This is a relatively newly discovered specimen from the Nemegt Basin of the Gobi Desert in Mongolia. Only one specimen is known that consists of a well-preserved skull and partial postcranial skeleton (Lü et al., 2004).

The position of these taxa at the base of the oviraptorid tree is not completely surprising. Clark et al. (2002) postulated that *Oviraptor philoceratops* might occupy a basal position based on its more elongate rostrum than is present in other oviraptorids; although, neither *Nemegtia barsboldi* nor *Rinchenia mongoliensis* share this maxillary morphology. *Oviraptor philoceratops* possesses a maxillary morphology similar to that of *Chirostenotes pergracilis* (Sues, 1997; Clark et al., 2002). There are six characters that are synapomorphic for Clade N. One of these characters is unambiguous: the presence of only two large denticles on the triturating surface of the premaxilla (266.0; Fig. 3.3). Other oviraptorosaurs have at least four denticles.

**Clade O (Fig. 3.2B)**

This unnamed clade is formed by *Oviraptor philoceratops* (Osborn, 1924) and *Rinchenia mongoliensis* (Barsbold, 1986). This close relationship is not surprising given that they once were included within *Oviraptor*. The name of ‘*Oviraptor’ mongoliensis’ was changed by Barsbold (1997) because of morphological differences in the crest of these taxa. The legitimacy of the name is disputed based on ICZN rules, and many analyses refer to this taxon simply as ‘*Oviraptor’ mongoliensis’.
relationship between *Oviraptor philoceratops* and *Rinchenia mongoliensis* is supported by two characters, one of which is unambiguous. Both taxa lack jugal that participation in the margin of the antorbital fenestra (405.0).

**Support Values for Species Level Analysis**

Most of the coelurosaur relationships are well supported in this analysis, having Bremer support values over five. The only clades that receive low support values at the higher level of coelurosaur relationships are compsognathids and maniraptorans (Fig. 3.5), which have a Bremer support value of one and alvarezsaurids and paravians (Fig. 3.5), which have a Bremer support value of three. It is not surprising that these relationships receive low support values because they are different from the relationships found in the last TWiG analysis (Turner et al., 2007). The sister group relationship between therizinosaurs and oviraptorosaurs is support by a value of six.

Within Oviraptorosauria, the Bremer support values are somewhat lower (Fig. 3.5). The clades along the stem of Oviraptoridae have fairly good support. Oviraptorosauria as a whole has a Bremer value of eight. The more exclusive clades within Oviraptorosauria have support values of 3, 2, 3, 1, 8, and 7, respectively leading up to Oviraptoridae (see Fig. 3.5). Oviraptoridae is relatively well supported, requiring an additional three steps to collapse the clade (Fig. 3.5). Oviraptorid clades, however, all have low Bremer values, reflecting the low level of character support for their relationships. The sister group relationship between *Oviraptor philoceratops* and *Rinchenia mongoliensis* has a Bremer support value of 2. The clade formed by IGM 100/42, *Gigantoraptor erlianensis*, and *Citipati osmolskae* has a value of 2, and the sister
Figure 3.5. Bremer support values for clades within **A**, Coelurosauria; and **B**, Oviraptorosauria.
Figure 3.5 (cont). Bremer support values for clades within A, Coelurosauria; and B, Oviraptorosauria.
group relationship between *Citipati osmolskae* and *Gigantoraptor erlianensis* is supported by a value of 3. The remaining nodes within Oviraptoridae have Bremer support values of one. Such low values suggest that the discovery and addition of new taxa have the potential to overturn some of the relationships presented here.

**DISCUSSION**

**OVIRAPTOROSAURS AS NON-AVIAN THEROPODS**

A number of past analyses have placed Oviraptorosauria well within Avialae, making this morphologically bizarre group secondarily flightless birds (Paul, 2002; Lü, 2002; Maryańska et al., 2002; Osmólska et al., 2004). Senter (2007) erroneously states that Lü et al (2004) returns a tree with oviraptorosaurs included within Avialae; although, that analysis places oviraptorosaurs as the sister taxon to a clade composed of troodontids + avialans. Such a result is unique relative to most other analyses, as it breaks up Deinonychosauria—a fairly well supported clade (Turner, 2008). Oviraptorosaurs as avialans, however, is not found in most other analyses of coelurosaurian relationships (e.g., Holtz, 1998; Hwang et al., 2004; Rauhut, 2003; Senter, 2007; most recent iteration of TWiG [see Turner et al., 2007]; Zanno et al., 2009), which instead recover the traditional position of Oviraptorosauria as a non-avian theropod, although the placement within non-avian Coelurosauria has not been consistent. Most phylogenetic trees from these analyses positioned oviraptorosaurs as the sister group to therizinosaurs, and in turn Oviraptorosauria + Therizinosauria as the sister taxon to Paraves (Holtz, 1998; Sues, 1997; Makovicky and Sues, 1998; TWiG [Turner et al., 2007]). Sereno (1999), Rauhut
(2003), Senter (2007), and Zanno et al. (2009) do not preserve the sister group relationship between oviraptorosaurs and therizinosaurs, but rather position oviraptorosaurs as the sister taxon to Paraves, with therizinosaurs residing in a more basal position on the coelurosaur tree.

Maryańska et al. (2002) and Osmólska et al. (2004) recover an avialan position for oviraptorosaurs, but omit several taxa in their final analyses, including troodontids and alvarezsaurids. In addition, these studies do not include in their final analysis the oviraptorosaurs *Incisivosaurus gauthieri* or *Microvenator celer*. *Incisivosaurus gauthieri*, in studies returning a non-avian coelurosaurian position for the group, has been posited as the basal-most taxon in Oviraptorosauria. Maryańska et al. (2002)’s unusual results, accordingly, were thought to be an artifact of taxon sampling due to the absence of these phylogenetically important taxa. The cause of their recovered topology, however, might be more complicated than such a simplistic explanation provides. Another hypothesis would be that this topology diverges from others because of character selection. The analysis presented here as well as previous analyses (i.e., Lü et al., 2004; Lü, 2005; Senter, 2007) contain a large number of characters from Maryańska et al. (2002) and yet retrieve a position for oviraptorosaurs as non-avian coelurosaurians, which seems to complicate the picture further.

To see what effect taxon sampling has on the Maryańska et al. (2002) tree, their character analysis was reanalyzed including the omitted groups, troodontids and alvarezsaurids. That reanalysis resulted in a tree that places Oviraptorosauria being the sister taxon to *Confuciusornis sanctus*, well within Avialae (Fig. 3.6; personal observation; Senter, 2007). Taxon sampling outside of Oviraptorosauria, therefore,
Figure 3.6. Maryanska et al. (2002) analysis including troodontids and alvarezsaurids.
appears to have little affect on this tree. The Maryańska et al. (2002) character matrix was run again with the addition of troodontids, alvarezsaurids, and *Incisivosaurus gauthieri*. This iteration produced a tree very much like the Maryańska et al. (2002) tree except *Incisivosaurus gauthieri* occupies the basal oviraptorosaur position and *Confuciusornis sanctus* is no longer the sister taxon to oviraptorosaurs, but rather *Archaeopteryx lithographica* (Fig. 3.7). This result shows that there does appear to be a long branch problem, but it is more likely along the oviraptorosaur branch rather than those groups outside of Oviraptorosauria.

A subsequent iteration of the Maryańska et al. (2002) matrix was run using the additional taxa and *Allosaurus fragilis* rather than *Herrerasaurus ischigualastensis* as the outgroup. *Herrerasaurus ischigualastensis* and *Coelophysis bauri*, the chosen outgroups for the aforementioned study, seem to be unnecessarily distantly related to the ingroup taxa (Sereno, 1999; Rauhut, 2003). This reanalysis of the data resulted in three MPTs (Fig. 3.8), none of which are consistent with the original tree recovered by Maryańska et al. (2002). In these three topologies oviraptorosaurs are either most closely related to alvarezsaurids or *Archaeopteryx lithographica*, with *Confuciusornis sanctus* consistently falling out as the sister taxon to this group (Fig. 3.8). Changing the outgroup also resulted in a destabilization of the relationships within Oviraptorosauria in one of the three trees (Fig. 3.9). This scenario breaks up the sister group relationship between *Nomingia gobiensis* and *Chirostenotes per gracilis*. Interestingly, when *Incisivosaurus gauthieri* is removed from the analysis and *Allosaurus fragilis* again is used as the outgroup, the original Maryańska et al. (2002) tree is recovered (Fig. 3.1).
Figure 3.7. Maryanska et al. (2002) analysis including troodontids, alvarezsaurids, and *Incisivosaurus gauthieri*. 
Figure 3.8. Coelurosaur relationships obtained by a reanalysis of Maryanska et al. (2002) analysis including troodontids, alvarezsaurids, and *Incisivosaurus gauthieri* with *Allosaurus* as the outgroup rather than *Herrerasaurus*. 
Figure 3.9. Oviraptorosaur relationships obtained by a reanalysis of Maryanska et al. (2002) analysis including troodontids, alvarezsaurids, and *Incisivosaurus gauthieri* with *Allosaurus* as the outgroup rather than *Herrerasaurus*. 
Senter (2007) hypothesized that the tree recovered by Maryańska et al. (2002) and others was caused by their use of higher taxa as OTUs outside of Oviraptorosauria, essentially resulting in the use of composite taxa. This situation, compounded by the lack of more basal species that might better approximate the primitive condition within the groups outside of Oviraptorosauria, possibly produced the unusual results. These various iterations of the Maryańska et al. (2002) analysis performed here, however, show that several factors contribute to the placement of oviraptorosaurs within Avialae. Their unusual results appear to be caused by the long branch along the oviraptorosaur lineage that can be broken up with additional taxa such as *Incisivosaurus gauthieri*. The reinstatement of troodontids and alvarezsaurids into the analysis at the very least will have an affect on the character polarization within Oviraptorosauria. Switching outgroups for the analysis also seems to have a large affect on the resultant topology when *Incisivosaurus gauthieri* is included. A distantly related outgroup can cause erroneous relationships in the ingroup due primarily to long branch attraction (Gauthier et al., 1988; Lyons-Weiler et al., 1998; Bergsten, 2005). This scenario is a likely contributor to the relationships retrieved by Maryańska et al. (2002). The addition of characters also has a large impact on the analysis. The present analysis returns a tree in which Oviraptorosauria is heavily supported as a non-avian coelurosaur (Fig. 3.6). The additional taxa and characters, many drawn from the postcranial skeleton rather than the highly apomorphic cranium of oviraptorids, which is highly convergent with derived avialans, also helps to elucidate the relationships.
AVIAN-OVIRAPTORID SYNAPOMORPHIES

Analyses that recover Oviraptorosauria within Avialae have focused primarily on cranial characters. The Maryańska et al. (2002) tree identified four unambiguous synapomorphies that supposedly are diagnostic for the ((Oviraptorosauria +Confuciusornis)+Archaeopteryx) clade under an accelerated transformation optimization (ACCTRAN). These unambiguous synapomorphies include a ventral margin of the external naris that is dorsal to the maxilla, a quadratojugal process of the jugal in lateral view that tapers, a parasphenoid rostrum that slants anterovertrally, and the presence of a long and shallow posterovertral process of the dentary (Maryańska et al., 2002; Osmólska et al., 2004). The following is a preliminary discussion of these characters with observations concerning their primary and secondary homology based on the tree derived from the current phylogenetic hypothesis (Fig. 3.2).

Ventral margin of the external naris dorsal to the maxilla

Oviraptorids possess an extremely modified rostral region due to extreme pneumatization and retraction of the skull. The ventral margin of the external naris lies dorsal to the main body of the maxilla in all oviraptorosaurs (20.1). This morphology differs somewhat within the clade, with the more basal forms such as Incisivosaurus gauthieri and Caudipteryx zoui, having an external naris that sits dorsal only to the maxillary body instead of sitting dorsal to the entire maxilla (the body of the element as well as the dorsal process) as in oviraptorids (Fig. 3.10). Furthermore in the more exclusive group of oviraptorids this pattern of transformation is continued so that the
Figure 3.10. Rostrum of A, *Incisivosaurus gauthieri*; B, *Khaan mckennai*; C, *Velociraptor mongoliensis*; and, D, *Anas platyrhynchos* demonstrating the posterior position of the external naris (arrow) and reduction of the ascending (nasal) process of the maxilla.
external naris is not only dorsal to the entire maxilla, but its ventral border also is formed exclusively by the premaxilla and nasal—prohibiting a contact between the maxilla and nasal (Fig. 3.10).

Paravians (including *Archaeopteryx* and crown birds) possess a similar condition to *Incisivosaurus gauthieri* and *Caudipteryx zoui* in that the naris sits at least level with the dorsal process of the maxilla (Fig. 3.10; Wellnhofer, 1974; Elzanowski and Wellnhofer, 1996; Norell et al., 2006; Norell et al., 2009). One difference between these taxa and oviraptorids is the reduction in the size of the dorsal process of the maxilla. The character, therefore, concerns both where the naris lies relative to the maxilla because of the posterior displacement of elements in the oviraptorid skull and the subsequent reduction of the maxilla (a separate character in this analysis; character 17). This morphology is found in the derived condition only within Oviraptoridae (crested and crestless forms) and is only superficially similar to the condition in either basal oviraptorosaurs nor those taxa outside of the clade such as therizinosaurs and paravians (including crown Aves; Fig. 3.10). Accordingly, the morphology, though similar, is not homologous in avialans and oviraptorids. Inclusion of basal oviraptorosaurs, which share the outgroup condition in the morphology of the maxilla, breaks up the character and provides evidence of a transition along the oviraptorosaur lineage. The maxilla of *Oviraptor philoceratops* and *Chirostenotes pergracilis* provides an interesting transitional form with more elongate maxillae, similar to that in the basal oviraptorosaurs (see Clark et al., 2002; Sues, 1997); however, the maxillae of these taxa also lack the dorsal process.

*Quadratojugal process of the jugal tapers in lateral view*
Following the analyses of Maryańska et al., (2004), Lü et al., (2004), and Lü (2005) the quadratojugal process of the jugal in oviraptorosaurs and avialans tapers in lateral view rather than being forked (Fig. 3.11). Oviraptorids as well as *Caudipteryx zoui* all lack a distinctly forked posterior end of the quadratojugal process of the jugal. Although the jugal appears to taper in *Incisivosaurus gauthieri* this area has been reconstructed (see Balanoff et al., 2009:Fig. 3); therefore, the character state cannot be assessed for this taxon. The process is forked in the sister taxon to oviraptorosaurs, therizinosaurs, and dromaeosaurs (Osborn, 1924) (Fig. 3.11). The character state in troodontids is more difficult to determine because the process is not preserved in most specimens. The jugal in *Mei long* is preserved and does not appear to be forked posteriorly (Xu and Norell, 2004), but the morphology needs to be more thoroughly analyzed within this group.

The jugal in crown Aves is a highly modified element and undergoes a significant transformation within this lineage. The postorbital bar, formed by the contact of the postorbital and jugal, that separates the orbit from the infratemporal fenestra is reduced in birds, and accordingly the postorbital process of the jugal also is reduced (this structure is retained in all oviraptorosaurs; see Osmólska et al., 2004). The contact, however, may still be present or at the very least the two elements approach each other in both *Archaeopteryx lithographica* (Wellnhofer, 1974; Elzanowski and Wellnhofer, 1996) and *Confuciusornis sanctus* (Chiappe et al., 1999). The quadratojugal process of the jugal in these taxa is reduced to a more rodlike structure in cross section (resembling oviraptorids); however more importantly, the process does appear to retain a forked suture with the quadratojugal (Fig. 3.11). The tapering morphology of the jugal,
Figure 3.11. Skulls of A, *Anas platyrhynchos*; B, *Tsaagan mangas*; C, *Khaan mckennai*; and, D, *Caudipteryx zoui* demonstrating the morphology of the posterior margin of the jugal (arrow).
therefore, can be considered to be a convergently derived morphology within all oviraptorosaurs and crown birds—separate from that of other maniraptorans. The ambiguous nature of the character within troodontids does not affect the pattern (i.e., even if there is a tapering jugal in troodontids, it most likely evolved independently from that of oviraptorosaurs).

*Parasphenoid rostrum slanted in a anteroventral orientation*

The parasphenoid rostrum is stated to slant in an anteroventral direction in oviraptorosaurs and avialans (Maryańska et al., 2002). The structure is often obscured on the oviraptorosaur skull because of the presence of an extensive palate and the delicate nature of the structure. More recent CT analyses, however, have been able to shed light on the nature of the parasphenoid rostrum within this group. *Incisivosaurus gauthieri* possesses a parasphenoid rostrum that slants dorsally with respect to the ventral surface of the braincase (Xu et al., 2002a; Balanoff et al., 2009). *Caudipteryx zoui* appears to have a similar morphology to *Incisivosaurus gauthieri*; however, it is difficult to state with certainty because of the disarticulation of the skull (Ji et al., 1998; Zhou et al., 2000).

In modern birds the parasphenoid rostrum typically is in the same horizontal plane as the ventral surface of the braincase if not somewhat dorsally oriented (Fig. 3.12). The more exclusive group within oviraptorosaurs, oviraptorids, have a divergent morphology as compared to other maniraptorans and the more basal oviraptorosaurs. These taxa possess an anteroventrally slanting parasphenoid rostrum with respect to the floor of the braincase (Fig. 3.12). Therefore, it does not appear that there is a shared morphology
Figure 3.12. Skulls of A, *Dromaius novaehollandae*; and B, *Citipati osmolskae*. Arrows indicate parasphenoid rostrum.
between these groups at the level of Oviraptorosauria (nor Oviraptoridae) and Avialae. The pattern, instead, seems to be a shared morphology between oviraptorosaurs and paravians, with a uniquely derived condition within Oviraptoridae.

*Long and shallow posteroventral process of the dentary*

The mandibles of Oviraptorosauria and Avialae are highly derived. These groups share features such as an edentulous and a slightly downturned symphyseal region. Oviraptorosaurs also have unique features of the mandible that differ considerably from avialans. Oviraptorosaurs exclusively possess an enlarged mandibular foramen. In derived oviraptorids, an anteriorly projecting process of the surangular divides this foramen. Oviraptorids also possess an expanded coronoid process—a feature distinguishing this group from all other maniraptorans—which is alternately present and absent in the more inclusive group Oviraptorosauria (see *Microvenator celer*, Makovicky and Sues, 1998).

The presence of a long and shallow posteroventral process of the dentary, however, has been cited as being synapomorphic for an Avialae that includes Oviraptorosauria (Maryańska et al., 2002). The process in both groups extends posteriorly ventral to the mandibular foramen for almost the entire length of the opening. The dentary is the only bone that is preserved from the mandible of *Incisivosaurus gauthieri*, and the posteroventral process is preserved as well. Although expanded, the length of the posteroventral process in reference to the mandibular fenestra cannot be confidently assessed. The posteroventral process in *Caudipteryx zoui* does extend the entire length of the mandibular fenestra, and the same morphology is present in
caenagnathids (see Currie et al., 1993) and oviraptorids (Osmólska et al., 2004). The morphology of avians is more difficult to discern. The dentary extends beneath the mandibular fenestra in some stem members of the clade (see *Confuciusornis sanctus*, Chiappe et al., 1999). The mandibular fenestra is absent in *Archaeopteryx lithographica*; however, a posteroventral process is present in the taxon (Wellnhofer, 1974). In the crown group, Aves, the mandibular fenestra is not always present. In some taxa, two mandibular fenestrae may be found (an anterior and posterior fenestra; Baumel and Witmer, 1993). An extended posteroventral process of the dentary consistently appears throughout the crown clade. The condition in paravians is more difficult to discern. Although a posteroventral process is present in groups such as dromaeosaurids, it does not extend the length of the mandibular fenestra. The character, therefore, may more properly be assessed as either a blunt or posteriorly forked dentary. A posteriorly forked dentary is a derived condition within oviraptorosaurs relative to other maniraptorans. Although sometimes possessing a posteroventral process, the basal avialans *Archaeopteryx lithographica* as well as the stem taxon *Ichthyornis dispar* lack the forked morphology of the dentary. This character, however, is alternately present and absent in the crown clade; thus, it appears to be subject to a large amount of homoplasy.

**Previous Analyses of Oviraptorosaur Ingroup Relationships**

One of the more recent phylogenetic analyses of oviraptorosaur relationships was performed by Lü et al. (2004). This study included 20 taxa and a total of 200 characters from both the cranial and postcranial skeleton. They published only one resulting tree recovered through parsimony analysis that retrieved a monophyletic Oviraptorosauria
Incisivosaurus gauthieri lies in the basal-most position, followed by Caudipteryx zoui and Microvenator celer, respectively. This phylogeny is notable in that there is not a monophyletic Caenagnathidae, but rather the taxa that have been variably included within this group (i.e., Chirostenotes pergracilis, Avimimus portentosus, Microvenator celer) are recovered as a paraphyletic assemblage with respect to Oviraptoridae (Barsbold, 1976). Oviraptorid relationships, alternatively, are completely resolved (Fig. 3.1C). Most notable is the basal position of Khaan mckennai and the sister group relationship between Oviraptor philoceratops and GIN 100/42, a specimen that Clark et al. (2002) hypothesized to be more closely related to Citipati osmolskae rather than Oviraptor philoceratops.

Unfortunately Lü et al. (2004), published few details about the methodology used in their phylogenetic analyses; therefore, reproducing these trees proved to be difficult. In a reanalysis of the Lü et al. (2004) study I recovered 13 most parsimonious trees and much of the resolution within Oviraptoridae was lost in the consensus tree. Incisivosaurus gauthieri was not recovered at the base of the tree; instead, Caudipteryx zoui, Microvenator celer, and then (Incisivosaurus gauthieri + Avimimus portentosus) respectively are recovered as the basal most taxa (Fig. 3.13). Some relationships within Oviraptoridae, however, are retained including the basal position of Khaan mckennai and the clade composed of ((Nomingia + Rinchenia) + Ingenia). All other regions of this clade collapsed (Fig. 3.13).

Lü (2005) includes additional taxa and characters and postulates an oviraptorid clade composed of Nomingia gobiensis, Rinchenia mongoliensis, Ingenia yanshini, Citipati osmolskae, Nemegtia barsoldi, Heyuannia huangi, Oviraptor philoceratops,
Figure 3.13. Consensus tree (from 13 MPTs) recovered from a reanalysis of the Lu et al. (2004) data matrix.
Conchoraptor gracilis, and Khaan mckennai and a Caenagnathidae composed of Chirostenotes pergracilis and an unnamed taxon (BPV-112). A reanalysis of the Lü (2005) data matrix also failed to recover the tree that was recovered in that analysis. The reanalysis recovered a total of two MPTs retaining the positions for the basal assemblage of taxa (Fig. 3.14). The primary differences between these analyses was found within Oviraptoridae; the only congruent topology between trees is a recovered sister taxon relationship between Rinchenia mongoliensis and Nomingia gobiensis. Lü (2005) follows Maryanska et al. (2002) closely yet fails to recover the same topology presented in their tree for oviraptorosaur relationships (Fig. 3.1D).

Recent hypotheses put forward by the Theropod Working Group (TWiG; see Turner et al., 2007) recover two monophyletic clades similar to those recovered by Lü (2005). Their analysis includes an expanded taxon sampling that differs slightly from Lü (2005) (i.e., included Microvenator celer and excluded the other unnamed taxa and Khaan mckennai) and differs primarily in the position of Avimimus portentosus. The explicit purpose of the TWiG matrix, however, is not to test the relationships among oviraptorosaurus but rather those of Coelurosauria (more specifically paravians); therefore, in this analysis relationships within these clades of interest remain unresolved (Fig. 3.1E). There is so little overlap in recovered relationships in Oviraptoridae between analyses that it is difficult to pinpoint the reasons for the conflict. These studies do not use the same taxa or characters, of course adding to the confusion.
Figure 3.14. Consensus tree (from 2 MPTs) recovered from a reanalysis of the Lu (2005) data matrix. Black dot represents Oviraptorosauria.
INGROUP RELATIONSHIPS RECOVERED FROM THE PRESENT ANALYSIS

Stem taxa

The topology of the stem recovered in this analysis does not diverge widely from that recovered in previous analyses. Those analyses that do differ did not include *Incisivosaurus gauthieri* (i.e., Maryańska et al., 2002; Osmólska et al., 2004). Maryańska et al. (2002) was conducted before the description of that taxon was published (Xu et al., 2002; Balanoff et al., 2009) and therefore cannot be evaluated in this respect. The inclusion of *Incisivosaurus gauthieri* in any subsequent analyses, however, is imperative for tracing character evolution along the oviraptorosaur lineage. The basal position of the taxon in this analysis is not surprising, given that all recent phylogenetic studies of Coelurosauria that have included Oviraptorosauria recover it in the same position (e.g., Hwang et al., 2004; Lu et al., 2004; Turner et al., 2007).

The position of *Avimimus pergracilis*, *Caudipteryx zoui*, and *Microvenator celer* has varied from analysis to analysis (Figs. 3.1 and 3.2); however, these taxa consistently fall out near the base of the oviraptorosaur tree. TWiG analyses sometimes find a sister group relationship between *Avimimus portentosus* and *Microvenator celer* (e.g., Norell et al., 2006; Turner et al., 2007). Holtz (2007) recovered a somewhat different topology in this region of the tree, with *Avimimus portentosus* being the more basal of the aforementioned taxa and *Caudipteryx zoui* and *Microvenator celer* residing in a polytomy in a slightly more exclusive clade (Fig. 3.2). The analysis presented here finds a relationship between these taxa that is consistent with Maryańska et al. (2002) and Osmólska et al. (2004) with *Avimimus pergracilis* at the base of the tree and *Caudipteryx*
zoui in a slightly more exclusive clade (Figs. 3.1 and 3.3). The aforementioned studies, however, do not include *Microvenator celer* in their matrices.

**IGM 100/42, *Citipati osmolskae*, and *Oviraptor philoceratops***

IGM 100/42 first was associated with *Oviraptor philoceratops* when Barsbold (1981) described the specimen as belonging to the taxon. The holotype specimen of *Oviraptor philoceratops* is a fragmentary specimen, and thus it is not surprising that IGM 100/42 would have been assigned to the taxon, especially at a time when the full diversity of this clade was not yet apparent. Most crested oviraptorosaurs, at that time, were included within *Oviraptor*. Subsequent phylogenetic analyses and a better understanding of the diversity within the oviraptorid clade (Clark et al., 2002), however, have shown that this specimen is morphologically distinct from *Oviraptor philoceratops* (which occupies the senior name; Osborn, 1924) in the morphology of its ossified crest, maxilla, and premaxilla. The holotype (AMNH 6517) and IGM 100/42 now occupy disparate positions on the oviraptorid tree (Figs. 3.1 and 3.2). It is interesting to note that IGM 100/42 was used by the Maryańska et al. (2002) analysis as their representative specimen for *Oviraptor philoceratops*, and must be taken into consideration when evaluating their results.

**Ingeniinae**

The Ingeniinae initially was erected by Barsbold (1976) as a “family” level group that would encompass all non-crested oviraptorid taxa. Ingeniinae was not recovered in this analysis. Instead, the taxa that are typically included in this group (i.e., *Conchoraptor*...
gracilis and Ingenia yanshini) are arranged as a paraphyletic assemblage along the stem leading to another group of crested oviraptorids, (((Citipati osmolskae + Gigantoraptor erlianensis) + IGM 100/42) (Fig. 3.2). In one of the MPTs, Khaan mckennai is recovered as the sister taxon to the specimen IGM 100/1253, a specimen that may in the future likely be assigned to Khaan mckennai (Clark et al., 2001).

**Evolution of the Cranial Crest within Oviraptoridae**

The recovery of Oviraptor philoceratops at the base of Oviraptoridae is not surprising. Clark et al. (2002) hypothesized that this taxon likely was “primitive” among oviraptorids based on its maxillary morphology, which much more closely resembles that found in caenagnathids than that observed in other oviraptorids (Clark et al., 2002:fig. 12). A noteworthy observation about the topology recovered in this analysis is the implications it has for the evolution of the cranial crest among oviraptorids. Both of the clades (((Oviraptor philoceratops + Rinchenia mongoliensis) + Nemegtia barsboldi) and (((Citipati osmolskae + Gigantoraptor erlianensis) + IGM 100/42) have bony crests on their skulls. Therefore instead of the crest evolving only once within the lineage in the Oviraptorinae as was hypothesized by Barsbold (1976), there are now topology a several different scenarios that can account for the evolution of the cranial crest (Fig. 3.15).

Bony crests on the dorsal skull are not unusual among dinosaurs, especially within avians, which have evolved this feature numerous times (e.g., bucerotiforms and ratites); therefore, independent origins of this feature within oviraptorids would not be unrealistic. The most parsimonious reconstruction of the evolution of this feature would be the occurrence of the crest as two separate evolutionary events (convergent evolution):
Therizinosauria

*Incisivosaurus gauthieri*

*Caudipteryx zoui*

*Avimimus portentosus*

*Similcaudipteryx*

*Microvenator celer*

*Chirostenotes pergracilis*

*Namingia gobiensis*

*Nemegtia barsboldi*

*Oviraptor philoceratops*

*Rinchenia mongoliensis*

*Oviraptoridae*

*Heyuannia huangi*

*ZPAL MgD/I/106*

*Ingenia yanshini*

*Conchoraptor gracilis*

*Khaan mckennai*

*IGM 100/1253*

*IGM 100/1253*

*IGM 100/42*

*Gigantoraptor erlianensis*

*Citipati osmolskae*

Figure 3.15. Perceived evolutionary history for the acquisition of a bony cranial crest.
one along the branch leading to the clade \((Oviraptor\ philoceratops + Rinchenia\ mongoliensis) + Nemegtia\ barsboldi\) and another at the base of the \((Citipati\ osmolskae + Gigantoraptor\ erlianensis) + IGM\ 100/42\) clade (Fig. 3.15).

It should be noted that the undescribed “caenagnathids” that are not included in this phylogenetic analysis possess large cranial crests (Triebold and Russell, 1995). If these specimens do sit within Caenagnathidae, this would have an effect on the reconstructions of the evolutionary history of this character system. Such a scenario would require either three separate acquisitions of the crest or an evolution of the feature at the base of the Caenagnathidae + Oviraptoridae clade, a reversal of this feature within the oviraptorid clade, and a subsequent re-evolution of the crest in the \((Citipati\ osmolskae + Gigantoraptor\ erlianensis) + IGM\ 100/42\) clade. Because I was not able to incorporate these undescribed specimens into my phylogenetic analysis, this scenario remains uncertain because their exact phylogenetic position at this moment is unknown.

**Protarchaeopteryx robusta and Incisivosaurus gauthieri**

*Protarchaeopteryx robusta* (Ji and Ji, 1997; Ji et al., 1998) was not included in the initial analysis of oviraptorosaur relationships; although it and *Incisivosaurus gauthieri* (Xu et al., 2002a) have been proposed to be either the same taxon or sister taxa (each being a monospecific taxon within the same genus) (Senter et al., 2004; Senter, 2007). The inclusion of *Protarchaeopteryx robusta* within the species level analysis does not affect the stability of the relationships within Oviraptorosauria but does result in ten most parsimonious trees with three separate positions for this taxon (Fig. 3.16). These various

---

252
positions destabilized the relationships between those taxa that lie outside of Oviraptorosauria.

In four of these trees, *Protarchaeopteryx robusta* does fall out as the sister taxon to *Incisivosaurus gauthieri*, supported by dental characters (Fig. 3.16A, B). Two of these four topologies have a (*Protarchaeopteryx* + *Incisivosaurus*) clade that in turn is the sister taxon to the rest of Oviraptorosauria (Fig. 3.16A). Characters supporting this relationship are the same types of dental characters that Holtz (2007) used to tie these taxa together. Both *Incisivosaurus* and *Protarchaeopteryx* possess a first premaxillary tooth that is much larger than the size of the crowns of premaxillary teeth two and three (230.2). The morphology of the first premaxillary tooth in these two taxa is spatulate (251.2). In the other two reconstructions in which these taxa are considered most closely related to each other, the clade they form is then the sister taxon to *Similcaudipteryx yixianensis* (Fig. 3.16B). The relationship between these three taxa, however, is not supported by any unambiguous synapomorphies.

Other evolutionary scenarios retain the oviraptorosaur affinities of *Protarchaeopteryx robusta* and posit this taxon either as the sister taxon to Oviraptoridae or (Oviraptoridae + *Chirostenotes pergracilis*) (Fig. 3.16C, D). Oviraptorids and *Protarchaeopteryx robusta* share 25 to 40 caudal vertebrae (117.1), a preacetabular length of the ilium that is approximately equal to or shorter than the postacetabular length (152.0), and a rounded anteroventral process on the preacetabular blade (155.1). The clade of (*Chirostenotes pergracilis* + Oviraptoridae) shares with *Protarchaeopteryx robusta* a preacetabular process to the ilium that is not or weakly expanded ventrally below the level of the acetabulum. This character is a reversal in this group from the
Figure 3.16. Alternate positions for the taxon *Protarchaeopteryx robusta*. 
Figure 3.16 (cont). Alternate positions for the taxon *Protarchaeopteryx robusta*. 
condition that is present in therizinosaurs and basal oviraptorosaurs. All coelurosaur taxa outside of Oviraptorosauria and Therizinosauria lack this derived condition; therefore, its absence in Protarchaeopteryx robusta is not necessarily strong support for its position as sister taxon to the aforementioned clade.

A final reconstruction positions Protarchaeopteryx robusta as the sister taxon to Alvarezsauridae (Fig. 3.16E). This relationship is supported by three characters. These taxa share a similar hand to forearm ratio, both having a short manus (146.2). The fibula fails to contact the tarsus in both of these taxa (183.1). They also lack distinct xiphoid processes on the sternum (186.1). It can be concluded from the disparate positions that this taxon occupies on the coelurosaur tree that additional material of this taxon will need to be incorporated in the analysis, as its oviraptorosaur affinities are based primarily on ambiguous character reconstructions.

SUMMARY AND CONCLUSIONS

The addition of taxa in this analysis (i.e., as compared to Maryańska et al. [2002], which did not include alvarezsaurids, troodontids, Incisivosaurus gauthieri, and Microvenator celer) and a more rigorous analysis of the anatomical structures themselves clearly have an effect on the perceived relationships within Oviraptorosauria, the position of the clade within Coelurosauria, and how morphological characters map onto the coelurosaur tree. The analysis presented here supports the position of Oviraptorosauria as non-avian coelurosaurian taxa, well outside of Avialae (following the results of Holtz, 1998; Sereno, 1999; Rauhut, 2003; Norell et al., 2006; and Turner et al., 2007; Zanno,
2009, among others). This position clarifies the evolution of many characters leading not only to the oviraptorosaur lineage but also the avian lineage as well. Furthermore, the relationships within Oviraptorosaura are clarified and many of the previously recovered relationships again are supported here. *Incisivosaurus gauthieri, Caudipteryx zoui, Avimimus portentosus, Similcaudipteryx yixianensis* and *Microvenator celer* are all found, as expected, along the stem leading to *Chirostenotes pergracilis* and Oviraptoridae. The relationships within Oviraptoridae are elucidated and consist of a basal Oviraptorinae and a paraphyletic ‘Ingeniinae’ (Fig. 3.2). A second crested clade is recovered within Oviraptoridae consisting of IGM 100/42, *Citipati osmolskae*, and *Gigantoraptor erlianensis* (Fig. 3.2).

Understanding the relationships within this lineage is imperative for further analysis (see following chapter) to polarize characters within the lineage and to establish non-independence of data points with respect to phylogeny in regression analyses when testing correlations (Felsenstein, 1985). *Incisivosaurus gauthieri* presents an important datapoint that breaks up the long branch that exists within Oviraptorosaura and overturns some of the putative synapomorphies used in previous analyses. With such additional resolution, those characters that were inferred by previous analyses to be unambiguous synapomorphies become either ambiguous (being present in more than just avialans and oviraptorosaurs) or synapomorphic for a much more inclusive group, including paravians.

In conclusion, what appears to be unique about Oviraptorosaura is not its placement among birds, but rather it is the opportunity to understand how the ‘avian’ characters are acquired along each lineage in question (Oviraptorosaura and Avialae). Once fully understood, the transformations can be compared to see the various ways in
which those groups of interest were able to acquire similar characters phylogenetically as well as ontogenetically. Oviraptorosauria, because of the number and the nature of specimens, provides an unparalleled opportunity to study the evolution and the development of character systems in an entirely extinct clade (e.g., looking at the endocranial evolution along this lineage as is done in the following chapter).
INTRODUCTION

For well over a century morphologists have taken advantage of the fact that casts of the endocranial cavity (endocasts) in organisms whose brain fills the majority of the cranial cavity (i.e., mammals and birds) provide a close approximation to the morphology of the brain as it appeared during life (see Marsh 1880; Edinger, 1929). Only a handful of early paleontological researchers such as Tilly Edinger used cranial endocasts to study the neuroanatomy of extinct animals (e.g., Edinger, 1929; 1951; Osborn, 1912; Radinsky, 1977; Hopson, 1979). Theropod endocasts in general are not known in large numbers, but early descriptions can be found such as Osborn’s initial description of a natural endocast from *Tyrannosaurus rex* (Osborn, 1912). In the absence of naturally occurring endocasts, synthetically prepared ones also have been used to investigate the endocranial morphology of extinct organisms (e.g., Wiman and Edinger, 1940; Radinsky, 1974; Hopson, 1979; Burnham, 2004). Hopson (1979) presents an almost comprehensive examination of the natural and synthetic dinosaurian endocasts that were known up to that point. The advent of non-destructive digital technologies such as computed tomography (CT) has more recently provided a means to visualize the endocranium and to reconstruct three dimensional models of this space with which to study the
neuroanatomy of fossils (e.g., Brochu, 2000; Carlson et al., 2003; Witmer et al., 2003; Franzosa, 2004; Macrini et al., 2007; Sampson and Witmer, 2007; Brusatte et al., 2009; Witmer and Ridgely, 2009).

As CT becomes standard protocol for describing specimens and a continually increasing number of datasets are becoming available in the archosaur literature, the number of archosaur endocasts will continue to grow. The large quantity of sauropod endocasts (natural, synthetic, and digital) has allowed researchers to assess endocranial variation along this lineage of morphologically unique saurischians (e.g., Janensch, 1935–36; Hopson, 1979; Galton, 1985; Tidwell and Carpenter, 2003; Chatterjee and Zheng, 2005; Balanoff et al., 2010). Some of the more comprehensive studies of archosaurian endocranial evolution in recent years not surprisingly have been focused on the theropod lineage, as the expansion of the brain in these taxa leaves traces of individual structures on the endocranial cavity by which the “neuroanatomy of the brain” can be identified.

Recent and thorough descriptions of theropod endocranial anatomy include a description by Sampson and Witmer (2007) of *Majungasaurus crenatissimus*, an abelisaurid near the base of Theropoda. Sanders and Smith (2005) describe a digitally generated endocast of the ceratosaur, *Ceratosaurus*. Further up the tree, the endocast of the carcharodontosaurid, *Giganotosaurus carolinii* is described by Carabajal and Canale (2010). Allosoroids have been described by Franzosa and Rowe (2005), who published a description of the endocast of the allosoroid *Acrocanthosaurus atokensis*, and by Rogers (1998; 1999), who provided descriptions of *Allosaurus fragilis*. The base of
Coelurosauria has been covered by Brochu (2000), Witmer and Ridgely (2009) Bever et al. (submitted) and Brusatte et al. (2009) with descriptions of tyrannosaurid endocranial casts.

Excepting Tyrannosauridae, most descriptions have concentrated at the base of the theropod lineage, while Coelurosauria has experienced relatively less growth in the number of published endocranial cast descriptions (Franzosa, 2004; Sampson and Witmer, 2007). Therapoda, and particularly Maniraptora, is of great interest because of the distinctive changes in the brain that coincide with the transition from ‘cursorial’ non-avian theropods to volant avians. Until recently, however, specimens were not available to study the more distal region of the coelurosaur tree. Looking more intensely at the distribution of endocranial variation in this important region of the tree will facilitate the understanding of the changes associated with attaining a characteristically avian brain.

Historically, analyses have tried to quantify the morphological transitions of paraphyletic groups, from non-dinosaurian reptiles to basal theropods and subsequently to crown birds (Jerison, 1968; 1969; 1977). The aim of such studies was not, however, to describe or quantify the morphology of the endocast but rather to examine the expansion in the volume of the entire brain as a representative measure of cognition or intelligence. An encephalization quotient (EQ) was propounded as a measure of brain expansion (see Jerison, 1977). The EQ thereafter became the most prominent measure of brain expansion within extinct organisms along both the mammalian and avian lineages (Hopson, 1979; Hurlburt, 1996). The initial attempt to create the EQ as a measure of cognition is problematic because endocranial volume and cognition have not yet reliably been shown
to exhibit a one-to-one correlation in extant taxa (Healy and Rowe, 2006; Lefebvre and Sol, 2008).

Larsson et al. (2000) put forth a more conservative hypothesis concerning the enlargement of the endocranium and forebrain within Coelurosauria; however, this study is in essence based on two data points. One point consisting of theropods outside of Coelurosauria (Allosaurus fragilis and Carcharodontosaurus saharicus) and the basal coelurosaur Tyrannosaurus rex, and the other datapoint being avialans as represented by Archaeopteryx lithographica. The sampling from this study in effect excludes a large segment of the more distal part of the avian stem. Although Larsson et al. (2000) provided a rigorous assessment of total endocranium and forebrain enlargement, again with such a large region of the coelurosaur tree from Tyrannosauridae to Avialae not being sampled, these results likely simplify the transition. A relatively straightforward, linear expansion in volume may or may not exist within this region of the tree. Reality probably bears some similarity to other transitions such as body size (Turner et al., 2007), in which a perceived trend, in reality, exhibits more complexity than previously had been shown.

The present study builds on such previous analyses, and also establishes that more morphological variation is present in the theropod endocast than previously indicated. This is accomplished by focusing on the more distal region of the coelurosaur lineage relative to birds. The addition of taxa from this region demonstrates that the transition from the relatively simple endocranial morphology present at the base of the coelurosaur tree (Larsson, 2000; Brochu, 2000; Brusatte et al., 2009; Sampson and Witmer, 2009) to
the complex morphology of the avian brain (Pearson, 1972; Niewenhuys, 1997) likely does not exist (see Larsson et al., 2000). Concentration is focused on a single lineage, Oviraptorosauria, which is positioned close to the avialan clade introducing additional variation and producing a more intricate story. A better understanding of the morphology of the cranial endocast in this important region of the tree will help us grasp the changes within the brain that may be associated with the acquisition of flight.

This analysis segments the endocranial cast into six separate regions that correspond closely with neuroanatomical partitions of the brain. Although previous studies of fossil taxa have partitioned the endocast (i.e., cerebral cast and everything else; Larsson et al., 2000), those analyses were not able to observe changes in the various neuronatomical divisions with respect to each other, body size, or total endocranial volume. This study, therefore, is able to assess more rigorously evolutionary patterns in the major anatomical regions of the ‘brain’ through the use of principal components analysis and bivariate regressions.

More specific questions regarding oviraptorosaur and avialan endocranial evolution also can be addressed with this data. As has been noted earlier concerning other character systems such as osteology and behavior, some studies have recognized that ‘derived’ characteristics in the oviraptorid endocast also are present in the endocranial cast of modern avians, and these similarities recently have been used to advance the hypothesis that Oviraptorosauria is not a non-avian theropod but rather a member of Avialae (Kundrát, 2007). Although such observations of similarity are interesting, they have been proffered without reference to an explicit phylogenetic hypothesis such as the
one presented in the previous chapter. It, therefore, remains to be identified whether such features are shared derived characters (synapomorphic of a clade including both Aves and Oviraptorosauria) or convergences (derived independently along the two separate lineages). A clearer understanding of these character acquisitions can only be identified within the larger context of the evolutionary history of not only Oviraptorosauria, but also Coleurosauria. Accordingly, this chapter both presents morphological descriptions of several oviraptorosaur endocasts, and also places character transformations within the evolutionary context of the previous chapter so as to identify phylogenetically informative characters derived from the endocranial morphology of Oviraptorosauria and Avialae. Also included in this analysis are specimens from important systematic positions (e.g., the basal oviraptorosaur Incisivosaurus gauthieri) that are able break up effects caused by long branches.

MATERIALS AND METHODS

TAXON SAMPLING

This study includes a comparative sample of taxa across a broad phylogenetic range of recent birds and non-avian theropods (Appendix 5). Concentration is given to the oviraptorosaur lineage, including crested (e.g., Citipati osmolskae) and non-crested (e.g., Khaan mckennai) forms. A large number of avian endocasts also are included in the dataset (Appendix 5). The vast majority of compared volumes reflect new data.
The use of computed tomography (CT) provides a nondestructive means to view and study the internal structures of the vertebrate braincase (Carlson et al., 2003). In addition, CT allows the extraction of digital endocasts from the endocranial cavity and its related structures in fossilized taxa. These casts can preserve fine-scale anatomical detail such as the cranial nerves and vessels through the skull as well as the morphology of the sinus cavities (e.g., Brochu, 2000; Franzosa, 2004; Franzosa and Rowe, 2005; Balanoff et al., 2009; Norell et al., 2009; Balanoff et al., 2010).

I extract digital endocasts using the CT data from the endocranial cavity of several specimens, both within and outside of Oviraptorosauria (Appendix 6). The endocranial endocasts were reconstructed using the original imagery, either tiff or DICOM images, in the volumetric rendering program VGStudioMax© 2.0.1. The reconstructions were made by adjusting the grayscale contrast in the images until bone and matrix were distinguishable from one another. The endocranial cavity was selected using the segmentation tools available in the program, and exported as isosurface volumes. Measurements taken from the endocast (including volume) were done using the same version of VGStudioMax©. Endocast volume measurements were taken by calculating the volume of negative space of the endocranial cavity. For ease of description, features of the endocranial casts are referred to by the names of the soft tissues of the brain that they reflect (e.g., cerebrum rather than cast of cerebrum). It is important to note, however, that what actually is preserved is a cast of the endocranial space, which may reflect structures other than the brain, such as meninges and sinuses. The endocast, however,
does help to determine relative size and shape of regions of the brain as well as recognizing the branching points of the cranial nerves (Hopson, 1979).

**SEGMENTATION OF THE ENDOCAST INTO ANATOMICAL REGIONS**

Osteological markers were used during the segmentation of the endocasts to distinguish six separate anatomical regions of the “brain” based as far as possible on the gross anatomical descriptions given by Iwaniuk and Hurd (2005). The divisions along tissue layers that are discussed in that paper are not possible when segmenting the endocranial space into separate regions. It is important to note that these regions are casts and may contain more neurological tissues than are implied by the descriptors that are used in the text. For example, the pituitary fossa encloses the pituitary body as well as transmitting the cranial carotid vessels and abducens nerves (cranial nerve VI). As preservation allowed, these regions were isolated from each endocast so that their volumes could be measured independently (Fig. 4.1; Appendix 5). The six segments included in this analysis comprise the olfactory bulbs, cerebrum, and pituitary (forebrain); the optic lobes (midbrain); and the cerebellum and brain stem (hindbrain) (Butler and Hodos, 1996). The osteological landmarks used to define the regions were identified in the two-dimensional, coronal CT slices (except the olfactory bulbs, which were identified in the sagittal slices) and delineated from each other using the computer program VGStudioMax 2.0.1. Standard segmentation tools from this program were used in the isolation of anatomical regions.
Figure 4.1. Endocranial cast of the tropicbird, *Phaethon rubricada*, demonstrating the six neuroanatomical partitions distinguished in this analysis: olfactory tracts and bulbs (light blue), cerebrum (yellow), pituitary (dark blue), optic lobes (purple), cerebellum (orange), and brain stem (green).
In this analysis, the region defined as the olfactory bulbs is delineated from the rest of the forebrain anteriorly by the anterior-most constriction of the endocranial space before it opens into the nasal cavity and posteriorly by the unnamed crista that lies between the olfactory bulb fossa and the anterior cerebral cavity (Baumel and Witmer, 1993; Fig. 4.2).

The cerebral region is defined anteriorly by the same crista that delineates the posterior margin of the olfactory bulbs, dorsally by the roof of the cranial cavity formed by the frontals and parietals, posteriorly by the crista between the cerebral and the cerebellar fossae, and ventrally by the crista between the optic lobe fossa and the cerebral fossa (Fig. 4.3). There is no clear posterior border of the cerebral fossa in the cranial space, so a straight line was drawn dorsally between the paired cristae that lie at the junction of the cerebral and cerebellar fossae and ventrally between the paired cristae lying at the junction of the cerebral and optic lobe fossae. These were followed posteriorly until they converged (Fig. 4.4), simulating the folding of the cerebellum over the cerebrum (Fig. 4.5).

The pituitary fossa was the simplest to isolate because it is fully enclosed except for its dorsal border. This line was drawn at the dorsal border of the sella turcica, which is the crista that lies between the pituitary stalk (infundibulum) and the optic lobe fossae (Fig. 4.6).

The cast of the optic lobes are the only anatomical structures from the midbrain that are isolated on the prepared endocasts. These are easily identified dorsally by drawing a line between the crista lying between the cerebral and optic lobe fossae to their
Figure 4.2. Sagittally sectioned skull of *Phaethon rubricada*, with digitally created endocast. Osteological markers used to delineate the olfactory bulbs are indicated in the enlarged image below.
Figure 4.3. Sagittally sectioned skull of *Phaethon rubricada*, with digitally created endocast. Osteological markers used to delineate the cerebrum are indicated in the enlarged image below.
Figure 4.4. Two dimensional CT slice through braincase of *Phaethon rubricada*. Arrows indicate osteological markers used to delineate posterior border of cerebrum.
Figure 4.5. Sagittally sectioned endocast of *Phaethon rubricada*. Colors correspond to: olfactory tracts and bulbs (light blue), cerebrum (yellow), pituitary (dark blue), optic lobes (purple), cerebellum (orange), and brain stem (green).
Figure 4.6. Sagittally sectioned skull of *Phaethon rubricada*, with digitally created endocast. Osteological markers used to delineate the pituitary are indicated in the enlarged image below.
Figure 4.7. Sagittally sectioned skull of *Phaethon rubricada*, with digitally created endocast. Osteological markers used to delineate the optic lobes are indicated in the enlarged image below.
Figure 4.8. Sagittally sectioned skull of *Phaethon rubricada*, with digitally created endocast. Osteological markers used to delineate the cerebellum are indicated in the enlarged image below.
Figure 4.9. Sagittally sectioned skull of *Phaethon rubricada*, with digitally created endocast. Osteological markers used to delineate the brain stem are indicated in the enlarged image below.
opposite on the other side of the braincase. Ventrally, the border of the optic lobe cast is defined as the crista between these structures and the pituitary fossa until the fossa closes posteriorly. Posterior to the pituitary fossa a line is drawn along the crista between the fossa for the brain stem and the optic lobe fossa. The posterior border is formed as the dorsal line and ventral line converge towards the midpoint of the endocranial space (Fig. 4.7). The optic nerve cast is included in the midbrain and is terminated anteriorly at the level of the optic foramen.

The two isolated regions in the hindbrain comprise the casts of the cerebellum and brain stem (Fig. 4.1). The cerebellar cast at its anterior margin can overlie or lie just posterior to the posterior margin of the cerebral fossa. In life, the cerebellum resides in a distinctive fossa on the roof of the endocranial cavity, delineated by a surrounding crista, crista marginalis (Baumel and Witmer, 1993; Fig. 4.8). The fossa for the brain stem underlies both those of the optic lobes and the cerebellum. Again, a distinctive crista is present at the dorsal border of the brain stem fossa and transverses both of these sections (Fig. 4.9). The posterior margin of this region is determined by the opening of the foramen magnum (Fig. 4.9).

**Statistical Analysis**

Several different analyses were run on the volumetric data gained from the digital endocasts of both avian and non-avian theropods. The initial analysis was a simple regression run between body mass and total endocranial volume, similar to the analyses reported by previous papers (e.g., Jerison, 1969; Hopson, 1979; Larsson et al., 2000;
Franzosa, 2004; Dominguez Alonso et al., 2004, Kundrát, 2007). In addition, body mass was plotted against each of the endocranial regions. Endocast volumes were obtained from the volume of negative space as calculated by VGStudioMax 2.0.1. Endocranial volumes in crown birds were found to be an accurate measure of brain volume (Iwaniuk and Nelson, 2002); and it is assumed that this also holds for non-avian theropods given that impressions of the brain on the endocranial cavity indicate that the brain was sufficiently expanded so as to fill the space. Cranial nerves were cut off as close to the “brain” as possible to cut down their influence on the total volume (Iwaniuk and Hurd, 2005). Body masses for both avian and non-avian theropods were calculated using femur length, based on the algorithm proposed by Christiansen and Fariña (2004). All of the volumetric and body mass data were log transformed to accommodate them onto a single chart and to facilitate ease of pattern recognition. Best fit lines were mapped onto the data using least squares regression. These lines were fit to the coelurosaurian and crown bird datapoints. A best fit line also was drawn for the paraphyletic group “non-avian theropods” to approximate the ancestral condition in the data.

The Phenotypic Diversity Analysis Program (PDAP; Midford et al., 2010) subsequently was used on bivariate data to test for non-independence of variables due to phylogenetic influence (Felsenstein, 1985), and a second set of regressions was run using independent contrasts. Because the inclusion of fossils required the use of strictly morphological trees, branch lengths were set at one. Phylogenetic topologies are based on the hypothesis of oviraptorosaur relationships presented in the previous chapter, Smith et al. (2007), Turner et al. (2007), and Mayr and Clarke (2003). Interpretations of the
bivariate graphs are based on a consideration of both the initial bivariate analysis and those corrected for phylogeny due to problems that might arise by setting all branch lengths to one when considering fossil data.

A principal components analysis (PCA) was run on the volumes of all of the six regions of the endocranium that were isolated in this analysis (olfactory bulbs, cerebrum, pituitary, optic lobes, cerebellum, and brain stem; Appendix 7). Rather than running the PCA on the absolute values of the volumes, each region was divided by the overall endocranial volume both for consistency with previous analyses performed on crown birds and mammals and to minimize errors that may be associated with shape and distortion (Appendix 7) (Clark et al., 2001; de Winter and Oxnard, 2001; Iwaniuk and Hurd, 2005). The PCA was run in SPSS ver. 19. Minimal polygons were drawn around the taxa belonging to the clades Oviraptorosauria, Aves, and Paraves for ease of comparisons.

ENDOCRANIAL CAST DESCRIPTIONS

AVIAN ENDOCRANIAL ANATOMY

(*Struthio camelus* Fig. 4.10 and *Anas platyrhynchos* Fig. 4.11)

Avians have an endocranial morphology distinct from that of basal coelurosaurs (see Brochu, 2000; Brusatte et al., 2009; 2010; Witmer and Ridgely, 2009). Their brains fill the cranial cavity with little to no overlying dural matter (Sedlmayr, 2002), allowing a fairly accurate estimation of brain morphology from the endocranial casts (Fig. 4.10, 3.11). Avians retain prominent cephalic and pontine flexures, a plesiomorphic feature that
Figure 4.10. Endocranial cast of the ostrich, *Struthio camelus*. 
Figure 4.11. Endocranial cast of the common duck, *Anas platyrhynchos*. 
can be traced at least to the base of Maniraptora (Franzosa, 2004). These two flexures, which occur just posterior to the cerebral hemispheres (cephalic) and within the hindbrain (pontine) are absent in crocodilian (Hopson, 1979; Franzosa, 2004), basal theropod (Franzosa, 2004; Sampson and Witmer, 2009), and basal coelurosaur (Brochu, 2000; Brusatte et al.; 2009; 2010; Witmer and Ridgely, 2010) endocasts. It is interesting to note that these flexures are convergently evolved along the sauropod lineage (see Balanoff et al., 2010).

In the forebrain, the olfactory tracts of avians are retracted, leaving the olfactory bulbs pressed against the anterior surface of the cerebrum with little anterior extension (Figs. 4.10 and 4.11). This arrangement is drastically different from the plesiomorphic condition in deinonychosaurs and most other coelurosaurs in which the olfactory bulbs sit at the distal end of elongate tracts that project anteriorly towards the nasal passage. A somewhat intermediate morphology is present in Archaeopteryx lithographica where the olfactory tracts are retracted to a greater degree than in more basal coelurosaurs, but are still visible on the endocast (Dominguez Alonso et al., 2004:Fig. 4).

The cerebrum is by far the largest region of the avian forebrain (Figs. 4.10 and 4.11). The cerebral hemispheres have a pyriform shape so that the posterior region of these structures is the widest and the anterior region is the narrowest. This same shape is present in deinonychosaurs (Fig. 4.12), basal avialans (Dominguez Alonso et al., 2004:Fig. 4), and some oviraptorosaurs (Figs. 4.13 and 4.14). The cerebrum also exhibits a dorsoventral expansion, as is characteristic of crown birds. Crown birds possess a unique feature of the cerebrum, the wulst or sagittal eminence, the function of which
spans a wide range from integumentary control to song learning (Fig. 4.10) (Pearson, 1972; Butler and Hodos, 1996). The cast of a large trochlear nerve canal (cranial nerve IV) can be seen on the anteroventral surface of the cerebrum, exiting through the laterosphenoid. A cast of the small oculomotor foramen (cranial nerve III) lies on the cerebrum ventral to the trochlear nerve cast. The arrangement of these cranial nerves does not diverge significantly from the generalized amniote pattern.

Morphology of the pituitary body varies widely within avians, and it has been suggested that the size of the pituitary can be correlated with the size of the organism as this structure is often enlarged in “gigantic” taxa such as whales and large birds (e.g., the ratites Struthio camelus or the extinct elephant bird, Aepyornis maximus) (see Edinger, 1942; Balanoff and Rowe, 2007). Cranial carotid canals enter the pituitary fossa ventrally and alternately anastamose (as they do in Anas platyrhynchos, Fig. 4.11A) or remain separate (as they do in Struthio camelus, Fig. 4.10A) before entering the cavity in various avian taxa (Baumel and Witmer, 1993). The abducens nerve (cranial nerve VI) enters the sella turcica (posterior wall of the pituitary fossa) at its dorsal edge and can be seen on the endocast of the infundibulum (pituitary stalk). Again, this arrangement does not differ significantly from the plesiomorphic amniote condition.

Visible structures in the midbrain of the avian endocast include the optic lobes (optic tectum) and nerves (cranial nerve II). The optic lobes of crown birds are located ventrolaterally. This arrangement differs from crocodilians in which these structures are positioned dorsally and contact each other along the midline (Butler and Hodos, 1996). More basal theropods also retain this plesiomorphic condition (Sampson and Witmer,
2007); however, the derived state is present at least at the base of Maniraptora (being present in *Zanabazar junior* [Norell et al., 2009] and *Incisivosaurus gauthieri*). The optic lobes have a spherical outline and can be assumed to have lacked any type of significant overlying dural structures because of their prominence (as opposed to the condition in tyrannosaurids; Brochu, 2000; Brusatte et al., 2009; Witmer and Ridgely, 2009). Anterior to the optic lobes, the associated optic nerve penetrates the braincase through the foramen formed at the midline of the laterosphenoids and orbitosphenoids. The openings for the optic nerve may be single (as in *Anas platyrhynchos*, Fig. 4.11) or paired (as in *Struthio camelus*, Fig. 4.10).

The cerebellum and brain stem comprise the majority of the hindbrain and are the only gross anatomical structures from this region that can be discerned on the endocast (Figs. 4.10E and 4.11E). While the cerebellum may fold over the posterior edge of the cerebrum, the cerebrum more typically is inflated to such a degree that it extends far dorsally to the cerebellum. The total proportion that the cerebellum contributes to the endocast volume in birds is relatively small, and its size varies somewhat with aerial ability. Highly aerial birds such as caprimulgiforms have a relatively larger cerebellum than poor fliers and flightless birds (Iwaniuk et al., 2005b). The cerebellum in all avians is folded to increase surface area—a convergent feature with mammals (Butler and Hodos, 1996)—and the cerebellar folds sometimes leave impressions that are visible on the endocranial cast (Fig. 4.10D). Laterally, floccular lobes protrude from the cerebellum occupying the space between the semicircular canals of the inner ear. The flocculus of crown birds is small, which appears to be a derived character of paravians (Figs. 4.10 and
4.11 compare to Zanabazar junior, Fig. 4.12; Dominguez Alonso et al., 2004:fig. 3). Dorsal to the flocculus is a transverse sinus, a plesiomorphic feature present in all theropod endocasts (Franzosa, 2004; Sampson and Witmer, 2007).

The brain stem (medulla oblongata) of crown birds is relatively wide and has a distinct pontine flexure point (Figs. 4.10C, D and 4.11C, D), as is present in all maniraptoran endocasts (Figs. 4.10–4.12). A number of cranial nerves extend from the lateral surface of the brain stem. In crown birds the trigeminal (cranial nerve V) divides within the braincase into ophthalmic and maxillomandibular branches. Both branches are associated with the laterosphenoid, the ophthalmic branch between the laterosphenoid and parabasisphenoid and the maxillomandibular branch between the laterosphenoid and prootic (Baumel and Witmer, 1993; Balanoff and Rowe, 2007). The cast of the internal acoustic fossa may sometimes be visible on the endocast, and forms the surface from which the facial nerve (cranial nerve VII) and both branches of the acoustic nerve (cranial nerve VIII) emanate (Figs 4.10 and 4.11). Posterior to the internal acoustic fossa and just ventral to the flocculus is the cast of the vagus foramen from which cranial nerves IX (glossopharyngeal), X (vagus), and XI (accessory) extend. The hypoglossals (cranial nerve XII) typically exit through two foramina within the basioccipital, although the number of foramina for the hypoglossal nerves may vary. More basally diverging theropods and coelurosauras have a single hypoglossal foramen (Franzosa, 2004; Sampson and Witmer, 2007; Witmer and Ridgely, 2009; Brusatte et al., 2009; Balanoff et al., 2010).
ZANABAZAR (=SAURNORNITHOIDES) JUNIOR (IGM 100/1; Fig. 4.12)

The exceptional preservation of the braincase of IGM 1/100 allowed the completion of an almost completely undistorted digital endocranial cast of Zanabazar junior (Fig. 4.12). The endocranial cavity has a length of 7.2 cm from the anterior extent of the olfactory tracts to the posterior border of the cerebellum. The greatest width of the endocast is 3.9 cm across the cerebral hemispheres. The total volume is approximately 26.0 cm$^3$. This volume differs considerably from the 45 cm$^3$ and 49 cm$^3$ previously estimated for Troodon formosus (Currie and Zhao [1993a] and Russell [1969], respectively)—a taxon whose overall cranial length is slightly smaller than that of Zanabazar junior. This relatively high endocranial volume for Troodon formosus suggests it may have had an autapomorphically large index of endocranial volume to body size among troodontids. The endocasts of Troodon formosus that formed the bases for these volumetric assessments largely were reconstructed from specimens with incomplete endocranial cavities; however, the disparity in preservational quality and methodology (CT versus physical reconstructions) complicates the direct comparison of these data. For example, the cerebellum in Zanabazar junior is considerably narrower than that reconstructed for Troodon formosus (Currie and Zhao, 1993a; Russell, 1969). This difference, whether accurate or exaggerated, likely is a major contributor to the volumetric disparity between these taxa.

Features of the forebrain that are identifiable on the endocast of Zanabazar junior include the olfactory tracts, cerebral hemispheres, pituitary body, and the optic nerve (cranial nerve II). The olfactory tract makes up the anterior-most portion of the endocast
Figure 4.12. Endocranial cast of *Zanabazar junior.*
(Fig. 4.12), but the absence of bones enclosing the ventral portion of the olfactory bulbs and tract makes the exact length and shape difficult to determine. Posterior to the olfactory tracts, the cerebral hemispheres are pyriform in shape—similar to those of *Archaeopteryx lithographica* (Dominguez Alonso et al., 2004) and *Troodon formosus* (Russell, 1969). The same region in more basal theropods, such as *Acrocanthosaurus atokensis* (Franzosa and Rowe, 2005) and *Tyrannosaurus rex* (Brochu, 2000; Larsson et al., 2000; Brusatte et al., 2009; Witmer and Ridgely, 2009), lacks distinctive expansion and is instead tubular in shape (Larsson et al., 2000). The optic nerves (cranial nerve II) enter the braincase through a single midline opening between the paired laterosphenoids, and are represented on the endocast as a large midline structure. The pituitary body lies anteroventral to the level of the optic nerve exit (Fig. 4.12C, D). The overall orientation of the pituitary body is oblique to the axis of the endocast as a whole. The paired internal carotid canals penetrate the basisphenoid, anastomose, and enter the posteroventral end of the pituitary fossa through a single opening.

The only portions of the midbrain that are observable on the endocast are the optic lobes and trochlear nerves (cranial nerve IV). The lateral exposure of the optic lobe is located posteroventral to the expanded cerebral hemispheres. The posteroventral displacement of the optic lobes and their relative degree of development is more similar to the condition in modern birds than in most non-avian theropods (Larsson et al., 2000; Dominguez Alonso et al., 2004). This degree and direction of development of the optic lobes, however, is present in some other non-avian coelurosaur lineages, such as ornithomimosuars and oviraptorosaurs. The cerebellum is expanded anterodorsally and
overlies the dorsal surface of the optic lobes. The transverse distance across both optic lobes is nearly the same length as across the cerebral hemispheres (Fig. 4.12E; compare to Fig. 4 in Dominguez Alonso et al., 2004). The trochlear nerves (cranial nerve IV) exit between the orbitosphenoid and laterosphenoid and are visible on the endocast on the ventral surface of the cerebral hemispheres approximately midway along their length (Fig. 4.12A, B). A pair of foramina for the exit of the oculomotor nerves (cranial nerve III) lies between the laterosphenoid and orbitosphenoid just posterior and ventrolateral to the foramen for the optic nerve. The paths of these foramina are not readily apparent on the endocast.

The prominent features of the hindbrain identifiable on the endocast include the cerebellum, floccular lobes, brain stem (medulla oblongata), and the majority of the cranial nerves of this region. These nerves include the trigeminal (cranial nerve V), facial (cranial nerve VII), vagus canal (cranial nerves X–XI), and hypoglossals (cranial nerve XII). Unfortunately, the middle and inner ear, such as the semicircular and cochlear canals, are not visible in the CT data because of damage in this region and a lack of adequate grayscale contrast between matrix and bone in the CT scans.

The cerebellum is compressed mediolaterally and lacks the lateral expansion present in avialans (Dominguez Alonso et al., 2004; Kurochkin et al., 2006). There also is no apparent folding of the cerebellum as in avialans (Kurochkin et al., 2006) and possibly oviraptorosaurs (Kundrát, 2007; Balanoff et al., 2009). Lateral to the cerebellum are the paired floccular lobes (Fig. 4.12A, B). These relatively small structures protrude from the endocast in a ventrolateral direction and are surrounded by the bones that enclose the
semicircular canals. In this specimen, only the right floccular lobe is distinguishable because of a concentration of dense minerals in this area on the left side of the skull (only the base of the left floccular lobe can be identified). Only a short length of the medulla oblongata is visible on the endocranial cast, but this portion is mediolaterally compressed as in most other theropods (Balanoff et al., 2009).

The trigeminal nerve (cranial nerve V) foramen lies between the prootic and laterosphenoid, and the path of this nerve is prominent on the endocranial cast. In contrast to Troodon formosus and avians where the gasserian ganglion typically is positioned intracranially with separate openings for the ophthalmic and maxillomandibular branches of the trigeminal nerve (Baumel and Witmer, 1993; Currie and Zhao, 1993a), this nerve appears to exit the braincase of Zanabazar junior before branching (as in Saurornithoides mongoliensis, Byronosaurus jaffei, and most non-avian theropods; Makovicky et al., 2003; Bever and Norell, 2009). The abducens nerve (cranial nerve VI), which typically extends through the basisphenoid to exit the braincase lateral to the pituitary fossa, is not visible. The facial nerve (cranial nerve VII) exits the braincase posteroventral to the trigeminal nerve within the lateral depression (Fig. 4.12A, B), an apparently derived condition shared only with Saurornithoides mongoliensis. The path of the facial nerve on the right side cannot be determined because of damage to this region. The direct paths of the branches of the vestibulocochlear nerve (cranial nerve VIII) are difficult to follow. The foramina for the posterior-most cranial nerves are located posteroventral to the lateral depression. Three prominent structures are visible in this region posteroventral to the floccular lobe. The largest is the cast of the vagus foramen, which transmits cranial
nerves X–XI. A small branch exits dorsal to the vagus canal and may represent the glosopharyngeal nerve (cranial nerve IX). The glosopharyngeal nerve also may exit with cranial nerves X and XI or it may exit the metotic fissure through the fenestra pseudorotunda, as generally is assumed in theropods (Currie, 1997). The two smaller median foramina represent exits for branches of the hypoglossal nerve (cranial nerve XII).

**Incisivosaurus gauthieri (IVPP V 13326; Fig. 4.13)**

The braincase of *Incisivosaurus gauthieri* is complete, and therefore a complete reconstruction of both the endocranial volume (endocast) and of the inner ear structures was possible (Fig. 4.13). The volume of the cranial cavity is 5.69 cm$^3$. Overall, the endocranial cast is mediolaterally compressed. This shape is reflected most prominently in the hindbrain (Fig. 4.13E). The cerebral and pontine flexures are well developed (Fig. 4.13A, B). The apex of the cerebral flexure is at the optic lobes and that of the pontine flexure is at the cerebellum (as defined by Hopson, 1979). The endocast has an unusual orientation within the braincase of *Incisivosaurus gauthieri*, with the cerebral hemispheres sitting entirely dorsal to the orbits and not extending posteriorly. The widest portion of the endocast is approximately two-thirds of the way along the anteroposterior length of the cerebral hemispheres. A fracture runs transversely across the braincase. This taphonomic structure is reflected on the endocranial cast (Fig. 4.13C, E).

The forebrain includes the olfactory bulbs, cerebral hemispheres, and pituitary body (Fig. 4.13). The olfactory bulbs of *Incisivosaurus gauthieri* lie within the frontals
Figure 4.13. Endocranial cast of *Incisivosaurus gauthieri*. Cast of inner ear rendered in pink.
and orbitosphenoid. The olfactory tracts are anteroposteriorly reduced so that they are not visible and the olfactory bulbs do not extend anteriorly as far as in other theropods but rather only to the anterior extent of the orbit (Fig. 4.13). The reduction of the olfactory tracts may be a result of an anterior rotation of the cranial cavity within the braincase or the reduction of the rostrum relative to the skull as a whole (This latter scenario is the more likely as it is present in other oviraptorosaurs) (Figs. 4.13–4.16). The parabasisphenoid is not well ossified in the region of the hypophyseal fossa; therefore, the pituitary body is not well defined (Fig. 4.13C, D). The only characteristic that reasonably can be determined about this structure is that it is relatively small compared with the rest of the endocranial volume. Compared with other theropods, the pituitary body also is relatively small in Incisivosaurus gauthieri. The carotid arteries can be seen anastomosing within the basisphenoid and separating again before entering the sella turcica; however, this feature is not reflected on the endocast (Fig. 4.13C, D).

The cerebral hemispheres are the most prominent structure of the forebrain and have a volume of approximately 2.38 cm$^3$. These structures are oblong and anteroposteriorly elongate. The cerebral hemispheres extend from the posterior margin of the orbit anteriorly to approximately two-thirds of the anteroposterior length of the orbit. A large interhemisphere sulcus is present along the midline of the dorsal surface of the endocast (Fig. 4.13A, B, E). Little lateral expansion of the cerebral hemispheres is present. Although the cerebral hemispheres represent the widest region of the endocast, they are only 27% wider than the optic tectum (the next widest region). The anterior extent of the cerebral hemispheres (as mentioned earlier) is unique among theropods.
Most other theropods do not have cerebral hemispheres that extend as far anteriorly. Again, this may represent an anterior extension of the forebrain or simply the anterior rotation of the cranial cavity within the skull due to a telescoping of the rostrum as a whole.

The only structure of the midbrain that is visible on the endocast of *Incisivosaurus gauthieri* is the optic tectum (Fig. 4.13). The paths of oculomotor (cranial nerve III) and trochlear (cranial nerve IV) nerves cannot be determined from the endocranial cast. The optic tectum is housed almost entirely within the laterosphenoid with a small contribution from the frontal/parietal. The irregularly shaped structure covers a large area on the lateral surface, extending from the posterior limit of the cerebral hemispheres to approximately one-third the length of the cerebellum. The optic tectum is located posteroventral to the cerebrum (comparable to the placement in troodontids – oppressed to the anterior region of the cerebellum; Hopson, 1979; Franzosa, 2004). Although the optic tectum covers a large amount of surface area, the lateral protrusion is restricted. The optic nerve exits through a large single opening formed by the junction of the laterosphenoids (Fig. 4.13A).

The regions of the hindbrain (rhombencephalon) that are visible on the endocranial cast include the cerebellum, and cast of the vagus foramen, which in life transmits the trigeminal (V), abducens (VI), and facial (VII) nerves. The brain stem, glossopharyngeal (IX), vagus (X), and hypoglossal (XII) nerves also are visible. The cerebellum is a pronounced structure that is extremely mediolaterally compressed (Fig. 4.13B, C, D), and runs about half of the length of the endocast. A distinct but narrow
ridge runs along the midline of the cerebellum, likely representing the sagittal sinus. Running transversely along the cerebellum are a series of indentions that may correspond to cerebellar fissures, which suggest that the cerebellum was folded. Kundrát (2007) observed similar structures in *Conchoraptor gracilis* and suggested that these were traces of a folded cerebellum. At least four distinct impressions (fissures) are present on the cerebellum in *Incisivosaurus gauthieri*; however, their correlation to cerebellar fissures cannot be established.

The floccular recess lies within the prootic, opisthotic, and exoccipital. The corresponding cast of the floccular recess projects posteroventrally. The flocculus is mediolaterally compressed but fills the space between the semicircular canals. The facial (cranial nerve VII) and both branches of the acoustic (cranial nerve VIII) nerves are present on the endocast anteroventral to the flocculus (Fig. 4.13C, D). The cochlear branch of the acoustic nerve extends ventrolaterally towards the cochlear duct. The vestibular branch reaches posteriorly to enter the inner ear. The facial nerve extends laterally to pierce the lateral surface of the prootic. The cast of the metotic foramen is located posterior to these nerves. The structure is elongate anteroventrally to posterodorsally and lies directly posterior to the cochlear duct. The glossopharyngeal, vagus, accessory nerves and possibly the jugular vein traversed this space. Two small nerves that pierce the basioccipital are present posterior to the cast of the metotic foramen. These are interpreted as a pair of hypoglossals (cranial nerve XII). The medulla oblongata is anteroposteriorly short in *Incisivosaurus gauthieri*. The mediolateral width of the medulla oblongata is compressed, but this structure is not out of proportion with
the remainder of the hindbrain, which overall is mediolaterally compressed (Fig. 4.13E, F).

The structure of the ear region of *Incisivosaurus gauthieri* is similar to the condition found in avians and some paravians (Makovicky et al., 2003; Dominguez Alonso et al., 2004; Norell et al., 2004; Norell et al., 2006). The osseous portion of the anterior semicircular canal is kidney shaped, and the long axis is rotated somewhat posteriorly (Fig. 4.13C, D, E). The posterior-most extent of the anterior semicircular canal also is exposed on the occipital surface of the braincase. The osseous portion of the horizontal semicircular canal is circular in shape (Fig. 4.13E). A small foramen branches off the posterior ramus of the posterior semicircular canal and travels posteriorly to exit on the supraoccipital on the occipital surface of the braincase. The posterior and lateral semicircular canals meet in a common crus, and there is a large vestibule anteriorly (Fig. 4.13). The cochlea also is similar to the typical avian type and curves ventromedially (Fig. 4.13C, D).

**Conchoraptor gracilis** (IGM 100/3006; Fig. 4.14)

In addition to the endocranial cast generated for this analysis, another endocranial cast of *Conchoraptor gracilis* was prepared by Kundrát (2007) from a different specimen of this taxon (ZPAL MgD-I/95), thus allowing a degree of interspecific variation to be assessed. The cranial endocast of *Conchoraptor gracilis* has an overall morphology that is similar to *Incisivosaurus gauthieri* but with a cerebrum that is expanded relatively more laterally. This morphology is in contrast to the long, narrow endocranial cast of
Figure 4.14. Endocranial cast of *Conchoraptor gracilis.*
more basal tetanurans, whose shape reflects the relative lack of forebrain inflation as well as the presence of a loose association between the brain and the dural sinuses that envelop it (most significant in the mid- and hindbrain regions; Sedlmayr, 2002; Franzosa, 2004; Sampson and Witmer, 2007).

Visible regions of the forebrain in IGM 100/3006 include the olfactory bulbs, cerebral hemispheres, and pituitary body. The absence of visible olfactory tracts reflects an extreme reduction of this structure that is shared with ZPAL MgD-I/95 (Kundrát, 2007), Citipati osmolskae (Fig. 4.15), Incisivosaurus gauthieri (Fig. 4.13; Balanoff et al., 2009), Khaan mckennai (Fig. 4.16) and crown birds (Figs. 4.10 and 4.11). The olfactory tracts of Archaeopteryx lithographica are reduced but still visible (Dominguez Alonso et al., 2004:fig. 3). A reduction of the olfactory tracts is convergently evolved in oviraptorosaurs and avialans (not reduced in deinonychosaurus [e.g., Zanabazar junior, Fig. 4.12; Norell et al., 2009]); whereas, extreme reduction so that the tracts are not visible dorsally would be convergent between oviraptorosaurs and crown birds. The cerebral hemispheres are pyriform in dorsal view—distinctly wider caudally than rostrally. This basic shape is shared with Incisivosaurus gauthieri, Archaeopteryx lithographica, crown birds, and Zanabazar junior, but is somewhat in contrast to the more oval reconstructed cerebrum of ZPAL MgD-I/95 (Kundrát, 2007:fig. 2) and that of Citipati osmolskae and Khaan mckennai (Figs. 4.15 and 4.16). This observed disparity in the ZPAL MgD-I/95 endocast as compared to the one prepared for this analysis may be due to over smoothing of the Kundrát reconstruction. It appears that the cerebral expansion in theropods took place largely in the caudal portion of the cerebral
hemispheres, resulting in the pyriform shape, which is retained (in slightly varying
degrees) in all taxa sharing the apomorphic expanded condition. The lateral margins of
the cerebral hemispheres constitute the widest part of the endocast, which is also true in
more basal taxa that lack distinct cerebral expansion (e.g., *Manjugasaurus crenatissimus*,
Sampson and Witmer, 2007; *Alioramus altai*, Brusatte et al., 2009; 2010). Although the
lateral expansion of the oviraptorid cerebral hemispheres is a characteristic shared with
paravians, the cerebrum of oviraptorids lacks the extreme dorsoventral expansion that
characterizes the caudal forebrain in crown birds, with *Archaeopteryx lithographica*
exhibiting an intermediate dorsoventral expansion. In oviraptors, the cerebral
hemispheres maintain a relatively even height along their entire rostrocaudal length (Fig.
4.14C, D; compare to fig. 2 in Kundrát [2007]). A wide but shallow inter-hemispherical
fissure (sagittal cerebral fissure) runs along the dorsal midline, present in all
maniraptorans including crown avians (Fig. 4.14E).

Kundrát (2007) describes an epiphysial projection at the frontal-parietal suture
directly in the middle of the sagittal cerebral fissure. A slight protuberance also is present
at the fronto-parietal suture in IGM 100/3006. This structure may correspond to the
epiphyse, which is not present in any other oviraptorosaurs, possibly making this feature
an autapomorphy of *Conchoraptor gracilis*. It is unlikely that the structure has a one-to-
one correspondence to pineal tissue, but the presence of such tissue is likely present (see
Discussion of Sampson and Witmer, 2007). The fronto-parietal suture itself falls at an
unusual position relative to the endocast. In most theropod taxa, including basal
theropods, the fronto-parietal suture falls at the posterior margin of the cerebrum;
however, in *Conchoraptor gracilis* this suture is located in the middle of the cerebrum in both specimens.

The elongate, rectangular pituitary body constitutes approximately 0.74% of the total endocranial volume. The infundibular stalk, which connects the pituitary to the main body of the endocast, is not well-defined osteologically due to relatively poor ossification of the surrounding basisphenoid and is not visible in the endocast reconstruction (Fig. 4.14C, D). The ventrally situated cerebral carotid canals enter the sella turcica of the pituitary fossa separately and do not anastomose medially; although, they do converge towards the midline.

The only discernable features of the midbrain are the optic lobes and optic nerve roots (cranial nerve II). The optic lobes are positioned directly caudal to the cerebral hemispheres and rostral to the transverse sinus and middle cerebral veins. The optic lobes of IGM 100/3006 are displaced lateroventrally (a derived maniraptoran condition shared with other oviraptorosaurs and birds that may be a result of expansion of the cerebrum and cerebellum; Sampson and Witmer, 2007). The optic lobes are large and spherical. Their shape compares closely with that of ZPAL MgD-I/95 (Kundrát, 2007). Most theropods possess this spherical morphology (see Franzosa et al., 2004; Sampson and Witmer, 2007; Norell et al., 2009). *Incisivosaurus gauthieri*, in contrast, possesses a more rectangular optic lobe (Balanoff et al., 2009). This disparity may reflect differences in the true shape of the optic lobes or perhaps more accurately reflect a dural sinus or some other structure that obscures the true shape of the optic tecta. Either way, the condition in *Incisivosaurus gauthieri* is interpreted as derived. Kundrát (2007) notes
that the optic lobes do not extend as far laterally as the cerebral hemispheres, a condition also found in the ostrich *Struthio camelus* (Fig. 4.10) but not in *Archaeopteryx lithographica*. He states that this may be a synapomorphy of birds and oviraptors to the exclusion of *Archaeopteryx lithographica* or a case of convergence (if oviraptors are non-avian theropods). It would appear that the oviraptorid and *Struthio camelus* condition is plesiomorphic (based on more basal taxa like *Majungasaurus crenatissimus* and *Alioramus altai*; Sampson and Witmer, 2009; Brusatte et al., 2009), which would mean that *Archaeopteryx lithographica* would possess the derived condition.

The visible partitions of the hindbrain include a pronounced cerebellum, medulla oblongata, and a number of cranial nerves. The cerebellum, the most prominent feature of the hindbrain, is expanded dorsally and anteriorly, although its anterior extent does not equal that of paravians (Fig. 4.12E; Dominguez Alonso et al., 2004). In crown birds, the rostral margin of the cerebellum overlies the caudal margin of the cerebral hemispheres, whereas in IGM 100/3006, a small but distinct space separates these structures (Fig. 4.14E). This space is present in all oviraptorosaurs; but absent in paravians (Fig. 4.12E; Dominguez Alonso et al., 2004:Fig. 4b). The cerebellum in *Conchoraptor gracilis* is wider than that of *Incisivosaurus gauthieri*, nearly reaching the lateral extent of the optic lobes, but lacking the extreme lateral expansion of *Citipati osmolskae* or *Khaan mckennai*. IGM 100/3006 lacks the cerebellar folds that are described for ZPAL MgD-I/95 (compare Fig. 4.14F with Kundrát [2007]:fig. 2). The floccular lobe of the cerebellum is visible projecting caudolaterally along the lateral surface of the hindbrain. This structure closely resembles the morphology of that in all known maniraptorans including
other oviraptorosaurs, Zanabazar junior (Fig. 4.14C, D, E; Norell et al., 2009), *Archaeopteryx lithographica* (Dominguez Alonso et al., 2004), and crown birds (see *Struthio camelus*; Fig. 4.10). The size of the floccular lobes, however, are relatively larger in oviraptorosaurs, especially oviraptorids, than in other maniraptorans (Figs. 4.10–4.16).

The medulla oblongata of *Conchoraptor gracilis* (both IGM 100/3006 and ZPAL MgD-I/95) possesses a prominent pontine flexure (Hopson, 1979; Kundrát, 2007). Kundrát (2007) suggests that this curved morphology could be a maniraptoran apomorphy. Although this may be true, the medulla oblongata is hard to compare in more basal tetanurans because the hindbrain of these taxa is obscured by dural sinuses (Sedlmayr, 2002; Witmer and Ridgely, 2009; Brusatte et al., 2009). Within oviraptorosaurs, the pontine flexure is present and pronounced in the basal *Incisivosaurus gauthieri* (Fig. 4.13C, D); however, in *Citipati osmolskae* and *Khaan mckennai* the flexure is more subtle. Thus, *Conchoraptor gracilis* is the only oviraptorid to display the plesiomorphic condition. The medulla oblongata of IGM 100/3006 is narrow overall, but because of extensive pneumaticity in the hindbrain region, much of its structure is indistinguishable.

Only a few cranial nerves can be discerned protruding from the surface of the medulla oblongata. The trigeminal nerve (cranial nerve V) is large, undivided and lies along the anterior margin of the medulla oblongata. The postnatal remnant of the metotic fissure is reflected on the endocast (caudoventral to the flocculus) as the rostral fenestra pseudorotunda and caudal vagus foramen through which cranial nerves IX–XI most likely exited. This arrangement indicates a divided metotic fissure.
The overall morphology of the *Citipati osmolskae* (IGM 100/798) endocranial cast closely resembles that of the oviraptorid, *Khaan mckennai*. The olfactory tracts and bulbs are more clearly defined in this endocast than in any other published specimen (Kundrát, 2007). The cerebral hemispheres are expanded laterally and appear to have filled the cranial cavity, but they lack the dorsoventral expansion found in avialans. The optic lobes are spherical and located ventrolaterally. The cerebellum of *Citipati osmolskae*, however, lacks the dorsal expansion that is present in the specimen of *Conchoraptor gracilis* (ZPAL MgD-I/95; Fig. 4.14) described by Kundrát (2007) or *Incisivosaurus gauthieri* (Fig. 4.13). The major difference between the endocasts of *Citipati osmolskae* and *Conchoraptor gracilis* is in the degree of flexure along the length of the endocast. There is little curvature present at the cephalic and pontine flexures (corresponding to curvature between the fore- and midbrain and the metencephalon and myelencephalon, respectively; Hopson [1979]). The cephalic flexure is not unlike that of *Conchoraptor gracilis*; however, the pontine flexure is much less pronounced in *Citipati osmolskae*, being much more closely allied with *Khaan mckennai* (Fig. 4.16). The shape of the endocast overall therefore has a much more elongate shape, and structures of the hindbrain are spread further apart anteroposteriorly than in either *Incisivosaurus gauthieri* or *Conchoraptor gracilis*.

The visible structures on the forebrain of the *Citipati osmolskae* endocast include the olfactory bulbs and the cerebral hemispheres (Fig. 4.15). While the pituitary fossa is
Figure 4.15. Endocranial cast of *Citipati osmolskae.*
visible in the two dimensional CT slice images, the walls of the basisphenoid surrounding
this space are not well ossified. It is therefore difficult to reconstruct this fossa on the
endocast. The pituitary fossa nonetheless appears to have a similar shape to that of
Conchoraptor gracilis. The structures associated with the olfactory system are retracted
posteriorly to such an extent that they are pressed against the anteroventral surface of the
cerebral hemispheres, as in all other examined oviraptorosaurs including the basal
Incisivosaurus gauthieri. The olfactory bulbs of Citipati osmolskae are larger than those
present in Khaan mckennai or Conchoraptor gracilis and are slightly upturned at the
distal end. Deinonychosaurus (see Zanabazar junior; Fig. 4.12) possess the plesiomorphic
morphology of extended olfactory tracts. Crown birds (see Struthio camelus; Dominguez
Alonso et al., 2004:Fig. 4) also have retracted olfactory structures that bear a striking
resemblance to those present in oviraptorosaurs.

The cerebral hemispheres in Citipati osmolskae are the largest region of the
endocast, comprising approximately 42% of the entire volume. This region is also the
widest part of the endocast. The cerebrum is oval in shape so that the anteroposterior
midpoint extends far laterally compared to any part of the mid- or hindbrain including the
optic tectum (Fig. 4.15E), similar to Khaan mckennai. Incisivosaurus gauthieri and
Conchoraptor gracilis have a more pyriform shape with the posterior region of the
cerebrum being the widest, similar to paravians. A slight constriction of the cerebrum
approximately two-thirds along the anteroposterior length is an artifact of the
frontoparietal suture. Because of the shortened frontals of oviraptorids, this contact
occurs within the cerebrum rather than at its posterior margin. A large, shallow
interhemisphere sulcus separates the paired cerebral hemispheres from each other. No trace of a midline ‘epiphysis’ can be seen at the posterior margin of the cerebrum in *Citipati osmolskae* as it is in the endocast reconstructed for both specimens of *Conchoraptor gracilis* (Fig. 4.14E and ZPAL MgD-I/95, Kundrát, 2007).

Structures from the midbrain that are visible on the endocast of *Citipati osmolskae* include the optic lobes and optic nerves (cranial nerve II). The optic lobes are large, occupying approximately 16% of the entire endocranial cast and extending laterally past the cerebellum in the hindbrain. They lie just posterior and ventral to the cerebral hemispheres and do not contact each other along the midline as they do in more basal theropods (Sampson and Witmer, 2007). The optic lobes have a distinctly spherical shape that is similar to other oviraptorids, but is markedly different from the more rectangular shape of the optic lobes in the more basal *Incisivosaurus gauthieri* (Fig. 4.13C, D). The optic lobes do not extend laterally past the cerebral hemispheres as they do in avialans (Dominguez Alonso et al., 2004; Kurochkin et al., 2006) or to the same lateral extent as they do in troodontids (see *Zanabazar junior*, Fig. 4.12) or avialans (Dominguez Alonso et al., 2004; Kurochkin et al., 2007). The optic nerves exit through a single large midline opening between the laterosphenoids as in all observed oviraptorosaurs.

The structures visible in the hindbrain of *Citipati osmolskae* include the cerebellum, brain stem (medulla oblongata), flocculus, cranial nerves, and vessels. The inner ear region also is present overlying this region of the brain. The most prominent feature of the hindbrain is the cerebellum, which is expanded anteriorly and laterally but not dorsally. The dorsal surface of the cerebellum in *Citipati osmolskae* is low and
rounded; it does not expand dorsally over the cerebral hemispheres when the lateral semicircular canals are oriented completely horizontally. This arrangement is in contrast to that described for *Conchoraptor gracilis* (ZPAL MgD-I/95; Kundrát, 2007).

*Conchoraptor gracilis* has a distinctly triangular apex on the dorsal surface of the cerebellum that reaches the cerebrum (Fig. 4.14C, D; Kundrát, 2007). The dorsal surface of the cerebellum lacks any type of ridges unlike the cerebellar morphology that is present in *Incisivosaurus gauthieri* (Fig. 4.13E) or reported for *Conchoraptor gracilis* (Kundrát, 2007).

The floccular lobe (auricula cerebelli in Kundrát [2007]) in *Citipati osmolskae* resembles other maniraptorans in that it projects posterolaterally. The shape of the flocculus is conical with a circular cross-sectional morphology, similar to that of *Khaan mckennai* (Fig. 4.16) and differing from the flattened morphology present in *Incisivosaurus gauthieri* and *Conchoraptor gracilis* (Figs. 4.13 and 4.14, respectively). The flocculus makes up a large portion of the total volume of the cerebellum, much larger than in other maniraptorans (Figs. 4.10–4.12). All observed oviraptorosaurs also have an enlarged floccular lobe and this morphology may be synapomorphic for the group as a whole. Oviraptorids, however, take this enlargement to a much greater degree (see *Khaan mckennai*, Fig. 4.16).

The cranial nerves of the hindbrain of *Citipati osmolskae* are positioned in a similar arrangement to *Khaan mckennai*. The trigeminal nerve is large and undivided. The foramen does possess a slightly constricted center similar to that present in *Incisivosaurus gauthieri*. The placement of the trigeminal nerve (crani


almost identical to that in *Conchoraptor gracilis, Khaan mckennai*, and *Incisivosaurus gauthieri*, being at the anterior margin and ventral to the flocculus. The extension of the hindbrain overall (there is a less pronounced pontine flexure in *Citipati osmolskae* than in *Conchoraptor gracilis*) may have an influence on the placement of the posterior cranial nerves in relation to the flocculus. The cast of the vagus foramen (cast of cranial nerves IV–XI) is located well posterior to the flocculus as opposed to the condition in *Conchoraptor gracilis* in which these nerves are located on the posteroventral edge of the flocculus (Figs. 4.14C, D and 4.15C, D). This derived arrangement of the cranial nerves also is present in *Khaan mckennai* (Fig. 4.16C, D).

*Citipati osmolskae* has an inner ear that takes up a large proportion of the length of the hindbrain (Fig. 4.15), and overall is somewhat dorsoventrally flattened. The flattened morphology is different from that exhibited by *Khaan mckennai* in that *Citipati osmolskae* preserves the kidney-shaped anterior semicircular canal that is present in all other maniraptorans. *Citipati osmolskae* also preserves a general triangular shape formed by the semicircular canals, and the vestibule does not extend dorsal to the lateral semicircular canal. This latter feature is characteristic of all maniraptorans including crown birds (Witmer and Ridgely, 2009). The semicircular canals are slender, much more so than the same structures in *Khaan mckennai*. The anterior semicircular canal preserves its kidney shape but, does not extend far dorsally beyond the posterior semicircular canal as it does in most other maniraptorans including crown birds and the more closely related *Incisivosaurus gauthieri* (Fig. 4.13C, D) (Witmer and Ridgely, 2009:Fig. 4). As in all coelurosaurians, there is a distinct anterior curvature in the posterior canal at the common
crus (Sampson and Witmer, 2007; Witmer and Ridgely, 2009). The lateral semicircular canal forms a wide lateral arc. This canal extends posteriorly approximately to the same level as the posterior semicircular canal. These two canals, however, remain separate posteriorly. This condition is reported by Witmer and Ridgely (2009) as being absent in tyrannosaurids and *Archaeopteryx lithographica* but present in the oviraptorosaur *Chirosstenotes pergracilis* and crown birds. *Citipati osmolskai*e also lacks the enlarged ampulla that is apparent in the endocast of the ear of *Khaan mckennai*.

**Khaan mckennai** (IGM 100/973; Fig. 4.16)

In overall appearance, the endocast of *Khaan mckennai* more closely resembles that of the crested oviraptorid *Citipati osmolskai*e than the other uncrested form included in this study, *Conchoraptor gracilis*, in that it is long and has a much more tubular shape. The endocasts of *Khaan mckennai* and *Citipati osmolskai*e lack the distinct cerebral and pontine flexures that are characteristic of maniraptorans in general (Figs. 4.15C, D and 4.16C, D). Given the presence of this feature in other oviraptorosaurs, it can be considered a derived characteristic of a group including these two taxa. Some dorsoventral compression may be present in this endocast, as it is apparent in the outward appearance of the skull of IGM 100/973. *Khaan mckennai*, similar to other oviraptorids, has a wide and shallow endocast with a laterally expanded cerebrum. The expansion of the forebrain is enough to infer that this structure filled the majority of the cranial cavity as it does in all other oviraptorosaurs and maniraptorans (Figs. 4.10–4.16; Osmólska, 2004).
Figure 4.16. Endocranial cast of *Khaan mckennai*. 
The entire forebrain is visible in *Khaan mckennai* including the olfactory bulbs, cerebrum, and pituitary body. The olfactory tracts, like all other oviraptorosaurs and crown birds (Figs. 4.13–4.16), are retracted and therefore not visible on the endocast. The olfactory bulbs are present and clearly reduced in size as compared to the morphology in more basal coelurosaurs and deinonychosaurs (see Brusatte et al., 2009:fig. 2 and Zanabazar junior, Fig. 4.12, respectively); however, these structures are reduced to a greater degree than in the oviraptorid *Citipati osmolskae* (Fig. 4.15). Crown birds undergo convergent evolution in this region and have olfactory tracts that are similar to oviraptorosaurs in that they are pressed against the anterior surface of the cerebrum (Fig. 4.16A). The avialan *Archaeopteryx lithographica* possesses an intermediate morphology between the extended olfactory tracts of deinonychosaurs and the extremely reduced ones of crown birds (Domínguez Alonso et al., 2004:Fig. 4).

The cerebrum of *Khaan mckennai* has an oval shape in dorsal view with a wide and deep interhemisphere sulcus that is especially visible towards the anterior margin (Fig. 4.16E). The oval shape of the cerebrum is shared only with the oviraptorid *Citipati osmolskae*. The widest region of the cerebrum lies at the anterior-posterior midpoint of the region. *Conchoraptor gracilis* and the basal oviraptorosaur *Incisivosaurus gauthieri*, in contrast, possess a cerebrum that is closer to a pyriform shape in dorsal view. The pyriform morphology, in which the anterior margin of the cerebrum is tapered and the caudal margin is the widest region, also is shared by paravians (Figs. 4.10–4.12). The lateral margin of the cerebrum is the widest point of the entire endocast of *Khaan mckennai*, extending well past the optic lobes. The dorsoventral depth of the cerebrum is
shallow in *Khaan mckennai*, as it is in *Citipati osmolskae* and *Conchoraptor gracilis* but not *Incisivosaurus gracilis*, making this a derived feature for Oviraptoridae. Crown birds have a much deeper cerebrum dorsoventrally than either oviraptorosaurs or deinonychosaurus, a feature that is derived for that clade. This specimen also lacks the epiphyseal projection seen in *Conchoraptor gracilis* (Kundrát, 2007). No cranial are nerves are visible in the forebrain. The pituitary fossa of *Khaan mckennai* is not visible in the two-dimensional CT scans due to either a lack of ossification or damage in this region of the braincase.

The optic lobes and associated optic nerves (cranial nerve II) are the only parts of the mesencephalon that are preserved on the endocast of *Khaan mckennai* (Fig. 4.16). The optic lobes lie immediately posterior to the cerebrum and have been ventrolaterally displaced. It is obvious from the endocast that the optic lobes did not meet along the midline as they do in more basal tetanurans (Sampson and Witmer, 2007), likely having been displaced by the expansion of the cerebrum and cerebellum. The optic lobes do not extend as far laterally as the cerebrum. In paravian taxa (including *Archaeopteryx lithographica*) the optic lobes extend laterally approximately to the same lateral level as the cerebrum (compare Fig. 4.16F and Dominguez Alonso et al., 2004:fig. 2). The shape of the optic lobes is spherical, as it is in most other maniraptorans. *Incisivosaurus gauthieri* has a more rectangular shaped optic bulb; however, this morphology appears to be a derived feature of that taxon. The optic nerve roots also are preserved on the endocast (Fig. 4.16). These appear to exit through a single opening formed by the junction of the laterosphenoids as they do in *Citipati osmolskae* (Clark et al., 2002),
Conchoraptor gracilis, Incisivosaurus gauthieri, and Zanabazar junior (Norell et al., 2009).

The hindbrain, composed of a visible cerebellum and brain stem (medulla oblongata), is completely intact. More basal theropods have an overlying dural sinus that obstructs the morphology of the cerebellum on the endocast (see Franzosa, 2004; Franzosa and Rowe, 2005; Sampson and Witmer, 2007; Brusatte et al., 2009; Witmer and Ridgely, 2009); however, as in other maniraptorans, this region filled the majority of the cranial cavity and is clearly visible in Khaan mckennai. As in many of the other regions of the endocranium, the hindbrain of Khaan mckennai resembles that of Citipati osmolskae. The cerebellum is low, not extending dorsally to the level of the cerebrum, but it is also wide (Figs. 4.15 and 4.16). The cerebellum of both Incisivosaurus gauthieri and Conchoraptor gracilis is closer to the morphology observable in Zanabazar junior by being narrow and extending farther dorsally (Figs. 4.12–4.14). A wide cerebellum also characterizes the avialan endocast (Dominguez Alonso et al., 2004:fig. 3). Extending posterolaterally from the lateral surface of the cerebellum is the flocculus (Fig. 4.16C, D). The flocculus of Khaan mckennai and all other oviraptorosaurs is conical in shape and makes up a large portion of the cerebellum. An enlarged flocculus appears to be a derived characteristic of Oviraptorosauria, reaching an extreme morphology in the more exclusive Oviraptoridae (Figs. 4.13–4.16).

The brain stem of most maniraptorans has a distinct curve, giving the endocast an overall “s-shaped” appearance (see Zanabazar junior, Fig. 4.12C). The flexure of the hindbrain in Khaan mckennai is much more subdued so that the endocast approaches a
straight line in lateral view (relaxing of the cephalic and pontine flexures) (Fig. 4.16C).

The lack of flexure in the hindbrain also gives it a shallow dorsoventral depth as compared to other maniraptorans, including *Incisivosaurus gauthieri* and *Conchoraptor gracilis*. The hindbrain of *Citipati osmolskae* possesses a morphology similar to *Khaan mckennai*. The brain stem of *Khaan mckennai* is wider than the cerebellum in dorsal view, again approaching the morphology of *Citipati osmolskae* (Figs. 4.15 and 4.16). The lateral width may be a result of surrounding basioccipital pneumaticity or dural sinuses, but this cannot be established at this time (Kundrát and Janáček, 2007). The only cranial nerves that can be discerned on the endocast of the brain stem are the trigeminal (cranial nerve V) and the cast of the vagus foramen (cranial nerves IX–X). The trigeminal cast is large and lies just posterior to the optic lobe on the brain stem as it does in other non-avian theropod dinosaurs. The cast of the vagus foramen lies posterior to the base of the flocculus. This derived position may be a product of the shape of the brain stem in general as it is also present in *Citipati osmolskae*.

The inner ear of *Khaan mckennai* comprises a large portion of the lateral surface of the hindbrain (Fig. 4.16). Its anterior margin lies almost at the posterior margin of the optic tectum and extends posteroirly to the foramen magnum. The unusual size of the inner ear most likely is a result of the expansion of the floccular lobes, a correlation that is also present in pterosaurs (Witmer et al., 2003). The vestibule is not well preserved, but does not extend dorsally to the lateral semicircular canal. The inner ear canals are triangular in shape, and the width of the canals is thin, as in most theropods (Witmer and Ridgely, 2009). The anterior semicircular canal morphology diverges from most
theropods in having an oval shape and not extending far dorsally beyond the posterior semicircular canal as it does in most other maniraptorans including crown birds (Witmer and Ridgely, 2009:Fig. 4). The posterior semicircular canal is slightly shorter than the anterior semicircular canal and has an anterior curvature at the common crus, a morphology present in all coelurosaurs (Sampson and Witmer, 2007; Witmer and Ridgely, 2009). The lateral semicircular canal is similar to all other coelurosaurs in forming a fairly large arc laterally. This canal reaches posteriorly at least to the posterior semicircular canal. This posterior semicircular canal appears to reach ventral to the lateral canal, the two remaining separate posteriorly. This condition is reported by Witmer and Ridgely (2009) as being absent in tyrannosaurids and *Archaeopteryx lithographica* but present in the oviraptorosaur *Chirostenotes pergracilis* and crown birds.

**PHYLOGENETICALLY VARIABLE ENDOCRAINAL MORPHOLOGY**

*Absence of a pontine flexure in the hindbrain (Fig. 4.17A)*

Two flexures help diagnose the maniraptoran endocast in general, an anterior cephalic flexure between the fore- and midbrain and a pontine flexure in the hindbrain, most easily observed in the brain stem (Figs. 4.10–4.12; Hopson, 1979). More basal coelurosaurs lack these flexures and overall have a cylindrical appearance (see tyrannosaurids, Brusatte et al., 2009:fig. 2; Brusatte et al., 2010). The cephalic and especially the pontine flexures are prominent and easily observed oviraptorosaurs in *Incisivosaurus gauthieri* and *Conchoraptor gracilis* (Figs. 4.13 and 4.14, respectively). The derived oviraptorids *Citipati osmolskae* and *Khaan mckennai*, however, have relaxed
Figure 4.17. Endocranial morphological characters traced onto the maniraptoran tree. Black dot indicates Oviraptorosauria.
Figure 4.17 (cont). Endocranial morphological characters traced onto the maniraptoran tree. Black dot indicates Oviraptorosauria.
Figure 4.17 (cont). Endocranial morphological characters traced onto the maniraptoran tree. Black dot indicates Oviraptorosauria.
the curvature of the cephalic and pontine flexures and appear to have undergone a
reversal towards the plesiomorphic cylindrical morphology that is apparent in
tyranosaurus (Figs. 4.15 and 4.16).

Retraction of the olfactory bulbs (Fig. 4.17B)

The olfactory bulbs characteristic of most non-avian theropods (and amniotes in
general; Butler and Hodos, 1996) are relatively large and located at the anterior end of the
olfactory tract (e.g., Brochu, 2000; Franzosa, 2004; Sampson and Witmer, 2007; Ali et
al., 2008; Zelenitsky et al., 2008). This morphology is readily apparent in the non-avian
and non-oviraptorosaur theropod endocasts segmented for this study (e.g., Zanabazar
junior; Fig. 4.12). In crown birds the olfactory tracts also are retracted so that the
olfactory bulbs press against the anterior margin of the cerebrum (Figs. 4.10 and 4.11).
This morphology has been thought to be distinctive for the crown, a unique feature that
evolved somewhere along the avian stem, with the avialans Archaeopteryx lithographica
(Dominguez Alonso et al., 2004) and PIN 5028/2 (Kurochkin, 2007) showing shortened,
but still anteriorly extended, olfactory tracts.

The olfactory tracts in Oviraptorosauria exhibit a similar morphology to that of
crown birds (Figs. 4.13–4.16). As mentioned previously, Oviraptorosauria undergoes a
shortening of the rostrum, which likely is responsible for the retraction of the olfactory
tracts (Franzosa, 2004; Kundrát, 2007). The shortened morphology appears in all
oviraptorosaurs including the basal Incisivosaurus gauthieri (even though this taxon has
experienced only a small amount of rostral shortening, the telencephalon lies largely
above the orbit unlike the situation of the endocast in paravians [Fig. 4.18; Balanoff et al., 2009]. A shortened olfactory tract and reduced olfactory bulb, therefore, characterizes all of Oviraptorosauria (Fig. 4.17B).

**Shape of cerebrum (Fig. 4.17C)**

The shape of the cerebral hemispheres in paravians is pyriform in dorsal view, being somewhat elongate along the anterior-posterior axis and narrowest at their anterior margin (Figs. 4.10E and 4.12E; Larsson et al., 2000; Kundrát, 2007). This same morphology can be seen in the basal oviraptorosaur *Incisivosaurus gauthieri* (Fig. 4.13E). In contrast, the shape of the cerebral hemispheres in the oviraptorids *Khaan mckennai* and *Citipati osmolskai* is distinctly oval (Figs. 4.15E and 4.16E). The cerebral hemispheres in these taxa are relatively shorter with very little tapering present at the anterior margin towards the olfactory bulbs. The oviraptorid *Conchoraptor gracilis* has an intermediate morphology between *Incisivosaurus gauthieri* and *Citipati osmolskai* and *Khaan mckennai*. *Conchoraptor gracilis* has a pyriform morphology that tapers anteriorly, but is less elongate than either paravians or *Incisivosaurus gauthieri* (Fig. 4.13; Kundrát, 2007:Fig. 4).

**Fronto-parietal suture (Fig. 4.17D)**

As noted by Kundrát (2007), the fronto-parietal contact along the anterior-posterior axis lies near the posterior edge of the cerebrum in at least allosaurids, tyrannosaurs, and paravians (Franzosa and Rowe, 2005; Kurochkin et al., 2007; Witmer...
Figure 4.18. Endocast of *Incisivosaurus gauthieri* with skull rendered semitransparent.
and Ridgely, 2009; Brusatte et al., 2010; Dominguez Alonso et al., 2004). In oviraptorids, this suture does not lie at the posterior margin but rather near the middle of the fossa for the cerebrum at approximately the largest expansion point, leaving a deep groove on the endocast (Figs. 4.14–4.16). Based on CT imagery, the basal oviraptorosaur *Incisivosaurus gauthieri*, similar to the outgroup morphology, possesses a fronto-parietal suture that lies near the posterior margin of the cerebrum (Fig. 4.13E). The location of the fronto-parietal suture with respect to the cerebrum, therefore, is derived in oviraptorids and likely is correlated with the short length of their frontal bone, which is much shorter in oviraptorids than it is in taxa outside of Oviraptoridae.

**Epiphyseal fossa (Figs. 4.14E and 4.17E)**

A clear protuberance present near the midlength of the dorsal surface of the cerebrum in the oviraptorid *Conchoraptor gracilis* (Fig. 4.14E; Kundrát, 2007:fig. 3), was interpreted by Kundrát (2007) as being an epiphyseal body, although this relationship cannot be established. In that paper this structure is shown to lie at the fronto-parietal suture near the middle of the cerebrum. Both endocranial casts completed for *Conchoraptor gracilis* possess the same structure (Kundrát, 2007 and Fig. 4.14). It is absent in taxa outside of Oviraptorosauria (Figs. 4.10–4.12) as well as the oviraptorosaur *Incisivosaurus gauthieri* (Fig. 4.13) and other oviraptorids (Figs. 4.15 and 4.16). The presence of an “epiphyseal body”, therefore, can be considered at present an autapomorphic feature of *Conchoraptor gracilis*. 
**Ventrolateral displacement of optic bulbs (Fig. 4.17F)**

A purportedly unique placement of the optic bulbs has been identified previously as a characteristic feature of crown birds. The expansion of the cerebral hemispheres displaces the optic bulbs laterally and ventrally from their dorsal position in the brain in more basal taxa (Hopson, 1979; Burnham, 2004; Franzosa, 2004; Sampson and Witmer, 2007). Franzosa (2004) noted that this character is present in taxa at least as far down the theropod tree as Maniraptorida, being dorsally placed and likely possessing a midline contact in allosaurids and tyrannosaurids (Witmer and Ridgely, 2009). This study also supports this hypothesis by identifying laterally displaced optic lobes in all oviraptorosaur taxa including *Incisivosaurus gauthieri* as well as derived oviraptorids and paravians (Figs. 4.10–4.16).

**Dorsal expansion of cerebellum and presence of a dorsal sagittal sinus (Fig. 4.17G)**

The expansion of the cerebellum is difficult to compare between coelurosaur clades because of the presence of a dorsal sagittal sinus overlying this region in several groups. This sinus is especially pronounced in tyrannosaurids such as *Alioramus altai* (Brusatte et al., 2009:fig. 2) as well as in taxa lying outside of Coelurosauria (see Franzosa, 2004; Sampson and Witmer, 2007; Balanoff et al., 2010). Within Oviraptorosauria and Paraves, however, this dorsal sinus is reduced to a point where it is either not visible or strongly reduced on the endocasts. A dorsal expansion of the cerebellum can be considered a shared, derived character within Paraves. The troodontid *Zanabazar junior* has a narrow, expanded cerebellum that extends dorsally beyond the
cerebrum (Fig. 4.12C, D). This same dorsal expansion can be seen in *Archaeopteryx lithographica* (Dominguez Alonso et al., 2004:Fig. 4). In crown birds, however, the extreme expansion of the cerebrum often overwhelms the cerebellum so that the relative expansion of this region is not evident.

The basal oviraptorosaur *Incisivosaurus gauthieri* also has a dorsally expanded cerebellum that extends to (but not above) the level of the cerebrum (Fig. 4.13C, D). Similar to *Incisivosaurus gauthieri*, *Conchoraptor gracilis* has a dorsally expanded cerebellum that almost reaches the dorsal level of the cerebrum. A small ridge, the reduced dorsal sagittal sinus cast, runs along the midline of the cerebellum in *Incisivosaurus gauthieri*, though not adding significantly to the volume of the endocast. There is no indication of this sinus in *Citipati osmolskae* and *Khaan mckennai* (Figs. 4.15 and 4.16); however, *Conchoraptor gracilis* may still have a small remnant present (Fig. 4.14). Kundrát (2007) suggested that the cerebellum of *Conchoraptor gracilis* was folded based on a series of transverse ridges found in this region. Although the presence of these structures could not be confirmed in the endocast of *Conchoraptor gracilis* constructed for this study, *Incisivosaurus gauthieri* does possess similar ridges (Fig. 4.13E). Such structures could indicate a folding of the cerebellum (a uniquely avian and mammalian characteristic; Butler and Hodos, 1996), or it could merely reflect the morphology of the sagittal sinus. Folds of the cerebellum often are present in the endocast of avians (Fig. 4.10). The morphology of the cerebellum of *Citipati osmolskae* and *Khaan mckennai* lacks any trace of a sagittal sinus, and has an unusual shape in being low and laterally expanded (Figs. 4.15 and 4.16).
Width of the cerebellum (Fig. 4.17H)

The width of the cerebellum in the oviraptorids *Citipati osmolskae* and *Khaan mckennai* is well expanded relative to that present in other maniraptorans or more basally positioned oviraptorosaurs. Considering only those taxa in which the morphology of the cerebellum is visible, *Zanabazar junior*, *Incisivosaurus gauthieri* and *Conchoraptor gracilis* all have a relatively narrow cerebellum (Figs. 4.12–4.14). The endocast of *Incisivosaurus gauthieri* and *Conchoraptor gracilis* possesses a small sagittal sinus (described above) running along the midline of the structure, the presence of which cannot be determined in *Zanabazar junior*. A similar expansion of the cerebellar morphology is present within the avian lineage, including the basal *Archaeopteryx lithographica* (Dominguez Alonso et al., 2004). Avialans also have a laterally expanded cerebellum.

Flocculus and size of the inner ear (Fig. 17I)

The flocculus is a lateral protrusion of the cerebellum into the inner ear that is completely surrounded by the semicircular canals. The presence of a flocculus is plesiomorphic for coelurosaurs, extending down the vertebrate tree to at least *Gnathostomata* (Butler and Hodos, 1996). The flocculus typically is a prominent feature of the coelurosaur hindbrain, but taxa outside of Coelurosauria sometimes exhibit flocculi that are much smaller in size. Described taxa with relatively small flocculi include the abelisaurid *Majungasaurus crenatissimus* (Sampson and Witmer, 2007), the sauropod...
Apatosaurus (Balanoff et al., 2010), and the allosaurid Acrocanthosaurus atokensis (Franzosa and Rowe, 2005). Tyrannosaurids also have a relatively small flocculus (Ridgely and Witmer, 2009; Brusatte et al., 2009). The size of this structure cannot be determined in Shuvuuia deserti.

An enlarged flocculus characterizes Maniraptor. This structure is noticeably larger in paravians than in more basal coelurosaurs (Figs. 4.10–4.16); however, Oviraptorosauria undergoes a dramatic inflation of this structure exceeding that present in any of the paravian taxa (Figs. 4.13–4.16). Incisivosaurus gauthieri has an expanded flocculus, but it is also somewhat flattened laterally (Fig. 4.13). All of the oviraptorids have a flocculus that is more rounded in cross section and occupies a majority of the lateral extent of the cerebellum exceeding that of any other coelurosaurs (Figs. 4.14–4.16). The only other group that compares in floccular size to oviraptorids is Pterosauria, which expands its floccular lobes even to a greater degree than the size of the structure in oviraptorids (Witmer et al., 2003:fig. 2). It is interesting to note that in both of these groups a correlated change also takes place in the bony canals of the inner ear. Both pterosaurs and oviraptorids expand the inner ear labyrinths surrounding the flocculus so that they also are enlarged beyond the size apparent in outgroups (Witmer et al., 2003:fig. 2; Figs. 4.13–4.16). Witmer et al. (2003) hypothesizes that the expansion of the inner ear simply is a result of the expansion of the flocculus—as the flocculus gets larger it displaces the semicircular canals outwardly.
Position of the vagus foramen (Fig. 4.17J)

On theropod endocasts, the cast of the vagus foramen, through which cranial nerves IX–X exit, typically is positioned on theropod endocast directly below or at the posterior margin of the flocculus (Ridgely and Witmer, 2009). This is also the arrangement present in the basal oviraptorosaur *Incisivosaurus gauthieri* and the oviraptorid *Conchoraptor gracilis* (Figs. 4.13 and 4.14). The oviraptorids *Citipati osmolskae* and *Khaan mckennai* have a slightly different arrangement with the cast of the vagus foramen lying completely posterior to the flocculus (Figs. 4.15C, D and 4.16C, D).

STATISTICAL RESULTS

Body size and endocranial volume (Figs. 4.19–4.24; Table 4.1)

*Total volume* (Fig. 4.19)

The volume of the total segmented endocranial space relative to body size is consistently higher in crown birds than in any taxon currently hypothesized to lie along the avian stem (including pterosaurs; Witmer et al., 2003) (Fig. 4.19). Based on the examined sample of crown birds, the correlation between endocranial volume and body size is moderately strong (corrected $r^2 = 0.694$; uncorrected $r^2 = 0.784$) and trends slightly positively. The addition of the fossil paravians *Archaeopteryx lithographica*, *Tsaagan mangas*, and *Zanabazar junior* lowers this correlation (corrected $r^2 = 0.544$) and reduces the rate at which this volume increases with body size. The addition of the
oviraptorosaurs, *Shuvuuia deserti*, and the non-maniraptoran theropods *Alioramus altai*, *Tyrannosaurus rex*, and *Allosaurus fragilis* actually strengthens the correlation slightly for the phylogeny corrected data ($r^2 = 0.475$; uncorrected $r^2 = 0.646$) and slightly flattens the rate of evolutionary scaling. Inclusion of the large-bodied ostrich, *Struthio camelius*, allows a more direct comparison between the expectations of crown birds and all but the largest examined stem taxa. Each of the stem birds whose body size falls within the range of examined crown birds exhibits an endocranial volume that is distinctly less than that expected of a crown bird. The stem taxon plotting most closely to the crown is the troodontid *Zanabazar junior*, followed by the oviraptorids *Conchoraptor gracilis*, *Citipati osmolskae*, and *Khaan mckennai* (*Incisivosaurus gautheri* could not be considered in these body size comparisons because it lacks postcranial material or from which a meaningful estimate of body size could be drawn). The relative endocranial volume of the fossil avialan *Archaeopteryx lithographica* is smaller than any of these four taxa, although it is distinctly larger than the dromaeosaurid *Tsaagan mangas* or the alvarezsaurid *Shuvuuia deserti*. The surprisingly high encephalization values for *Allosaurus fragilis* and the two examined tyrannosaurs, *Tyrannosaurus rex* and *Alioramus altai*, is still less than that expected of a similarly sized crown bird, and it is likely overestimated because their estimated endocranial volumes include a substantial dorsal sagittal sinus overlying the hindbrain, a structure that lacks any type of neurological tissues in life (Sedlmayer, 2002; Franzosa and Rowe, 2005; Sampson and Witmer, 2007; Witmer and Ridgely, 2009).
Cerebrum (Fig. 4.20)

Cerebral volume exhibits a moderately strong correlation with body size in crown birds (corrected $r^2 = 0.608$; uncorrected $r^2 = 0.745$) that weakens when the stem taxa to birds are considered (Fig. 4.20). In agreement with relative endocranial volume, the stem taxon plotting closest to the morphometric range of crown birds is Zanabazar junior, followed by Conchoraptor gracilis. The large-bodied Alioramus altai, Tyrannosaurus rex, and Allosaurus fragilis more obviously fall below the trend line of crown birds for this regression than for that of total endocranial volume, reinforcing the interpretation that, in these taxa, a posterior sagittal sinus makes an important contribution to the volume of the endocranial space.

Optic lobes (3.21)

The correlation between volume of the optic lobes and body size within the avian crown (corrected $r^2 = 0.717$; uncorrected $r^2 = 0.817$) is stronger than that observed for the cerebrum, although the strength of this relationship exhibits a considerable drop when stem taxa are considered (e.g., total sample corrected $r^2 = 0.428$; Fig. 4.21). The relative size of the optic lobes in Archaeopteryx lithographica, Shuvuuia deserti, and Tsaagan mangas places them well away from the morphometric space defined by the avian crown. The oviraptorosaurs Conchoraptor gracilis, Khaan mckennai, and Citipati osmolskae, and the troodontid Zanabazar junior plot distinctly closer to the observed range of the crown. Citipati osmolskae and especially Zanabazar junior fall within the expected range of crown birds if the amount of morphometric variation observed in crown birds at small
and medium body sizes is maintained at a larger body size. The sampling of large-bodied birds, however, is relatively small in this analysis.

**Cerebellum (Fig. 4.22)**

A relatively weak correlation exists between volume of the cerebellum and body size, both within the crown and when stem taxa are considered (a distinctly stronger correlations is recovered for crown birds for the uncorrected versus corrected data, \( r^2 = 0.655 \) versus \( r^2 = 0.498 \), respectively). The rate at which the volume of the cerebellum increases with body size transforms from a slightly positive trend within the crown to a slightly negative trend when fossils are considered (for both corrected and uncorrected data). Once again, *Shuvuuia deserti* plots further from the avian crown than does *Archaeopteryx lithographica*. The oviraptorosaurs *Khaan mckennai* and *Citipati osmolskae* and the troodontid *Zanabazar junior* plot within the range of variation expected of a crown bird of similar body size (if the range of variation observed in small and medium-sized crown birds is maintained at large body sizes), while *Conchoraptor gracilis* lies fully within the observed range of the avian crown.

**Brain stem (Fig. 4.23)**

The correlation between brain stem volume and body size is relatively strong compared to the examined neuroanatomical partitions. The strength of this correlation drops approximately 10% when the data are corrected for phylogeny but the \( r^2 \) value still exceeds 0.7 within the crown. The rate at which this partition increases in volume with
body size trends slightly negative in each of the examined data sets (corrected and uncorrected). The resulting spatial relationship closely resembles that based on the optic lobes, with the exception of the relatively large brain stem of *Khaan mckennai*, which places it on the margin of the observed range, and within the expected range, defined by the avian crown.

*Olfactory bulbs (Fig. 4.24)*

The volume of the olfactory bulbs exhibits the lowest correlation with body size of all the examined neuroanatomical partitions both within the crown and when stem taxa are considered. Applying a correction for phylogeny, the $r^2$ values plummet (e.g., $r^2 = 0.022$ within the crown). The inclusion of stem taxa strengthens this correlation in both data sets, and in the uncorrected data, the $r^2$ exceeds 0.6. The rate at which olfactory lobe volume increases with body size generally trends moderately negative although for the corrected values of crown birds, a slightly positive trend is recovered. The relative size of the olfactory bulbs in *Shuuvia deserti* and *Archaeopteryx lithographica* place them within the observed range for crown birds. The large amount of observed variation within the avian crown (most notably at medium body sizes) suggests that all examined stem taxa, with the possible exception of *Alioramus altai* and *Zanabazar junior*, fall within the expected range of variation of the crown. *Alioramus altai* and *Zanabazar junior* may actually express a higher ratio than that expected for a crown bird.
Table 4.1. Regression statistics for body mass against volume of each region.

<table>
<thead>
<tr>
<th>region</th>
<th>statistic</th>
<th>Whole Sample</th>
<th>Paraves</th>
<th>Crown Birds</th>
<th>‘Non-avian’ Theropods</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>uncorrected</td>
<td>corrected</td>
<td>uncorrected</td>
<td>corrected</td>
</tr>
<tr>
<td>total endocranium</td>
<td>slope</td>
<td>0.3515</td>
<td>0.6501</td>
<td>0.3223</td>
<td>0.7445</td>
</tr>
<tr>
<td></td>
<td>y-intercept</td>
<td>0.8764</td>
<td>-0.0753</td>
<td>0.9213</td>
<td>-0.1710</td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.6463</td>
<td>0.4748</td>
<td>0.4997</td>
<td>0.5436</td>
</tr>
<tr>
<td>olfactory bulbs</td>
<td>slope</td>
<td>0.5144</td>
<td>0.6192</td>
<td>0.4473</td>
<td>0.5448</td>
</tr>
<tr>
<td></td>
<td>y-intercept</td>
<td>-1.3644</td>
<td>-0.1679</td>
<td>-1.3922</td>
<td>-0.2012</td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.6477</td>
<td>0.2359</td>
<td>0.5378</td>
<td>0.1809</td>
</tr>
<tr>
<td>cerebrum</td>
<td>slope</td>
<td>0.2871</td>
<td>0.6243</td>
<td>0.3107</td>
<td>0.7469</td>
</tr>
<tr>
<td></td>
<td>y-intercept</td>
<td>0.6300</td>
<td>-0.0631</td>
<td>0.7176</td>
<td>-0.1691</td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.5151</td>
<td>0.4264</td>
<td>0.4381</td>
<td>0.5039</td>
</tr>
<tr>
<td>pituitary</td>
<td>slope</td>
<td>0.5134</td>
<td>0.5579</td>
<td>0.5166</td>
<td>0.5985</td>
</tr>
<tr>
<td></td>
<td>y-intercept</td>
<td>-1.3505</td>
<td>0.0035</td>
<td>-1.3178</td>
<td>-0.0385</td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.8055</td>
<td>0.5488</td>
<td>0.7895</td>
<td>0.5418</td>
</tr>
<tr>
<td>region</td>
<td>statistic</td>
<td>Whole Sample</td>
<td>Paraves</td>
<td>Crown Birds</td>
<td>‘Non-avian’ Theropods</td>
</tr>
<tr>
<td>---------------</td>
<td>-----------</td>
<td>--------------</td>
<td>---------</td>
<td>-------------</td>
<td>-----------------------</td>
</tr>
<tr>
<td></td>
<td></td>
<td>uncorrected</td>
<td>corrected</td>
<td>uncorrected</td>
<td>corrected</td>
</tr>
<tr>
<td>optic lobes</td>
<td>slope</td>
<td>0.2709</td>
<td>0.5963</td>
<td>0.3207</td>
<td>0.7172</td>
</tr>
<tr>
<td></td>
<td>y-intercept</td>
<td>-0.0108</td>
<td>-0.0738</td>
<td>0.0722</td>
<td>-0.1795</td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.4729</td>
<td>0.4280</td>
<td>0.6198</td>
<td>0.6051</td>
</tr>
<tr>
<td>cerebellum</td>
<td>slope</td>
<td>0.2901</td>
<td>0.5506</td>
<td>0.2994</td>
<td>0.7020</td>
</tr>
<tr>
<td></td>
<td>y-intercept</td>
<td>-0.0505</td>
<td>-0.0248</td>
<td>-0.0119</td>
<td>-0.1480</td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.3730</td>
<td>0.2653</td>
<td>0.4080</td>
<td>0.4524</td>
</tr>
<tr>
<td>brain stem</td>
<td>slope</td>
<td>0.3792</td>
<td>0.5806</td>
<td>0.3957</td>
<td>0.6946</td>
</tr>
<tr>
<td></td>
<td>y-intercept</td>
<td>-0.2699</td>
<td>-0.0409</td>
<td>-0.2251</td>
<td>-0.1397</td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.6315</td>
<td>0.4127</td>
<td>0.6719</td>
<td>0.5785</td>
</tr>
</tbody>
</table>
Figure 4.19. Log transformed values of total endocranial volume and body mass plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurus in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.1.
Figure 4.20. Log transformed values of total cerebral volume and body mass plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.1.
Figure 4.21. Log transformed values of total optic lobe volume and body mass plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurus in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.1.
Figure 4.22. Log transformed values of total cerebellar volume and body mass plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurus in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.1.
Figure 4.23. Log transformed values of total volume of brain stem and body mass plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurus in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.1.
Figure 4.25. Log transformed values of total pituitary volume and body mass plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for non-avian theropods. Regression statistics can be found in Table 4.1.
Pituitary (Fig. 4.25)

The relationship between pituitary volume and body size is unique among the examined neuroanatomical partitions in the strength of its correlation across the various clades based on uncorrected data. These values drop considerably when the data are corrected for phylogeny. In both data sets, the strength of the correlation increases when the crown is examined in combination with stem taxa. The rate at which the pituitary increases with body size trends slightly negatively in all the examined data sets, with the exception of the uncorrected crown where it trends slightly positively. Based on the relative size of their pituitary fossa, Shuuvia deserti and Archaeopteryx lithographica plot within the observed range defined by the avian crown, while Alioramus altai, Zanabazar junior, and Conchoraptor gracilis fall within the expected range of variation of crown birds of comparable body sizes (again, assuming a similar range of variation at large body size as that observed at small and medium body sizes).

Neuroanatomical Partitions: Proportional Volumetric Comparisons

(Figs. 4.26–4.31; Table 4.2)

Cerebrum (Fig. 4.26)

The cerebrum consistently represents the largest single neuroanatomical partition among the examined taxa, and its volume scales, with a startlingly strong correlation, with total endocranial volume (Fig. 4.26; Table 4.2). The degree to which the cerebrum dominates the endocranial cavity varies considerably among examined taxa. In the non-
coelurosaurian tetanuran *Allosaurus fragilis*, the cerebrum fills approximately 28 percent of the endocranial cavity, whereas that of the extant parakeet, *Brotogeris chrysopteris*, accounts for nearly 80 percent of its endocranial space (Fig 3.26; Appendix 7). The examined taxon with the smallest proportional cerebral volume is the tyrannosaur *Alioramus altai* whose cerebrum fills only 24 percent of the endocranial cavity. This low value (the proportional cerebral volume of *Tyrannosaurus rex* is 33%) may reflect the immaturity of the only known specimen of *Alioramus altai* (Brusatte et al., 2009). If so, the endocranial cavity at the base of Coelurosauria is characterized by an ontogenetic trajectory in which the cerebrum continues to expand in relative volume (positive allometry) during the later portions of post-natal development (Bever et al., in review). The next smallest cerebrum among the examined taxa is that of oviraptorosaurs whose proportional values range from 42% (*Citipati osmolskae* and *Khaan mckennai*) to 48% (*Conchoraptor gracilis*). The phylogenetically most basal oviraptorosaur, *Incisivosaurus gautheri*, expresses a proportional cerebral volume of 43% and thus most closely resembles *Citipati osmolskae* and *Khaan mckennai*. The cerebrum of the alvarezsaur *Shuvuuia deserti* is highly comparable to that of *Conchoraptor gracilis* in filling nearly 50% of the endocranial cranial space despite being hypothesized in many analyses to lie phylogenetically outside the clade defined by Oviraptorosauria and Paraves (see Turner et al., 2007). The troodontid *Zanabazar junior* contains the proportionally largest cerebrum among examined fossil paravians (56%). It fills a slightly larger proportion of the endocranial cavity than in the dromeosaur *Tsaagan mangas* (52%) and the fossil avialan *Archaeopteryx lithographica* (55%). The cerebral proportions of these fossil paravians
are comparable to those found at the lower range of crown birds (e.g., common nighthawk, *Chordeiles minor* [52%]; ostrich, *Struthio camelus* [54%]). The mean proportion of the endocranial cavity filled by the cerebrum in the examined crown birds is 65.3%.

*Optic lobes (Fig. 4.27)*

The optic lobes account for the second largest volumetric partition of the endocranial cavity in 13 of the 25 examined taxa including the stem taxa *Shuvuuia deserti*, *Incisivosaurus gautheri*, *Tsaagan mangan*, *Zanabazar junior*, and *Archaeopteryx lithographica*. Among crown birds, the observed mean proportional volume contributed by the optic lobes is 14.1% with a range that extends from 9.2% in the golden-fronted woodpecker (*Melanerpes aurifrons*) to 27.7% in the nocturnal common nighthawk (27.2%). Along the avian stem, the lowest proportional volumes contributed by the optic lobes are in the oviraptorosaurs *Conchoraptor gracilis* (10.6%), *Khaan mckennai* (14.8%) and *Citipati osmolskae* (15.8%). The same proportion in the basal oviraptorosaur *Incisivosaurus gautheri* is 21.8%, which also is higher than the comparable optic lobe contributions of *Shuvuuia deserti* (18.3%), *Zanabazar junior* (18.0%), and *Archaeopteryx lithographica* (18.3%). *Tsaagan mangas* exhibits the proportionally largest optic lobes among examined fossil taxa (22.7%). The volumetric contribution of the optic lobes in each of the fossil taxa fall within the range of variation observed within the avian crown.

*Cerebellum (Fig. 4.28)*
The cerebellum contributes the second largest volumetric partition of the endocranial cavity in 11 of the 25 examined taxa, including the oviraptorosaurs *Conchoraptor gracilis* and *Citipati osmolskae*. Among crown birds, the observed mean proportion of the endocranial cavity filled by the cerebellum is 12.6% with a range that extends from 5.9% in the sandhill crane, *Grus canadensis*, to 19.5% in the common loon, *Gavia immer*. The cerebellum of the stem birds *Shuuvia deserti*, *Tsaagan mangas*, *Zanabazar junior*, and *Archaeopteryx lithographica* accounts for a comparably small proportion of the endocranial space (10.8%, 10.0%, 12.0%, and 12.2%, respectively) comparing closely with the smallest observed values for crown birds. In contrast, the proportional volume filled by the cerebellum in oviraptorosaurs begins near the upper range of crown birds (*Incisivosaurus gautheri, 19.4%) and increases significantly from there (*Khaan mckennai, 18.0%; Citipati osmolskae, 22.7%; Conchoraptor gracilis, 33.7%)

*Brainstem (Fig. 4.29)*

The observed mean contribution of the brainstem to total endocranial volume in crown birds is 6.5%. The smallest observed brainstem proportion among crown birds is 3.1% in the ground hornbill, *Bucorvus abyssinicus*, with the largest being 10.0% in the ostrich, *Struthio camelus*. Comparably large brainstem contributions are found in the endocranial cavities of *Shuuvia deserti* (13.7%), *Tsaagan mangas* (13.0%), and *Archaeopteryx lithographica* (11.0%). These are smaller than the same contribution in the oviraptorosaurs *Incisivosaurus gautheri* (15.0%), *Citipati osmolskae* (16.6%), and
especially *Khaan mckennai* whose proportional brainstem contribution (24.4%) is second only to the cerebrum. In contrast, *Conchoraptor gracilis* joins *Zanabazar junior* as the only observed stem birds with a proportional brain stem contribution that falls within the observed upper range of crown birds.

*Olfactory bulbs (Fig. 4.30)*

The olfactory bulbs are among the smallest proportional contributors to the endocranial cavity of crown birds where they form between 0.03% (ground hornbill, *Bucorvus abyssinicus*) and 2.7% (black vulture, *Coragyps atratus*) of the total endocranial volume (observed mean value for the crown is 0.5%). Among the examined fossils, the largest proportional contributions from the olfactory bulbs are found in the tyrannosaurid *Alioramus altai* (7.6%) and the alvarezsaurid *Shuvuuia deserti* (5.9%). A relatively large olfactory contribution also is present in the troodontid *Zanabazar junior* (4.1%), but the other fossil paravians, *Tsaagan mangas* and *Archaeopteryx lithographica*, both exhibit olfactory contributions that fall within the upper range of examined crown birds (1.4 and 2.1%, respectively). In oviraptorosaurs, the proportional olfactory contribution ranges from 0.5% and 0.3% in *Incisivosaurus gautheri* and *Khaan mckennai*, respectively, to 2.5% in *Citipati osmolskae*.

*Pituitary (Fig. 4.31)*

The pituitary fossa forms only a small contribution to the total endocranial volume in the examined crown and stem birds. The mean value of this contribution
Table 4.2. Regression statistics for total endocranial volume against each region.

<table>
<thead>
<tr>
<th>region</th>
<th>statistic</th>
<th>Whole Sample</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>uncorrected</td>
<td>corrected</td>
<td>uncorrected</td>
<td>corrected</td>
<td>uncorrected</td>
<td>corrected</td>
<td>uncorrected</td>
<td>corrected</td>
<td>uncorrected</td>
<td>corrected</td>
<td>uncorrected</td>
</tr>
<tr>
<td>olfactory bulbs</td>
<td>slope</td>
<td>1.0047</td>
<td>0.5928</td>
<td>0.8662</td>
<td>0.7752</td>
<td>0.8473</td>
<td>0.6156</td>
<td>1.1378</td>
<td>0.8856</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>y-intercept</td>
<td>-2.2394</td>
<td>0.0438</td>
<td>-2.2511</td>
<td>-0.0380</td>
<td>-2.359</td>
<td>-0.0289</td>
<td>-1.8244</td>
<td>0.1418</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.4682</td>
<td>0.1455</td>
<td>0.4192</td>
<td>0.2228</td>
<td>0.4774</td>
<td>0.1090</td>
<td>0.7221</td>
<td>0.2436</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cerebrum</td>
<td>slope</td>
<td>0.9014</td>
<td>0.9752</td>
<td>1.0236</td>
<td>0.9963</td>
<td>1.0198</td>
<td>0.9844</td>
<td>0.8868</td>
<td>0.8638</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>y-intercept</td>
<td>-0.1713</td>
<td>0.0163</td>
<td>-0.2184</td>
<td>0.0152</td>
<td>-0.2045</td>
<td>0.0159</td>
<td>-0.2543</td>
<td>0.0532</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.9639</td>
<td>0.9592</td>
<td>0.9884</td>
<td>0.9754</td>
<td>0.9889</td>
<td>0.9521</td>
<td>0.9876</td>
<td>0.9083</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>pituitary</td>
<td>slope</td>
<td>1.0858</td>
<td>0.8458</td>
<td>1.0949</td>
<td>0.9666</td>
<td>1.1430</td>
<td>1.0885</td>
<td>0.9991</td>
<td>1.0562</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>y-intercept</td>
<td>-2.3914</td>
<td>0.0228</td>
<td>-2.4487</td>
<td>0.0033</td>
<td>-2.5393</td>
<td>-0.0281</td>
<td>-2.0334</td>
<td>-0.1125</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.7672</td>
<td>0.6768</td>
<td>0.8224</td>
<td>0.6742</td>
<td>0.8700</td>
<td>0.6542</td>
<td>0.7505</td>
<td>0.6580</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>optic bulbs</td>
<td>slope</td>
<td>0.8717</td>
<td>0.9768</td>
<td>0.8604</td>
<td>0.8649</td>
<td>0.8486</td>
<td>1.0639</td>
<td>0.9390</td>
<td>0.6811</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>y-intercept</td>
<td>-0.7363</td>
<td>-0.0353</td>
<td>-0.7362</td>
<td>-0.0489</td>
<td>-0.7483</td>
<td>-0.0682</td>
<td>-0.7202</td>
<td>0.1289</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.9299</td>
<td>0.8490</td>
<td>0.9274</td>
<td>0.8649</td>
<td>0.9311</td>
<td>0.8188</td>
<td>0.9619</td>
<td>0.8708</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
## ENDOCRANIAL VOLUME

<table>
<thead>
<tr>
<th>region</th>
<th>statistic</th>
<th>Whole Sample</th>
<th>Paraves</th>
<th>Crown Birds</th>
<th>‘Non-avian’ theropods</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>uncorrected</td>
<td>corrected</td>
<td>uncorrected</td>
<td>corrected</td>
</tr>
<tr>
<td>cerebellum</td>
<td>slope</td>
<td>1.0358</td>
<td>0.9411</td>
<td>0.9911</td>
<td>0.9746</td>
</tr>
<tr>
<td></td>
<td>y-intercept</td>
<td>-0.9097</td>
<td>0.0231</td>
<td>-0.9176</td>
<td>0.0074</td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.9041</td>
<td>0.7762</td>
<td>0.9295</td>
<td>0.8152</td>
</tr>
<tr>
<td>brain stem</td>
<td>slope</td>
<td>1.0109</td>
<td>0.8773</td>
<td>1.5503</td>
<td>0.9603</td>
</tr>
<tr>
<td></td>
<td>y-intercept</td>
<td>-1.1161</td>
<td>0.0229</td>
<td>-1.6097</td>
<td>-0.0135</td>
</tr>
<tr>
<td></td>
<td>r²</td>
<td>0.8486</td>
<td>0.8146</td>
<td>0.9095</td>
<td>0.9186</td>
</tr>
</tbody>
</table>
Figure 4.26. Log transformed values of total cerebral volume and endocranial volume plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurus in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for ‘non-avian theropods’. Regression statistics can be found in Table 4.2.
Figure 4.27. Log transformed values of total optic lobe volume and endocranial volume plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurus in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for ‘non-avian theropods’. Regression statistics can be found in Table 4.2.
Figure 4.28. Log transformed values of total cerebellar volume and endcranial volume plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurus in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for ‘non-avian theropods’. Regression statistics can be found in Table 4.2.
Figure 4.29. Log transformed values of total brain stem volume and endcranial volume plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurus in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for ‘non-avian theropods’. Regression statistics can be found in Table 4.2.
Figure 4.30. Log transformed values of total olfactory bulb volume and endcranial volume plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurus in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for ‘non-avian theropods’. Regression statistics can be found in Table 4.2.
Figure 4.31. Log transformed values of total pituitary volume and endcranial volume plotted against each other. Oviraptorosaurs are shown in red, deinonychosaurs in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Solid line represents best fit line for whole sample. Small dotted line represents best fit line for crown birds. Large dotted line represents best fit line for ‘non-avian theropods’. Regression statistics can be found in Table 4.2.
among crown birds is 0.4%, with the smallest observed value being 0.1% in the parakeet, *Brotogeris chrysopteris*, and the largest being 1.1% in the ostrich, *Struthio camelus*. The largest proportional pituitary contributions are in the alvarezsaurid *Shuvuuia deserti* (2.2%) and the tyrannosaurid *Alioramus altai* (2.0%). The contribution in *Zanabazar junior* and *Archaeopteryx lithographica* (1.0 and 1.3%, respectively) is comparable to that of the ostrich, whereas the contribution of oviraptorosaurs *Incisivosaurus gautheri* and *Conchoraptor gracilis* is distinctly small among the observed fossils (0.2 and 0.7%, respectively).

**Principal Components Analysis (Figs. 4.32 and 4.33; Table 4.3)**

Principal components analysis of the correlation matrix of the six examined neuroanatomical volumes relative to the total endocranial volume reveal five principal components representing 47.5%, 23.5%, 16.5%, 8.2%, and 4.3% of the total sample variation, respectively. A taxonomic plot of the examined specimens multivariate positions along the axes defined by the first and second principal components reveals complete morphometric isolation of the following clades: the avian crown, Paraves, Oviraptorosauria, and Oviraptorosauria+Paraves.

The first principal component (PC I), which accounts for nearly half of the total sample variance, is defined largely by the inverse relationship between the proportional cerebral volume—the only variable with a negative correlation coefficient (loading)—and the comparably positive loadings of the other examined variables (Table 4.3). The individual relationships between the proportional contribution of the cerebrum and the
Table 4.3. Loadings obtained from a principal component analysis of the six isolated brain regions.

<table>
<thead>
<tr>
<th>structure</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
<th>PC5</th>
</tr>
</thead>
<tbody>
<tr>
<td>olfactory bulbs</td>
<td>0.219</td>
<td>0.445</td>
<td>0.283</td>
<td>0.374</td>
<td>1.350</td>
</tr>
<tr>
<td>cerebrum</td>
<td>-0.322</td>
<td>0.265</td>
<td>0.086</td>
<td>-0.091</td>
<td>0.059</td>
</tr>
<tr>
<td>optic lobe</td>
<td>0.192</td>
<td>0.048</td>
<td>-0.791</td>
<td>0.572</td>
<td>-0.117</td>
</tr>
<tr>
<td>pituitary</td>
<td>0.260</td>
<td>0.324</td>
<td>0.346</td>
<td>0.062</td>
<td>-1.472</td>
</tr>
<tr>
<td>cerebellum</td>
<td>0.118</td>
<td>-0.560</td>
<td>0.415</td>
<td>0.610</td>
<td>0.141</td>
</tr>
<tr>
<td>brain stem</td>
<td>0.285</td>
<td>-0.140</td>
<td>-0.074</td>
<td>-1.085</td>
<td>0.393</td>
</tr>
</tbody>
</table>
Figure 4.32. Plots of endocranial partition data on first and second principal component axes. Oviraptorosaurs are shown in red, deinonychosaurus in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Dotted line drawn around paravians. Loadings given in Table 4.3.
Figure 4.33. Plots of endocranial partition data on second and third principal component axes. Oviraptorosaurs are shown in red, deinonychosaurus in yellow, *Archaeopteryx lithographica* by a green dot, and crown birds in blue. Dotted line drawn around paravians. Loadings given in Table 4.3.
proportional volumes of the other examined neuroanatomical partitions do trend consistently negative (Fig. 4.32). These correlations, however, are not strong, with $r^2$ values ranging from 0.314 for the optic lobes to 0.621 for the brain stem. The relatively expanded cerebrum of crown birds results in their complete taxonomic separation from stem birds along PC I (Fig. 4.32), although the oviraptorosaur *Conchoraptor gracilis* and the common night hawk *Chordeiles minor* nearly overlap along this axis. The fossil paravians *Tsaagan mangas*, *Zanabazar junior*, and *Archaeopteryx lithographica* are nearly equal in their multivariate position along PC I and fall within the morphometric space defined by oviraptorosaurs. This range is defined by the morphometric separation between *Conchoraptor gracilis* on one end and *Khaan mckenaai* and *Citipati osmolskae* on the other end. The phylogenetically basal oviraptorosaur *Incisivosaurus gautheri* plots in an intermediate position between these taxa and in this regard is nearly identical to the fossil paravians. The alvarezsaurid, *Shuvuuia deserti*, which may lie phylogenetically outside the clade defined by oviraptorosaurs and paravians (see Turner et al., 2007), plots farthest from the avian crown along PC I.

The second principal component axis (PC II), which describes slightly less than a quarter of the total sample variance, results in slightly less taxonomic separation than PC I (Fig. 4.32). The multivariate position of the dromaeosaur *Tsaagan mangas* lies well within the range delimited by the avian crown, whereas the other fossil paravians, *Archaeopteryx lithographica* and *Zanabazar junior* plot successively outside of crown birds on the positive end of PC II. The morphometric range defined by the oviraptorosaurs is fully distinct from that of crown birds, although only by the slightest
margin. *Citipati osmolskae* plots just outside the common loon, *Gavia immer*, and the red-billed tropicbird, *Phaethon rubricada*, at the negative end of the axis. The morphometric variance described by PC II is defined largely by the relatively large negative loading of the cerebellum’s contribution to the endocranial space and the relatively large positive loading of the volumetric contribution of the olfactory bulbs. The avian crown thus plots at an intermediate position between the relatively large cerebellum of oviraptorosaurs and the relatively large olfactory bulbs and pituitary fossa of fossil paravians and *Shuvuuia deserti*.

The third principal component (PC III) is defined largely by the relatively strong negative loading of the optic lobes and the comparably positive loadings of the cerebellum and pituitary fossa (Table 4.3). The variance described by PC III, which accounts for less than 17% of the total sample variance, results in little taxonomic separation with only *Shuvuuia deserti* and *Conchoraptor gracilis* plotting outside the range defined by the avian crown (both plotting at the negative end of the axis) (Fig. 4.33). The fourth principal component (PC IV) describes less than 10% of the total sample variance, but is notable for the distinct morphometric positions of *Khaan mckennai* and *Conchoraptor gracilis*, which plot outside the range defined by crown birds but at opposite ends of the axis. Separation along this axis is defined largely by the relatively strong negative loading of the brain stem and the strong positive loadings of the cerebellum and optic lobes. The especially distinct morphometric position of *Khaan mckennai* along this axis is thus largely explained by its relatively large brain stem. The fifth principal component (PC V) explains less than 5% of the total sample variance and
each of the examined fossil taxa falls with the range of variance defined by the examined
crown birds.

**DISCUSSION**

The relatively few previous studies that considered the evolution of the avian
neurocranial configuration from their extinct theropod ancestors do so only in relatively
broad terms, relying largely on comparative observations with taxa that are distantly
related to the crown. These comparisons also often are made through characterization of
paraphyletic taxonomic assemblages that can create or enhance perceived gaps in the
data. The present study differs because, in addition to restricting comparisons to
monophyletic groups, it concentrates comparisons at the distal end of the avian stem—to
those taxa most closely related to the origin of birds. This approach allows a more refined
discrimination of what endocranial apomorphies actually diagnose crown birds and what
avian-like neuroanatomy was already in place well before the origin of the crown,
sometime in the Late Cretaceous (Clarke et al., 2005). Establishing an objective method
for dividing the endocranial space into discrete neuroanatomical regions furthermore
allows the first investigation of mosaic evolution between these partitions and its role in
producing the modern avian endocranium. In addition, clarifying the endocranial
morphology of the paravians Zanabazar junior and Tsaagan mangas allows more specific
questions to be addressed. One important example is whether the endocranial
configuration of oviraptorosaurs supports their phylogenetic placement inside or outside of Avialae.

Morphological observations of endocranial casts suggest that relatively few endocranial characters actually diagnose an avialan clade—only the presence of reduced olfactory tracts. Instead, the base of the avialan clade as exemplified by Archaeopteryx lithographica exhibits a plesiomorphic morphology that can be diagnosed by characters shared with maniraptorans and paravians. The distinctive maniraptoran morphology is diagnosed by pronounced pontine and cephalic flexures (convergently evolved in Sauropoda; Balanoff et al., 2010), ventrolaterally displace optic lobes, and an inflation of the cerebrum relative to more basal coelurosaurs. The paravian endocast is distinguished by yet another expansion of the cerebrum and relatively small floccular lobes.

Oviraptorosaurs also possess relatively few diagnostic endocranial features. These characters include reduced olfactory tracts and an unusually large flocculus. Within oviraptorids, the sister group relationship (relative to those taxa included in the morphological analysis) between Khaan mckennai and Citipati osmolskae is supported by a relatively large number of characters such as the relaxation of cephalic and pontine flexures, an oval-shaped cerebrum in dorsal view, a low but broad cerebellum, and a vagus foramen placed well behind the flocculus.

Several studies of coelurosaur evolutionary relationships have hypothesized that Oviraptorosauria is nested within Avialae (see Discussion of Chapter 2), being more closely related to crown birds than to any of the non-avian coelurosaur clades (Lü, 2002; Maryańska et al., 2002; Osmólska et al., 2004). This hypothesis garnered support from
the study of Kundrát (2007), which concluded that the relationship of endocranial volume to body size in the oviraptorid *Conchoraptor gracilis* was equal to that of some extant birds (Kundrát, 2007:Fig. 4). In contrast, my analysis of total endocranial volume relative to body size recovered distinctly high values for the avian crown. The large endocranial cavities of *Conchoraptor gracilis*, *Khaan mckennai*, and *Citipati osmolskae* did result in their plotting closer to the crown than *Archaeopteryx lithographica*, which could be interpreted as supporting an avialan status for Oviraptorosauria. This interpretation, however, is weakened by the fact that the relative endocranial volume of the troodontid *Zanabazar junior* also plots closer to the crown than does *Archaeopteryx lithographica*.

The relationship between the volume of the six partitioned neuroanatomical regions and body size reveals a pattern in which the relative volume of the cerebrum is uniquely large in crown birds and thus can be optimized as an unambiguous synapomorphy of that clade. The strong similarity between the relative cerebral volumes in *Archaeopteryx lithographica*, the oviraptorosaurs, and *Zanabazar junior* are inferred to reflect the ancestral maniraptoran condition. The implication of this inference is that the cerebral volume to body size relationship in *Archaeopteryx lithographica* is not uniquely avian but rather plesiomorphic for a larger maniraptoran clade (as also seen in morphology). The volumes of the optic lobes, cerebellum, and brain stems relative to body size also are distinctly larger in the crown than in *Archaeopteryx lithographica* and thus reflect synapomorphic expansions that transformed sometime after the Jurassic divergence of *Archaeopteryx lithographica*. Overlap in these values between crown birds, *Zanabazar junior*, and at least some of the oviraptorosaurs indicate that the expansions
are not unambiguous synapomorphies of the crown but rather evolved at least three times in Maniraptora—once in Avialae (after the split of *Archaeopteryx lithographica*), once in Deinonychosauria (as evidenced by *Zanabazar junior*), and once in Oviraptorosauria (Fig. 4.34). An alternative interpretation is that these expansions reflect maniraptoran synapomorphies and that the relatively small values observed in *Archaeopteryx lithographica* are autapomorphies of that taxon. This interpretation is hampered by the fact that not all of oviraptorosaurs overlap with crown birds for these variables.

The strong correlation between cerebral volume and total endocranial volume is expected if cerebral expansion is a primary driver of the general endocranial expansion that is characteristic of the theropod portion of the avian stem (Larsson et al., 2000). The relatively high correlations between total endocranial volume and the volumes of the other neuroanatomical partitions (Figs. 4.26–4.31) indicate that all of these regions, with the possible exception of the olfactory lobes, are expanding along the avian stem. The implication of these strong correlations is that total endocranial volume does not appear to be structurally constrained. If such a constraint, even a weak one, were in place and cerebral expansion were being driven by strong selection pressure, then the expansion of this region should be accomplished at the expense of one or more of the other regions. That all or most of these regions are expanding together attests to the high potential of the surrounding skeleton to respond to the tissues they envelop (Rowe, 1996).

The relationship between the volume of the examined neuroanatomical partitions and total endocranial volume presents a different, and in some ways clearer, evolutionary pattern. These data indicate that an increase in proportional volume of the cerebrum to
Figure 4.34. Inferred pattern of neuroanatomical expansion relative to body size. The alternative interpretation that the relative expansion of the optic lobes, cerebellum, and brain stem is a synapomorphy deep within Maniraptora and that *Archaeopteryx lithographica* reflects an autapomorphic reversal is hampered by similarly small values in some oviraptorosaurs (suggesting a homoplastic expansion within that clade). The possibility that the expansions expressed in *Zanabazar junior* and the crown reflect paravian synapomorphies, with secondary contraction in *Archaeopteryx lithographica* is ambiguous with the above interpretation. Cerebral expansion relative to body size is an unambiguous synapomorphy of the avian crown.
50% or more of the total endocranial volume is an unambiguous synapomorphy of Paraves that supports the phylogenetic exclusion of Oviraptorosauria from that group. The overlap between the lower range of crown birds and the fossil paravians, suggest that the proportional volume of the cerebrum may not have exhibited another distinct increase until after the origin of the avian crown. The validity of this prediction will depend to a large degree on the reconstructed value for the ancestral crown bird, which currently is unclear. The relatively small value in the paleognath *Struthio camelus* as well as multiple neognaths suggests this scenario is a possibility.

The cerebrum, of course, expands at the expense of other regions if the proportional data are considered alone. Such a consideration reveals interesting patterns, including a seemingly distinct increase in the proportional volume of the cerebrum at the origin of Paraves (Fig. 4.35). No undisputed paravian taxon, including both the stem and crown members, possesses a cerebrum that fills less than half of the total endocranial cavity. The proportional cerebral volume of the putative avialans examined, including the oviraptorosaurs (Maryańska et al., 2002; Osmólska et al., 2004; Kudrát, 2007) and the alvarezsaurid *Shuvuuia deserti* (Perle et al., 1993; Chiappe et al., 1998; 2002), possess a proportional cerebral volume less than 50%, suggesting that they lie phylogenetically outside not only Avialae but also Paraves (in congruence with recent phylogenetic analyses; see Turner et al., 2007). The proportional cerebral volume of the avialan *Archaeopteryx lithographica*, while slightly larger than that of the dromaeosaur *Tsaagan mangas*, is slightly smaller than that of the troodontid *Zanabazar junior*. It therefore is likely that the cerebral proportion expressed in *Archaeopteryx lithographica* closely
Regional Volumes Relative to Total Endocranial Volume

Oviraptorosauria  Zanabazar  Archaeopteryx  crown birds

secondary expansion of proportional cerebral volume (may have occurred inside the crown)

cerebral volume over 50% of total endocranial volume

(this unambiguous synapomorphy supports the phylogenetic exclusion of Oviraptorosauria from Paraves, and thus Avialae)

Figure 4.35. Inferred pattern of neuroanatomical expansion relative to total endocranial volume. Possessing a cerebral volume over 50% of the total endocranial volume optimizes as a synapomorphy of Paraves. A subsequent cerebral expansion may also have taken place within crown birds.
reflects the ancestral condition for Paraves and is not a uniquely avialan feature. Perhaps more surprising than the non-unique proportional volume of the *Archaeopteryx lithographica* cerebrum is the overlap between the proportional cerebral volumes of the examined paravians and the lower end of the observed range for the avian crown (Fig. 4.33). Five of the observed crown birds express a proportional cerebral volume that closely approximates or is less than that of *Archaeopteryx lithographica* and *Zanabazar junior* (Appendix 7). These five taxa bracket crown birds so it is possible that the proportional cerebral volume diagnostic of Paraves is retained in the ancestor of the avian crown. This would mean that no significant increase in the relative size of the cerebrum occurred within Avialae until after the origin of the avian crown, and that cerebral increase is not a synapomorphy of the crown clade Aves. It is also possible that these low values for extant birds reflect derived conditions (e.g., the relatively small proportional value observed for the paleognath *Struthio camelus* may reflect its secondarily acquired flightless condition if flight can be correlated with size of the cerebrum). Apparent support for the derived hypothesis is found in the relatively high proportional volume of the cerebrum in the examined galloanseriforms. Denser sampling within the crown and the stem of Paraves will clarify these questions but currently it is not clear whether even the ancestral crown avian possessed a cerebrum that is reconstructed as filling a apomorphically large proportion of the endocranial cavity within theropods.

The expansion of the cerebrum has important implications for behavior and cognition in the fossil record. Correlating size of the brain or specific regions to functions should be approached with caution. Interconnected networks exist between
neuroanatomical partitions and functions often are the product of multiple regions (Barton and Harvey, 2000; Healy and Rowe, 2006). It has been established, however, that an expansion in the forebrain does correlate to some degree with cognition (Iwaniuk et al., 2005a; Lefebvre et al., 2004). Even more interestingly, an expanded forebrain also has been shown to be strongly correlated with developmental mode in birds. Boire and Baron (1994) states that “. . . altricial birds tend to achieve a low level of embryonic brain growth and have larger brains as adults than precocial species” (Portmann, 1946; 1947; Bennett and Harvey, 1985a; 1985b). Although not as pronounced as the inflation apparent in Paraves, the enlarged forebrain of maniraptorans in general coincides with one of the rare examples of behavior that is preserved in the fossil record. Oviraptorosaur specimens have been discovered “nesting” their eggs similar to behavior in modern birds (Norell et al., 1994; 1995; Dong and Currie, 1996). The parental care indicated by these brooding oviraptorosaur specimens is supported also by the neuroanatomy of this group. Considering that an expanded cerebrum is characteristic of a larger group of maniraptorans, it would not be surprising to find examples of additional taxa exhibiting this same behavior (e.g., the *Troodon formosus* nesting trace reported by Varricchio et al., 1999). Further analysis is needed to test this hypothesis and can be done by setting up a phylogenetic bracket using he only other living clade of archosaurs, crocodilians.

Gross anatomical observation (Figs. 4.13–4.16) and principal components analysis (Fig. 4.32, 3.33) both identify a unique morphological space for oviraptorosaurs. These taxa possess an unusually large cerebellum, especially pronounced in *Citipati osmolskae* and *Conchoraptor gracilis*. An increase in size of the cerebellum typically is
correlated with increased coordination and orientation. A pattern of expansion not surprisingly is seen in extremely aerial birds such as caprimulgiforms, although it should be noted some behavioral functions also may take place in this region of the brain (Butler and Hodos, 1996; Iwaniuk et al., 2005b). The relative expansion of the cerebellum in oviraptorids, however, cannot be explained by complex flight, as these taxa exhibit an obviously cursorial postcranial skeleton (Fig. 1.14–1.15). The largest portion of the cerebellum is composed of the floccular lobes, a feature that appears to be convergent with the same expansion in Pterosauria, although not expanding quite to the same extent as in pterosaurs (Witmer et al., 2003). Witmer et al. (2003) proposed that the enlarged flocculus might be correlated with “gaze stabilization” so that a predator is able to fix its gaze on a target while moving in pursuit (Witmer et al., 2003). In addition, the flocculus is responsible for coordinating cutaneous signals (Witmer et al., 2003; Iwaniuk et al., 2005b), suggesting that there might have been some sort of extensive integumentary covering capable of receiving sensory signals in these taxa. Such an evolutionary scenario is not unlikely, considering that oviraptorids lie phylogenetically among taxa that possess at least some sort of integumentary structures (e.g., *Caudipteryx zoui*, Ji et al., 1997; *Beipiaosaurus inexpectus*, Xu et al., 2009).

**SUMMARY AND CONCLUSIONS**

This study represents the first attempt to objectively partition the endocranial cavity of both crown and stem birds into discrete neuroanatomical regions and then to use these partitions to investigate the role of mosaic evolution in the origin of the avian
endocranial space. Such an approach lends itself to address both specific questions concerning the endocranial morphology within oviraptorosaurs and more general questions about the origin of the avian brain. These results, both morphological and volumetric, support an Oviraptorosauria that lies phylogenetically outside of Avialae, contrary to the findings of Kundrát (2007). Reduced olfactory tracts are shown to be the only morphological character that supports a clade composed of Oviraptorosauria and Aves to the exclusion of other paravians (i.e., Zanabazar junior). However in the context of the maniraptoran tree, this character can be shown to be convergently evolved in the two clades. The other character that has been proposed as being synapomorphic of a clade composed of Oviraptorosauria and crown birds (to the exclusion of deinonychosaurus and *Archaeopteryx lithographica*) is the expansion of the cerebrum. An expanded cerebrum instead is shown to be a diagnostic feature of paravians to the exclusion of oviraptorosaurs (see below).

In reference to the evolution of the avian brain, Larsson et al. (2000) predicted that the comparative size of the cerebrum in *Archaeopteryx lithographica* would be in the range of closely related maniraptorans such as *Troodon formosus* and *Caudipteryx zoui*. That study was found to be both correct and incorrect in its predictions. The cerebrum of oviraptorosaurs, which includes *Caudipteryx zoui*, was found to fall below the 50 percent line and thus not in the range of *Archaeopteryx lithographica*. Larsson (2000) is correct in the sense that the cerebral volume of both *Archaeopteryx lithographica* and troodontids exceeds 50 percent of the total endocranial volume. These results suggest that there is not a unique morphology or cerebral volume that is indicative of the avialan
endocast, but rather that exhibited by *Archaeopteryx lithographica* is plesiomorphic for the paravian clade.

If the tree is correct and *Archaeopteryx lithographica* does represent the ancestral morphology of the subsequent length of Avialae, then the avian crown is diagnosed by a volumetric increase in all six of the examined neuroanatomical partitions relative to body size. Only in the cerebrum is the relative volume uniquely large in the crown when the other stem paravians and oviraptorosaurs also are considered. This indicates that the high values expressed in crown birds relative to *Archaeopteryx lithographica* were achieved independently at least three times—one in Avialae (after the divergence of *Archaeopteryx lithographica*), once in Deinonychosauria, and once in Oviraptorosauria (assuming that the brain of *Archaeopteryx lithographica* is not secondarily reduced).

Looking at the volumes of these regions relative to the total endocranial volume reveals a more straightforward, although, slightly different pattern. The size of the cerebrum in these considerations no longer indicates a unique status of the avian crown but rather overlap between birds and fossil paravians (Fig. 4.35). A jump is present between oviraptorosaurs and Paraves, which supports Oviraptorosauria outside of Paraves.

Future studies should sample more densely along these lineages to determine the incidence parallel evolutions and if the *Archaeopteryx lithographica* endocast actually is representative of the ancestral morphology of the avialan lineage. Our data indicate that *Archaeopteryx lithographica* can be inferred as largely plesiomorphic not only for Avialae and the crown but for the entire paravian radiation. In addition, an increased sample should allow more rigorous comparisons of endocranial evolution with other
clades that also exhibit a cerebral expansion, such as the crown and stem of Mammalia (e.g., Radinsky, 1967; 1974; 1977).
CHAPTER FIVE
CONCLUSIONS

The stem avian clade Oviraptorosauria, which previous to this study was poorly understood both morphologically and phylogenetically, presents a unique opportunity to study morphological evolution close to the origin of flighted coelurosaurs. This dissertation endeavors to thoroughly describe morphologies that are characteristic for the different forms of oviraptorosaurs and subsequently presents a phylogenetic hypothesis of relationships within both Oviraptorosauria and Coelurosauria so that any morphological observations can be analyzed within a broader evolutionary context. Thus, the results of this analysis are able to elucidate the important evolutionary relationships within Coelurosauria near the origin of flight, namely that the data support Oviraptorosauria as the sister taxon to Therizinosauria and this larger clade is positioned outside of Avialae. These results are contrary to some recent phylogenetic analyses that posit an avialan position for Oviraptorosauria (Maryańska et al., 2002; Lü, 2004; Osmólska et al., 2004). Clarifying the position of Oviraptorosauria within Coelurosauria as well as the interrelationships of the group is especially important in light of the many avian-like features that are derived within this clade. A non-avialan position of Oviraptorosauria further suggests that these avian-like characters exhibit some degree of plasticity at the base of Maniraptora, sometimes convergently evolving several different times in this region of the tree (e.g., within Oviraptorosauria, Paraves, and/or Avialae).

These convergently evolved characteristics are present not only in the external skeletal morphology of coelurosaurian theropods, but also extend to the morphology and volumetric
changes in various regions of the endocranial cast (endocast). The shape of the endocranial space in extinct coelurosaurs has long been an area of interest to biologists; however, the region of the tree proximal to Avialae historically has been neglected. This neglect largely reflects the lack of available specimens and the logistical difficulty of accessing the necessary anatomy. The discovery of new specimens as well as technological innovations such as computed tomography and associated software for manipulating digital data are helping to resolve this problem. The present study adds several new morphological descriptions of endocasts to the literature and also determines what endocranial features are phylogenetically informative within this region of the coelurosaur tree. These characters indicate that Oviraptorosauria possesses an endocranial morphology distinct from paravians, reinforcing a position for this group outside of Avialae.

Furthermore, the phylogenetic hypothesis presented in this dissertation is used to investigate the evolution not only of the morphological changes in Oviraptorosauria and more broadly those of Coelurosauria, but it also is used to address what types of volumetric changes occur within the endocranial space. Previous studies of endocranial volume have attempted to quantify the volumetric changes that occur along the avian stem; however, they have only been able to do this by looking at total endocranial volume with respect to body size in crown birds and taxa that are distantly related to Avialae such as tyrannosaurids (Jerison, 1969; Hopson, 1979; Larsson et al., 2000). This study, firstly, employs taxa that are more closely related to Avialae and crown birds and thus nearer the origin of flight. The use of computed tomography also allows the partitioning of the endocranial cast into six separate segments corresponding closely to neuroanatomical regions of the brain (Iwaniuk and Nelson, 2005). No previous studies had the technology with which to perform this type of analysis. These neuroanatomical regions
include the olfactory tracts and bulbs, cerebrum, pituitary, optic lobes, cerebellum, and brain stem. Segmentation of the endocast affords the opportunity to address specific questions concerning the volumetric changes with respect to body size as well as how these different regions are changing with respect to each other and total endocranial volume.

These novel comparisons revealed a large amount of plasticity in the maniraptoran tree and a more complex pattern of endocranial evolution than was previously hypothesized to be present. If the volumetric values for Archaeopteryx lithographica are taken to represent the ancestral condition in avialans, then several instances of cerebral expansion occur in parallel (within Oviraptorosauria, Deinonychosauria, and Avialae). Most interestingly, the endocast at the base of Avialae does not appear to be unique either morphologically or volumetrically; rather, it is the more inclusive clade Paraves that expresses distinctive neuroanatomical innovation. If Archaeopteryx lithographica is hypothesized to have a “flight-ready brain” (Domínguez Alonso et al., 2004), then this generalization actually can be extended down the tree and is also applicable to Deinonychosauria, which lends credence to the idea that dromaeosaurids such as Microraptor zhaoianus may have had a brain that was neurologically capable of some level of volant activity such as gliding flight (Xu et al., 2003).

This dissertation presents the important first step towards a greater understanding of the evolution of the brain within stem avians. A large amount of data is available for crown birds (Iwaniuk et al., 2003; Burish et al., 2004; Iwaniuk et al., 2004; Iwaniuk and Hurd, 2005); however, relatively little is known about endocranial anatomy within the region of the tree that lies at the base of Maniraptora. Neuroanatomical patterns within Oviraptorosauria are elucidated here, and preliminary hypotheses about these same patterns in the more inclusive clade
Maniraptora also are put forth. Future studies should place a greater focus on filling out the deinonychosaur and avialan clades. This present analysis shows that a large amount of variation is present at the maniraptoran node if *Archaeopteryx lithographica* is taken to be representative of the ancestral condition within Avialae, and many features that were thought to be characteristic of avialans have evolved several different times. The apomorphic expansion of the forebrain (which is at least partially correlated with cognition; Burish et al., 2004) has occurred at least twice within amniotes (i.e., birds and mammals), and elucidating the avian pattern of forebrain expansion will lend greater understanding to the mechanisms behind this convergence.
LITERATURE CITED


Bever, G.S. et al. submitted to *PLOS One*.


Galton, P.M. 1985. Cranial anatomy of the prosauropod dinosaur Plateosaurus from the Knollenmergel (Middle Keuper, Upper Triassic) of Germany. Geologica et Palaeontologica 19: 119–159.


Appendix 1. Anatomical abbreviations.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>an</td>
<td>angular</td>
</tr>
<tr>
<td>aof</td>
<td>antorbital fenestra</td>
</tr>
<tr>
<td>ar</td>
<td>articular</td>
</tr>
<tr>
<td>asc</td>
<td>anterior semicircular canal</td>
</tr>
<tr>
<td>ax</td>
<td>axial vertebra</td>
</tr>
<tr>
<td>bo</td>
<td>basioccipital</td>
</tr>
<tr>
<td>bsp</td>
<td>parabasisphenoid</td>
</tr>
<tr>
<td>bt</td>
<td>basal tubera</td>
</tr>
<tr>
<td>cc</td>
<td>cranial carotid canal</td>
</tr>
<tr>
<td>ccr</td>
<td>common crux</td>
</tr>
<tr>
<td>ch</td>
<td>choana</td>
</tr>
<tr>
<td>cif</td>
<td>crista interfenestralis</td>
</tr>
<tr>
<td>cnII</td>
<td>cranial nerve II (optic)</td>
</tr>
<tr>
<td>cnV</td>
<td>cranial nerve V (trigeminal)</td>
</tr>
<tr>
<td>cnVI</td>
<td>cranial nerve VI (abducens)</td>
</tr>
<tr>
<td>cnVII</td>
<td>cranial nerve VII (facial)</td>
</tr>
<tr>
<td>cnVIIIc</td>
<td>cranial nerve VIII (cochlear branch)</td>
</tr>
<tr>
<td>cnVIIIv</td>
<td>cranial nerve VIII (vestibular branch)</td>
</tr>
<tr>
<td>coc</td>
<td>cochlear canal</td>
</tr>
<tr>
<td>d</td>
<td>dentary</td>
</tr>
<tr>
<td>dtr</td>
<td>dorsal tympanic recess</td>
</tr>
<tr>
<td>ec</td>
<td>ectopterygoid</td>
</tr>
<tr>
<td>ecs</td>
<td>endocranial space</td>
</tr>
<tr>
<td>eo</td>
<td>exoccipital</td>
</tr>
<tr>
<td>eov</td>
<td>external occipital vein</td>
</tr>
<tr>
<td>f</td>
<td>frontal</td>
</tr>
<tr>
<td>fm</td>
<td>foramen magnum</td>
</tr>
<tr>
<td>fps</td>
<td>fenestra pseudorotundum</td>
</tr>
<tr>
<td>fr</td>
<td>floccular recess</td>
</tr>
<tr>
<td>frac</td>
<td>fracture</td>
</tr>
<tr>
<td>frps</td>
<td>frontoparietal suture</td>
</tr>
<tr>
<td>fv</td>
<td>foramen vestibuli</td>
</tr>
<tr>
<td>h</td>
<td>hyoid</td>
</tr>
<tr>
<td>hsc</td>
<td>horizontal semicircular canal</td>
</tr>
<tr>
<td>icf</td>
<td>intercerebral fissure</td>
</tr>
<tr>
<td>ifb</td>
<td>interfenestral bar</td>
</tr>
<tr>
<td>inf</td>
<td>infratemporal fenestra</td>
</tr>
<tr>
<td>j</td>
<td>jugal</td>
</tr>
<tr>
<td>l</td>
<td>lacrimal</td>
</tr>
<tr>
<td>lat</td>
<td>laterosphenoid</td>
</tr>
<tr>
<td>lc</td>
<td>lacrimal canal</td>
</tr>
<tr>
<td>Abbreviation</td>
<td>Full Name</td>
</tr>
<tr>
<td>--------------</td>
<td>-----------------------------------------------</td>
</tr>
<tr>
<td>lsc</td>
<td>lateral semicircular canal</td>
</tr>
<tr>
<td>mdf</td>
<td>mandibular fenestra</td>
</tr>
<tr>
<td>mef</td>
<td>metotic fenestra</td>
</tr>
<tr>
<td>mf</td>
<td>metotic fissure</td>
</tr>
<tr>
<td>mo</td>
<td>medulla oblongata</td>
</tr>
<tr>
<td>mx</td>
<td>maxilla</td>
</tr>
<tr>
<td>mxf</td>
<td>maxillary fenestra</td>
</tr>
<tr>
<td>n</td>
<td>nasal</td>
</tr>
<tr>
<td>na</td>
<td>naris</td>
</tr>
<tr>
<td>nc</td>
<td>nuchal crest</td>
</tr>
<tr>
<td>ncr</td>
<td>nuchal crest</td>
</tr>
<tr>
<td>np</td>
<td>nasal passage</td>
</tr>
<tr>
<td>nr</td>
<td>nasal recess</td>
</tr>
<tr>
<td>o</td>
<td>orbit</td>
</tr>
<tr>
<td>oc</td>
<td>occipital condyle</td>
</tr>
<tr>
<td>op</td>
<td>opisthotic</td>
</tr>
<tr>
<td>osc</td>
<td>otosphenoidal crest</td>
</tr>
<tr>
<td>osp</td>
<td>orbitosphenoid</td>
</tr>
<tr>
<td>p</td>
<td>parietal</td>
</tr>
<tr>
<td>pal</td>
<td>palatine</td>
</tr>
<tr>
<td>par</td>
<td>prearticular</td>
</tr>
<tr>
<td>pf</td>
<td>palatine fenestra</td>
</tr>
<tr>
<td>pit</td>
<td>pituitary</td>
</tr>
<tr>
<td>Abbr</td>
<td>Term</td>
</tr>
<tr>
<td>------</td>
<td>-----------------------</td>
</tr>
<tr>
<td>st</td>
<td>sella turcica</td>
</tr>
<tr>
<td>stf</td>
<td>supratemporal fenestra</td>
</tr>
<tr>
<td>t</td>
<td>tooth</td>
</tr>
<tr>
<td>v</td>
<td>vomer</td>
</tr>
<tr>
<td>vc</td>
<td>vagus canal</td>
</tr>
<tr>
<td>vest</td>
<td>vestibule</td>
</tr>
<tr>
<td>vf</td>
<td>vagus foramen</td>
</tr>
</tbody>
</table>
Appendix 2. List of institutional abbreviations.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Full Name</th>
</tr>
</thead>
<tbody>
<tr>
<td>AMNH</td>
<td>American Museum of Natural History, New York, USA</td>
</tr>
<tr>
<td>CMN</td>
<td>Canadian Museum of Nature, Ottawa, Canada</td>
</tr>
<tr>
<td>IGM</td>
<td>Geological Institute, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia</td>
</tr>
<tr>
<td>IVPP</td>
<td>Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China</td>
</tr>
<tr>
<td>LH</td>
<td>Long Hao Institute of Geology and Paleontology, Hohhot, Inner Mongolia, China</td>
</tr>
<tr>
<td>PIN</td>
<td>Paleontological Institute, Russian Academy of Sciences, Moscow, Russia</td>
</tr>
<tr>
<td>ROM</td>
<td>Royal Ontario Museum, Ontario, Canada</td>
</tr>
<tr>
<td>RTMP</td>
<td>Royal Tyrrell Museum of Palaeontology, Drumheller, Canada</td>
</tr>
<tr>
<td>UMNH</td>
<td>Utah Museum of Natural History, Salt Lake City, Utah</td>
</tr>
<tr>
<td>ZPAL</td>
<td>Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland</td>
</tr>
</tbody>
</table>
Appendix 3. List of characters used in the phylogenetic analysis. Characters 1-219 correspond to the same characters in Lu (2005), unless otherwise noted. Lu (2005) in turn is based in large part on Maryanska et al. (2002), Osmolska et al. (2004), Gauthier (1986), Rauhut (2003), and the Theropod Working Group (TWiG) character list. Corresponding TWiG character numbers are given for each character based on the most recent publication of that character list (Turner et al., 2007).

1. Ratio of preorbital skull length to basal skull length:

   (0) 0.6 or more

   (1) 0.5 or less

   The skull is shortened in all oviraptorids relative to other examined taxa, except the modern chicken (*Gallus gallus*—birds are variable for this character). *Oviraptor philoceratops* has a longer rostrum than other oviraptorids; however, overall it still possesses a derived, shortened skull length.

2. Longitudinal pneumatized crest-like prominence along midline of skull:

   (0) absent

   (1) present

   This character is modified from Maryanska et al. (2002). The wording was slightly altered from “skull roof” to “midline of skull” to make it more specific to oviraptorosaurs. Cranial ornamentation on the dorsal surface of the skull has evolved multiple times in different theropod clades including ceratosaurs, tyrannosaurids,
oviraptorosaurs, and crown birds. Within Oviraptorosauria this feature seems to appear on those taxa that achieve large body sizes.

3. Orbit:

(0) round in lateral or dorsolateral view

(1) dorsoventrally elongate

TWiG (character 2)

4. Premaxilla main body length (ventral) to height (below naris):

(0) roughly as tall as long (1.0-1.4)

(1) premaxilla extremely long and shallow (more than 1.7)

(2) premaxilla has a shorter length than height (0.7 or less)

The character states were changed in this analysis from the ratios (given in parentheses) to discreet character states that are more easily analyzed. The typical theropod condition—including crown avians—is a premaxilla that is longer than tall. The oviraptorosaurs *Incisivosaurus gauthieri, Avimimus portentosus,* and *Caudipteryx zoui* possess a premaxilla that is approximately as long as tall. A shortened premaxilla is synapomorphic of Oviraptoridae.

5. Otosphenoidal crest:

(0) vertical on basisphenoid and prootic, and does not border an enlarged pneumatic recess
(1) well-developed, crescent shaped, thin crest forms anterior edge of an enlarged pneumatic recess

Among oviraptorosaurs, only *Incisivosaurus gauthieri* and *Chirottenotes pergracilis* possess a well-developed otosphenoidal crest. It also can be found in troodontids, *Shuvuuia deserti*, and some extant birds.

TWiG (character 6)

6. Subnarial (maxillary) process of the premaxilla:

(0) contacts the nasal, the maxilla excluded from the narial border

(1) does not contact the nasal, the maxilla participates in formation of the narial border

**EXCLUDED.** Describes the same morphology present in character 17.

7. Premaxillae of adults:

(0) not fused

(1) fused

The premaxillae are fused in all oviraptorosaurs except the basal taxa *Incisivosaurus gauthieri* and *Caudipteryx zoui*.

Chiappe (1996)

8. Pneumatization of the premaxilla:

(0) absent

(1) present
9. Basisphenoid recess:

   (0) present between basisphenoid and basioccipital
   
   (1) entirely within the basisphenoid
   
   (2) absent
   
   Rauhut (2003)
   
   TWiG (character 9)

10. Subantorbital portion of maxilla:

   (0) not inset medially
   
   (1) inset medially

   The maxilla in all oviraptorids that were scored is inset ventral to the antorbital fossa and not confluent with the lateral surface of the skull.

11. Palatal shelves of the maxillae:

   (0) completely separated by the vomer
   
   (1) in contact for most of their length

12. Maxilla, palatal shelf:

   (0) flat
   
   (1) with paired ventral “tooth-like” projections

   This feature is synapomorphic of a group formed by oviraptorids and Chirostenotes pergracilis. The ventral margin of the palatal surface in these taxa possess a raised
protuberance that with the vomer form a toothlike structure. Osmolska et al. (2004; character 11) combines this morphology with the ridges and troughs that also are present on the palatal surface of some oviraptorosaurs; however, these should be considered separate morphologies as *Chirostenotes pergracilis* possesses “teeth” but not the ridges and troughs.

TWiG (character 26)

13. Rim around the antorbital fossa:

(0) poorly delimited

(1) well-pronounced

14. Antorbital fossa:

(0) not bordered rostrally by the premaxilla

(1) bordered rostrally by the premaxilla

This morphology likely is a result of the shortening of the facial region in oviraptorosaurs so that the maxilla no longer forms the anterior margin of the antorbital fossa. Among oviraptorosaurs *Incisivosaurus gauthieri, Caudipteryx zoui, Chirostenotes pergracilis*, and *Oviraptor philoceratops* have an antorbital fossa that is bordered anteriorly by the maxilla.

15. Accessory maxillary fenestrae:

(0) absent
(1) at least one accessory fenestra present

This analysis uses the TWiG version of this character as opposed to that used in the
Maryanska et al. (2002), Osmolska et al. (2004), Lu et al. (2004), and Lu (2005)
analyses. Those analyses refer to presence and size of the accessory maxillary fenestrae.

16. Skull proportions:

(0) preorbital region distinctly longer than postorbital region

(1) preorbital and postorbital regions subequal in length

This character is modified from the original, which refers to the relative lengths of the
frontals, maxilla, and premaxilla. The preorbital region of all oviraptorosaurs is shortened
to some degree. *Incisivosaurus gauthieri* has a preorbital region that is longer than its
postorbital region, and *Caudipteryx zoui* has preorbital and postorbital regions that are
approximately the same length.

17. Maxillary process of premaxilla:

(0) contacts nasal to form posterior border of naris

(1) maxillary process of premaxilla reduced so that maxilla participates broadly in
external naris

(2) maxillary process of premaxilla extends posteriorly to separate maxilla from nasal
posterior to naris

This character is scored differently from Turner et al. (2007). *Incisivosaurus gauthieri*
and *Caudipteryx zoui* are scored as having state 0. Oviraptorosaurids (contrary to TWiG)
have a maxillary process of the premaxilla that extends posterodorsally and completely separates the nasal and maxilla so that these elements do not contact each other at all. In *Velociraptor mongoliensis* and other dromaeosaurs, the maxilla does not participate in the external naris, but still contacts the nasal posterior to the external naris.

TWiG (character 17)

18. Nasal recesses:

(0) absent

(1) present

19. Caudal margin of naris:

(0) farther rostral than the rostral border of the antorbital fossa

(1) nearly reaching or overlapping rostral border of the antorbital fossa

(2) overlapping most of the antorbital fossa

This analysis, similar to Lu et al. (2004) and Lu (2005), uses an additional character state, so that it differentiates a external naris that lies at the rostral margin of the antorbital fossa and one that is overlaps the fossa.

TWiG (character 23)

20. Ventral margin of the external naris:

(0) at the level of the body of the maxilla

(1) dorsal to the body of the maxilla
This character is slightly modified from Maryanska et al. (2002; character 20) by specifying the body of the maxilla (not inclusive of the dorsal process).

21. Prefrontal:

(0) present  
(1) absent  

This character is slightly modified from the one used by Lu et al. (2004), and Lu (2005). That analysis describes character state 1 as “absent or fused with the lacrimal”. This state appears to describe two different character states and two different homology statements.

TWiG (character 40)

22. Lacrimal recess:

(0) absent  
(1) present  

23. Premaxillary symphysis:

(0) acute, v-shaped  
(1) rounded, u-shaped  

The premaxillary symphysis of both therizinosaurs and oviraptorosaurs has a u-shape when viewed ventrally rather than having straight mandibular rami that do not possess any curvature and thus form a v-shape.

TWiG (character 24)
24. Secondary palate:

(0) formed by premaxilla only

(1) by premaxilla, maxilla, and vomer

**EXCLUDED.** A secondary palate is present in all coelurosaurians, and therefore not useful for determining relationships in this analysis.

TWiG (character 25)

25. Pronounced, round accessory antorbital fenestra:

(0) absent

(1) present

**EXCLUDED.** Describes the same morphology as that in character 15.

26. Parietal:

(0) equal to or shorter than the length of the frontal (0.6 or less)

(1) longer than the frontal (1.0 or more)

Oviraptorids have an extremely reduced frontal bone, typically about half of the length of the parietal. The more basal taxa *Incisivosaurus gauthieri*, *Caudipteryx zoui*, and *Avinimimus portentosus* have a parietal that is either the same length as the frontal or shorter than the frontal. The ratio numbers are redescribed from Maryanska et al. (2002; character 26) and made into more qualitative characters.
27. Narial region:

(0) apneumatic or poorly pneumatized

(1) with extensive pneumatic fossae, especially along posterodorsal rim of fossa

An extremely pneumatized narial region is present in all oviraptorosaurs and can be considered a synapomorphy for this group.

TWiG (character 30)

28. Sagittal crest on the parietals:

(0) absent

(1) present

EXCLUDED. This character is repetitive with character 46.

29. Jugal pneumatic recess in posteroventral corner of antorbital fossa:

(0) present

(1) absent

TWiG (character 33)

30. Infratemporal fenestra:

(0) ventrally nearly as long as rostrally high

(1) shorter ventrally than high

(2) large, square

(3) not separated from the orbit
31. Descending (prequadratic) process of the squamosal:

(0) constricting the dorsal part of the infratemporal fenestra

(1) not constricting the infratemporal fenestra

32. Quadratojugal and jugal:

(0) separate

(1) fused and not distinguishable from one another

TWiG (character 36)

33. Jugal shape beneath infratemporal fenestra:

(0) tall, twice or more as tall dorsoventrally as it is wide transversely

(1) rod-like

This character has been used as a classic synapomorphy of oviraptorids; however, this analysis finds that several oviraptorids, *Conchoraptor gracilis* and ZPAL MgD-I/106, do not have the typical rod-like jugal. Maryanska et al. (2002; character 33) and Lu (2005; character 33) is modified from this character. Those analyses refer to the shape of the jugal beneath the antorbital fenestra.

TWiG (character 32)

34. Jugal-postorbital contact:

(0) present
(1) absent

TWiG (character 31)

35. Quadratojugal process of the jugal in lateral view:

(0) forked
(1) tapering
(2) fused with the quadratojugal

This character is found by Maryanska et al. (2002) to be an unambiguous synapomorphy of *Confuciusornis sanctus* and Oviraptorosauria, making oviraptorosaurs avialans (both possessing tapering quadratojugal processes of the jugal). This analysis finds, instead, that the jugal and quadratojugal are fused. This region in *Incisivosaurus gauthieri* cannot be assessed because it has been reconstructed.

36. Quadratojugal-squamosal contact:

(0) tips of the bones closely approaching but not contacting each other
(1) bones widely separated
(2) contact present

TWiG (character 48)

37. Ascending (squamosal) process of the quadratojugal:

(0) massive, bordering about the ventral half of the infratemporal fenestra
(1) slender, bordering the ventral half of the infratemporal fenestra
(2) slender, bordering the ventral two-thirds or more of the infratemporal fenestra
(3) absent

38. Dorsal (otic) process of the quadrate:

(0) erect
(1) directed (curves) posteriorly

TWiG (character 51)

39. Otic process of the quadrate:

(0) articulating only with the squamosal
(1) articulating with the squamosal and the lateral wall of the braincase

This character also is used by Maryanska et al. (2002) and Osmolska et al. (2004) as a character linking Oviraptorosauria and avialans. Both avialans and oviraptorids do possess a quadrate with a double head that articulates both with the squamosal and the braincase; but, the unusual quadrate morphology of oviraptorids can be considered to have evolved convergently as *Incisivosaurus gauthieri* has a single headed quadrate.

TWiG (character 50)

40. Quadrate:

(0) solid
(1) hollow, with depression on posterior surface
Characters states in Maryanska et al. (2002) differ from this analysis by describing the quadrate as simply solid or hollow.

TWiG (character 52)

41. Accessory process for the contact with the quadratojugal on the distal end of the quadrate:

   (0) absent
   (1) present

42. Quadratojugal:

   (0) sutured to the quadrate
   (1) joined through a ligamentary articulation

43. Mandibular condyles of the quadrate situated:

   (0) caudal to the occipital condyle
   (1) in the same vertical plane as the occipital condyle
   (2) rostral to the occipital condyle

44. Enlarged foramen or foramina opening laterally at the angle of the lacrimal:

   (0) absent
   (1) present

TWiG (character 38)
45. Paroccipital process:

(0) straight, projects laterally or posterolaterally

(1) straight, projecting ventrolaterally

(2) distal end curves ventrally, pendant

All taxa scored for Oviraptorosauria possess ventrally curving paroccipital processes with a pendant shape so that this can be considered a synapomorphy of the group as a whole.

TWiG (character 57)

46. Dorsal surface of parietals:

(0) flat, with lateral ridge bordering the supratemporal fenestra

(1) parietals dorsally convex with very low sagittal crest along midline

(2) parietals dorsally convex with well-developed sagittal crest

TWiG (character 45)

47. Foramen magnum:

(0) smaller than or equal to the occipital condyle

(1) larger than the occipital condyle

48. Basal tubera:

(0) set far apart, level with or beyond lateral edge of occipital condyle and/or foramen magnum (may connected by a web of bone or separated by a large notch)
(1) tubera small, directly below condyle and foramen magnum, and separated by a narrow notch.

The character states in Maryanska et al. (2002), Osmolska et al. (2004), Lu et al. (2004), and Lu (2005) are slightly different. Those analyses have the states “basal tubera: modestly pronounced (0); well pronounced, widely separated (1).” The character used by TWiG is much more descriptive.

TWiG (character 225)

49. Pneumatization of the basisphenoid:

(0) weak or absent

(1) extensive

50. Basipterygoid process:

(0) well developed, extending as a distinct process from the base of the basisphenoid

(1) abbreviated or absent

Oviraptorosaurs and therizinosaurs have state basipterygoid processes that are not well ossified and can be considered either abbreviated or absent. The Maryanska et al. (2002) and following analyses break character state 1 into two states: “strongly reduced (1) or absent (2)”. It is difficult to distinguish between these states; therefore, the TWiG character is used.

TWiG (character 13)
51. Posterior end of dentary:

(0) without posterodorsal process dorsal to mandibular fenestra
(1) with dorsal process above anterior end of mandibular fenestra
(2) with elongate dorsal process extending over most of fenestra

Oviraptorosaurs more derived than *Caudipteryx zoui* have a posterodorsal process of the dentary that extends over almost the entire mandibular fenestra.

TWiG (character 68)

52. Parasphenoid rostrum with palate held in horizontal orientation:

(0) horizontal or directed rostrodorsally
(1) slanting rostroventrally

This character was found to be synapomorphic of a group composed of *Confuciusornis sanctus* and oviraptorids (making oviraptorosaurs avialans)--both having a parasphenoid rostrum that was slanted anteroventrally. This analysis, however, finds that this morphology is synapomorphic only for oviraptorids. Avialans have either a horizontal or anterodorsal slant to their parasphenoid rostrum. The basal oviraptorosaur, *Incisivosaurus gauthieri*, also is revealed through the use of CT to have a rostrocaudal orientation to its parasphenoid rostrum. The character is slightly modified from Maryanska et al. (2002) by adding the qualifier “with palate held in horizontal orientation”.

53. Tibiofibular crest in the lateral condyle of femur:

(0) absent
This morphology is present in all oviraptorosaurs including more basal forms such as *Similcaudipteryx yixianensis*, *Avimimus portentosus*, and *Microvenator celer*.

54. Parietals:

   (0) separate
   (1) fused
   TWiG (character 56)

55. Foramen magnum:

   (0) subcircular, slightly wider than tall
   (1) oval, taller than wide
   TWiG (character 54)

56. Medially extended pterygoids meet each other along the midline ventrally underlie the basisphenoid and parasphenoid:

   (0) absent
   (1) present

57. Quadrate wing of the pterygoid:

   (0) distant from the braincase wall
   (1) overlapping the braincase
The quadrate wing of the pterygoid in Oviraptorosauria extends dorsally so that it covers part of the lateral surface of the braincase.

58. Pterygoid basal process for contact with the basisphenoid:

   (0) absent
   (1) present

59. Ectopterygoid situated:

   (0) lateral to the pterygoid
   (1) rostral to the pterygoid

   All oviraptorosaurs that could be scored have an ectopterygoid that articulates with the anterior margin of the pterygoid instead of articulating with its lateral border.

60. Ectopterygoid:

   (0) lateral contact exclusively with jugal
   (1) lateral contact includes the maxilla and lacrimal

   The ectopterygoid in oviraptorosaurs has a lateral articulation with both the maxilla and jugal as opposed to only the jugal as is found in other theropods. The original Maryanska et al. (2002) character reads: “Ectopterygoid contacts with the maxilla and lacrimal: absent (0); present (1)”. This analysis modifies the character to be more explicit about what element the ectopterygoid is contacting.
61. Hook-like jugal process on ectopterygoid:

(0) present

(1) absent

**EXCLUDED.** This character is present in all coelurosaurs, therefore, lending no resolution to this analysis.

62. Massive pterygoid-ectopterygoid longitudinal bar:

(0) absent

(1) present

**EXCLUDED.** This character is describing the same morphology and can be considered correlated with character 59.

63. Palate extending below the cheek margin:

(0) absent

(1) present

**EXCLUDED.** “Cheek margin” was not defined in the original character; therefore, this character is excluded from the analysis.

64. Snout width (across the premaxilla-maxilla suture) to snout length:

(0) 0.1 or less

(1) 0.3 to 0.4

(2) 0.5 or more
65. Palatine shape:

(0) rectangular
(1) tetraradiate, with jugal process
(2) triradiate, jugal process absent

The palatine of *Incisivosaurus gauthieri* and *Microvenator celer* have a unique triradiate morphology. Although a palatine was not described by Makovicky and Sues (1997), Ostrom (1970) mentions its presence. All other coelurosaurs have a tetraradiate palatine including oviraptorids and *Chirostenotes pergracilis*.

TWiG (character 63)

66. Maxillary process of the palatine:

(0) shorter than vomeral process
(1) longer than vomeral process

**EXCLUDED.** This character is excluded from the analysis because it is difficult to establish homology between taxa, especially those taxa that have a triradiate palatine.

67. Vomer:

(0) distant from parasphenoid rostrum
(1) approaching or in contact with rostrum

The vomer in oviraptorosaurs, therizinosaurus, and crown birds does approach or contact the parasphenoid rostrum and was used by Maryanska et al. (2002; character 67) as a
synapomorphy of a clade including all three of these groups. The state in *Incisivosaurus gauthieri* could not be ascertained even with the use of CT data.

68. Suborbital (ectopterygoid-palatine) fenestra:

(0) well developed

(1) closed or reduced

A reduced suborbital fenestra is a synapomorphy of therizinosours and oviraptorosaurs. Described originally in Clark et al. (1994).

TWiG (character 64).

69. Pterygopalatine fenestra:

(0) absent

(1) present

70. Jaw joint:

(0) distant from skull midline

(1) close to the skull midline (mandibular articulation surface underlies basisphenoid)

This character is modified from Maryanska et al. (2002). Character state one is defined further so as to avoid confusion. The mandibular articulation in oviraptoroids is expanded medially and partially underlies the braincase in ventral view.

71. Occipital condyle:
(0) without constricted neck

(1) subspherical with constricted neck

TWiG (character 55)

72. Mandibular symphysis:

(0) loose

(1) tightly sutured

(2) fused

73. Extended symphyseal shelf at the mandibular symphysis:

(0) absent

(1) present

An extended symphyseal shelf is present in all oviraptorosaurs including *Incisivosaurus gauthieri*, *Microvenator celer*, *Chirostenotes pergracilis*, and oviraptorids.

*Confuciusornis sanctus*, *Apsaravis ukhaana*, and crown birds also possess an extended symphyseal shelf.

74. Dentary symphyseal region:

(0) in line with main part of buccal edge

(1) symphyseal end downturned
Oviraptorosaurs and therizinosaurs possess a symphyseal region of the dentary that is
downturned as does not lie in line with the rest of the element. This analysis uses the
TWiG version of this character as opposed to the one stated in Maryanska et al. (2002).

TWiG (character 66)

75. Mandibular symphysis in ventral view:

(0) acute, v-shaped
(1) u-shaped

Ornithomimids, therizinosaurs, oviraptorosaurs, and some crown birds are found to have
a u-shaped morphology.

76. Retroarticular process:

(0) short, stout
(1) elongate and slender

All oviraptorosaurs are found to possess an elongate and slender retroarticular process of
the mandible. This region of the mandible is now missing in *Incisivosaurus gauthieri*;
however, before going missing it was figured in Xu et al. (2002) and shows an slender
retroarticular process. This analysis uses the TWiG version of this character as opposed to
that used by Maryanska et al. (2002), which states this character as a ratio.

TWiG (character 78)

77. Mandible maximum height to length ratio:
78. External mandibular fenestra’s height to length ratio:

(0) 0.2 to 0.5
(1) 0.7 to 1.0
(2) fenestra absent

The external mandibular fenestra is large and tall in oviraptorids. *Incisivosaurus gauthieri*, *Caudipteryx zoui*, *Avimimus portentosus*, and *Chirostenotes pergracilis* have a external mandibular fenestra that is longer than tall.

79. External mandibular fenestra length to total mandibular length ratio:

(0) 0.20 or less
(1) 0.25 or more
(2) fenestra absent

80. Articular and surangular:

(0) remain as separate elements
(1) co-ossified

81. Mandibular rami in ventral view:
(0) straight

(1) bowed laterally at midlength

82. Rostrodorsal margin of the dentary:

(0) straight or weakly concave

(1) deeply concave

83. Caudal margin of the dentary:

(0) incised, producing two caudal processes

(1) oblique

**EXCLUDED.** This incorporates characters 84, 85, and 51. This character is broken into two (characters 51 and 85) that are used in its place.

84. Long and shallow caudodorsal process of the dentary:

(0) present

(1) absent

**EXCLUDED.** This character is a repeat of character 51 and 83. Character 51 is retained.

85. Long and shallow caudoventral process of the dentary:

(0) extending at least to the caudal border of the external mandibular fenestra

(1) not reaching the caudal border of the external mandibular fenestra
86. Mandible:

(0) without coronoid prominence

(1) with coronoid prominence

An enlarged coronoid prominence is found in *Microvenator celer, Avimimus portentosus*, and all oviraptorids. A reversal of this condition occurs in *Chirostenotes pergracilis*.

TWiG (character 67).

87. External mandibular fenestra:

(0) oval

(1) subdivided by a spinous rostral process of the surangular

The enlarged mandibular fenestra of oviraptorids is subdivided by a spinous process of the surangular.

TWiG (character 72)

88. Mandibular articular facet for the quadrate:

(0) formed of the surangular and articular

(1) formed exclusively of the articular

89. Mandibular articular facet for the quadrate:

(0) with one or two cotyles

(1) convex in lateral view
The mandibular articular facet for the quadrate on the mandible is convex in lateral view and projects above the dorsal margin of the mandibular rami. A plesiomorphic condition of having at least one cotyle is present in *Avimimus portentosus*. The morphology cannot be confidently assessed in *Caudipteryx zoui*, but it appears to be coincident with that of *Avimimus portentosus*.

90. Articular facet for the mandibular joint positioned:

(0) below the dorsal margin of the caudal part of the mandibular ramus

(1) above this margin

**EXCLUDED.** This character is correlated with the preceding character also concerning the morphology of the mandibular articular facet.

91. Rostral part of the prearticular:

(0) deep, approaching the dorsal margin of the mandible

(1) shallow, strap-like, not approaching the dorsal margin of the mandible

*Caudipteryx zoui*, *Chirostenotes pergracilis*, and oviraptorids have a prearticular that is shallow and strap-like in morphology.

92. Splenial:

(0) subtriangular, approaching the dorsal margin of the mandible

(1) strap-like, shallow, not approaching the dorsal margin of the mandible
*Caudipteryx zoui* has the plesiomorphic morphology of a subtriangular splenial. The splenial is missing from *Incisivosaurus gauthieri*. The articular surface on the dentary suggests that it was subtriangular, but it is scored as missing in this analysis.

*Chirostenotes pergracilis* and oviraptorids all possess a strap-like splenial.

93. Mandibular adductor fossa:

(0) rostrally delimited, occupying the caudal part of the mandible

(1) large, rostrally and dorsally extended, not delimited rostrally

94. Coronoid ossification:

(0) large

(1) only a thin splint

(2) absent

In all oviraptorosaurs that can be scored the coronoid bone is only a thin splint. The Maryanska et al. (2002) and successive analyses use only two characters (states 1 and 2 combined) for this character. This analysis uses the TWiG version of this character.

TWiG (character 76)

95. Premaxilla, dentition:

(0) toothed

(1) edentulous

In oviraptorosaurs, the premaxillary dentition is the last to be lost.
96. Maxillary tooth row:

(0) extends at least to the level of the preorbital bar
(1) does not reach the level of the preorbital bar
(2) the maxillary teeth absent

**EXCLUDED.** This character is used in a slightly modified form later in the analysis (character 205).

97. Dentary:

(0) fully toothed
(1) no teeth rostrally
(2) edentulous

Unlike the dentition of the skull, that of the dentary is lost anteriorly first. Neither therizinosaurus nor *Incisivosaurus gauthieri* have teeth at the anterior margin of the dentary. The Maryanska et al. (2002) and following analyses use only two character states for this character, toothed or edentulous. This analysis follows TWiG and adds the state “no teeth rostrally” to describe additional morphology that is present in coelurosaurians.

TWiG (character 220)

98. Number of cervicals (excluding cervicodorsal):
(0) not more than 10
(1) twelve or more

TWiG (character 92)

99. Number of pleurocoels on cervicals:

(0) absent
(1) two arranged horizontally
(2) one

TWiG (character 100)

100. Cranial articular facets of the centra in the anterior postaxial cervicals:

(0) subcircular or square
(1) distinctly wider than deep

TWiG (character 98)

101. Cranial articular facets of the centra in the anterior postaxial cervicals:

(0) not inclined or only slightly inclined
(1) strongly inclined ventrocaudally, almost continuous with the ventral surfaces of the centra
(2) ball-shaped

102. Anterior cervical centra:
(0) not extending posteriorly beyond the respective neural arches
(1) extending posteriorly beyond the respective neural arches

TWiG (character 96)

103. Cervical neural spines:
   (0) anteroposteriorly long
   (1) short and centered on neural arch so that arch is x-shaped in dorsal view

TWiG (character 99)

104. Epipophyses on the postaxial cervicals:
   (0) in the form of a low crest or rugosity
   (1) large, prong-shaped

105. Cervical ribs:
   (0) loosely attached to vertebrae in adults
   (1) fused

106. Shafts of the cervical ribs:
   (0) longer than the respective centra
   (1) not longer than the respective centra

TWiG (character 124)
107. Pleurocoels or lateral excavations on the dorsal centra:

(0) absent

(1) present

108. Postzygapophyses on the dorsals:

(0) not extending beyond the respective centra

(1) markedly extending beyond the centra

109. Number of sacrals:

(0) 2

(1) 3

(2) 4

(3) 5

(4) 6

(5) 7

(6) 8

(7) 9

(8) 10

(9) 11 or more

This character is modified from the form used by Maryanska et al. (2002) and Turner et al. (2007) to account for all possible variation (Turner, 2008).

TWiG (character 110)
110. Sacral spines in adults:

(0) unfused
(1) fused

111. Continuous sulcus along the ventral side of the mid-sacral centra:

(0) absent
(1) present

112. Pleurocoels on the sacral centra:

(0) absent
(1) present

**EXCLUDED.** This character is repetitive with char. 175, which also is concerned with pleurocoels in the sacral centra.

113. Scapula and coracoid:

(0) separate
(1) fused into scapulocoracoid

TWiG (character 135)

114. Hyposphene-hypantrum articulations in the trunk vertebrae:

(0) present
115. Pleurocoels on the caudal centra:

(0) absent
(1) present at least in the proximal part of the tail

Oviraptorids and *Nomingia gobiensis* are the only oviraptorosaurs to have pleurocoels in any caudal vertebrae.

116. Distal caudal centra:

(0) about as long as the proximal ones or insignificantly shorter
(1) longer than the proximal caudal centra
(2) about half as long as the proximal caudal centra

**EXCLUDED.**

117. Number of caudal vertebrae:

(0) more than 40
(1) 25 to 40
(2) no more than 24

TWiG (character 121)

118. Pygostyle:
The distal-most vertebrae of *Nomingia gobiensis* are fused to form a pygostyle; however, this morphology is convergently evolved with that of derived avialans—not being present in *Archaeopteryx lithographica*.

119. Scapular caudal end:

(0) blunt and expanded

(1) tapered to a sharp point or slightly expanded

This character is slightly modified from that used by Lu et al. (2004) and Lu (2005). State 1 is changed from “blunt and much expanded” to “blunt and expanded”. The more distinctive morphologies that need to be distinguished between are scapulas that have a blunt end or a tapered end.

120. Scapula and coracoid:

(0) nearly in the same plane, forming an arc

(1) forming a distinct angle

TWiG (character 137)

121. Distal caudal prezygapophyses:

(0) overlapping less than a half of the centrum of the preceding vertebra

(1) overlapping at least a half of the preceding vertebra
122. Hypapophyses in the cervicodorsal vertebral region:

(0) absent or small

(1) prominent

This character is slightly modified from that used by Maryanska et al. (2002), Osmolska et al. (2004), Lu et al. (2004), and Lu (2005) and uses only two character states rather than three. Those analyses broken state 0 into two states, absent and small. Because it is difficult to establish a qualifier for what should be considered small or prominent, these states are combined.

123. Distal chevrons:

(0) deeper than long

(1) longer than deep

124. Sternal plates:

(0) separate in adults

(1) fused

(2) not ossified

TWiG (character 128)
125. Scapula length to humerus length ratio:

(0) scapula significantly longer than humerus
(1) humerus longer than scapula

This character is modified from that used by Maryanska et al. (2002) and successive analyses. Those analyses used ratios instead of qualitatively describing the characters.

TWiG (character 139)

126. Acromion:

(0) projecting dorsally
(1) everted laterally
(2) projecting cranially

TWiG (character 133)

127. Caudoventral process on the coracoid:

(0) absent
(1) short, not extending beyond the glenoid diameter
(2) long, caudoventrally extending beyond the glenoid

_Caudipteryx zoui_, _Microvenator celer_, and _Chirostenotes pergracilis_ have a short caudoventral process on the coracoid. All other oviraptorosaurs possess a long process.

TWiG (character 136)

128. Orientation of the glenoid on the pectoral girdle:
(0) posteriorly/posterolaterally

(1) lateral

*Chirostenotes pergracilis, Rinchenia mongoliensis, Ingenia yanshini, Heyuannia huangi,*
and *Citipati osmolskae* among oviraptorosaurs have a glenoid that is oriented more laterally.

TWiG (character 138)

129. Humerus, deltopectoral crest:

(0) large and distinct, proximal end of humerus quadrangular in anterior view

(1) less pronounced, forming an arc rather than being quadrangular

(2) very weakly developed, proximal end of humerus rounded edges

(3) extremely long

(4) proximal end of humerus broad, triangular in anterior view

TWiG (character 140)

130. Internal tuberosity on the humerus:

(0) weakly pronounced or absent

(1) well pronounced but low

(2) subtriangular, distinctly extended medially

(3) in form of a longitudinally short, tuberlike extension, sharply delimited from the shaft and usually also from the humeral head
131. Distal condyles of the humerus facing:

(0) distally

(1) cranially or craniodistally

132. Deltopectoral crest (measured from the humeral head to the apex) extending for:

(0) about the proximal third of the humerus length or less

(1) about 40 to 50% of the humerus length

133. Epicondyles on the humerus:

(0) absent or poorly developed

(1) the ectepicondyle more prominent than the entepicondyle

(2) the entepicondyle more prominent than the ectepicondyle

(3) the ectepicondyle and entepicondyle about equally prominent

134. Shaft of the ulna:

(0) straight

(1) bowed

*Rinchenia mongoliensis, Ingenia yanshini, and Gigantoraptor erlianensis* have an ulna with a straight shaft. All other coelurosaurids are scored as having a bowed shaft.

135. Radius length to humerus length ratio:

(0) 0.8 or less
136. Carpus including:

(0) more than four free carpals
(1) three or four free carpals
(2) the carpometacarpus

TWiG (character 147)

137. Distal carpals:

(0) flat, mostly separate
(1) carpals I and II separate, carpal I with the proximal trochlea
(2) carpals I and II fused, with the trochlea on carpal I, covering only metacarpal I
(3) carpals I and II fused, half-moon shaped, with the trochlea on the proximal surface, covering metacarpals I and II

138. Manual digit II:

(0) shorter than or sub-equal to manual digit III
(1) or longer than manual digit III

139. Combined lengths of manual phalanges III-1 and III-2:

(0) greater than the length of phalanx III-3
(1) or less than or equal to the length of phalanx III-3
140. Metacarpal I length to metacarpal II length ratio:

   (0) 0.5 or more
   (1) less than 0.5

   *Khann mckennai, Ingenia yanshini,* and *Conchoraptor gracilis* possess character state 0 in contrast to all other scored oviraptorosaurs.

   TWiG (character 149)

141. Proximal margin of metacarpal I in dorsal view:

   (0) straight, horizontal
   (1) angled due to the medial extent of the carpal trochlea

142. Metacarpal II relative to metacarpal III:

   (0) shorter
   (1) subequal
   (2) longer

143. Metacarpal II length to humerus length ratio:

   (0) 0.4 or less
   (1) more than 0.4

144. Metacarpal III:
(0) unmodified

(1) very slender

145. Lip or nubbin on the proximodorsal edge of the manual unguals:

(0) absent

(1) present

TWiG (character 153)

146. Manus length to humerus length plus radius length ratio:

(0) 0.50-0.65

(1) more than 0.65

(2) or less than 0.50

147. Manus length to humerus length ratio:

(0) more than 1.0

(1) 0.8 or less

EXCLUDED. This character is repetitive with the preceding character (character 146).

148. Manus length to femur length ratio:

(0) 0.3-0.6

(1) more than 0.7

(2) less than 0.2
149. Humerus length to femur length ratio:

(0) 0.5 to 0.6
(1) less than 0.4
(2) 0.7 or more

150. Dorsal margins of the opposite iliac blades:

(0) well separated from each other
(1) close to or contacting each other along their medial sections

151. Dorsal margin of the ilium along the central portion of the blade:

(0) straight
(1) arched

Among oviraptorosaurs only *Chirostenotes pergracilis*, *Nomingia gobiensis*, *Rinchenia mongoliensis*, and *Heyuannia huangia* possess a rounded dorsal margin of the ilium.

152. Preacetabular process relative to postacetabular process (the lengths measured from the center of the acetabulum):

(0) shorter or equal
(1) longer
Among oviraptorosaurs the more basal taxa *Caudipteryx zoui*, *Chirostenotes pergracilis*, *Nomingia gobiensis*, and *Similcaudipteryx yixianensis* have a preacetabular process that is longer than the postacetabular process of the ilium.

TWiG (character 155)

153. Preacetabular process:

(0) not expanded or weakly expanded ventrally below the level of the dorsal acetabular margin

(1) expanded ventrally well below the level of the dorsal acetabular margin

Makovicky and Sues (1998; character 75)

154. Ilium, cuppedicus fossa:

(0) deep, ventrally concave

(1) shallow or flat, with no lateral overhang

(2) absent

TWiG (character 164)

155. Cranioventral process on the preacetabular blade:

(0) absent

(1) rounded

(2) hooklike

TWiG (character 154)
156. Distal end of the postacetabular process:
   (0) truncated or broadly rounded
   (1) narrowed or acuminate
   TWiG (character 158)

157. Supracetabular crest:
   (0) well developed
   (1) reduced or absent
   TWiG (character 157)

158. Craniocaudal length of the pubic peduncle:
   (0) about as long as the ischiadic peduncle
   (1) distinctly longer than the ischiadic peduncle

159. Dorsoventral extension of the pubic peduncle:
   (0) level with the ischiadic peduncle
   (1) deeper than the ischiadic peduncle

160. Pubis orientation:
   (0) propubic
   (1) vertical
(2) opisthopubic (posteriorly oriented)

All oviraptorosaurs have a pubis that is vertically oriented, differing from the opisthopubic morphology of paravians, therizinosaurs, and alvarezsaurids.

TWiG (character 177)

161. Pelvic elements:
   (0) unfused
   (1) fused or partially fused

162. Brevis fossa:
   (0) absent or small
   (1) large

   TWiG (character 161)

163. Ilium, antitrochanter posterior to acetabulum:
   (0) absent/poorly developed
   (1) present and prominent

   TWiG (character 162)

164. Ilium length to femur length ratio:
   (0) 0.5 to 0.7
   (1) 0.8 or more
165. Hypocleidium on furcula:

(0) absent

(1) present

A distinct hypocleidium is present on the furcula of all oviraptorosaurs that could be scored except *Caudipteryx zoui*.

TWiG (character 132)

166. Pubic shaft:

(0) straight

(1) distal end curves anteriorly, anterior surface of shaft concave

(2) shaft curves posteriorly, anteriorly convex curvature

The pubic shaft of oviraptorids and *Microvenator celer* has an anterior margin that is concave. *Avimimus portentosus*, *Chirostenotes pergracilis*, and *Nomingia gobiensis* have an anterior margin of the pubic shaft that is straight. This character is more consistent with the one used by TWiG as opposed to that of Maryanska et al. (2002), Osmolska et al. (2004), Lu et al. (2004), and Lu (2005). Those analyses use only two character states, straight or concave anteriorly.

TWiG (character 180)

167. Pubic boot:

(0) projects anteriorly and posteriorly
(1) has little or no anterior process

(2) has no anterior or posterior projections

TWiG (character 178)

168. Pubic apron length:

(0) about half of pubic shaft length

(1) less than one-third of shaft length

TWiG (character 181)

169. Caudal margin of the ischiadic shaft:

(0) straight or almost straight

(1) strongly concave

170. Ischium, obturator process:

(0) absent

(1) proximal in position

(2) located near middle of ischiadic shaft

(3) located near distal end of ischium

TWiG (character 169)

171. Distal end of the ischium:

(0) not expanded
(1) expanded

TWiG (character 175)

172. Ischium length:

(0) more than two-thirds of pubis length
(1) two-thirds or less of pubis length

TWiG (character 173)

173. Posterior (greater) trochanter:

(0) weakly separated or not separated from the femoral head
(1) distinctly separated from the femoral head

174. Craniocaudal extend of the posterior trochanter of femur:

(0) short
(1) long

EXCLUDED. This character is ambiguous in its description of the morphology.

175. Sacral vertebrae, foramina or fossae:

(0) absent
(1) present on anterior sacrals only
(2) present on all sacrals

TWiG (character 113)
176. Femur, lesser trochanter and greater trochanter:

(0) separated by deep cleft
(1) separated by small groove
(2) completely fused (or absent) to form a trochanteric crest

*Citipati osmolskae* and *Gigantoraptor erlianensis* share the unique morphology of having a trochanteric crest (greater and lessert trochanter fused). Most other oviraptorosaurs have a small groove separating the greater and lesser trochanter including oviraptorids, *Nomingia gobiensis*, and *Caudipteryx zoui*, Only *Chirostenotes pergracilis* and *Microvenator celer* have femur with a deep cleft separating the greater and lessert trochanters.

Maryanska et al. (2002), Osmolska et al. (2004), Lu et al. (2004), and Lu (2005) use a slightly different form of this character. Their analyses have the states “well separated (0); contacting (1); or fused (2).” This analysis uses the character from the TWiG dataset, which is more descriptive concerning the morphology.

TWiG (character 184)

177. Dorsal extremity of the lesser trochanter of femur:

(0) well below the greater trochanter
(1) about level with the greater trochanter

178. Fourth trochanter of femur:
(0) well developed
(1) weakly developed or absent

TWiG (character 187)

179. Adductor fossa and associated craniomedial crest on the distal femur:

(0) weak or absent
(1) well developed

TWiG (character 189)

180. Strong distal projection of the fibular condyle on the femur:

(0) absent
(1) present

Avimimus portentosus, Nomingia gobiensis, Microvenator celer, and Gigantoraptor erlianensis lack a strong distal projection of the fibular condyle of the femur. All other oviraptorosaurs oviraptorids possess this character.

181. Number of cnemial crests on the tibia:

(0) one, cranial
(1) two, cranial and lateral

EXCLUDED. Describes the same morphology that is present in another character.

182. Medial surface of the fibular head:
(0) flat or shallowly concave
(1) with a deep fossa

**EXCLUDED.** Describes the same morphology that is present in another character.

183. Contact of the fibula with the tarsus:

(0) present
(1) absent

TWiG (character 191)

184. Ossified sternal plates:

(0) separate in adults
(1) fused

**EXCLUDED.** The character is a repeat of character 124.

185. Ascending process of the astragalus:

(0) as tall as wide across the base
(1) taller than wide

186. Sternum:

(0) without distinct lateral xiphoid process posterior to costal margin
(1) with lateral xiphoid process

TWiG (character 129)
187. Distal tarsals:

   (0) not fused with metatarsals
   (1) fused with metatarsals

   TWiG (character 199)

188. Proximal co-ossification of metatarsals II through IV:

   (0) absent
   (1) present

   TWiG (character 200)

189. MT III proximal shaft:

   (0) exposed prominently between MT II and MT IV along the entire metapodium
   (1) MT III proximal shaft constricted and much narrower than either II or IV, but still exposed along most of metapodium, subarctometatarsal
   (2) very pinched, not exposed along proximal section of metapodium, arctometatarsal
   (3) proximal part of MT III lost

   This character, taken from the TWiG matrix, is a modified version of the one used by Maryanska et al. (2002), Osmolska et al. (2004), Lu et al. (2004), and Lu (2005). Those analyses use the character “Arctometatarsus: absent (0); or present (1).”

   TWiG (character 203)
190. Metatarsals II and IV:

(0) not in contact on the plantar surface

(1) contacting distally

**EXCLUDED.** Repeat of arctometatarsal character.

191. Metatarsal I length:

(0) more than 50% of metatarsal II length

(1) less than 50% of metatarsal II length

(2) metatarsal absent

**EXCLUDED.** Not useful for coelurosaur relationships.

192. Metatarsal IV length relative to metatarsal II length:

(0) about equal

(1) longer

193. Epipterygoid:

(0) present

(1) absent

194. Tibia length to femur length ratio:

(0) less than 1

(1) more than 1
**EXCLUDED.** This character is state 1 in all examined coelurosaurs; therefore, providing no useful information for relationships within this group.

195. Metatarsus length to femur length ratio:

- (0) 0.4 to 0.6
- (1) about 0.3
- (2) 0.7 to 0.8

196. Dorsal vertebral count:

- (0) 13 to 14
- (1) 11 to 12
- (2) fewer than 11

197. Ossified uncinate processes:

- (0) absent
- (1) present

   TWiG (character 125)

198. Coracoid shape:

- (0) short
- (1) elongated with trapezoidal profile
- (2) strutlike
199. Proximal end of metacarpal III:
   (0) contacts the distal carpals
   (1) does not contact distal carpals

200. Metacarpals I and II:
   (0) fused proximally
   (1) not fused along their entire length

201. Ectopterygoid fossa:
   (0) absent
   (1) with constricted opening into fossa
   (2) with open ventral fossa into the main body of the element

   TWiG (character 59)

202. Palatal flange of pterygoid:
   (0) well developed
   (1) reduced in size or absent

   TWiG (character 61)

203. Symphyseal region of dentary:
   (0) broad and straight, paralleling lateral margin
(1) medially recurved slightly
(2) strongly recurved medially

TWiG (character 203)

204. Mandibular articulation surface:

(0) as long (anteroposteriorly) as distal end of quadrate
(1) twice or more as long as quadrate mandibular surface, allowing anteroposterior movement of the mandible

TWiG (character 79)

205. Maxillary teeth:

(0) present
(1) absent

TWiG (character 82)

206. Lower margin of the external nasal opening:

(0) below the level of the upper corner of the antorbital fenestra
(1) close to or above the level of the upper corner of the antorbital fenestra

EXCLUDED. The morphology described in this character is repetitive with character 20.

207. Quadratojugal and quadrate contact:

(0) far from the lateral surface of the mandibular articulation
(1) near the lateral surface of the mandibular articulation.

This character is describing where on the quadrate the quadratojugal articulates, whether it is near the mandibular surface or dorsal to this surface.

208. Nasals and premaxillae:

(0) do not form a crest

(1) form a crest

209. The top of the crest of skull lies:

(0) posterior to the anterior margin of premaxilla

(1) at the top of the anterior margin

(2) anterior to the vertical margin (crest strongly extends forwards as it does in IGM 100/42)

210. Shape of narial opening:

(0) rounded, circular

(1) angular, elongate

211. The maxillary fenestra:

(0) relatively smaller than the antorbital fenestra or absent

(1) larger than the antorbital fenestra
212. Large openings on the base of the neural arches of anterior caudal vertebrae:

(0) absent
(1) present

213. Large openings (fossae) on the neural arches of anterior cervical vertebrae:

(0) present
(1) absent

214. Constriction between articulated premaxillae and maxillae:

(0) absent
(1) present

215. Nasals, shape in dorsal view:

(0) parallel sided
(1) hourglass shaped, expanded posteriorly

216. Postorbital part of skull roof:

(0) as high as orbital region
(1) deflected ventrally in adult individuals

217. Number of pleurocoels in cervicals:

(0) absent
(1) two, arranged horizontally

(2) one

**EXCLUDED.** This character is a repetitive with character 99.

218. Cervical pleurocoels developed as:

(0) deep depressions

(1) foramina

219. Nasal fusion:

(0) absent, nasals separate

(1) present, nasal fused together

220. Length of the premaxilla on the palatal surface to the basal skull length (from premaxilla to occiptal condyle):

(0) 0.10 or less

(1) 0.15 or more

221. Maxilla length (in lateral view) to basal skull length ratio:

(0) 0.4 to 0.7

(1) about 0.3

222. Postorbital:
(0) T-shaped

(1) with distinct frontal process that is upturned ~90 degrees in lateral view

TWiG (character 4)

223. Nuchal transverse crest:

(0) pronounced

(1) not pronounced

224. Ratio of orbit length to antorbital fossa length:

(0) 0.7–0.9

(1) 0.6 or less

(2) 1.2 or more

225. Surangular foramen (rostral to mandibular articulation):

(0) absent

(1) present

TWiG (character 74)

226. Caudal vertebrae, regionalization:

(0) distinct transition point

(1) without transition point, vertebrae homogeneous in shape

TWiG (character 115)
227. Number of caudals with transverse processes:

   (0) 15 or more
   (1) less than 15

228. Neural spines confined to:

   (0) 23 proximal caudals or more
   (1) at most 17 proximal caudals

229. Crenulate margin on buccal edge of premaxilla:

   (0) absent
   (1) present

230. First premaxillary tooth size compared with crowns of premaxillary teeth 2 and 3:

   (0) slightly smaller or same in size
   (1) much smaller
   (2) much larger

231. Jugal process of maxilla ventral to external antorbital fenestra:

   (0) dorsoventrally shallow
   (1) dorsoventrally deep
232. Jugal participation in margin of antorbital fenestra:

(0) absent

(1) present, narrowly contributes

233. Vomer:

(0) fused along entire length

(1) fused only at anteriormost extent

234. Paroccipital process:

(0) elongate and slender, with dorsal and ventral edges nearly parallel

(1) process short, deep with convex distal end

TWiG (character 56)

235. Lateral border of the quadrate shaft:

(0) straight

(1) with lateral tab that touches squamosal and quadratojugal above an enlarged quadrate foramen

TWiG (character 53)

236. Prootic, accessory tympanic recess dorsal to crista interfenestralis:

(0) absent

(1) present as dorsally open fossa on prootic-opisthotic
(2) present as deep, posterodorsally directed concavity

TWiG (character 16)

237. Tertiary antorbital fenestra (fenestra promaxillaris):

(0) absent

(1) present

TWiG (character 29)

238. In lateral view, dorsal border of antorbital fenestra formed by:

(0) maxilla and/or lacrimal

(1) lacrimal and nasal

(2) premaxilla, maxilla, and lacrimal

239. Supratemporal fossa:

(0) limited extension onto dorsal surfaces of frontal and postorbital

(1) covers most of frontal process of the postorbital and extends anteriorly onto dorsal surface of frontal

TWiG (character 245)

240. Cervical vertebrae, carotid processes:

(0) absent

(1) on posterior cervicals
(2) throughout most of the cervical series

TWiG (character 97)

241. Neural spines on distal caudals:

(0) form a low ridge
(1) spine absent
(2) midline sulcus in center of neural arch

TWiG (character 119)

242. Humerus, anterior surface of deltopectoral crest:

(0) smooth
(1) with distinct groove or ridge near lateral edge along the distal end of crest

TWiG (character 141)

243. Ilium, orientation of the postacetabular blades in dorsal view:

(0) parallel
(1) diverge posteriorly

TWiG (character 159)

244. Shelf on pubic shaft proximal to symphysis (‘pubic apron’):

(0) extends medially from middle of cylindrical pubis shaft
(1) shelf extends medially from anterior edge of anteroposteriorly-flattened shaft
245. Ischium, lateral face of ischiadic blade:
   (0) flat (or round in rodlike ischia)
   (1) laterally concave
   (2) with longitudinal ridge subdividing lateral surface into anterior (including obturator
      process) and posterior parts (2).

246. Distal ends of ischium:
   (0) form symphysis
   (1) approach one another but do not form symphysis
   (2) widely separated

247. Scars for interspinous ligaments:
   (0) terminate at apex of neural spine in dorsal vertebrae
   (1) terminate below apex of neural spine

248. Ungual and penultimate phalanx of pedal digit II:
   (0) similar to those of III
(1) penultimate phalanx highly modified for extreme hyperextension, ungual recurved and significantly larger than that of digit III

TWiG (character 204)

249. Ascending (nasal) process of the premaxilla with palate held horizontally:

(0) vertical

(1) sloping posteriorly

This is a newly described character and varies among oviraptorosaurs. *Rinchenia mongoliensis*, IGM 100/42, *Conchoraptor gracilis*, *Nemegtia barsboldi*, and *Citipati osmolskae* have a vertically oriented nasal process.

250. Ridges and troughs on palatal surface of premaxilla and maxilla:

(0) absent

(1) present

This character was incorporated into character 12 of Maryanska et al. (2002); however, the palatal teeth and the ridges and troughs of the palatal surface are not necessarily correlated. The teeth are present in *Chirostenotes pergracilis* but the ridges are not.

251. Morphology of premaxillary teeth:

(0) recurved

(1) peg-like

(2) spatulate
*Incisivosaurus gauthieri* possess two different morphologies of premaxillary teeth, the anterior teeth being spatulate and those more lateral teeth being more peg like.

252. Accessory fossa on the lateral surface of the ascending ramus of premaxilla anterior to naris:

(0) present

(1) absent

This is a newly described character first described by Clark et al. (2002). In oviraptorids, a fossa is present on the ascending ramus of the premaxilla. Not present in other coelurosaurs, *Ingenia yanshini*, and *Incisivosaurus gauthieri*, *Caudipteryx zoui*, and *Avimimus portentosus*.

253. Frontal contact with parietal:

(0) sinuous

(1) angular

(2) straight

This is a newly described character. The contact with the suture in oviraptorosaurs has one of two morphologies. This contact can either be sinuous, with a saddle shape outline or can slant posteriorly (with the midline being most anteriorly placed). *Avimimus portentosus*, *Conchoraptor gracilis*, *Nemegtia barsboldi*, *Khaan mckennai*, and ZPAL MgD-I/106 all possess a sinuous contact. *Citipati osmolskae* has an angled contact, and *Incisivosaurus gauthieri* has a straight contact. Coelurosaurs outside of Oviraptorosauria also have a straight, transverse contact.
254. Pneumatic recesses on the anterior margin of the frontals:

(0) present and invade frontals

(1) absent, no pneumatic recesses

This is a newly described character. The facial region of oviraptorosaurs is highly pneumatic and this pneumaticity extends onto the frontal in all taxa except *Incisivosaurus gauthieri*, *Caudipteryx zoui*, and *Avimimus portentosus*. No other coelurosaurians have pneumatic foramina in the frontal.

255. Postorbital process of jugal:

(0) angled vertically

(1) posterodorsally angled

(2) absent

256. Slope of the occiput:

(0) vertical

(1) distinctly slanted anteroventrally

This is a newly added character that was first discussed by Clark et al. (2002). *Citipati osmolskae* and IGM 100/42 both have an anteroventrally slanted occipital surface of the skull that approaches 45 degrees.

257. Lateral flange comprised of pterygoid, quadrate (optic wing) and epipterygoid:
(0) covering lateral wall of braincase
(1) not developed, lateral wall visible

This is a newly added character. In all oviraptorosaurs, including the basal taxon *Incisivosaurus gauthieri*, the lateral surface of the braincase is obscured by a large flange that is comprised of the optic process of the quadrate, the quadrate process of the pterygoid, and the epipterygoid.

258. Articular surface for the pterygoid (on quadrate):

(0) extends to the articular surface of the medial mandibular condyle
(1) does not reach mandibular condyle, dorsal

This is a newly added character. The articulation for the pterygoid on the quadrate is located at the mandibular articulation in all oviraptorosaurs except *Incisivosaurus gauthieri*. In that taxon and in coelurosaurs outside of Oviraptorosauria the articulation point for the pterygoid on the quadrate lies anterior to the mandibular articulation surface.

259. Quadrate:

(0) wide mandibular process (width constituting 50-60% of the height of the quadrate)
(1) narrow mandibular process (width constituting approximately 40% of the height of the quadrate)

260. Squamosal:

(0) broadly overlaps optic wing of quadrate, forming an immovable joint
(1) not overlapping, freely movable quadrate

This is a newly described character. The squamosal in oviraptorids overlaps the quadrate covering the majority of the optic wing and forming an immovable joint. A freely movable squamosal is present in coelurosaurs outside of Oviraptorosauria, *Incisivosaurus gauthieri*, and *Avimimus portentosus*. The state cannot be determined in *Caudipteryx zoui*.

261. Orientation of the antorbital fenestra:

(0) horizontally elongate

(1) vertically elongate

(2) subequal

This character is newly described. All oviraptorids that could be scored have a vertically elongate antorbital fenestra except *Nemegtia barsboldi*. *Caudipteryx zoui* and *Chirostenotes pergracilis* have a horizontally elongate antorbital fenestra.

262. External narial opening:

(0) same or smaller than antorbital fenestra

(1) larger than the antorbital fenestra

This a newly described character. *Confuciusornis sanctus*, crown birds, and oviraptorids have an external narial opening that is larger than the antorbital fenestra. Within oviraptorosaurs only *Incisivosaurus gauthieri* and *Caudipteryx zoui* have an external narial opening smaller than the antorbital fenestra.
263. Sacral centra:

(0) subequal in width

(1) centrum width decreasing posteriorly

Makovicky and Sues (1998)

264. Parietal:

(0) extends ventrally onto the lateral surface of the braincase to make up all of the medial wall of the supratemporal fossa

(1) the ventral extension of the parietal laterally is short and the medial wall of the supratemporal fossa is formed by the parietal and laterosphenoid

This is a newly described character. The parietal in IGM 100/42, Citipati osmolskae, and Khaan mckennai does not extend far ventrally into the supratemporal fossa, but instead the lateral wall of the supratemporal fossa is formed by the parietal and the laterosphenoid.

265. Accessory openings on the anterior surface of the premaxilla:

(0) absent

(1) present

In crested forms of oviraptorid there is variation in the presence or absence of accessory openings on the anterior surface of the premaxillae. Citipati osmolskae and IGM 100/42 both have these openings.
266. Number of denticles on the triturating surface of the premaxilla:

(0) two
(1) three
(2) four
(3) five
(4) absent

This is a newly described character. All oviraptororosaurs have a crenulate margin on the premaxilla. Variation exists in the number of denticles that are present. *Incisivosaurus gauthieri*, *Caudipteryx zoui*, *Avimimus portentosus* and GIN 100/42 all have four denticles. *Conchoraptor gracilis*, *Citipati osmolskae*, and *Khaan mckennai* have five denticles. *Rinchenia mongoliensis* and *Nemegtia barsboldi* have two large undulations on the triturating surface of the premaxilla.

267. Trigeminal fenestra:

(0) branched, at least two openings present
(1) single
(2) branches within laterosphenoid, pinched

This character is newly described. Therizinosaurs, *Incisivosaurus gauthieri*, and *Chirostenotes pergracilis* all have an incipient split in the trigeminal fenestra.

268. Configuration of palatal “teeth” formed by the maxilla and vomer:
(0) along the midline, one large palatal “tooth”

(1) more laterally placed, two distinct processes

This is a newly described character. Oviraptorids and Chirostenotes pergracilis possess palatal teeth. *Ingenia yanshini* and *Khaan mckennai* both have more laterally placed palatal teeth on the maxillae rather than being situated near the midline.

269. Ungual phalanx of manual digit I:

(0) possesses an upturned proximodorsal lip

(1) upturned lip is absent

270. Ascending process of the astragalus:

(0) pinched at the base so that it is narrower than the trochlear process

(1) not pinched at the base, same width as the trochlear process

This is a newly described character. *Ingenia yanshini*, *Citipati osmolskae*, *Khaan mckennai*, and *Gigantoraptor erlianensis* all have an astragalus that is pinched at the base of the ascending process so that it is not confluent with the trochlear surface.

271. Anterior cervical vertebrae in dorsal view:

(0) have a distinctly rectangular shape, web of bone spreading between the zygapophyses

(1) regions between the zygapophyses are excavated, creating a x-shape in dorsal view

This is a newly described character. The anterior cervical vertebrae in *Citipati osmolskae* and *Gigantoraptor erlianensis* have a derived morphology in which the regions between
the zygapophyses are highly excavated (and x-shaped) and have a morphology that is similar to the more posterior cervical vertebrae.

272. Accessory antorbital fenestrae on floor of antorbital fossa:

(0) absent

(1) present

This is a newly described character. *Citipati osmolskae*, *Khaan mckennai*, and ZPAL MgD-I/106 all have at least one fenestra on the floor of the antorbital fossa.

273. Orbitosphenoid:

(0) not ossified in adult

(1) ossified in adult

This is a newly described character. An ossified orbitosphenoid is present in all oviraptorosaurs for which this region of the skull is visible. CT scans confirm that an orbitosphenoid also is present in *Khaan mckennai*.

274. Vaned feathers on forelimb:

(0) symmetric

(1) asymmetric

TWiG (character 1)

275. Anterior process of postorbital:
(0) projects into orbit

(1) does not project into orbit

TWiG (character 3)

276. Crista interfenestralis:

(0) confluent with lateral surface of prootic and opisthotic

(1) distinctly depressed within middle ear opening

TWiG (character 7)

277. Subotic recess (pneumatic fossa ventral to fenestra ovalis):

(0) absent

(1) present

TWiG (character 8)

278. Posterior opening of basisphenoid recess:

(0) single

(1) divided into two small, circular foramina by a thin bar of bone

TWiG (character 10)

279. Base of cultriform process:

(0) not highly pneumatized
(1) base of cultriform process (parasphenoid rostrum) expanded and pneumatic
(parasphenoid bulla present)

TWiG (character 11)

280. Basipterygoid processes:

(0) ventral or anteroventrally projecting
(1) lateroventrally projecting

TWiG (character 12)

281. Basipterygoid processes:

(0) solid
(1) hollow

TWiG (character 14)

282. Basipterygoid recesses on dorsolateral surfaces of basipterygoid processes:

(0) absent
(1) present

TWiG (character 15)

283. Caudal (posterior) tympanic recess:

(0) absent
(1) present as opening on anterior surface of paroccipital process
(2) extends into opisthotic posterodorsal to fenestra ovalis, confluent with this fenestra

TWiG (character 18)

284. Exits of C. N. X-XII:

(0) flush with surface of exoccipital

(1) cranial nerve exits located together in a bowl-like depression

TWiG (character 19)

285. Premaxilla internarial bar:

(0) rounded

(1) flat

TWiG (character 21)

286. Accessory antorbital fossa:

(0) situated at rostral border of antorbital fossa

(1) situated posterior to rostral border of fossa

TWiG (character 29)

287. Medial jugal foramen:

(0) present on medial surface ventral to postorbital bar

(1) absent

TWiG (character 34)
288. Quadratojugal:

(0) without horizontal process posterior to ascending process (reversed “L” shape)

(1) with process (i.e., inverted ‘T’ or ‘Y’ shape)

TWiG (character 35)

289. Supraorbital crests on lacrimal in adult individuals:

(0) absent

(1) dorsal crest above orbit

(2) lateral expansion anterior and dorsal to orbit

TWiG (character 37)

290. Lacrimal:

(0) anterodorsal process absent (inverted ‘L’ shaped)

(1) lacrimal ‘T’ shaped in lateral view

(2) anterodorsal process much longer than posterior process

TWiG (character 39)

291. Frontals:

(0) narrow anteriorly as a wedge between nasals

(1) end abruptly anteriorly, suture with nasal transversely oriented

TWiG (character 41)
292. Anterior emargination of supratemporal fossa on frontal:

(0) straight or slightly curved
(1) strongly sinusoidal and reaching onto postorbital process

Currie (1995)
TWiG (character 42)

293. Frontal postorbital process (dorsal view):

(0) smooth transition from orbital margin
(1) sharply demarcated from orbital margin

Currie (1995)
TWiG (character 43)

294. Frontal edge:

(0) smooth in region of lacrimal suture
(1) edge notched

Currie (1995)
TWiG (character 44)

295. Descending process of squamosal:

(0) parallels quadrate shaft
(1) nearly perpendicular to quadrate shaft
296. Posterolateral shelf on squamosal overhanging quadrate head:

   (0) absent
   (1) present

   Currie (1995)

TWiG (character 49)

297. Dorsal recess on ectopterygoid:

   (0) absent
   (1) present

   Currie (1995)

TWiG (character 60)

298. Palatine and ectopterygoid:

   (0) separated by pterygoid
   (1) contact

   Currie (1995)

TWiG (character 62)

299. Labial face of dentary:

   (0) flat
   (1) with lateral ridge and inset tooth row
Russell and Dong (1993)

TWiG (character 69)

300. Dentary:

(0) subtriangular in lateral view

(1) with subparallel dorsal and ventral edges

Currie (1995)

TWiG (character 70)

301. Nutrient foramina on external surface of dentary:

(0) superficial

(1) lie within deep groove

Currie (1987)

TWiG (character 71)

302. Internal mandibular fenestra:

(0) small and slit-like

(1) large and rounded

Currie (1995)

TWiG (character 73)

303. Splenial:
(0) not widely exposed on lateral surface of mandible
(1) exposed as a broad triangle between dentary and angular on lateral surface of mandible

TWiG (character 75)

304. Articular:

(0) without elongate, slender medial, posteromedial, or mediiodorsal process from retroarticular process
(1) with process

TWiG (character 77)

305. Second premaxillary tooth:

(0) approximately equivalent in size to other premaxillary teeth
(1) second tooth markedly larger than third and fourth premaxillary teeth

Currie (1995)

TWiG (character 81)

306. Maxillary and dentary teeth:

(0) serrated
(1) some without serrations anteriorly
(2) all without serrations

TWiG (character 83)
307. Dentary and maxillary teeth:

(0) large

(1) small (25-30 in dentary)

TWiG (character 84)

308. Dentary teeth:

(0) in separate alveoli

(1) set in open groove

Currie (1987)

TWiG (character 85)

309. Serration denticles:

(0) large

(1) small

TWiG (character 86)

310. Serrations:

(0) simple, denticles convex

(1) distal and often mesial edges of teeth with large, hooked denticles that point toward the tip of the crown

TWiG (character 87)
311. Teeth:

(0) constricted between root and crown

(1) root and crown confluent

TWiG (character 88)

312. Dentary teeth:

(0) evenly spaced

(1) anterior dentary teeth smaller, more numerous, and more closely appressed than those in middle of tooth row

TWiG (character 89)

313. Dentaries:

(0) lack distinct interdental plates

(1) with interdental plates medially between teeth

TWiG (character 90)

314. In cross section, premaxillary tooth crowns:

(0) sub-oval to sub-circular

(1) asymmetrical (D-shaped in cross section) with flat lingual surface

TWiG (character 91)
315. Axial epipophyses:
   (0) absent or poorly developed, not extending past posterior rim of postzygopophyses
   (1) large and posteriorly directed, extend beyond postzygapophyses
   TWiG (character 93)

316. Axial neural spine:
   (0) flared transversely
   (1) compressed mediolaterally
   TWiG (character 94)

317. Epipophyses of cervical vertebrae:
   (0) placed distally on postzygapophyses, above postzygopophyseal facets
   (1) placed proximally, proximal to postzygapophyseal facets
   TWiG (character 95)

318. Cervical and anterior trunk vertebrae:
   (0) amphiplatyan
   (1) opisthocoelous
   (2) heterocoelous
   TWiG (character 101)

319. Parapophyses of posterior trunk vertebrae:
(0) flush with neural arch
(1) distinctly projected on pedicels

(Norell and Makovicky, 1999)

TWiG (character 103)

320. Zygapophyses of trunk vertebrae:

(0) abutting one another above neural canal, opposite hyposphenes meet to form lamina
(1) zygapophyses placed lateral to neural canal and separated by groove for interspinuous ligaments, hyposphenes separated

TWiG (character 327)

321. Vertebral pneumaticity:

(0) cervical vertebrae but not dorsal vertebrae pneumatic
(1) all presacral vertebrae pneumatic

TWiG (character 106)

322. Transverse processes of anterior dorsal vertebrae:

(0) long and thin
(1) short, wide, and only slightly inclined

TWiG (character 107)
323. Neural spines of dorsal vertebrae:

(0) not expanded distally

(1) expanded to form ‘spine table’

TWiG (character 108)

324. Sacral vertebrae:

(0) with unfused zygapophyses

(1) with fused zygapophyses forming a sinuous ridge in dorsal view

TWiG (character 111)

325. Ventral surface of posterior sacral centra:

(0) gently rounded, convex

(1) ventrally flattened, sometimes with shallow sulcus

(2) centrum strongly constricted transversely, ventral surface keeled

TWiG (character 112)

326. Last sacral centrum:

(0) with flat posterior articulation surface

(1) convex articulation surface

TWiG (character 114)

327. Transition point in caudal series begins:
(0) distal to the 10th caudal
(1) between the 7th and 10th caudal vertebra
(2) proximal to the 7th caudal vertebra
TWiG (character 116)

328. Anterior caudal centra:

(0) tall, oval in cross section
(1) with box-like centra in caudals I-V
(2) anterior caudal centra laterally compressed with ventral keel
Modified from (Gauthier, 1986)
TWiG (character 117)

329. Neural spines of caudal vertebrae:

(0) simple, undivided
(1) separated into anterior and posterior alae throughout much of caudal sequence
(Russell and Dong, 1993)
TWiG (character 119)

330. Proximal end of chevrons of proximal:

(0) caudals short anteroposteriorly, shaft cylindrical
(1) proximal end elongate anteroposteriorly, flattened and plate-like
TWiG (character 122)
331. Distal caudal chevrons:
   (0) simple
   (1) anteriorly bifurcate
   (2) bifurcate at both ends
   TWiG (character 123)

332. Ossified ventral (sternal) rib segments:
   (0) absent
   (1) present
   TWiG (character 125)

333. Lateral gastral segment:
   (0) shorter than medial one in each arch
   (1) distal segment longer than proximal segment
   TWiG (character 127)

334. Anterior edge of sternum:
   (0) grooved for reception of coracoids
   (1) sternum without grooves
   TWiG (character 130)
335. Articular facet of coracoid on sternum (conditions may be determined by the articular facet on coracoid in taxa without ossified sternum):

(0) anterolateral or more lateral than anterior
(1) almost anterior

Xu et al. (1999)

TWiG (character 131)

336. Acromion margin of scapula:

(0) continuous with blade
(1) anterior edge laterally everted

TWiG (character 133)

337. Posterolateral surface of coracoid ventral to glenoid fossa:

(0) unexpanded
(1) posterolateral edge of coracoid expanded to form triangular subglenoid fossa bounded laterally by enlarged coracoid tuber

TWiG (character 134)

338. Ulna, olecranon process:

(0) weakly developed
(1) distinct and large

TWiG (character 142)
339. Distal articular surface of ulna:

(0) flat
(1) convex, semilunate surface

TWiG (character 143)

340. Proximal surface of ulna:

(0) single continuous articular facet
(1) divided into two distinct fossae (one convex, the other concave) separated by a median ridge

TWiG (character 144)

341. Lateral proximal carpal (ulnare?):

(0) quadrangular
(1) triangular in proximal view

TWiG (character 145)

342. Distal carpals:

(0) two distal carpals in contact with metacarpals, one covering the base of metacarpal I (and perhaps contacting metacarpal II) the other covering the base of metacarpal II
(1) a single distal carpal capping metacarpals I and II

TWiG (character 146)
343. Distal carpals:

(0) not fused to metacarpals

(1) fused to metacarpals, forming carpometacarpus

TWiG (character 147)

344. Third manual digit:

(0) present, phalanges present

(1) reduced to no more than metacarpal splint

TWiG (character 150)

345. Manual unguals:

(0) strongly curved, with large flexor tubercles

(1) weakly curved with weak flexor tubercles displaced distally from articular end

(2) straight with weak flexor tubercles displaced distally from articular end

(3) absent

TWiG (character 151)

346. Unguals on all digits:

(0) generally similar in size

(1) digit I bearing large ungual and unguals of other digits distinctly smaller

TWiG (character 152)
347. Tuber along dorsal edge of ilium, dorsal or slightly posterior to acetabulum:

(0) absent
(1) present

TWiG (character 160)

348. Ridge bounding cuppedicus fossa:

(0) terminates rostral to acetabulum or curves ventrally onto anterior end of pubic peduncle
(1) rim extends far posteriorly and is confluent or almost confluent with acetabular rim

TWiG (character 163)

349. Posterior edge of ischium:

(0) straight
(1) with proximal median posterior process

TWiG (character 165)

350. Ischiadic shaft:

(0) straight
(1) ventrodistally curved anteriorly
(2) hooked posteriorly

TWiG (character 167)
351. Ischium, obturator process:
   (0) does not contact pubis
   (1) contacts pubis
   TWiG (character 170)

352. Obturator notch:
   (0) present
   (1) notch or foramen absent
   TWiG (character 171)

353. Semicircular scar on posterior part of the proximal end of the ischium:
   (0) absent
   (1) present
   TWiG (character 172)

354. Tubercle on anterior edge of ischium:
   (0) absent
   (1) present
   TWiG (character 176)

355. Contact between pubic apron:
(0) contributions of both pubes meet extensively
(1) contact disrupted by a slit
(2) no contact

Makovicky et al. (2005)
TWiG (character 182)

356. Femoral head:

(0) without fovea capitalis (for attachment of capital ligament)
(1) circular fovea present in center of medial surface of head

TWiG (character 183)

357. Lesser trochanter of femur:

(0) absent, indistinct
(1) present as a trochanteric shelf or spike
(2) alariform
(3) cylindrical in cross section

TWiG (character 185)

358. Femur, lateral ridge:

(0) absent or represented only by faint rugosity
(1) distinctly raised from shaft, moundlike

TWiG (character 186)
359. Femur, accessory trochanteric crest distal to lesser trochanter:

(0) absent
(1) present

TWiG (character 188)

360. Popliteal fossa between end of femur:

(0) open distally
(1) closed off distally by contact between distal condyles

TWiG (character 190)

361. Deep oval fossa on medial surface of fibula near proximal end:

(0) absent
(1) present

TWiG (character 193)

362. Distal end of astragalus and calcaneum:

(0) with condyles separated by shallow, indefinite sulcus
(1) with distinct condyles separated by prominent tendon groove on anterior surface

TWiG (character 194)

363. Medial cnemial crest:
364. Ascending process of the astragalus:

(0) tall and broad, covering most of anterior surface of distal end of tibia

(1) process short and slender, covering only lateral half of anterior surface of tibia

(2) ascending process tall, but with medial notch that restricts it to lateral side of anterior face of distal tibia

TWiG (character 196)

365. Ascending process of astragalus:

(0) confluent with condylar portion

(1) separated by transverse groove or fossa across base

TWiG (character 197)

366. Astragalus and calcaneum:

(0) separate from tibia

(1) fused to each other and to the tibia in late ontogeny

TWiG (character 198)

367. Distal end of metatarsal II:
(0) smooth, not ginglymoid
(1) with developed ginglymus

TWiG (character 201)

368. Distal end of metatarsal III:
(0) smooth, not ginglymoid
(1) with developed ginglymus

TWiG (character 202)

369. Ungual and penultimate phalanx of pedal digit II:
(0) similar to those of III
(1) penultimate phalanx highly modified for extreme hyper-extension, ungual more strongly curved and significantly larger than that of digit III

TWiG (character 204)

370. Metatarsal I:
(0) articulates with the middle of the medial surface of metatarsal II
(1) metatarsal I attaches to posterior surface of distal quarter of metatarsal II
(2) metatarsal I articulates to medial surface of metatarsal II near its proximal end
(3) metatarsal I absent

TWiG (character 205)
371. Metatarsal I:

(0) attenuates proximally, without proximal articulating surface

(1) proximal end of metatarsal I similar to that of metatarsals II-IV

TWiG (character 206)

372. Shaft of MT IV:

(0) round or thicker dorsoventrally than wide in cross section

(1) shaft of MT IV mediolaterally widened and flat in cross section

TWiG (character 207)

373. Foot:

(0) symmetrical

(1) asymmetrical with slender MTII and very robust MT IV, excluding flange

TWiG (character 208)

374. Neural spines on posterior dorsal vertebrae in lateral view:

(0) rectangular or square

(1) anteroposteriorly expanded distally, fan-shaped

TWiG (character 209)

375. Shaft diameter of phalanx I-1 relative to diameter of radius:

(0) less than shaft diameter of radius
(1) greater than shaft diameter of radius

TWiG (character 210)

376. Angular:

(0) exposed almost to end of mandible in lateral view, reaches or almost reaches articular
(1) excluded from posterior end angular suture turns ventrally and meets ventral border of
mandible rostral to glenoid

TWiG (character 211)

377. Distal articular ends of metacarpals I + II:

(0) ginglymoid
(1) rounded, smooth

TWiG (character 213)

378. Radius and ulna:

(0) well separated
(1) with distinct adherence or syndesmosis distally

TWiG (character 214)

379. Jaws occlude:

(0) for their full length
(1) diverge rostrally due to kink and downward deflection in dentary buccal margin
380. Quadrat head:

(0) covered by squamosal in lateral view

(1) quadrat cotyle of squamosal open laterally exposing quadrat head

TWiG (character 216)

381. Vertical ridge on lesser trochanter:

(0) present

(1) absent

TWiG (character 218)

382. Supratemporal fenestra:

(0) bounded laterally and posteriorly by the squamosal

(1) supratemporal fenestra extended as a fossa on to the dorsal surface of the squamosal

TWiG (character 219)

383. Posterior edge of coracoid:

(0) not or only shallowly indented below glenoid

(1) posterior edge of coracoid deeply notched just ventral to glenoid, glenoid lip everted

TWiG (character 221)
384. Retroarticular process:

(0) points caudally

(1) curves gently dorsocaudally

TWiG (character 222)

385. Flange on supraglenoid buttress on scapula:

(0) absent

(1) present

Nicholls and Russell (1985)

TWiG (character 223)

386. Depression (possibly pneumatic) on ventral surface of postorbital process of laterosphenoid:

(0) absent

(1) present

Makovicky et al. (2003)

TWiG (character 224)

387. Dorsal edge of postacetabular blade:

(0) convex or straight

(1) concave, brevis shelf extending caudal to vertical face of ilium giving ilium a dorsally concave outline in lateral view

Novas (2004)
388. Postacetabular end of ilium:

(0) terminating in rounded or square end in dorsal view

(1) with lobate brevis shelf projecting from end of ilium and beyond end of postacetabular lamina

Character added by Makovicky et al. (2005)

TWiG (character 227)

389. Flexor heel on phalanx II-2:

(0) small and asymmetrically developed only on medial side of vertical ridge subdividing proximal articulation

(1) heel long and lobate, with extension of midline ridge extending onto its dorsal surface

Character added by Makovicky et al., 2005.

TWiG (character 228)

390. Large, longitudinal flange along caudal or lateral face of metatarsal IV:

(0) absent

(1) present

Modified from Novas and Pol (2005)

TWiG (character 229)
391. Proximodorsal process of ischium:

(0) small, tab-like or pointed process along caudal edge of ischium

(1) process large proximodorsally hooked and separated from iliac peduncle of the ischium by a notch (Chiappe et al., 1999)

Character added by Makovicky et al. (2005)

TWiG (character 230)

392. Lateral face of pubic shaft:

(0) smooth

(1) with prominent lateral tubercle about halfway down the shaft

Senter et al. (2004)

TWiG (character 231)

393. Distally placed dorsal process along caudal edge of ischidiac shaft:

(0) absent

(1) present

Forster et al. (1998)

TWiG (character 232)

394. Obturator process:

(0) square (i.e. with distinct caudal edge or notch)

(1) triangular with caudal end confluent with shaft
TWiG (character 233)

395. Triangular obturator process:

(0) with short rostral projection and wide base along ischial shaft

(1) with short base, long process extending rostrally

TWiG (character 234)

396. Tuber along extensor surface of MT II:

(0) absent

(1) present

Chiappe (2002)

TWiG (character 235)

397. Ulna/Femur length ratio:

(0) significantly less than one

(1) equal or greater than one

TWiG (character 236)

398. Dorsal displacement of accessory (maxillary) fenestra:

(0) absent

(1) present

TWiG (character 237); Turner et al., (2007)
399. Jugal process of maxilla ventral to the external antorbital fenestra:

(0) dorsoventrally narrow

(1) dorsoventrally wide

TWiG (character 238); Turner et al. (2007)

400. Accessory antorbital (maxillary) fenestra recessed within a shallow, caudally or caudodorsally open fossa, which is itself located within the maxillary antorbital fossa:

(0) absent

(1) present

TWiG (character 239); Turner et al. (2007)

401. Nasal process of maxilla, dorsal ramus (ascending ramus of maxilla):

(0) prominent, exposed medially and laterally

(1) absent or reduced to slight medial, and no lateral exposure

TWiG (character 240); Turner et al. (2007)

402. In lateral view, participation of the ventral ramus of the nasal process of the maxilla in the anterior margin of the internal antorbital fenestra:

(0) present, extensively

(1) small dorsal projection of the maxilla participates in the anterior margin

(2) no dorsal projection of the maxilla participates in the anterior margin
403. In lateral view, dorsal border of the internal antorbital fenestra:

(0) formed by lacrimal and maxilla
(1) by lacrimal and nasal

TWiG (character 242); Turner et al. (2007)

404. In lateral view, lateral lamina of the ventral ramus of nasal process of maxilla:

(0) present, large broad exposure
(1) present, reduced to small triangular exposure
(2) no dorsal projection of maxilla participates in the anterior margin

TWiG (character 244)

405. Jugal:

(0) does not particulate in margin of antorbital fenestra
(1) participates in antorbital fenestra

TWiG (character 246)

406. Anterior and posterior denticles of teeth:

(0) not significantly different in size
(1) anterior denticles, when present, significantly smaller than posterior denticles

TWiG (character 247)
407. Maxillary teeth:

(0) almost perpendicular to jaw margin
(1) inclined strongly posterodorsally

TWiG (character 248)

408. Maxillary tooth height:

(0) highly variable with gaps evident for replacement
(1) almost isodont with no replacement gaps

TWiG (character 248)

409. Splenial forms notched anterior margin of internal mandibular fenestra:

(0) absent
(1) present

TWiG (character 250)
507

Appendix 4. Data matrix.
Allosaurus fragilis
00100[01]00000010101[01]000100100[01]1100000200000001000000000000000000001
[01]0000100000000000[01]110000000000000200[01]1100103000000000001[01]00101002012
0002101020001001000000000[01]0[01]1[01][01]000[01]011000000010[01]10?0?0000100000?
00021000000-0101000110000001[01]000001[01]100011[01]00000000001001210?01111??000?
??????????1?0000010100111010??000000010010000001010101001000000000010001??00000
00?000000000000100010000100000000000000001000000000?0?000?00010000000000
Tyrannosaurus rex
00120[01]001000[01]0100000011110010100000200010001020[01]00000100000000011100[01]
01000000000001010000000000000200011001030?100000000101010101100000001-00201001
1[01]000001110001010000000[01]001001210?01111??00000-0-10101?0?01000121000010001
01000?00101101000010101110000010000000?00?1??00000???1000000001101?1010?0001000
0000000100000000000000?0?00100001000001000?
Struthiomimus altus
??0?0?0?10?0?0?0??0?0101??0?11100002110??1?00??0?01?00???????????????0?10000000000
00000000000?1-20210?1?01??3???110?1000101?00202100000100100100001[01]2??0??10010
0000010000?0-???11?1?01????0??-?-1110??1?10????1011100000000010?10000100??????????
01?0000000100000001??0100000?0100000100101000101000100003?0000111111101111000?0
?00100000000001????
Garudimimus brevipes
000100001010001000000011[01]000111000021001002000[01]0100000010000000?1??010020
110000000001000000002[01][01][02]021010001003111?00010??101???????0????????????????
??10??01001000110?000????0000001101001?002021?10?????2010[01]000-0111011011000010
00??0-01?00110000??100?0010-12111011010?20000-?-?1?00?1??0111????0?000?00?00?0?1?0
?0?0?????????????????0?????????????????????????0????????1????0??????00000?0??01??1?1?
??1?000?0?0??00010000000????
Huaxiagnathus orientalis
?000??00?????0100000?0????0?????0?1????????0??????0????????????????????000???22?????
10-???????0?00??000?00??????0?????0???1?00?00??1??0101?001110???2?10000011010??100
1?0100???0??????0?1?000??0??000000??0?0??0-100??1???0???????0110?01?????????????00?
01????11????????????0-??11?0??1?????????0???0?0?????????010????010?1010?0??0?????0???
0??1010??0000??010000000000?0???????0?010000?0?011??000????0?0?00?0?0010?0000000?
1?00?


Archaeopteryx lithographica

Apsaravis ukhaana
???????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
Caudipteryx zoui

Chirostenotes pergracilis
?????1????0?1000???????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????????
Conchoraptor gracilis

Ingenia yanshini

Heyuannia huangi

Nemegtia barsboldi

Citipati osmolskae
Incisivosaurus gauthieri

Oviraptor philoceratops

Khaan mckennai

Gigantoraptor erlianensis

Similcaudipteryx yixianensis
Protarchaeopteryx robusta
Appendix 5. Raw volumetric data for endocranial regions (cm$^3$). Body mass given in kilograms.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>specimen #</th>
<th>body mass</th>
<th>total endocranium</th>
<th>olfactory bulbs</th>
<th>cerebrum</th>
<th>optic lobes</th>
<th>pituitary</th>
<th>cerebellum</th>
<th>brain stem</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anas platyrhynchus</td>
<td>0.1668</td>
<td>6.8005</td>
<td>0.05481</td>
<td>4.69312</td>
<td>0.951</td>
<td>0.04103</td>
<td>0.5273</td>
<td>0.53324</td>
<td></td>
</tr>
<tr>
<td>Bucorvus abyssinicus</td>
<td>1.2609</td>
<td>22.0831</td>
<td>0.00615</td>
<td>16.81483</td>
<td>2.8396</td>
<td>0.03859</td>
<td>1.69881</td>
<td>0.685</td>
<td></td>
</tr>
<tr>
<td>Chordeiles minor</td>
<td>0.0117</td>
<td>0.8773</td>
<td>0.00568</td>
<td>0.45814</td>
<td>0.2384</td>
<td>0.00353</td>
<td>0.10697</td>
<td>0.06459</td>
<td></td>
</tr>
<tr>
<td>Ptilinopus melanospila</td>
<td>0.0987</td>
<td>1.1153</td>
<td>0.00322</td>
<td>0.63129</td>
<td>0.2711</td>
<td>0.00401</td>
<td>0.13303</td>
<td>0.07262</td>
<td></td>
</tr>
<tr>
<td>Coragyps atratus</td>
<td>0.8988</td>
<td>8.7080</td>
<td>0.23389</td>
<td>5.95214</td>
<td>0.995</td>
<td>0.0245</td>
<td>0.95531</td>
<td>0.54718</td>
<td></td>
</tr>
<tr>
<td>Haliaeetus leucocephalus</td>
<td>2.0601</td>
<td>17.7662</td>
<td>0.0318</td>
<td>12.24211</td>
<td>2.1649</td>
<td>0.07587</td>
<td>2.18085</td>
<td>1.07076</td>
<td></td>
</tr>
<tr>
<td>Chauna chavaria</td>
<td>1.1993</td>
<td>7.7370</td>
<td>0.03565</td>
<td>5.17842</td>
<td>0.8994</td>
<td>0.04624</td>
<td>0.99983</td>
<td>0.57749</td>
<td></td>
</tr>
<tr>
<td>Gavia immer</td>
<td>0.3046</td>
<td>9.9359</td>
<td>0.0414</td>
<td>5.50361</td>
<td>1.6177</td>
<td>0.05737</td>
<td>1.94034</td>
<td>0.77545</td>
<td></td>
</tr>
<tr>
<td>Grus canadensis</td>
<td>2.1797</td>
<td>15.1426</td>
<td>0.02634</td>
<td>11.08408</td>
<td>1.9537</td>
<td>0.03924</td>
<td>0.88928</td>
<td>1.14999</td>
<td></td>
</tr>
<tr>
<td>Struthio camelus</td>
<td>59.304</td>
<td>57.3888</td>
<td>0.18723</td>
<td>31.03093</td>
<td>6.5153</td>
<td>0.63607</td>
<td>7.266</td>
<td>5.75323</td>
<td></td>
</tr>
</tbody>
</table>

*body size estimated based on *Troodon formosus* (Turner et al., 2007). **Body size estimated based on *Linheraptor exquisitus* (Xu et al., 2010).
<table>
<thead>
<tr>
<th>Taxon</th>
<th>specimen #</th>
<th>body mass</th>
<th>total endocranium</th>
<th>olfactory bulbs</th>
<th>cerebrum</th>
<th>optic lobes</th>
<th>pituitary</th>
<th>cerebellum</th>
<th>brain stem</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Fregata magnificens</em></td>
<td></td>
<td>0.1709</td>
<td>9.1571</td>
<td>0.01533</td>
<td>6.09456</td>
<td>0.8831</td>
<td>0.05167</td>
<td>1.62222</td>
<td>0.49016</td>
</tr>
<tr>
<td><em>Phaethon rubricada</em></td>
<td></td>
<td>0.0276</td>
<td>4.0332</td>
<td>0.01035</td>
<td>2.22193</td>
<td>0.7329</td>
<td>0.01728</td>
<td>0.7562</td>
<td>0.29457</td>
</tr>
<tr>
<td><em>Phalacrocorax penicillatus</em></td>
<td></td>
<td>0.2573</td>
<td>12.3242</td>
<td>0.02665</td>
<td>8.36189</td>
<td>1.4016</td>
<td>0.0405</td>
<td>1.63195</td>
<td>0.86163</td>
</tr>
<tr>
<td><em>Melanerpes aurifron</em></td>
<td></td>
<td>0.0149</td>
<td>2.2063</td>
<td>0.00311</td>
<td>1.56714</td>
<td>0.2029</td>
<td>0.00608</td>
<td>0.34458</td>
<td>0.08249</td>
</tr>
<tr>
<td><em>Podilymbus podiceps</em></td>
<td></td>
<td>0.0471</td>
<td>2.4872</td>
<td>0.00776</td>
<td>1.62851</td>
<td>0.408</td>
<td>0.01092</td>
<td>0.25811</td>
<td>0.17394</td>
</tr>
<tr>
<td><em>Diomedea immutabilis</em></td>
<td></td>
<td>0.4344</td>
<td>14.3838</td>
<td>0.20619</td>
<td>9.44662</td>
<td>1.4368</td>
<td>0.04968</td>
<td>2.39647</td>
<td>0.84806</td>
</tr>
<tr>
<td><em>Brotogeris chrysopteris</em></td>
<td></td>
<td>0.0155</td>
<td>1.9778</td>
<td>0.00872</td>
<td>1.53269</td>
<td>0.2046</td>
<td>0.00226</td>
<td>0.1644</td>
<td>0.06514</td>
</tr>
<tr>
<td><em>Incisivosaurus gauthieri</em></td>
<td></td>
<td>-</td>
<td>5.53</td>
<td>0.029</td>
<td>2.38</td>
<td>1.20</td>
<td>0.008</td>
<td>1.07</td>
<td>0.82</td>
</tr>
<tr>
<td><em>Conchoraptor gracilis</em></td>
<td>IGM 100/xxxx</td>
<td>5.019</td>
<td>7.76</td>
<td>-</td>
<td>3.71</td>
<td>0.82</td>
<td>0.058</td>
<td>2.62</td>
<td>0.55</td>
</tr>
<tr>
<td><em>Citipati osmolskae</em></td>
<td>IGM 100/978</td>
<td>85.96</td>
<td>22.782</td>
<td>0.569</td>
<td>9.52</td>
<td>3.60</td>
<td>-</td>
<td>5.16</td>
<td>3.78</td>
</tr>
</tbody>
</table>

*body size estimated based on *Troodon formosus* (Turner et al., 2007). **Body size estimated based on *Linheraptor exquisitus* (Xu et al., 2010).
<table>
<thead>
<tr>
<th>Taxon</th>
<th>specimen #</th>
<th>body mass</th>
<th>total endocranium</th>
<th>olfactory bulbs</th>
<th>cerebrum</th>
<th>optic lobes</th>
<th>pituitary</th>
<th>cerebellum</th>
<th>brain stem</th>
</tr>
</thead>
<tbody>
<tr>
<td>Khaan mckennai</td>
<td>IGM 100/973</td>
<td>12.61</td>
<td>8.890</td>
<td>0.0284</td>
<td>3.71</td>
<td>1.31</td>
<td>-</td>
<td>1.60</td>
<td>2.17</td>
</tr>
<tr>
<td>Zanabazar junior</td>
<td>IGM 100/1</td>
<td>49.3*</td>
<td>26.41</td>
<td>1.08</td>
<td>14.81</td>
<td>4.75</td>
<td>0.266</td>
<td>3.16</td>
<td>2.34</td>
</tr>
<tr>
<td>Tsaagan mangas</td>
<td>IGM 100/1015</td>
<td>23.4**</td>
<td>3.092</td>
<td>0.49</td>
<td>1.61</td>
<td>0.70</td>
<td>-</td>
<td>0.31</td>
<td>0.40</td>
</tr>
<tr>
<td>Archaeopteryx</td>
<td>BMNH 37001</td>
<td>0.5</td>
<td>1.40</td>
<td>0.024</td>
<td>0.74</td>
<td>0.28</td>
<td>0.025</td>
<td>0.19</td>
<td>0.14</td>
</tr>
<tr>
<td>Shuvuuia deserti</td>
<td>IGM 100/977</td>
<td>0.248</td>
<td>0.85</td>
<td>0.05</td>
<td>0.41</td>
<td>0.16</td>
<td>0.019</td>
<td>0.09</td>
<td>0.12</td>
</tr>
<tr>
<td>Alioramus altai</td>
<td>IGM 100/1184</td>
<td>359.32</td>
<td>81.01</td>
<td>6.18</td>
<td>18.70</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Tyrannosaurus</td>
<td>AMNH 5029</td>
<td>6055.4</td>
<td>-</td>
<td>111.80</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Allosaurus</td>
<td>UUVP 294</td>
<td>1176</td>
<td>169.00</td>
<td>-</td>
<td>46.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

*Body size estimated based on *Troodon formosus* (Turner et al., 2007). **Body size estimated based on *Linheraptor exquisitus* (Xu et al., 2010).
Appendix 6. Computed tomography scanning parameters. All CT slices for extant birds are available at www.digimorph.org. Abbreviations: UT, University of Texas at Austin, High Resolution CT Facility; SUNY, Stony Brook Medical Center; OU, Ohio University.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Specimen #</th>
<th>Scanning Facility</th>
<th>Slice Thickness (mm)</th>
<th>Number of Slices through Endocranium</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anas platyrhynchos</td>
<td>UT</td>
<td>0.500</td>
<td>123</td>
<td></td>
</tr>
<tr>
<td>Bucorvus abyssinicus</td>
<td>UT</td>
<td>0.263</td>
<td>143</td>
<td></td>
</tr>
<tr>
<td>Chordeiles minor</td>
<td>UT</td>
<td>0.059</td>
<td>381</td>
<td></td>
</tr>
<tr>
<td>Ptilinopus melanospila</td>
<td>UT</td>
<td>0.121</td>
<td>290</td>
<td></td>
</tr>
<tr>
<td>Coragyps atratus</td>
<td>UT</td>
<td>0.121</td>
<td>300</td>
<td></td>
</tr>
<tr>
<td>Haliaeetus leucocephalus</td>
<td>UT</td>
<td>0.169</td>
<td>245</td>
<td></td>
</tr>
<tr>
<td>Chauna chavaria</td>
<td>UT</td>
<td>0.295</td>
<td>115</td>
<td></td>
</tr>
<tr>
<td>Gavia immer</td>
<td>UT</td>
<td>0.109</td>
<td>408</td>
<td></td>
</tr>
<tr>
<td>Grus canadensis</td>
<td>UT</td>
<td>0.166</td>
<td>246</td>
<td></td>
</tr>
<tr>
<td>Struthio camelus</td>
<td>SUNY</td>
<td>0.310</td>
<td>209</td>
<td></td>
</tr>
<tr>
<td>Fregata magnificens</td>
<td>UT</td>
<td>0.128</td>
<td>269</td>
<td></td>
</tr>
<tr>
<td>Phaethon rubricada</td>
<td>UT</td>
<td>0.174</td>
<td>171</td>
<td></td>
</tr>
<tr>
<td>Phalacrocorax penicillatus</td>
<td>UT</td>
<td>0.115</td>
<td>399</td>
<td></td>
</tr>
<tr>
<td>Melanerpes aurifrons</td>
<td>UT</td>
<td>0.060</td>
<td>311</td>
<td></td>
</tr>
<tr>
<td>Podilymbus podiceps</td>
<td>UT</td>
<td>0.056</td>
<td>379</td>
<td></td>
</tr>
<tr>
<td>Taxon</td>
<td>Specimen #</td>
<td>Scanning Facility</td>
<td>Slice Thickness (mm)</td>
<td>Number of Slices through Endocranium</td>
</tr>
<tr>
<td>-----------------------------</td>
<td>--------------</td>
<td>-------------------</td>
<td>----------------------</td>
<td>--------------------------------------</td>
</tr>
<tr>
<td><em>Diomedea immutabilis</em></td>
<td></td>
<td>UT</td>
<td>0.138</td>
<td>313</td>
</tr>
<tr>
<td><em>Brotogeris chrysopteris</em></td>
<td></td>
<td>UT</td>
<td>0.163</td>
<td>123</td>
</tr>
<tr>
<td><em>Incisivosaurus gauthieri</em></td>
<td>IVPP V 13326</td>
<td>SUNY</td>
<td>0.187</td>
<td>147</td>
</tr>
<tr>
<td><em>Conchoraptor gracilis</em></td>
<td>IGM 100/3006</td>
<td>OU</td>
<td>0.920</td>
<td>550</td>
</tr>
<tr>
<td><em>Citipati osmolskae</em></td>
<td>IGM 100/978</td>
<td>UT</td>
<td>0.250</td>
<td>360</td>
</tr>
<tr>
<td><em>Khaan mckennai</em></td>
<td>IGM 100/973</td>
<td>UT</td>
<td>0.164</td>
<td>328</td>
</tr>
<tr>
<td><em>Zanabazar junior</em></td>
<td>IGM 100/1</td>
<td>UT</td>
<td>0.500</td>
<td>195</td>
</tr>
<tr>
<td><em>Tsaagan mangas</em></td>
<td>IGM 100/1015</td>
<td>UT</td>
<td>0.500</td>
<td>124</td>
</tr>
<tr>
<td><em>Archaeopteryx lithographica</em></td>
<td>BMNH 37001</td>
<td>UT</td>
<td>0.023</td>
<td>996</td>
</tr>
<tr>
<td><em>Shuvuuia deserti</em></td>
<td>IGM 100/977</td>
<td>UT</td>
<td>0.251</td>
<td>195</td>
</tr>
<tr>
<td><em>Alioramus altai</em></td>
<td>IGM 100/1844</td>
<td>UT</td>
<td>0.250</td>
<td>490</td>
</tr>
</tbody>
</table>
Appendix 7. Proportion of endocranial regions relative to total endocranial volume.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>specimen #</th>
<th>olfactory bulbs</th>
<th>cerebrum</th>
<th>optic lobes</th>
<th>pituitary</th>
<th>cerebellum</th>
<th>brain stem</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anas platyrhynchus</td>
<td></td>
<td>0.0081</td>
<td>0.6898</td>
<td>0.1398</td>
<td>0.0060</td>
<td>0.0775</td>
<td>0.0784</td>
</tr>
<tr>
<td>Bucorvus abyssinicus</td>
<td></td>
<td>0.0003</td>
<td>0.7614</td>
<td>0.1286</td>
<td>0.0017</td>
<td>0.0769</td>
<td>0.0310</td>
</tr>
<tr>
<td>Chordeiles minor</td>
<td></td>
<td>0.0065</td>
<td>0.5222</td>
<td>0.2718</td>
<td>0.0040</td>
<td>0.1219</td>
<td>0.0736</td>
</tr>
<tr>
<td>Ptilinopus melanospila</td>
<td></td>
<td>0.0029</td>
<td>0.5660</td>
<td>0.2431</td>
<td>0.0036</td>
<td>0.1193</td>
<td>0.0651</td>
</tr>
<tr>
<td>Coragyps atratus</td>
<td></td>
<td>0.0269</td>
<td>0.6835</td>
<td>0.1143</td>
<td>0.0028</td>
<td>0.1097</td>
<td>0.0628</td>
</tr>
<tr>
<td>Haliaeetus leucocephalus</td>
<td></td>
<td>0.0018</td>
<td>0.6891</td>
<td>0.1219</td>
<td>0.0043</td>
<td>0.1228</td>
<td>0.0603</td>
</tr>
<tr>
<td>Chauna chavaria</td>
<td></td>
<td>0.0046</td>
<td>0.6693</td>
<td>0.1162</td>
<td>0.0060</td>
<td>0.1292</td>
<td>0.0746</td>
</tr>
<tr>
<td>Gavia immer</td>
<td></td>
<td>0.0042</td>
<td>0.5539</td>
<td>0.1628</td>
<td>0.0058</td>
<td>0.1953</td>
<td>0.0780</td>
</tr>
<tr>
<td>Grus canadensis</td>
<td></td>
<td>0.0017</td>
<td>0.7320</td>
<td>0.1290</td>
<td>0.0026</td>
<td>0.0587</td>
<td>0.0759</td>
</tr>
<tr>
<td>Struthio camelus</td>
<td></td>
<td>0.0033</td>
<td>0.5407</td>
<td>0.1135</td>
<td>0.0111</td>
<td>0.1266</td>
<td>0.1003</td>
</tr>
</tbody>
</table>

*Pituitary proportions estimated based on mean of oviraptorosaurs for use in PCA. **Pituitary proportion estimated based on mean of paravians. ***Olfactory bulb proportion of Conchoraptor gracilis based on measure for Khaan mckennai.
<table>
<thead>
<tr>
<th>Taxon</th>
<th>specimen #</th>
<th>olfactory bulbs</th>
<th>cerebrum</th>
<th>optic lobes</th>
<th>pituitary</th>
<th>cerebellum</th>
<th>brain stem</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Fregata magnificens</em></td>
<td>0.0017</td>
<td>0.6656</td>
<td>0.0964</td>
<td>0.0056</td>
<td>0.1772</td>
<td>0.0535</td>
<td></td>
</tr>
<tr>
<td><em>Phaethon rubricada</em></td>
<td>0.0026</td>
<td>0.5509</td>
<td>0.1817</td>
<td>0.0043</td>
<td>0.1875</td>
<td>0.0730</td>
<td></td>
</tr>
<tr>
<td><em>Phalacrocorax penicillatus</em></td>
<td>0.0022</td>
<td>0.6785</td>
<td>0.1137</td>
<td>0.0033</td>
<td>0.1324</td>
<td>0.0699</td>
<td></td>
</tr>
<tr>
<td><em>Melanerpes aurifron</em></td>
<td>0.0014</td>
<td>0.7103</td>
<td>0.0920</td>
<td>0.0028</td>
<td>0.1562</td>
<td>0.0374</td>
<td></td>
</tr>
<tr>
<td><em>Podilymbus podiceps</em></td>
<td>0.0031</td>
<td>0.6548</td>
<td>0.1640</td>
<td>0.0044</td>
<td>0.1038</td>
<td>0.0699</td>
<td></td>
</tr>
<tr>
<td><em>Diomedea immutabilis</em></td>
<td>0.0143</td>
<td>0.6568</td>
<td>0.0999</td>
<td>0.0035</td>
<td>0.1666</td>
<td>0.0590</td>
<td></td>
</tr>
<tr>
<td><em>Brotogeris chrysopteris</em></td>
<td>0.0044</td>
<td>0.7750</td>
<td>0.1034</td>
<td>0.0011</td>
<td>0.0831</td>
<td>0.0329</td>
<td></td>
</tr>
<tr>
<td>birds (mean)</td>
<td>0.005294</td>
<td>0.652929</td>
<td>0.14071</td>
<td>0.004288</td>
<td>0.12615882</td>
<td>0.064447</td>
<td></td>
</tr>
<tr>
<td><em>Incisivosaurus gauthieri</em></td>
<td>IVPP V 13326</td>
<td>0.0053</td>
<td>0.4312</td>
<td>0.2179</td>
<td>0.0015</td>
<td>0.1943</td>
<td>0.1498</td>
</tr>
<tr>
<td><em>Conchoraptor gracilis</em></td>
<td>IGM 100/xxx</td>
<td>0.0032***</td>
<td>0.4783</td>
<td>0.1062</td>
<td>0.0074</td>
<td>0.3374</td>
<td>0.0706</td>
</tr>
</tbody>
</table>

*Pituitary proportions estimated based on mean of oviraptorosaurs for use in PCA. **Pituitary proportion estimated based on mean of paravians. ***Olfactory bulb proportion of *Conchoraptor gracilis* based on measure for *Khaan mckennai*.  

521
<table>
<thead>
<tr>
<th>Taxon</th>
<th>specimen #</th>
<th>olfactory bulbs</th>
<th>cerebrum</th>
<th>optic lobes</th>
<th>pituitary</th>
<th>cerebellum</th>
<th>brain stem</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Citipati osmolskae</em></td>
<td>IGM 100/978</td>
<td>0.0250</td>
<td>0.4179</td>
<td>0.1579</td>
<td>0.0073*</td>
<td>0.2265</td>
<td>0.1658</td>
</tr>
<tr>
<td><em>Khaan mckennai</em></td>
<td>IGM 100/973</td>
<td>0.0032</td>
<td>0.4172</td>
<td>0.1480</td>
<td>0.0073*</td>
<td>0.1804</td>
<td>0.2443</td>
</tr>
<tr>
<td><em>Zanabazar junior</em></td>
<td>IGM 100/1</td>
<td>0.0409</td>
<td>0.5607</td>
<td>0.1798</td>
<td>0.0101</td>
<td>0.1196</td>
<td>0.0889</td>
</tr>
<tr>
<td><em>Tsaagan mangas</em></td>
<td>IGM 100/1015</td>
<td>0.0136</td>
<td>0.5212</td>
<td>0.2265</td>
<td>0.009**</td>
<td>0.1000</td>
<td>0.1298</td>
</tr>
<tr>
<td><em>Archaeopteryx lithographica</em></td>
<td>BMNH 37001</td>
<td>0.021</td>
<td>0.551</td>
<td>0.183</td>
<td>0.013</td>
<td>0.122</td>
<td>0.110</td>
</tr>
<tr>
<td><em>Shuvuuia deserti</em></td>
<td>IGM 100/977</td>
<td>0.0592</td>
<td>0.4853</td>
<td>0.1830</td>
<td>0.0222</td>
<td>0.1078</td>
<td>0.1367</td>
</tr>
<tr>
<td><em>Alioramus altai</em></td>
<td>IGM 100/1844</td>
<td>0.0763</td>
<td>0.2309</td>
<td>-</td>
<td>0.0197</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Tyrannosaurus rex</em></td>
<td>AMNH 5029</td>
<td>-</td>
<td>0.3259</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td><em>Allosaurus fragilis</em></td>
<td>UUVP 294</td>
<td>-</td>
<td>0.2763</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

*Pituitary proportions estimated based on mean of oviraptorosaurs for use in PCA. **Pituitary proportion estimated based on mean of paravians. ***Olfactory bulb proportion of *Conchoraptor gracilis* based on measure for *Khaan mckennai*. 