

# The skull of *Velociraptor* (Theropoda) from the Late Cretaceous of Mongolia

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The well preserved material of the Late Cretaceous dromaeosaurid, *Velociraptor mongoliensis*, has allowed us to supplement earlier descriptions of the skull in this species. The skull of *V. mongoliensis* is similar to that of *Deinonychus antirrhopus*, but differs from the latter by: (1) laterally convex supratemporal arcade resulting in short, rounded supratemporal fenestra; (2) depressed nasal; (3) longer maxillary process of premaxilla; (4) lack of separate prefrontal, and (5) convex ventral border of the dentary. These differences, especially that in the structure of the temporal region, support generic distinction of *Deinonychus* and *Velociraptor*. Skulls of other dromaeosaurids are compared.

Key words: Dinosauria, Theropoda, Dromaeosauridae, *Velociraptor*, skull, mandible, Late Cretaceous, Gobi Desert, Mongolia.

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## Introduction

Dromaeosaurids were small to medium size theropods, except for *Utahraptor* and an undetermined dromaeosaurid from Japan (Azuma & Currie 1995), which were relatively large animals. They were cursorial, moderately fast carnivores with large, rostrolaterally facing eyes. There is taphonomic evidence (Ostrom 1990; Maxwell & Ostrom 1995) that at least *Deinonychus antirrhopus* may have hunted in packs. On the other hand, *Velociraptor mongoliensis* may have also been a carrion feeder (Osmólska 1993; but see Kielan-Jaworowska & Barsbold 1972; Unwin *et al.* 1994; Fastovsky *et al.* 1997 for alternative interpretations). The Dromaeosauridae are Cretaceous maniraptoran theropods, and eight monotypic genera: *Adasaurus* Barsbold, 1983, *Deinonychus* Ostrom, 1969, *Dromaeosaurus* Matthew & Brown, 1922, *Hulsanpes* Osmólska, 1982, *Ornithodesmus* Seeley, 1887, *Saurornitholestes* Sues, 1978, *Utahraptor*

Kirkland, Burge, & Gaston, 1993, and *Velociraptor* Osborn, 1924 are presently assigned to this family. Three of these genera (*Adasaurus*, *Hulsanpes*, and *Ornithodesmus*), are based exclusively on incomplete postcrania.

The most peculiar dromaeosaurid feature is the opisthopubic pelvis (Barsbold 1976), which distinguishes these dinosaurs from other theropods, except for the distantly related therizinosauroids; the extremely long caudal zygapophyses and chevrons are probably also common to all dromaeosaurids, but caudal vertebrae are known only in *Deinonychus*, *Velociraptor*, and *Saurornitholestes* (Dr P.J. Currie's personal communication 1999)

The skull of *V. mongoliensis* has been known for more than 70 years. Over this time, it has been described, illustrated or commented by several authors, among them Sues (1977a), Barsbold (1983), Paul (1988), and Ostrom (1969b, 1990). Up to now, *Velociraptor* is represented by the most complete and most numerous skulls and postcrania among dromaeosaurids (in addition to the here described material, there are numerous still not described specimens recently collected by the AMNH Asiatic Expeditions).

It was Ostrom (1969a), who first recognised the close relationship of *Velociraptor* with the North American forms, *Dromaeosaurus* and *Deinonychus*, and assigned it to the Dromaeosauridae (= Dromaeosaurinae Matthew & Brown 1922). The skulls are largely complete in the two latter genera, whereas skulls of *Saurornitholestes* and *Utahraptor* are represented by a few bones each. The following description of the skull in *V. mongoliensis* supplements the earlier descriptions by Osborn (1924), Sues (1977a), and Barsbold (1983). The skull data for *D. antirrhopus*, *Dromaeosaurus albertensis*, and *Saurornitholestes langstoni* used in the comparisons below are respectively from Ostrom (1969b), Colbert & Russell (1969), Currie (1995), Sues (1977a), and Witmer & Maxwell (1996), unless stated otherwise.

**Institutional abbreviations:** AMNH, American Museum of Natural History, New York; GIN, Institute of Geology, Mongolian Academy of Sciences, Ulan Bator; PIN, Museum of Palaeontology, Russian Academy of Sciences, Moscow; ROM, Royal Ontario Museum, Toronto; TPM, Royal Tyrrell Museum of Palaeontology, Drumheller; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

## **Systematic palaeontology**

### **Theropoda Marsh, 1881**

### **Maniraptora Gauthier, 1986**

### **Family Dromaeosauridae Matthew & Brown, 1922**

### **Subfamily Velociraptorinae Barsbold, 1983**

### ***Velociraptor* Osborn, 1924**

Type species by monotypy: *Velociraptor mongoliensis* Osborn, 1924.

### ***Velociraptor mongoliensis* Osborn, 1924**

Figs 1–8.

Holotype: AMNH 6515, skull, mandible, manual digit I.

Type horizon and locality: Djadokhta Formation (?early Campanian), Bayn Dzak, Omnogov province, Gobi Desert, Mongolia.

**Material.** — The present description of the skull of *V. mongoliensis* is based on several skulls pertaining to more or less complete skeletons from the Upper Cretaceous sandstone deposits of the Mongolian Gobi. The specimens studied were found by the Polish-Mongolian Palaeontological Expeditions (specimens GIN 100/25 and ZPAL MgD-I/97, see Kielan-Jaworowska & Barsbold 1972; Gradziński *et al.* 1977), by the Soviet-Mongolian Palaeontological Expeditions (specimen PIN 3143/8), by a Mongolian expedition (specimen GIN 100/24, see Barsbold 1983) and by the Mongolian-Japanese Palaeontological Expeditions (specimen GIN 100/2000). Description of the postcrania preserved with these skulls will be published at a later date (Barsbold & Osmólska in preparation).

The following specimens derive from the Djadokhta Formation (?early Campanian, see Kielan-Jaworowska & Hurum 1997), Tugrikin-Shire, Omnogov, Mongolia:

GIN 100/24 – consists of an almost complete, articulated, but dorsoventrally flattened skull, both mandibular rami, and a few fragmentary postcranial bones. The premaxillae are damaged rostrally, as are the caudal ends of the nasals and the rostral tips of the frontals along their mutual contact; the shaft and the caudal end of the left lacrimal are missing; jugals, quadratojugals and quadrates are fragmentary; pterygoids and palatines are partly damaged, those on the left side having shifted caudally from their natural position; vomers are not exposed. The dentaries are positioned between the left and right maxillae and premaxillae; the postdentary portion of the right mandibular ramus is fragmentary, the left surangular lacks its rostradorsal part; the dentary teeth and articular region are not exposed.

GIN 100/25 – includes skeletons of two dinosaurs – *V. mongoliensis* and *Protoceratops andrewsi*. Remains of these dinosaurs are preserved in a position suggestive of combat and for that reason this specimen is widely known as one of the ‘fighting dinosaurs’. The *V. mongoliensis* skeleton is complete and articulated. It includes the skull, adducted mandibles and postcranium. The snout and mandible are somewhat compressed laterally and the dentaries are forced under the skull obscuring the palate and rostral part of the basicranium.

GIN 100/2000 – is represented by the complete skeleton of a young individual. It includes skull with mandible and postcranium.

PIN 3143/8 – almost complete skull with left mandibular ramus, lacking the right temporal region; tip of the rostrum is severely damaged.

The Barun Goyot Formation (?late Campanian: Kielan-Jaworowska & Hurum 1997), Khulsan, Bayankhongor, Mongolia, yielded one specimen ZPAL MgD-I/97 – included is the left, rostral half of the skull (exposed from the medial side) but lacks the premaxilla and tips of the vomers. Both mandibular rami are placed between the maxillae (as in all described *V. mongoliensis* specimens with the mandible preserved); the left ramus lacks the caudal articular region and the tip of the dentary; the fragmentary right ramus includes the splenial and an incomplete dentary. Associated with the skull was a distal part of the left hind limb.

The new, abundant *Velociraptor* material recently collected in Mongolia by the Mongolian Academy of Sciences – American Museum of Natural History Expeditions (Norell & Makovicky 1998) has not been studied by the present authors.

**Revised diagnosis** (based upon skull characters). — Skull shallow with long snout, preorbital length constituting 60% of total skull length (estimated at about 50% in *Dr. albertensis* and *D. antirrhopus*; proportions unknown in other dromaeosaurids); supratemporal fossa (and fenestra) subcircular, bound by laterally convex supratemporal arcade (elongate, with straight arcade in *D. antirrhopus*; shape of fossa unknown in other dromaeosaurids); frontal long, almost four times longer than wide across the orbital portion, and almost four times as long as parietal [wider in *S. langstoni*, frontal length at most three times the width across the orbital portion; in *Dr. albertensis* frontal shorter, about twice as long as wide; parietal/frontal length ratio unknown in both these species; in *D. antirrhopus*, frontal only three times longer than wide and twice as long as parietal (Dr L.M. Witmer's personal communication 1999)]; rostral border of internal antorbital fenestra broadly rounded (subtriangular in *D. antirrhopus*; shape unknown in other dromaeosaurids); premaxilla with long maxillary process reaching well beyond caudal margin of external naris (not extending beyond naris in *D. antirrhopus*; unknown or incomplete in other dromaeosaurids); nasal depressed, deepest just behind the external naris (not depressed in *D. antirrhopus*; unknown in other dromaeosaurids); maxilla with longitudinal ridge dorsal to a row of neuro-vascular foramina, which are arranged in one row (no ridge in *D. antirrhopus*; maxilla unknown in other dromaeosaurids); no separate prefrontal (prefrontal is separate in *D. antirrhopus* and probably also in *Dr. albertensis*); dentary very shallow, its depth constituting one-eighth to one-seventh of its length, ventral margin convex (dentary relatively deeper and with straight ventral margin in other dromaeosaurids); first and second premaxillary teeth larger than third and fourth.

Because of deficiency of the skull data for some dromaeosaurid taxa, all the above characters are equivocal synapomorphies of *V. mongoliensis*.

**Occurrence.** — Upper Cretaceous, ?lower–?upper Campanian, Djadokhta and Barun Goyot formations; Omnogov and Bayankhongor provinces, Gobi Desert, Mongolia.

## Description and comparisons

### Skull as a whole

The skull has a long, narrow and shallow snout, which constitutes 60% of the skull length (Table 1). In caudal view, the skull is almost as wide as deep (Figs 2A, 5); the rostral view shows the orbits rostrolaterally oriented for a stereoscopic vision (Norell & Makovicky 1998). In lateral view (Figs 1A, B, 3A, 4A), the skull profile weakly rises caudally; from about the mid-length of the nasals forwards, the rostral part of the snout is somewhat elevated above the narial opening and depressed behind it. The naris is large and oval, and set in a depression. The elongate subnarial foramen is pronounced. The antorbital fossa is long and shallow and occupies slightly more than a half of the snout length. Only the rostral and rostradorsal portion of its rim is well developed, while the ventral part of the rim is indistinct. More than a half of the antorbital fossa is occupied by the internal antorbital fenestra, the rostral margin of which is broadly rounded. The maxillary fenestra is much smaller, the interfenestral strut separating it from the internal antorbital fenestra is wide. The promaxillary fenestra is divided into two small openings in GIN 100/25, although it seems slit-like in other skulls. The orbit is almost circular, only slightly longer than high. The infratemporal fenestra is about three times higher than long, and is slightly inclined caudodorsally. Caudal to this fenestra, there is a tall, wide paraquadrate foramen that, because of its great size, is well exposed

both laterally and caudally. In dorsal view, the skull has a striking appearance, due to the narrowness of the snout, the width of which equals only about a third of the postorbital skull width. The snout is also long in comparison to the short frontoparietal part of the skull roof between the supratemporal fenestra (Figs 2B, 3B, 4B). The lateral apices of the lacrimals extend somewhat beyond the jugals. The supratemporal arcades are laterally convex making the supratemporal fossae (and fenestrae) almost circular. The skull is about twice as wide across the temporal arcades as between the orbits. The supraorbital fossae are bounded caudally by a steep, sharp nuchal crest. The nuchal crest is confluent medially with the sagittal crest, which is relatively low and short, and extends along the open sutural interparietal contact.

Table 1. Skull and mandible measurements (in mm) of *Velociraptor mongoliensis* (GIN 100/25)

Maximum length of skull (paroccipital process–tip of snout)	230
Medial length of skull (transverse nuchal crest–tip of snout)	213
<b>Width across supratemporal arcades</b>	77
Width across occiput	69
Width across lateral tips of lacrimals	<b>52</b>
Width across parietals (at about midlength)	27
Maximum depth	66
Length of snout (rostral margin of orbit–tip)	<b>140</b>
Width of snout (in front of rostral ends of lacrimals)	<b>22</b>
Depth of snout (in front of orbit)	45
Length of mandible	210
Maximum depth of mandible (behind external fenestra)	23

The distinctive appearance of the skull in *Velociraptor*, with its short temporal region, rounded temporal fenestrae and very long, narrow snout has not been noticed so far. The skull proportions, with the length of the preorbital region exceeding almost 4.5 times the length of the postorbital region, distinguish *Velociraptor* from *Dromaeosaurus* and *Deinonychus*, in which the preorbital lengths are about 2.5–3.5 times these of the postorbital regions. Among theropods, such a long snout occurs only in the ornithomimids. The subcircular shape of the temporal fenestra is the character that distinctly differs *Velociraptor* from *Deinonychus*. The right temporal arcade is complete in YPM 5210 specimen of *D. antirrhopus* and it seems subparallel to the medial line of the skull. As a result, the supratemporal fenestra is elongate and relatively narrow in *Deinonychus*, and its width (measured across its caudal portion) constitutes about 30% of the length of the fenestra. The temporal arcade is laterally convex in *Velociraptor*, and the width of the fenestra is more than 50% of its length. Due to the shape of the supratemporal arcade, the supratemporal fenestra is wider in *Velociraptor*, and it provided more space for the adductor muscles than the fenestra in *Deinonychus*. At the same time, the sagittal extent of the adductor origins was relatively greater in the American than in the Mongolian genus. It might result in a more oblique direction of some adductor fibres in *Deinonychus*. The unique specimen of *Dromaeosaurus* entirely lacks the temporal arcade, as well as most of the parietal; thus the shape of the

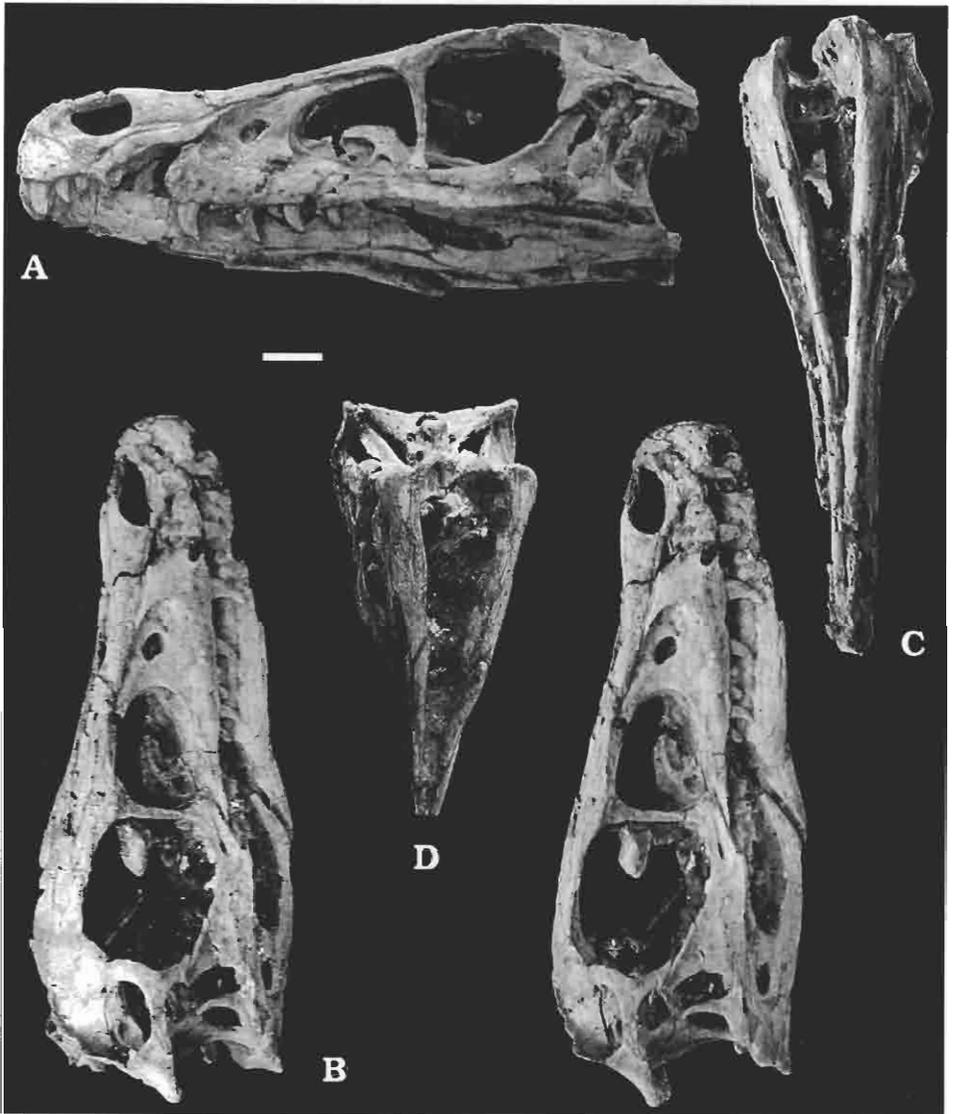


Fig. 1. Skull with mandible of *Velociraptor mongoliensis* GIN 100/25. A. Left lateral view. B. Right lateral view, stereophotograph. C. Ventral view. D. Left caudoventral view, showing contacts of quadrate heads with squamosals. Scale bar 2 cm.

supratemporal fenestra cannot be determined in this genus. Colbert & Russell (1969) reconstructed it as elongate, listing the long supratemporal arcade in *Dromaeosaurus* among differences to *Velociraptor*, while Currie's (1995) reconstruction shows a straight, but relatively shorter arcade and a rather rounded fenestra. The mode of preservation of the skulls at our disposal, and the loose contacts between some bones within the snout, show that the skull and mandible were not as rigid as in most other theropods.

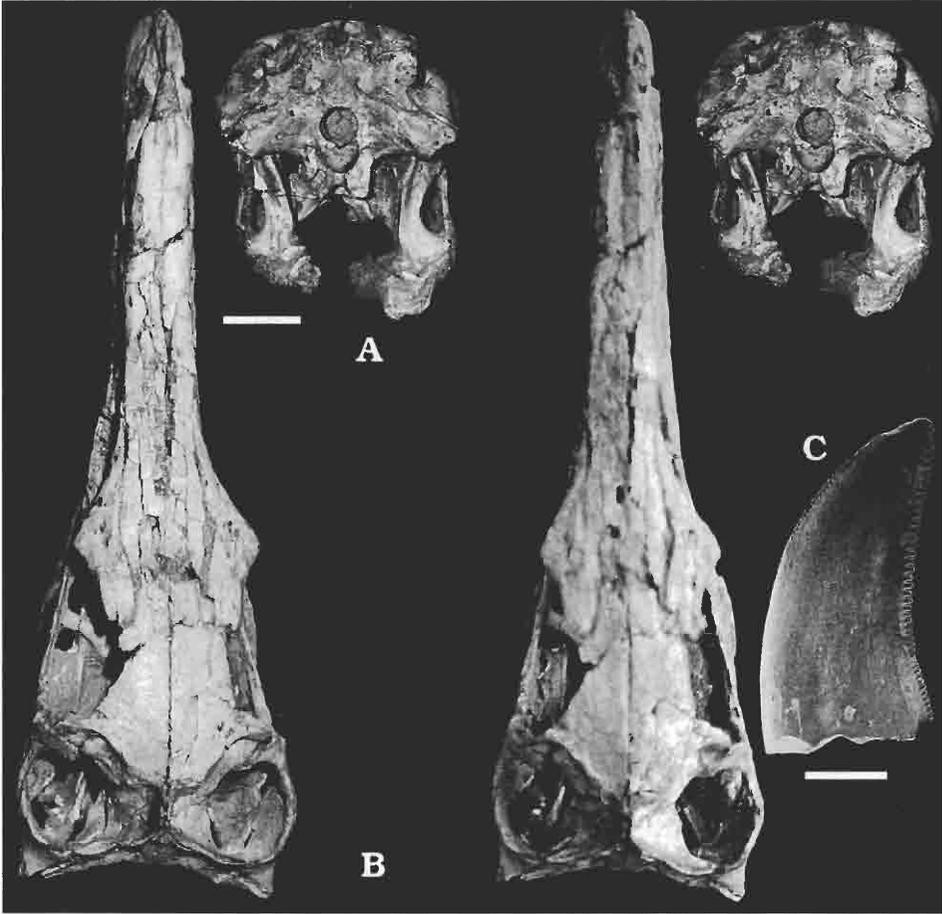


Fig. 2. Skull with mandible of *Velociraptor mongoliensis* GIN 100/25. A. Occipital view, stereophotograph. B. Dorsal view, stereophotograph, GIN 100/25. C. Tooth of *Velociraptor mongoliensis*, ZPAL MgD-I/97a. Scale bars 2 cm for A and B, 2 mm for C.

## Snout

**Premaxilla.** — The main body of the premaxilla is longer than high. A long, thin maxillary process of the premaxilla is wedged between the maxilla and nasal, reaching caudally to or close to the rostral margin of the antorbital fossa, and it separates the maxilla from the naris. In the extreme case (GIN 100/25), on the right side of the skull, this process extends even farther, to a point above the fifth/sixth maxillary teeth. The nasal process has a stout base, but its internarial portion is thin, and its end fits into a medial groove present along the tip of the nasal. A shallow depression in the premaxilla outlines the rostral and ventral margins of the narial opening. At the contact with the maxilla, the caudoventral border of the premaxilla is slightly embayed to mark the subnarial foramen. The surface of the rostral and alveolar parts of the premaxilla bears small, irregularly spaced foramina. In palatal view, the rostral portion of the premaxilla is steep, and only below the naris is there a narrow palatal shelf. The premaxillary shelves contact each other on the mid-line. They separate caudally, leaving a triangular space below the narial openings, where tip of the fused vomers is inserted.

**Maxilla.** — The lateral body of the maxilla has a low triangular outline. The nasal process of the maxilla is shorter than the jugal process. Along the alveolar margin, there is a row of small neuro-vascular foramina, above which extends a low, longitudinal ridge. The antorbital fossa is weakly delimited. It occupies almost two-thirds of the ventral length of the maxilla and the internal antorbital fenestra takes up about a third of that length. The rostral half of the fossa is shallow lateromedially and bears a small, teardrop-shaped maxillary fenestra. This fenestra is located halfway between the antorbital fenestra and the rostral margin of the antorbital fossa, and it leads into the maxillary sinus. Close to the rostral margin of the antorbital fossa, two small, rostrally directed openings (probably homologous to the promaxillary fenestra) penetrate the bone to enter the promaxillary sinus. This double promaxillary fenestra has been only noticed in GIN 100/25, while in AMNH 6515 (holotype), and possibly also in PIN 3143/8, the promaxillary fenestra is slit-like.

The maxillary recesses are exposed medially in ZPAL MgD-I/97 (Figs 7E, 8A). As preserved, they resemble the structures illustrated by Witmer (1997a: fig. 30) in *Albertosaurus*, with well pronounced *pila postantralis*, *antrum maxillaris*, and several *recessi pneumatici interalveolares*; the region of the promaxillary recess is poorly preserved. Owing to the damage of the rostralmost region of the maxilla in ZPAL MgD-I/97, it cannot be stated whether a *vestibular bulla* was present in *Velociraptor*. The left palatal shelf of the maxilla is partly preserved in ZPAL MgD-I/97, its rostral portion lacking. It is moderately wide rostrally (at least 7 mm), and has a smooth, upturned medial border. As preserved, a part of this border contacts the vomer along the region rostral to *pila interfenestralis*. The shelf is inclined dorsomedially–ventrolaterally. This inclination gradually decreases rostrally, and the shelf was probably almost horizontal at the contact with the premaxilla. Caudally, the palatal shelf underlies the medial surface of the jugal, close to the contact of the latter with the lacrimal shaft. Rostral to the lacrimal the medial border of the palatal shelf is in contact with the palatine. However, this contact is located more caudally than that of *Albertosaurus* (Witmer 1997a: fig. 30d). The position of the last maxillary tooth is opposite the mid-length of the internal antorbital fenestra.

**Nasal.** — The nasal is L-shaped in cross section and its dorsal portion is very narrow along more than its rostral half. In the rostral portion of the snout, the dorsal surfaces of each nasal incline slightly medially to produce a groove along the internasal contact. Judging from a vertical displacement along the internasal suture visible in the holotype, as well as in all other specimens at our disposal, this contact was loose. The caudalmost portion of the nasal is broken off in all our specimens, but the extensive caudal extent of this bone is evidenced by the presence of the longitudinally ridged dorsal surface on the rostralmost portion of the frontal in PIN 3143/8 (see below). Approximately from the fourth maxillary tooth position to the end of the maxillary fenestra, the nasal contacts the maxilla and this contact looks loose in the specimens at our disposal, as well as in the holotype. Contrary to that, the contact between the nasal and the maxillary process of the premaxilla seems more firm. Along its caudal third, the nasal contacts the lacrimal laterally. The nasal deepens rostrally and is the deepest behind the caudal boundary of the narial opening, producing a distinct elevation of the snout profile above the nares. The outer surface of the nasal is covered by irregularly spaced, small foramina.

Kirkland *et al.* (1993) drew attention to differences in shapes of the premaxillae in the dromaeosaurids, expressed as the length-to-depth ratio of the main body of the premaxilla. This index is the highest in *Velociraptor*: 164 in the holotype and 170 in GIN 100/25, while it is much lower in all other dromaeosaurids: 86 in *Dromaeosaurus*, about 90 in *Deinonychus*, and 101 in *Utahraptor*. Except in *Velociraptor*, the maxillary process is not completely preserved in any dromaeosaurid. In *Deinonychus* this process is not complete (Ostrom 1969b), and has been reconstructed as not extending beyond the caudal border of the external naris. On the illustrations of the holotype of *V. mongoliensis* skull in Osborn's (1924) and Sues' (1977a) papers, this process is short and ends just behind the naris, but in GIN 100/25 and 100/24 it extends much farther caudally. This region of the skull is not well preserved in the holotype and its interpretation by these au-



Fig. 3. A, B. Deformed skull and mandible of *Velociraptor mongoliensis*, GIN 100/24, in right lateral (A) and dorsal (B) views. Scale bar 2 cm.

thors may be incorrect. The respective regions of maxillae are damaged in *Dromaeosaurus*. To our knowledge, such a long and shallow maxillary process occurs only in the Ornithomimidae (a long process is also present in the Oviraptoridae, but its form is incomparable to that in the dromaeosaurids: Barsbold, Maryańska, & Osmólska in preparation). The maxillary process of the premaxilla separates the maxilla from the narial border only in some theropods, among them in the earliest ones, the Triassic *Eoraptor* Sereno *et al.*, 1993 and *Herrerasaurus* Reig, 1963 (Sereno & Novas 1992), but also in the Late Jurassic *Ornitholestes* Osborn, 1903, *Sinraptor* Currie & Zhao 1994) and the Cretaceous tyrannosaurids. The maxilla forms a part of the narial margin in *Compsognathus*, the ceratosaurs, allosaurids, therizinosaurids (*Erlikosaurus*), troodontids, and *Archaeopteryx*. The symphyseal edge of the premaxilla is rostroventrally inclined in *Deinonychus* whereas it is perpendicular to the long axis of the skull in *Velociraptor*. The maxilla in *Deinonychus* is relatively deeper caudally than that in *Velociraptor*, and the rostral margin of the internal antorbital fenestra is subtriangular, whereas this fenestra is broadly rounded rostrally in *Velociraptor*. *Deinonychus* and *Dromaeosaurus* lack the longitudinal ridge which runs above the alveolar border in *Velociraptor*. The outer surfaces of the maxillae in both North American genera are marked by more numerous neuro-vascular foramina, which are less regularly spaced, whereas these foramina are arranged in a single row in *Velociraptor*. The promaxillary fenestra is slit-like in *Deinonychus*, but not in all skulls of *Velociraptor*, but otherwise the maxillary recesses seem comparable to those in *Velociraptor*. The nasal of *Velociraptor* resembles that of *Deinonychus* in being relatively long, and in having the lateral and dorsal surfaces at right angles to each other, the dorsal one very narrow. However, in *Deinonychus*, the profile of the nasal slopes uniformly towards the rostral extremity of the snout, whereas

in *Velociraptor*, the nasal profile slopes only along about two thirds of its caudal length and it rises from about the level of the rostral boundary of the antorbital fossa. This results in the so called depressed 'nasal'. It is worth mentioning that the angles between the 'sloped' caudal and the 'raised' rostral parts of the nasal differ in skulls GIN 100/24, 25, PIN 3143/8, and AMNH 6515. The angle is insignificant in the first of these skulls (Fig. 3A), is small in the second (Fig. 1A, B) and third, and is most conspicuous in the holotype (Sues 1977a: pl. 16). This suggests that the nasals might be flexible in this region. The internasal contact seems weak rostrally in *Velociraptor* and *Deinonychus*, contrary to the contact between the nasal and maxillary process of the premaxilla, which seems firm in both genera.

### Skull roof, orbital and temporal region

**Frontal.** — The frontal is three times longer than wide at the level of the mid-length of the orbit. The interfrontal suture is easily discernible. At the caudodorsal corner of the orbit, the frontal abruptly widens into a rather narrow, transversely elongated postorbital process. Rostral to this process, the frontal gently narrows rostrally. On the outer surface of the frontal, there is a large, shallow depression in PIN 3143/8, which is weakly marked in other specimens. This depression extends along the mid-length of the frontal, and is separated from its fellow by a narrow and low ridge along the interfrontal suture, formed by the somewhat elevated medial margins of both frontals. The frontal is rough where it forms the caudal half of the dorsal margin of the orbit. Rostrolaterally, there is a subrectangular platform on the dorsal surface of the frontal for the extensive, overlapping contact with the caudal process of the lacrimal. The overlapping nasal-frontal contact was extensive judging by a longitudinally ridged surface exposed rostrally on the frontal in PIN 3143/8. This surface occupies about a fifth of the frontal length. In the region of the supratemporal fossa, there is a distinct S-shaped ridge extending caudomedially from the postorbital contact towards the interfrontal suture. The ridge marks the rostral extent of the fossa and of the temporal musculature. Caudal to that ridge, the frontal slopes towards the parietal and the slope is relatively steep laterally. Close to the contact with the postorbital, the frontal has a deep depression on its dorsal surface. The frontoparietal suture is interdigitate and tight. The ventral wing of the frontal is medially inclined and bounds laterally the rostral part of the brain cavity. Farther rostrally, it forms the thick lateral wall to the olfactory tract. The caudal margin of the ventral wing has an extensive sutural contact with the laterosphenoid, that extends medially from the tip of the transversely directed postorbital process of the frontal. In lateral view, the frontals gently rise towards the suture with the parietals and attain their highest level just in front of that contact.

**Parietal.** — The length of parietals equals to about a half of the combined (smallest) transverse width of both these bones. The parietals are suturally joined to each other along a sharp sagittal crest that rises slightly caudally. In lateral view, the parietals slope caudoventrally from their contact with the frontals, but close to the margin of the skull they turn abruptly dorsally to form a thin and high transverse nuchal crest. The crest caudally bounds the supratemporal fossae and is medially continuous with the sagittal crest. The dorsolateral apex of the parietal sets on the dorsal surface of the caudal process of the squamosal. On the occiput, the parietal occupies a relatively wide region lateral to the supraoccipital, where it overlies the caudal surface of the caudal process of the squamosal.

**Lacrimal (+prefrontal?).** — In all the specimens at our disposal, as well as in the holotype, there is definitely only one element present in the rostradorsal region of the orbit. For this reason it is here described as the lacrimal. However, this element may represent the fused prefrontal and lacrimal. The lacrimal is T-shaped in lateral view. Its dorsal portion is triangular, flat and horizontal, with a pointed lateral apex. The external margin is rough. The tip of the narrow, long rostral process of the lacrimal is wedged between the nasal and maxilla and dorsally bounds more than the half of the antorbital fossa. The caudal portion is short, wider than the rostral; it has the subrectangular shape and bounds dorsally the rostral half of the orbit. This portion of the lacrimal overlaps a relatively large lateral portion

of the frontal. As preserved in GIN 100/24 and 25, a small caudolateral angle of the lacrimal extends outwards, slightly beyond the orbital margin of the frontal. As seen on the broken surface of the lacrimal shaft in the ZPAL MgD-I/97, at least its dorsal portion was pneumatized, and there is a small ventral aperture at the base of the horizontal portion. This aperture is located above the much larger, funnel-like 'lacrimal canal' visible on the caudal surface of the shaft. The lacrimal recess seems to extend also into the base of the rostral process of the dorsal horizontal portion of the lacrimal. As seen from the side, the shaft is straight for most of its length. In the caudal view, however, it is arched dorsomedially. The shaft is narrow in the sagittal direction and expanded transversely. Its surface facing the antorbital fossa is excavated. This excavation extends dorsally and rostrally along the roof of the antorbital fossa. Ventrally, the concavity on the shaft becomes deeper, and close to the contact with the jugal it passes into a deep, funnel-like recess, which penetrates the base of the lacrimal ventrocaudally. The dorsal lacrimal-maxilla contact within the fossa is indistinct in all our specimens. The lacrimal shaft is well exposed medially in ZPAL MgD-I/97. This specimen shows that the ventral extremity of the shaft extends caudolaterally-rostromedially. The ventral end of the shaft has an extensive contact with the jugal and an inclined, triangular facet medially for contact with the palatine. In this specimen, there is no ventral contact with the maxilla, the maxillary process of the jugal separating these two bones ventrally.

**Postorbital.** — The triradiate postorbital forms most of the caudal boundary of the orbit in GIN 100/25, but not in PIN 3143/8, in which the jugal bounds most of the caudal orbital margin. The frontal process of the postorbital is directed dorsally and medially, and its end contacts the frontal above and the laterosphenoid below. Contact with the frontal is much more extensive than with the laterosphenoid. The medial flexion of the frontal process is almost at right angles to the squamosal process. The latter process deviates caudally  $20^{\circ}$ – $30^{\circ}$  from the longitudinal axis of the skull to help form the short, laterally bowed supratemporal arcade.

**Squamosal.** — The squamosal has four prominent processes: the ventral (= prequadratic) process, the caudal (= paroccipital) process, the rostral (= postorbital) process and the medial (= parietal) process. The prequadratic process is relatively short and subtriangular. Its extensive, oblique caudoventral edge contacts a triangular rostrolateral flange of the quadrate (Figs 1A, B, 4A). The ventral apex of this process also has a short contact with the ascending process of the quadratojugal (see below). On the occipital surface of the skull, the caudal process is well exposed dorsal to the opisthotic. It slopes slightly caudoventrally in lateral view. Rostrally, the postorbital process diverges from the long axis of the skull at an angle of about  $35^{\circ}$ . The parietal process is directed rostromedially and slightly ventrally, and invades a narrow sulcus on the parietal, above the ventral contact of the latter bone with the prootic. It forms the ventral part of the steep caudal wall to the supratemporal fossa. The angle between the parietal and postorbital processes is about  $80^{\circ}$ . The cotyla for the head of the quadrate is not well exposed. A sharp crest extends along the lateral surface of the squamosal, which caudally transforms into a shelf overhanging the prequadratic process and extends lateral to the quadrate cotyla.

**Quadrate.** — The quadrate seems not pneumatic and has a single-headed otic process. In lateral aspect, the ventral third of the quadrate shaft is perpendicular to the ventral margin of the skull. More dorsally, the shaft inclines somewhat backwards. Close to mid-height, the rostrolateral edge of the shaft expands into a large, triangular flange directed rostrally and slightly medially. The rostdorsal margin of this flange contacts, along its almost entire extent, the prequadratic process of the squamosal, except rostrally where a tip of the quadratojugal inserts between these bones. The head of quadrate is narrow. In caudal view, the shaft of the quadrate is bowed to produce a concave lateral edge which forms the medial boundary to the large, tall paraquadratic (= quadrate-quadratojugal) foramen. The mandibular process is transversely expanded and is divided into mandibular condyles by a shallow groove. The lateral condyle is larger than the medial one, and bears the mediolaterally extended articular surface. The articular surface on the medial condyle is oriented obliquely (rostromedially-caudolaterally) to the median axis of the skull. The mandibular articulation projects a little below the alveolar margin of the maxilla.

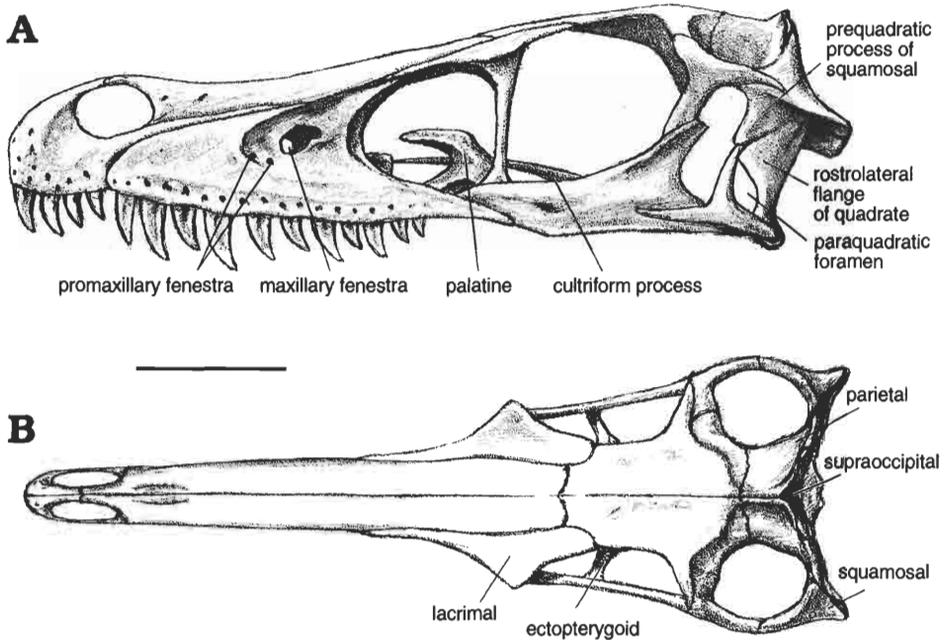


Fig. 4. Reconstruction of skull in *Velociraptor mongoliensis* in lateral (A) and dorsal (B) views. Scale bar 4 cm. Drawn by K. Sabath.

**Quadratojugal.** — The quadratojugal has the shape of an inverted *T*, which is characteristic of the dromaeosaurids (Paul 1988). It has two widely separated contacts (the dorsal and the ventral one) with the quadrate. The ascending process of the quadratojugal is slender and bounds almost two-thirds of the infratemporal fenestra. The dorsal tip of this process fits between the prequadratic process of the squamosal and the triangular, rostrolateral flange of the quadrate. The ascending process delimits rostrally the paraquadratic foramen. Because of the slenderness of the ascending process, this foramen is well exposed also laterally, not only caudally as is the case in most theropods. As in all dromaeosaurids, the quadrate (= caudal) process of the quadratojugal is stouter than the ascending and jugal processes. Its contact with the quadrate is limited: in fact, only the rounded end of this process bears medially a flat articular surface which adheres to the mandibular process of the quadrate, just above the lateral condyle. The jugal process of the quadratojugal is thin, and wedges deeply into the jugal.

**Jugal.** — In lateral view, the ventral margin of the jugal is horizontal, continuing the line of the alveolar border of the maxilla. Along the rostral three quarters of the orbit, the ventral margin of the jugal flares out, to cover the surangular when the mandible is adducted. The suborbital margin of the jugal is slightly concave in GIN 100/25, but rather straight in GIN 100/24 and PIN 3143/8. The postorbital process of the jugal inclines strongly caudodorsally. Its length is unknown in GIN 100/24 and 25, in which the postorbital processes are damaged distally. In PIN 3143/8, the complete left postorbital process (presently, its tip is broken off) reaches the supratemporal arcade, and forms the entire rostral margin of the infratemporal fenestra. The long and relatively shallow maxillary process dorso-medially overlaps the jugal process of the maxilla, ending just in front of the ventral extremity of the lacrimal, forming a small portion of the ventral border to the antorbital fossa. The rostral apex of the maxillary process is entirely occupied on its lateral surface by the jugal pneumatic recess (Witmer 1997a), which deepens caudally and seems to penetrate the suborbital ramus of the jugal. The quadratojugal process is relatively long and shallow, and caudally has a wedge-like incision for the

quadratojugal. The medial surface of the jugal (exposed in ZPAL MgD-I/97) is angled along and below the ventral margin of the orbit to produce a strong ridge, which continues caudodorsally along the orbital margin of the postorbital process of the jugal. Rostrally, the maxillary process of the jugal has an extensive medial contact with the ventral extremity of the lacrimal. Part of this contact is also overlapped medially by the maxillary ramus of the palatine. Below the palatine–jugal contact, the suborbital ramus of the jugal is underlain by the tapering caudal extremity of the maxilla. The caudal extent of this contact is along the rostral third of the orbital margin. Rostral to the base of the postorbital process of the jugal, there is a large depression on the medial surface. At the rostral limit of this depression, the jugal process of the ectopterygoid abuts against the jugal.

The complete skull roof is known only in *Velociraptor* and *Deinonychus*, but frontals are known also in *Saurornitholestes* and *Dromaeosaurus*. The frontals are relatively short and broad between the orbits in *Dromaeosaurus*, and the orbital portion of the frontal is subequal in length to the postorbital one. The adorbital part of the frontal is more elongate in *Velociraptor*. In *Dromaeosaurus*, and possibly also in *Saurornitholestes* (fide Currie 1987), there is a slot in the rostrolateral margin of the frontal for the contact with the lacrimal, whereas the articular surface is wide and extensively overlapped by the lacrimal in *Velociraptor*. The holotype of *S. langstoni*, which includes both frontals, represents an individual of similar size to GIN 100/25 (the maximum widths across the frontals are somewhat over 60 mm in both specimens). The interorbital width of the paired frontals (measured just behind lacrimal contacts) is about 70% of the maximum frontal length in *Saurornitholestes*, but is only about 50% in *Velociraptor*. The caudal portion of the frontal is somewhat bulbous centrally in *Saurornitholestes*, but it is only very weakly convex in all skulls of *Velociraptor* at our disposal.

As in *Dromaeosaurus* (Currie 1995), the nasal in *Velociraptor* extensively overlaps the frontal, differing in this respect from *Saurornitholestes*, in which the nasal–frontal contact seems shorter. Parietals are fragmentary in *Dromaeosaurus*. A striking feature of the lacrimal in *Velociraptor* is its slender and greatly elongated rostral process (it reaches almost to the mid-length of the long nasal). Although the external edge of the lacrimal seems smooth in the holotype of *V. mongoliensis*, in all skulls at our disposal the orbital margin of the lacrimal is somewhat thickened and rough. The lacrimal in *Deinonychus* also has the long rostral process (Dr L.M. Witmer's personal communication 1999). The shape of the lacrimal attributed to *Utahraptor* is distinctive in dorsal aspect, because it lacks the lateral projection, and is rather rectangular (not triangular as in *Velociraptor* and *Deinonychus*). In *Dromaeosaurus* only fragments of the lacrimal are known. However, also in this genus the lacrimal does not contact the maxilla ventrally. Lack of the ventral lacrimal–maxilla contact is a common character of theropods, the rare exceptions known to us being *Eoraptor* (Serenó *et al.* 1993), *Syntarsus rhodesiensis* (fide Colbert 1989), *Ceratosaurus* (Gilmore 1920), *Allosaurus* (Madsen 1976) and *Compsognathus* (Ostrom 1978). The prefrontal is absent (or completely fused with the lacrimal) in *Velociraptor*, while it is a separate bone in *Deinonychus* and probably also in *Dromaeosaurus*. In the presumably embryonic dromaeosaurid skulls (probably representing *Velociraptor*) preliminary described by Norell *et al.* (1994), the prefrontal is absent, which according to these authors contradicts the idea that the prefrontal was fused to the lacrimal.

The squamosal process of the postorbital is almost parallel to the long axis of the skull in *Deinonychus* showing but negligible outward inflexion, while this process dis-

tinctly deviates in *Velociraptor*. This results in a different shape of the supratemporal fenestrae in both genera (see above). As noticed by Paul (1988), the dorsally directed frontal process of the postorbital is the character occurring both in *Velociraptor* and *Deinonychus*. Although the postorbital is unknown in *Dromaeosaurus*, the shape of the frontal suggests (Currie 1995) that the frontal process of the postorbital was dorsally directed, as in *Deinonychus* and *Velociraptor*. The axis of the frontal process is at a distinct angle to the axis of the jugal process in *Velociraptor*, this angle is much greater in *Deinonychus*. The pronounced dorsal direction of the frontal process is a character occurring in a few theropods (e.g., in oviraptorids, see Barsbold, Maryańska, & Osmólska in preparation), but seems extreme in the dromaeosaurids.

The squamosal is generally similar in *Deinonychus* to that in *Velociraptor*, but shows a few differences: in *Deinonychus*, the prequadratic process is longer and more slender, the caudal process is more inclined ventrally, the occipital exposure of the squamosal above the paroccipital process is shallower, and the angle between the axes of the parietal and postorbital processes is only  $60^\circ$  ( $80^\circ$  in *Velociraptor*). The squamosal in *Dromaeosaurus* has a much shorter caudal process than those of *Velociraptor* and *Deinonychus*. The far caudal extension of this process produces in *Velociraptor* (and probably also in *Deinonychus*) a shelf built of the squamosal and opisthotic, which extends behind, as well as laterally, to the cotyla for the quadrate head. It seems that this shelf was less extensive in *Dromaeosaurus* (Currie 1995: fig. 1a). The prequadratic process in *Dromaeosaurus* is longer and narrower than in *Velociraptor*, and has a more extensive contact with the ascending process of the quadratojugal. In this respect, the prequadratic processes are similar in *Dromaeosaurus* and *Deinonychus*. The distinctly quadriradiate shape of the dromaeosaurid squamosal is peculiar, due to its widely separate prequadratic and caudal processes, the axes of which are at about right angle to each other. In most theropods, these two processes are at an angle of less than  $90^\circ$ , or are subparallel. The prequadratic process of a similar shape occurs also in *Troodon* (Currie 1985), but, unlike dromaeosaurids, it does not contact the ascending process of the quadratojugal (Russell & Dong 1994).

The quadrate of *Deinonychus* is similar to that of *Velociraptor* (Dr. L.M. Witmer's personal communication 1999). In *Dromaeosaurus*, there is only a slight rostral extension of the lateral edge of the shaft (Currie 1995: fig. 4b) instead of the large, triangular rostrrolateral flange characteristic of *Velociraptor*. Colbert & Russell (1969) emphasised that the mandibular articulation was well below the alveolar margin of the maxilla. This has been confirmed by Currie's reconstruction of the skull (1995: fig. 1a). The ventral projection of the mandibular articulation seems shallower in *Velociraptor*. The preserved portion of the left quadrate of *Saurornitholestes* shows a slight difference in the more oblique course of the intercondylar groove. The troodontid quadrate is poorly known. According to the schematic illustration of *Sinornithoides youngi* published by Russell & Dong (1994: fig. 3), the rostrrolateral flange is absent in this troodontid species. Unlike *Velociraptor*, the quadrate is pneumatic in troodontids (Currie & Zhao 1994). Within the Dromaeosauridae, the quadratojugal, especially its ascending process, is stoutest in *Dromaeosaurus*. In this genus, the ascending process has more extensive contacts with the quadrate process of the squamosal and the rostrrolateral flange of the quadrate. In *Deinonychus*, the ascending process is about as

slender as in *Velociraptor*, but its contact with the rostralateral flange of the quadrate is less extensive.

Note that in Ostrom 1969b: fig. 11, the quadratojugal is erroneously oriented and should be turned about 90° counter-clockwise on fig. 11a, and clockwise on fig. 11b. In fact, fig. 11 shows the right quadratojugal, not the right reversed as stated in the explanation. The process on which the articular surface for the jugal is indicated represents the ascending process of the quadratojugal, and this surface is not for the jugal but for the contact with the rostralateral flange of the quadrate. Consequently, the process directed upwards on the figure in question is the jugal process of the quadratojugal.

The nature of contact of the ascending process of the quadratojugal with the squamosal and quadrate is peculiar in *Velociraptor*, because it looks as if it were not rigid. Ostrom (1969b: p. 24) has also drawn attention to the fact that in this place the contact between the two bones 'does not appear to be a particularly solid union', although, due to his erroneous orientation of the quadratojugal, he regarded this contact as the 'clasping junction' of the quadratojugal and jugal. Because of the slenderness of the ascending process, the paraquadratic foramen is larger in *Velociraptor* than in *Dromaeosaurus* (and probably also *Deinonychus*). As observed by Paul (1988), the large paraquadratic ('quadrate') foramen is characteristic of the Dromaeosauridae. In most theropods the quadratojugal has a more extensive contact with the quadrate. In *Dromaeosaurus*, the end of the quadratojugal twists around the quadrate onto its caudal surface, as it does in most theropods. This is not the case in *Velociraptor*. In the troodontids, the quadratojugal is L-shaped and its ascending process does not reach the prequadratic process of the squamosal (Russell & Dong 1994). In the ornithomimids, the quadratojugal, as well as the entire infratemporal region, are not comparable with those of dromaeosaurids. Although the quadratojugal is also slender and reduced in the oviraptorids, and has a contact with the squamosal, it is rather L-shaped, and its ascending process attaches to the caudolateral margin of the quadrate, leaving only a small and caudally facing paraquadratic foramen. The contact of the quadratojugal with the quadrate is of the cotyla-condyle type in the oviraptorids (Maryńska & Osmólska 1997). The jugal of *Velociraptor* is similar to those of *Deinonychus* and *Dromaeosaurus*. However, in the latter genus, the ventral margin slopes slightly caudoventrally, and unlike *Velociraptor* does not continue the horizontal line of the alveolar border of the maxilla as does the ventral border of the jugal in *Velociraptor* (the maxilla and jugal are disarticulated in *Deinonychus*). Presence of the jugal pneumatic recess in *Deinonychus* has also been reported by Witmer (1997a).

## Occiput and braincase

Most of the bones forming the occiput and basicranium are fused. The occipital condyle is round and about as wide as the foramen magnum (Figs 2A, 5), although its depth is about a half of the vertical diameter of the foramen magnum. The major part of the condyle is formed by the **basioccipital**. The ventral articular surface of the condyle is well developed. The condylar neck is short. The basal tubers are well separated from each other by a deep broad sulcus. Damage to one of the tubers in GIN 100/25 shows that the basioccipital is pneumatic. The lateral and dorsomedial contacts of the **supraoccipital** with the parietals is well defined. This bone is roughly subrectangular and abuts dorsally against the caudal surface of the upturned parietals, participating in the formation of the central part of the transverse nuchal crest. Some distance above the level of the foramen magnum the supraoccipital bears a pair of vertical, crescent grooves. They apparently do not lead to any foramen. Sutures between the

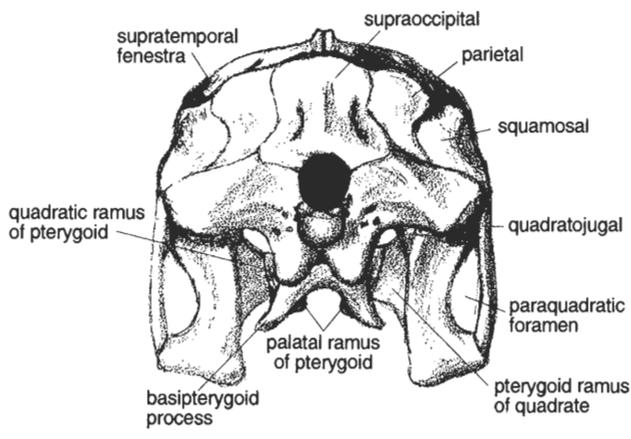


Fig. 5. Reconstruction of skull in *Velociraptor mongoliensis* in occipital view. Scale bar 4 cm. Drawn by K. Sabath.

supraoccipital and **exoccipitals** are obscure. The paroccipital process is stout, ends bluntly and is oriented almost entirely laterally with only a slight downward inclination. Distally, the end of paroccipital process is twisted and faces dorsocaudally. The dorsal contact of the exoccipital with the parietal and squamosal is distinct, but the sutures with the basioccipital and opisthotic are not discernible. Lateral to the foramen magnum three foramina pierce the exoccipital: two are the exits of cranial nerve XII, the third is probably for cranial nerve X (and most likely IX and XI).

**Basisphenoid + parasphenoid.** — Most of the basisphenoid contacts are not discernible, and the parasphenoid is fused with the basisphenoid. In front of the basioccipital tubera, there is a deep basin ventrally – the basisphenoid recess – that is bounded rostrally by a massive crest of bone from which extends rostrally the parasphenoid. Caudal to the basisphenoid recess, a pair of openings is visible in GIN 100/24 (this region is poorly displayed in GIN 100/25), which lead deep into the basisphenoid. They resemble the auditory tube foramina of birds, but their far caudal position would speak against such an interpretation. The crest which bounds rostrally the basisphenoid recess is continuous laterally with the basipterygoid processes, which project rostroventrally and laterally. The basipterygoid process is stout, and ends bluntly. Its medial side is entirely covered by a rough articular surface for the palatal ramus of the pterygoid, while the rostradorsal surface contacts the quadrate ramus. On the dorsal surface of the base of the basipterygoid process there is an extensive basipterygoid recess (Witmer 1997b). More dorsally, there are two smaller excavations close to base of the parasphenoid rostrum (Fig. 6B). The more caudal of the two might have contained the entrance to the carotid canal, but preservation of this region is too poor to be sure whether there was an opening within the excavation. The parasphenoid rostrum is broken off distally in all specimens at our disposal. Its preserved proximal portion bears a shallow, longitudinal sulcus dorsally, whereas ventrally, at the base of the rostrum, there is a concavity – the subsellar recess (Witmer 1997b).

The braincase is short but deep in *Velociraptor*. Its lateral wall is not well displayed in specimens GIN 100/25 and 24. As the brain cavity could not be studied in the specimens in our disposal, the following interpretation of the openings on the lateral wall of the braincase is tentative (Fig. 6). As in the occipital region, only a few contacts between the bones are distinguishable, but include those of the **laterosphenoid**. The rostradorsal process of the laterosphenoid forms a laterally curved cone, and its tip has rostrally a lateromedially elongate, well finished and convex articular surface. This process, along with the frontal, participates in the lateromedially elongate fossa for the postorbital. The bottom of this fossa is smooth. The nature of the dorsal articulation between the postorbital and the skull roof speaks in favour of a certain mobility of the postorbital at this contact. Caudally, the laterosphenoid–frontal suture is continuous with the laterosphenoid–parietal suture. Farther caudally, the

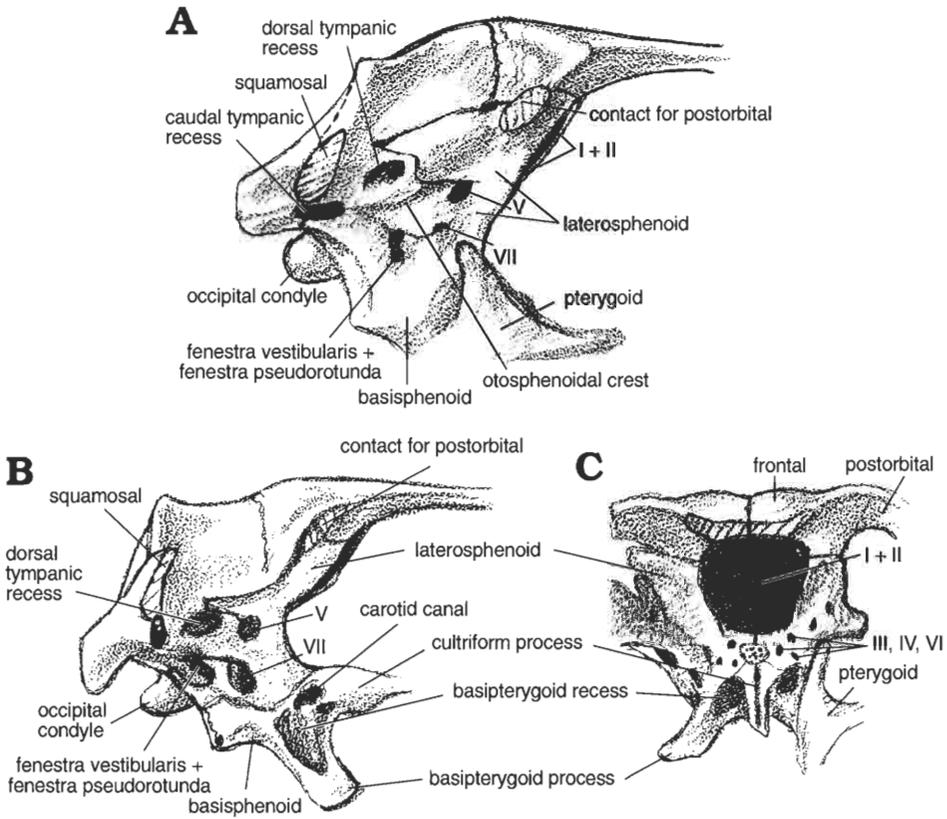


Fig. 6. Schematic drawing of braincase in *Velociraptor mongoliensis*. A. Lateral view, GIN 100/25. B. Dorsolateral view, GIN 100/24. C. Rostral view, GIN 100/24. I–V, VII – nerve exits. Not to scale. Drawn by K. Sabath.

latter suture is continued by the parietal–prootic suture, which slopes ventrally towards the back of the braincase. The caudal contact of the laterosphenoid is with the dorsal portion of the **prootic** along a distinct dorsoventral, zigzag suture. Just behind its contact with the laterosphenoid, the dorsal wing of the prootic bears a large, elongate depression. This depression is present in GIN 100/25 and 24 and it probably represents the dorsal tympanic recess. The rostroventral contact of the laterosphenoid with the prootic is not clearly marked, and it is unknown how far rostrally this contact continues. The otosphenoid crest is well pronounced. Below it, three openings pierce the prootic in GIN 100/25. The most rostral and dorsal one represents the exit of the trigeminal nerve; it is large, placed within a shallow concavity (there is a pair of openings in this position on the left side of the braincase), and is bounded dorsally by the laterosphenoid and caudally by the prootic. A horizontal groove runs rostral to this opening, which might conduct the ophthalmic branch of the trigeminal nerve (Currie 1995). A vertical groove runs ventrally from the exit of the fifth nerve. Caudoventral to this opening, another, much smaller one is visible in GIN 100/25. It is probably for the exit of the facial nerve. This opening is much larger in GIN 100/24 and may represent the prootic recess (Witmer 1997b) which probably contained the exit of the facial nerve. The third of these openings is most ventral and most caudal in position. It is large and vertically elongated and may correspond to the fenestra vestibularis + fenestra cochlearis. This opening seems to be bounded ventrally by a narrow tongue of the basisphenoid, rostradorsally by the prootic and caudodorsally by the opisthotic. In GIN 100/25, on the rostral surface of the paroccipital process and at its base, ventral and somewhat medially to the

quadrate cotyla, the opisthotic is pierced by a large, longitudinally extended fenestra, the caudal tympanic recess. In GIN 100/24, there is only a depression in this position. As preserved, the exits of optic nerves are confluent with that for the olfactory stalk to form a large, rostrally facing fenestra. The laterosphenoids meet rostrally on the mid-line of the braincase to form a dorsal portion of the caudal wall of the pituitary fossa. On each side, this wall is pierced by three small foramina (Fig. 6C). The most lateral of them, placed rostrally to the exit of the trigeminal nerve, may represent the exit for the abducens nerve (Currie 1995). Two others may correspond to exits of the trochlear and oculomotor nerves.

The occiput and the lateral braincase wall are known in *Dromaeosaurus*. The condylar neck is more pronounced in this genus than in *Velociraptor*, and the basal tubera are separated less distinctly. The tubera were considered by Colbert & Russell (1969) as lacking sinuses, but these are present in *Velociraptor*. The proportions of the braincase seem to be similar in both genera, although compared to the total skull length, the basicranium is shorter in *Velociraptor*. The basiptyergoid processes extend ventrally only to the level of the basal tubera in *Dromaeosaurus*. In *Velociraptor*, they extend farther ventrally, being well exposed in the occipital view. The dorsal surfaces of basiptyergoid processes are not preserved in *Dromaeosaurus* (Colbert & Russell 1969: fig. 5), thus it is impossible to state whether the basiptyergoid recesses were present, but the subsellar recess, as well as the basisphenoid recess, are pronounced in this genus; the basisphenoid recess is much deeper than this in *Velociraptor*. The depression on the prootic, here interpreted as the dorsal tympanic recess, seems homologous to the depression on the prootic in *Archaeopteryx* (see also Witmer 1997b).

## Palate

The palate is not seen in GIN 100/25 and is poorly displayed in GIN 100/24, because it is partly obscured in both specimens by the mandibles forced into the skull. The palate has also been crushed in the holotype and strongly damaged in PIN 3143/8. Only in ZPAL MgD-I/97 are some remains of the palate visible (Figs 7E, 8), although their mutual position is somewhat distorted due to the lateral flattening of the snout. The secondary palate is narrow and relatively highly vaulted, due to the inclinations of the palatal shelves of maxillae. This inclination increases caudally and so does the vault of the palate. Most probably, the palatal shelves of the maxillae did not suture to each other, being separated by the vomers. Any reconstruction of the shape of the exochoanal fenestra is impossible because of the lateral flattening of the snout in ZPAL MgD-I/97.

**Pterygoid.** — The pterygoid is a thin bone that is broken in the available specimens. It does not differ from other theropods. The basiptyergoid notch is deep, narrow and faces caudodorsally.

**Ectopterygoid.** — The ectopterygoids are exposed dorsally in GIN 100/25, and the left ectopterygoid has been found articulated in ZPAL MgD-I/97. This bone has a typical theropod shape, with a pocketed medial portion, and a slender, arched jugal process. The pterygoid margin of the ectopterygoid is thin and long, and the ectopterygoid–pterygoid contact is extensive. The caudal extremity of the ectopterygoid is overlapped laterally by the caudal end of the palatine. In ZPAL MgD-I/97, due to lateral compression of the skull, the ectopterygoid seems to be pushed medially onto the lateral surface of the pterygoid, without damage to the delicate adjoining bones. It has also been shifted slightly caudally and its caudomedial corner has been displaced and moved opposite the region of the basiptyergoid articulation. The pocketed portion of the ectopterygoid has its caudal margin broken. The pocket (ventral ectopterygoid recess, see Witmer 1997a) is elongate and includes two depressions separated by a wide but low elevation. As preserved, the recess faces medially, although originally, it might have faced more ventrally. The dorsal ectopterygoid recess has not been found in any of our specimens, but its absence may be due to inadequate preservation. The jugal ramus contacts the jugal behind mid-length of the ventral orbital margin.

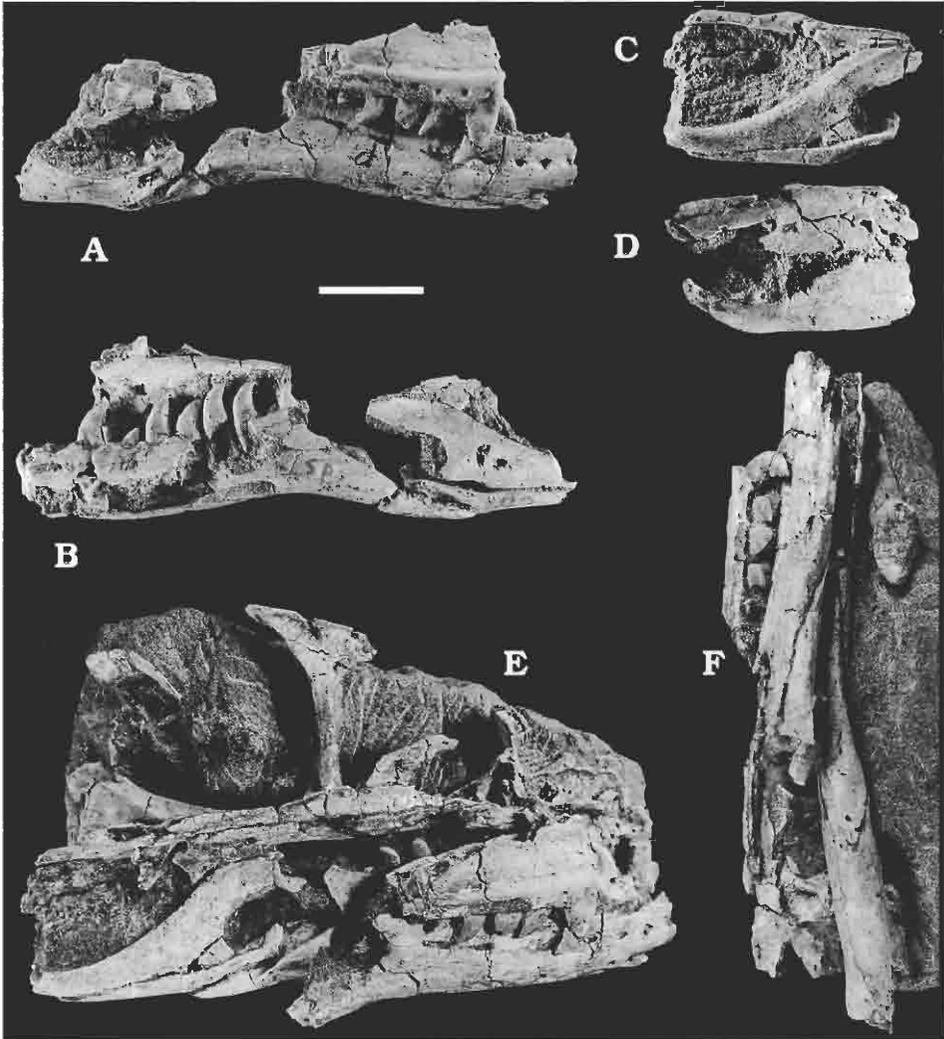


Fig. 7. *Velociraptor mongoliensis*, ZPAL MgD-I/97. A. Right mandible with fragment of maxilla, labial view. B. The same, lingual view. C. Caudal fragment of left mandible, lingual view. D. The same, labial view. E. Medial view of left half of fragmentary skull with mandible; fragments of right maxilla and dentary articulated and visible in lateral view. F. Same specimen, ventrolateral view; proximal surface of a pedal ungual visible to the right. Scale bar 2 cm.

**Palatine.** — The palatine is tetradiate and thin, except for its hatchet-shaped choanal process, which is more massive and has a thickened exochoanal margin (Fig. 8B, C). The palatine is steeply inclined, raising medially, the choanal process extending well dorsal to the pterygoid (Figs 1A, 4A). As a result, the exochoanal fenestra lies also in an inclined plane. Dorsal margins of the choanal processes of the opposite palatines meet well dorsal to the palatal rami of pterygoids. The maxillary process of the palatine is short, and bounds laterally less than the caudal half of the exochoanal fenestra. Close to its caudal end, the palatine abuts against the well pronounced subtriangular surface present on the medial surface of the lacrimal shaft, just above the contact of this latter bone with the jugal. Medially and dorsally to the maxillary contact, there is a relatively large palatine recess (Witmer

1997a) on the dorsal surface of the palatine, which is confluent with the floor of the antorbital fossa. This recess is bounded rostrally and caudally by thickened ridges that converge into the roller-like ridge reinforcing the caudomedial part of the exochoanal margin. Caudal to the lacrimal contact, the palatine protrudes into a long pterygoid process, the end of which covers the ectopterygoid dorsally. Both the suborbital and pterygopalatine fenestrae are present, although they are relatively narrow, because of the narrowness and strong vaulting of the mouth cavity.

**Vomer.** — The vomer is fragmentary in all specimens at our disposal. Its rostral section is visible in ZPAL MgD-I/97 (Fig. 8A), although the most rostral tip of the vomer is broken off in this specimen. In this specimen, the vomer is distinctly paired along its preserved rostral part. Each half extends slightly laterally, but medially they tightly adhere to each other, forming together a stout, elongate structure, that is ventrally flat and plough-like in lateral view. In ventral view, this structure has a subrhomboidal shape and bears a distinct sagittal suture, whereas dorsally there is a deep, longitudinal groove between both halves of the vomer. Caudally, the pterygoid rami of the vomer become less tightly joined, shallower and flatten transversely. As found, the rostral portion of the vomer adheres to the medial margins of the palatal shelves of the maxillae, closing medially the hard palate up to the level of the rostral end of the maxillary fenestra. The vomer–maxilla contact was not firm, because, during preparation of ZPAL MgD-I/97, the right maxilla was easily detached from the vomer, with no damage being done to the bones. Moreover, the articular surfaces of these bones are well preserved and smooth. The right vomer is displayed in GIN 100/24, but is fragmentary.

The poorly displayed palate in the skulls at our disposal makes it difficult to compare it with the palates of other dromaeosaurids. The pterygoid is fragmentary, but it does not seem to differ significantly from that in *Deinonychus*. Ostrom (1969b) suggested that the dorsally expanded sheet of bone on the palatal ramus was in this genus an articular surface for the vomer. Our *Velociraptor* skulls show that this surface is rather for a free contact with the palatine. This seems to be confirmed by the fact, that once the *Deinonychus* palatine (YPM 5210) is placed in a steeply inclined position (similar to the palatine position in *Velociraptor*) its choanal process is located almost exactly opposite the above mentioned dorsal extension of the palatal ramus of the pterygoid. Ectopterygoids are known in *Deinonychus*, *Dromaeosaurus*, and *Saurornitholestes*. They are generally similar to that in *Velociraptor*. However, in the Mongolian genus, the pterygoid flange of the ectopterygoid lies in the same plane as the base of the jugal process, while both parts are at an angle to each other in *Deinonychus* and *Dromaeosaurus*. It does not seem that this difference is due to a deformation of the ectopterygoid in *Velociraptor*, but it may reflect the more steep position of the pterygoid flange. The medial margin of the ectopterygoid is longer in the Mongolian genus than in *Dromaeosaurus* and *Deinonychus*, due to its longer rostral (palatine) process. The ventral pocket (= ventral ectopterygoid recess: Witmer 1997a) seems to be also shallower than in the compared genera. This difference may be related to the smaller size (?younger age) of our individuals. The dorsal ectopterygoid recess, which was described by Sues (1978) in *Saurornitholestes* and which is also present in *Deinonychus* (Witmer 1997a), is missing in *Velociraptor* and *Dromaeosaurus*. As compared with the palatine in *Deinonychus* (Witmer 1997a: fig. 32), the exochoanal margin is thicker in the Mongolian genus, due to the presence of the reinforcing ridge, and the palatine recess is bounded also rostrally in *Velociraptor*. Because of the steep inclination of the palatine, its rostral portion is visible through the internal antorbital fenestra in all *Velociraptor* skulls at our disposal, except for the dorsoventrally flattened skull in GIN 100/24. The steep position of the palatine (Osmólska 1985) and the dorsal contact between the margins of the opposite choanal processes are observed in

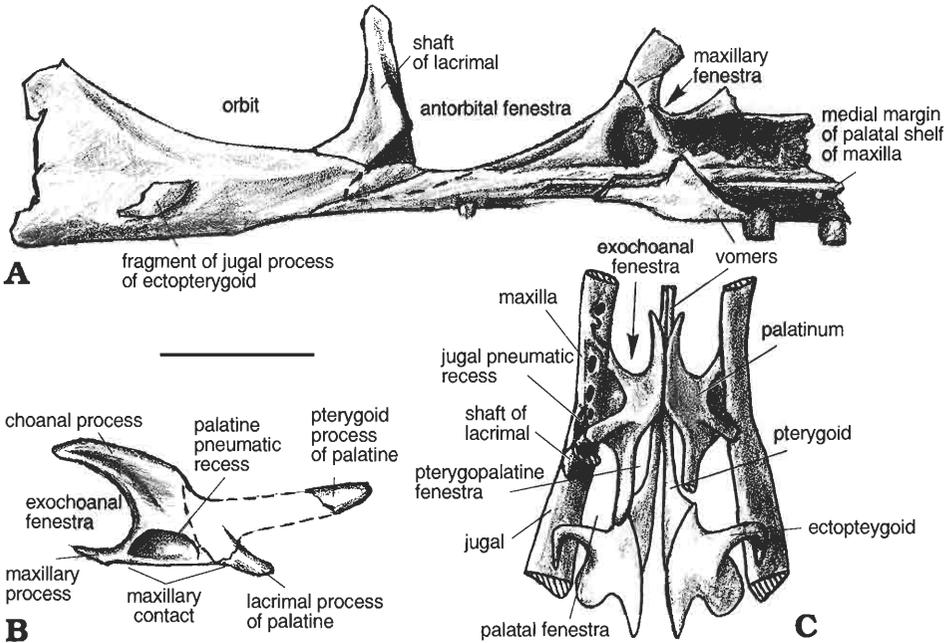


Fig. 8. *Velociraptor mongoliensis*, ZPAL MgD-I/97 (see also Fig. 7). A. Drawing of left half of fragmentary skull in medial view; surface for lacrimal contact of palatine delimited by broken line. B. Drawing of left palatine in dorsolateral view. C. Schematic reconstruction of palate in dorsal view. Scale bar 2 cm for A and B, C not to scale. Drawn by K. Sabath.

many theropods, resulting in a highly vaulted palate. Bones of the palate are disarticulated in *Deinonychus*. As reconstructed by Ostrom (1969b: fig. 5), the palatines are placed horizontally, contacting pterygoids and/or vomers with their medial margins. As a result, the palate in *Deinonychus* was reconstructed as being broad and flat. However, the very similar shapes of the palatine (and of other palate elements) in *Deinonychus* and *Velociraptor*, as well as the presence of the vertically extended contact surface on the palatal ramus of the pterygoid (possibly for the palatine, see above), provide evidence that the palatine was also inclined in *Deinonychus*. Thus, the palate was in fact vaulted and the skull much narrower than shown in the published reconstruction of this American genus. In perhaps all non-avian theropods, the vomers are indistinguishably fused rostrally, whereas in *Velociraptor* they are distinctly separate along their entire length. According to Ostrom (1969b), the paired construction of the rostral part of the vomer was marked by 'narrow dorsal and ventral grooves'. Although the most rostral (premaxillary) portion of the palate is not exposed in any of our specimens of *Velociraptor*, we assume that the vomers probably did not reach as far rostrally as in *Deinonychus* (fide Ostrom 1969b).

### Mandible

The mandibles are slightly damaged rostrally in GIN 100/25 but both rami seem to be naturally articulated in GIN 100/24 (see Barsbold 1983: fig. 13a). In all the specimens at our disposal, the mandibles are adducted and placed between the maxillae and premaxillae. In ventral view, the caudal ex-

termities of the mandibular rami curve towards each other, while the dentaries are almost parallel to each other. For most of their length the mandibular rami are close to each other. This is only partly due to a secondary lateral flattening, because the inter-ramal distance is also very small in the dorsoventrally flattened skull of GIN 100/24. In ZPAL MgD-I/97 (Fig. 7A–D, F), the mandibles have well exposed lingual sides, but lack rostral and caudal extremities. In PIN 3143/8, the left mandible is preserved to the very end, but bones are incomplete in many places. A relatively complete and well preserved lower jaw is known only in the holotype. It was described by Sues (1977a) and the description of bones that follows supplements Sues' data. At the tip, the mandibles lie inside the premaxillae in all specimens at our disposal. The mandible is slender and about twice as deep caudally as rostrally. In lateral view, the ventral mandibular margin is almost straight caudally, somewhat concave in the mid-length (along the splenial), and convex along the dentary. The external mandibular fenestra is shallow and elongate; its length equals about one-sixth of the total mandibular length. Caudal to this fenestra, there is a relatively large, longitudinally oval surangular foramen. Along the surangular, the dorsal mandibular border is flat, almost horizontal and wide; due to a medial eversion of the dorsal part of the surangular, the surangular ridge is prominent along the caudal third of the surangular length, and it overhangs the labial surface along the region of the surangular foramen. On the lingual side, there is a large Meckelian fenestra. In the mid-length, the mandible is divided by the intramandibular joint. The articular, angular, surangular and coronoid are incorporated into the caudal structural unit, while the splenial and dentary form the rostral one.

**Dentary.** — The dentary is shallow, its depth constituting only about 13% of its length. Both dentaries are parallel and close to each other for most of their length. In GIN 100/24, in which the symphyseal region is best preserved, the symphyseal articular surface extends almost in the longitudinal plane of the dentary and a narrow slit is left between the two opposing surfaces. There are two longitudinal rows of foramina on the dentary. The caudal margin of the dentary is oblique for most of its length, except dorsally where its short caudodorsal process contacts the surangular. The much longer caudoventral process is concave along its contact with the splenial ventrally, whereas dorsally it makes about a half of the rostroventral margin of the external mandibular fenestra. The tip of the caudoventral process fits into a shallow groove on the labial surface of the angular, just above the ventral contact of the latter bone with the splenial. On the lingual side, the alveolar margin is about on the same level as on the labial side. The lingual side of the dentary is well exposed in ZPAL MgD-I/97. It shows the Meckelian groove, which is rather wide, shallow, and runs close to the lower margin of the dentary. Just below the alveolar margin there runs a thin furrow, which fades away near the mid-length of the dentary; the rostral section of this furrow bears a row of tiny openings. No interdental plates were noticed. The lingual lamina of the dentary is damaged close to its caudal end in this specimen, but this region is broadly covered by a thin wing of the splenial in the holotype. A short portion of the ventral contact between the dentary and splenial is visible on the lingual side of the mandible; caudally, it passes onto the labial side, a narrow tongue of the splenial being visible here below the dentary and angular.

**Splenial.** — As in other dromaeosaurids, the splenial wraps ventrally around the angular, makes a short medial portion of the ventral mandibular margin and is exposed labially. This labial part of the splenial is narrow, subtriangular, and its rostral half dorsally contacts the dentary whereas the caudal one contacts the angular. On the lingual side of the mandible, the splenial is deep rostrally. Caudally, the lingual sheet of the splenial is deeply incised by a V-shaped notch resulting in formation of a short, thin dorsal flange and a long, stout, caudally tapering ventral (= angular) process. Most of the dorsal surface of the latter process is slightly concave transversely, but towards its end, this surface becomes convex, displaying two articular facets for contact with the angular. These facets are at an angle to each other; the medial one is narrow and steep, whereas the lateral is broad and only slightly inclined lateroventrally. The dorsal flange of the splenial covers medially the caudodorsal portion of the dentary and its margin reaches up to the bases of the last 2–3 teeth. The splenial–dentary contact is extensive here. The splenial–prearticular contact is not visible in GIN 100/25 and damaged in ZPAL MgD-I/97. However, this region looks almost intact in GIN 100/24, and it shows that margins of these two bones come very close to each other, but do not contact (contrary to Sues 1977a).

**Angular.** — On the labial side, the angular is shallow below the external mandibular fenestra, constituting here less than a quarter of the total caudal depth of the mandible. It deepens immediately behind the fenestra, narrowing again along its caudal extremity. The angular–surangular suture is easily visible. The stout, lateromedially extended splenial process of the angular rises rostrorodorsally and its end bears laterally a shallow groove for the tip of dentary. On its ventromedial surface this process has a broad, shallow and relatively long concavity that accommodates the angular process of the splenial. This articular surface is smooth, broader and longer than the respective process of the splenial; its lateral border is somewhat elevated. On the lingual side, the angular is shallow and is exposed below the prearticular. Its rostral portion overlaps the latter bone medially, and more caudally it underlies the ventral border of the prearticular. Mutual relations between the articular surfaces of the splenial and angular might allow some passive rotation of the tooth-bearing portion of the lower jaw. Rostrocaudal sliding was probably also possible; flexion of the rostral segment of the mandible at the angular–splenial joint does not seem likely, because contact between the two bones seems too long.

**Prearticular.** — Prearticulars are visible in all *V. mongoliensis* mandibles at our disposal. In ZPAL MgD-I/97 they are best displayed, but their caudal extremities are broken off. In this latter specimen, the rostral margin of the thin, vertical prearticular blade is deeply embayed along the caudal boundary of the Meckelian fenestra. The edge of the bone along the embayment is thin, unfinished and might be continued by an unossified membrane (Barsbold 1983). The contact with the angular seems to be loose rostrally, because, within both mandibular rami the thin, vertical blade has its ventral margin slightly displaced laterally, and separated from the dorsomedial edge of the angular by a narrow space filled with sediment. Close to its caudal end, the prearticular curves medially and it seems to be fused with the articular in GIN 100/24 and 25.

**Coronoid.** — The small, triangular coronoid is visible in ZPAL MgD-I/97. It has a sharp dorsal margin and is sandwiched between the prearticular and a thin plate of bone, which may be either a portion of the broken dorsal margin of the surangular or the caudodorsal end of the dentary. The rostral corner of the coronoid has a narrow long furrow, parallel to the dorsal margin of the prearticular.

**Surangular.** — The maximum length of the surangular is only somewhat less than that of the dentary. The dorsal half of the caudal margin of the external mandibular fenestra is formed by the surangular. At the end of the mandible, the surangular does not cover its entire labial surface and a narrow portion of the prearticular is visible just above the ventral margin. The surangular is pierced by a relatively large surangular foramen. The dorsal rim of the surangular is inflected medially along the dorsal boundary of the adductor fossa. It results in a flat, or even slightly concave broadening of the mandibular border. More rostrally, the dorsal surangular margin becomes sharp. Contact with the dentary along the dorsal mandibular border is not seen in our specimens. This contact is not visible in the holotype either (Sues 1977a: fig. 2).

**Articular.** — The articular region is either poorly seen or lost in our specimens, but it shows the short retroarticular process with a concave, weakly caudoventrally inclined dorsal surface. The very end of the retroarticular process is vertical, lateromedially wide and slightly concave. The dorsomedial vertical process seems short and dorsomedially inclined.

The exact size of the external mandibular fenestra is not known in *Deinonychus*, but it was probably similarly long. The fenestra is much smaller, only about one tenth of the mandibular length, in *Dromaeosaurus*. The resemblance between the lower jaws in *Velociraptor* and *Deinonychus* has been noticed by Paul (1988). The dentary in these two genera is less robust than that in *Dromaeosaurus*. The *Velociraptor* dentary differs from *Deinonychus* and *Dromaeosaurus* dentaries in having a convex ventral margin, but the *Saurornitholestes* dentary is also weakly convex (Sues 1977b: fig. 1). Splenials in *Velociraptor*, *Deinonychus*, *Saurornitholestes* and *Dromaeosaurus* are similar in every respect. The caudoventral (= angular process) of the splenial is concave along the articular surface for the angular in all dromaeosaurids, in which it resembles the respective

process in *Herrerasaurus*. In *Dromaeosaurus*, the caudal margin of the caudodorsal extension of the splenial dorsally contacts the rostral margin of the prearticular, just as it does in *Velociraptor* (Barsbold 1983: fig. 13a). Contacts of the caudodorsal and caudoventral flanges of the splenial in *Deinonychus* is erroneously reconstructed by Ostrom (1969b: fig. 16), among others, the Meckelian fenestra not being marked. However, judging from the incised rostral margin of the splenial, identical with those in *Dromaeosaurus* and *Velociraptor*, this fenestra had to be present also in *Deinonychus*. Thus differences with the *Velociraptor* mandible may be less significant than implied by Ostrom's reconstruction. The angular in *Deinonychus* is similar, although the contact surface for the splenial and the floor of the Meckelian canal are shallower. In *Dromaeosaurus*, the angular is relatively shallower: it forms at most a third of the height of entire labial wall of the mandible. In this respect, it resembles more the angular in some carnosaurus. The most rostral portion of the prearticular is not preserved in *Deinonychus*. In *Dromaeosaurus*, the rostral embayment of the prearticular is less deep and the splenial process more stout. The coronoid is very similar in *Dromaeosaurus* and *Velociraptor*, although the furrow along the rostral margin seems to be lacking in the former. The coronoid is unknown in *Deinonychus*. The surangular in *Deinonychus* is represented by an isolated caudal fragment and it differs from this bone in *Velociraptor* in the presence of a ridge that projects medially along the dorsal border of the adductor fossa. The marginal portion of the surangular is well exposed medially in ZPAL MgD-I/97 and it is flat, devoid of any ridge. In *Dromaeosaurus*, the surangular is relatively deeper behind the external mandibular fenestra and it forms caudally a larger portion of the ventral margin. The surangular foramen is much smaller in this genus than that in *Velociraptor*. The articular in *Velociraptor* seems similar to the articular in *Dromaeosaurus*. A comparison of casts of the right surangular (YPM 5234) and the right articular (YPM 5232) of *Deinonychus* (the two bones may come from the same mandible, because they articulate perfectly with each other) with our specimens of *Velociraptor* shows that the articular on Ostrom's figure (1969b: fig. 22) is incorrectly oriented. The 'medial' surface of the bone (fig. 22a) is actually the ventral one, while that determined as lateral (fig. 22b) appears to represent, in fact, the slanting caudal extremity of the bone. The surface indicated on this figure as the 'area overlain by the surangular' was located dorsal to the tuber labeled by Ostrom as the insertion site of *m. depressor mandibulae*; presumably it faced caudodorsally, as in *Velociraptor*. This surface occurs in many theropods, e.g., in the Tyrannosauridae (Osborn 1912: fig. 4) and *Bagaraatan*, although it is rather vertical in the tyrannosaurids, and slants slightly in *Bagaraatan* (Osmólska 1996: fig. 2e, f).

## Dentition

There are four premaxillary teeth in all our specimens, and they are weakly curved. The two rostralmost teeth preserved in GIN 100/24 are of about equal size and nearly twice as long as the third and fourth teeth (Fig. 3A). The maxilla bears 11 teeth and within the rostral half of the tooth row, every second tooth is longer than the neighbouring teeth. As a result, the tips of the functioning teeth are separated by large spaces. The maxillary teeth are slender and caudally curved. Carinae of these teeth are poorly preserved and it is only possible to note that serrations on the mesial carina are distinctly smaller than those on the distal carina. The denticles on the mesial carina are strongly worn and cannot be measured. Those on the distal carina are better preserved, and there are nine denticles per 2 mm along the medial section of the carina. The dentary teeth cannot be counted in specimens at our disposal, because mandibles are forced under the skull. However, in the holotype the number of dentary teeth is 14 to 15.

In the Djadokhta Fm sediments at Bayn Dzak (= Shabarakh Usu), the type locality of *V. mongoliensis*, numerous shed dromaeosaurid teeth were found that most probably are teeth of this species. All are between 9 and 14 mm (usually 10 mm) long and 3–5 mm (usually 5 mm) wide across the base of the crown. Some of them (Fig. 2C) have preserved serrations on the mesial carina, but these are most easily visible along the distal portion of the crown; close to the tip, the serrations are worn off. In these teeth, the average number of denticles on the mesial carinae is 7 per 1 mm. The distal carina is thin and serrated, the number of denticles being, on the average, 5 per 1 mm. Denticles are somewhat more crowded close to the base of the crown. Some of these teeth have a wear facet on one side, which is located near the tip of the crown.

The interdental plates are indistinguishable in *Velociraptor*, their presence being probably obscured by fusion, as in other dromaeosaurids. However, the lingual margin of the tooth sockets is as high as the labial margin, which, as suggested by Currie (1995), may indicate that the plates are present.

In *Deinonychus*, there are four premaxillary and 15 maxillary teeth, and a maximum of 16 dentary teeth. The discrepancy between numbers of teeth in the upper and lower jaws is smaller (or, maybe, none) in *Velociraptor*, 13–15 teeth being present in the upper jaw and 14–15 teeth in the mandible. Sues (1977a) has counted only three premaxillary teeth in the holotype of *V. mongoliensis*. However, on all other specimens there are four premaxillary teeth as in other dromaeosaurids and in most other theropods. According to Sues (1977a) there are nine or ?ten maxillary teeth in the holotype of *V. mongoliensis*. Nine teeth are present in the maxilla of *Dromaeosaurus*.

## Discussion

Skulls in *Deinonychus antirrhopus* and *Velociraptor mongoliensis*, as well as in *Saurornithoides langstoni* were considered by Paul (1988) as much more similar to each other than either is to the skull in *Dromaeosaurus albertensis*, and consequently he assumed that *Deinonychus* and *Saurornitholestes* are junior synonyms of *Velociraptor*. This opinion has not been supported by Witmer & Maxwell (1996), who have studied new, more complete material of *D. antirrhopus*, and have drawn attention to some previously unknown features of this species. For example, they stated that the skull was more robust in *D. antirrhopus* than in *V. mongoliensis*. These new data on *D. antirrhopus*, as well as the redescription of *Dr. albertensis* by Currie (1995), have rendered invalid some evidence quoted by Paul in favour of his hypothesis, whereas others appear to be dromaeosaurid synapomorphies. For example, the nasal is not 'depressed' in *Deinonychus* (it is unknown in *Dromaeosaurus* and other dromaeosaurids), the maxillary alveolar border is also slightly convex in *Dromaeosaurus* (Currie 1995: figs 1, 2), the cross-section of the lacrimal shaft is also U-shaped in *Utahraptor* (and in some other theropods; the shaft is not preserved in *Dromaeosaurus*; the lacrimal is unknown in *Saurornitholestes*), the quadratojugal also has the inverted T shape in *Dromaeosaurus*, and, as deduced by Currie (1995), the frontal process of the post-orbital was also upturned in *Dromaeosaurus*.

Our present study has farther increased the number of differences between *V. mongoliensis* and *D. antirrhopus*. In the latter species, the maxilla is more robust, the antorbital fenestra is longer and distinctly triangular, the supratemporal fenestra is narrower but longer, and is bounded laterally by the straight supratemporal arcade. In *V. mongoliensis*, the supratemporal arcade is laterally bowed and the fenestra is sub-

circular; this difference in shape most probably reflects a difference in the action of adductors in *D. antirrhopus* and *V. mongoliensis*. This seems to us of taxonomic importance, speaking for the separation of the two species at the generic level. The taxonomic status of *S. langstoni* remains unclear until the description of better material. Consequently, we agree with Witmer & Maxwell (1996) that *Deinonychus* is a valid genus. The greater number of maxillary teeth in *Deinonychus* (15, versus 11 in *Velociraptor*) may be an equivocal character, because the so far known *Deinonychus* skulls are larger than those in *Velociraptor*. However, it is unknown whether the tooth count correlated with size in dromaeosaurids.

Two subfamilies, the Dromaeosaurinae (with *Dromaeosaurus*, *Adasaurus* and *Deinonychus*) and the monotypic Velociraptorinae, have been recognised by Barsbold (1983) within the Dromaeosauridae. Later, basing upon distribution of 27 characters among the dromaeosaurids and some other theropod taxa, Currie (1995) concluded that *Deinonychus*, *Saurornitholestes*, and tentatively *Utahraptor*, should also be assigned to the Velociraptorinae. His opinion on the velociraptorine affinity of *Deinonychus* has been supported by Witmer & Maxwell (1996) and we have not found any evidence to falsify this hypothesis.

Currie (1995: pp. 587–588) recognised 15 dromaeosaurid autapomorphies among the skull and mandible characters (eighteen autapomorphic skull and mandible characters have been listed on pp. 590–591), but a few of them appear equivocal to us. These are: long and shallow maxillary process of the premaxilla (Currie 1995: p. 587 – character 1) – it is a widespread feature among theropods (this character is not included in the matrix on p. 591); absence of the ventrally extended pterygoid flange (l.c.: p. 587 – character 9; p. 591 – character 16) – the ventral extension, such as that found in the ‘large’ theropods, is missing in many coelurosaurs (e.g., in the ornithomimids, troodontids, oviraptorids and *Avimimus*); presence of a palatine-ectopterygoid contact (l.c.: p. 588 – character 10; p. 591 – character 17) – the palatine contacts the ectopterygoid in at least the ornithomimids and oviraptorids; presence of the caudal tympanic recess (l.c.: p. 587 – character 7; p. 591 – character 15) – Clark *et al.* (1994) rightly quote this character among tetanuran synapomorphies. The following apomorphic character states are absent in *Velociraptor* and cannot be considered as synapomorphies of the Dromaeosauridae: relatively short basiptyergoid processes, not extending ventrally beyond the level of the basal tubera (l.c.: p. 587 – character 8) – these processes extend well below the basal tubera in *Velociraptor*; slot-like frontal-lacrimal contact (l.c.: p. 591 – character 8) – there is no vertical slot on this contact in *Velociraptor*, instead, the lacrimal extensively overlaps the frontal dorsally; tall and labiolingually thin dentary (l.c.: p. 588 – character 11; 591 – character 19) – the dentary is thick in relation to height in *Velociraptor*.

## Geographic and stratigraphic record of the Dromaeosauridae

The only dromaeosaurid material determinable on the generic level comes from the Upper Cretaceous deposits in the southern Gobi (Mongolia and China) and from western North America (Alberta, Montana, Oklahoma, Wyoming, Utah). Some indetermi-

nate, or doubtful, dromaeosaurid remains have been also reported (see: Weishampel 1990) from the Lower or Upper Cretaceous deposits of the United States (Utah, Colorado, New Mexico, Texas), Mexico (Estado de Baja California Norte, Estado de Coahuila), Uzbekistan and Kazakhstan (Nessov 1995). Dromaeosaurid or dromaeosaurid-like teeth, with denticles differing in size between the mesial and distal carinae, have been reported from the presumably Lower Cretaceous deposits (Xinminbao Formation) of the Gansu Province in China (Dong 1997). These may constitute the earliest dromaeosaurid record, not supported as far by any bone material. Supposedly dromaeosaurid teeth, the more precise taxonomic assignment of which is at the moment impossible, have been found also in the European Upper Cretaceous deposits (France: Buffetaut *et al.* 1986; Romania: Grigorescu 1984; Csiki & Grigorescu 1998; Spain: Sanz & Frances in: Pol *et al.* 1992). As demonstrated by Howse & Milner (1993), the holotype sacrum of *Ornithodesmus cluniculus* Seeley, 1887 (England), determined by Seeley (1901) as belonging to a pterosaur, represents in fact a theropod. Contrary to Howse & Milner, who assigned *O. cluniculus* to the Troodontidae, Norell & Makovicky (1997), believe it should be placed within the dromaeosaurids.

Some small dromaeosaurid teeth have been reported from Alaska (Clemens & Nelms 1993) and Sudan (Rauhut & Werner 1995). The Sudan teeth are accompanied by some pedal phalanges and unguals; these remains constitute the first Gondwanan record of the Dromaeosauridae.

The stratigraphically oldest so far described dromaeosaurid species are known from North America (and from Europe, if the Barremian *O. cluniculus* is a dromaeosaurid, as suggested by Norell & Makovicky 1997). They are: the Barremian (Cedar Mountain Formation) *Utahraptor ostrommaysorum* Kirkland *et al.*, 1993, which is based upon fragmentary skull and postcranial material, and the Aptian–Albian (Cloverly Formation) *Deinonychus antirrhopus* Ostrom, 1969. *Velociraptor mongoliensis* Osborn, 1924 from Asia is younger, being found in deposits of the ?early and ?late Campanian age (Djadokhta, Bayan Mandahu and Barun Goyot formations, and probably also the Minhe Formation). Two North American species, *Dromaeosaurus alber-tensis* Matthew & Brown, 1922 and *Saurornitholestes langstoni* Sues, 1978 (both from the late Campanian Dinosaur Park Formation, see Eberth & Hamblin 1993), are roughly contemporaneous with *V. mongoliensis*, while the poorly known Mongolian *Adasaurus mongoliensis* Barsbold, 1983 (the ?early Maastrichtian Bugeen Tsav beds; contemporaneous with the tyrannosaurid *Tarbosaurus bataar*) represents the stratigraphically youngest dromaeosaurid so far known. If the determination of the stratigraphic age of the Bugeen Tsav beds is correct, the Dromaeosauridae persisted in Asia until at least the early Maastrichtian. It should be added, that Dr. P. J. Currie (personal communication 1995) kindly informed us of unquestionable dromaeosaurid teeth which are common in the Maastrichtian beds of North America. Another Asian species, *Hulsanpes perlei* Osmólska, 1982, sometimes assigned to the Dromaeosauridae (Ostrom 1990), is of the late Campanian age (Barun Goyot Formation). However, this species is so far known exclusively from a single, slender metatarsus of an immature individual, and may represent either a dromaeosaurid or a troodontid (Osmólska 1982). Even if its assignment to the Dromaeosauridae is correct, it may represent a juvenile *V. mongoliensis*, both occurring in the same locality and strata. It should be mentioned, that among the still undescribed Asian theropod materials, there are remains

(including the skull) of a new dromaeosaurid species from Mongolia (Dr. A. Perle's personal communication 1992) and of a giant Lower Cretaceous dromaeosaurid from Japan (Azuma & Currie 1995).

*Phaedrolosaurus ilikensis* Dong, 1973, from the Chinese Lower Cretaceous Tugulo series of the Junggar Basin, was originally assigned to the Dromaeosauridae but has been considered a *nomen dubium* by Norman (1990). The second author saw in the IVPP collection a fragmentary femur attributed by Dong (1973) to *Ph. ilikensis*. This femur has a well developed wing-like anterior trochanter, different from the finger-like dromaeosaurid anterior trochanter (see also comments upon the status of *Ph. ilikensis* by Sues in 1977a).

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## **Czaszka drapieżnego dinozaura *Velociraptor mongoliensis* z późnej kredy Mongolii**

RINCHEN BARSBOLD i HALSZKA OSMÓLSKA

### **Streszczenie**

W pracy opisano czaszkę i żuchwę niewielkiego, mierzącego około 2 m długości, drapieżnego dinozaura z rodziny Dromaeosauridae, *Velociraptor mongoliensis* Osborn, 1924, oraz przedstawiono rozprzestrzenienie geograficzne i stratygraficzne tej rodziny. Badany materiał pochodzi z osadów kampanu (górna kreda) pustyni Gobi (Mongolia) i został zebrany przez mongolskie, polsko-mongolskie, radziecko-mongolskie i japońsko-mongolskie ekspedycje paleontologiczne w latach 1970–1997. Dromeozauroidy żyły w okresie kredowym w Ameryce Północnej i Azji Środkowej. Z sześciu do ośmiu monotypowych rodzajów zaliczanych do tej rodziny, tylko mongolski *Velociraptor* jest reprezentowany przez dość liczne i kompletne szkielety, pozostałe rodzaje oparte są na pojedynczych i bardzo fragmentarycznych szczątkach, zaś czaszki (znacznie mniej kompletne) znane są tylko u dwóch północnoamerykańskich rodzajów *Deinonychus* i *Dromaeosaurus*. Przeprowadzona w pracy analiza anatomiczna kilku czaszek *V. mongoliensis* i porównanie ich z czaszką wczesnokredowego *Deinonychus antirrhopus* Ostrom, 1969 wykazały, że nie ma dostatecznych podstaw do uznania nazwy rodzajowej *Deinonychus* za młodszy synonim nazwy *Velociraptor*, co było sugerowane przez niektórych badaczy (Paul 1988). Potwierdzono, że oba te rodzaje są ze sobą bliżej spokrewnione niż z innymi przedstawicielami dromeozauroidów.