Cranial morphology of *Sinornithosaurus millenii* Xu et al. 1999 (Dinosauria: Theropoda: Dromaeosauridae) from the Yixian Formation of Liaoning, China

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Abstract: The recent discovery of the early dromaeosaurid *Sinornithosaurus millenii* Xu et al. 1999 is especially important for our understanding of maniraptoran evolution, particularly of avian origins. This paper presents a thorough description of the skull of this species, revises the diagnosis based on cranial features, and discusses similarities to those of other dromaeosaurids and *Archaeopteryx*. Distinctive cranial characteristics of *S. millenii* include the presence of a deep excavation on the posteroventral margin of the premaxilla, a diastema between the premaxillary and maxillary teeth, a number of pits and ridges on the anterolateral surface of the antorbital fossa, long posterolateral process of the parietal that are sharply posteriorly directed, the column-like margin of the pterygoid process of the quadrate, the bifurcated posterior end of the dentary, and a distinctive groove posterior to the anterior carina on the lingual surface of the premaxillary tooth crowns. The present study on the skull of *S. millenii* provides new information on the poorly known cranial anatomy of dromaeosaurid dinosaurs, revealing that dromaeosaurids share more similarities with *Archaeopteryx* than previously thought. It also provides evidence suggesting that early dromaeosaurids are more bird-like than the later, more derived ones, thus contradicting claims that more bird-like dinosaurs appeared later in fossil record than the earliest birds.

Résumé : La découverte récente du dromæosauridé précoce *Sinornithosaurus millenii* Xu et al., 1999, est spécialement importante pour notre compréhension de l'évolution des rapaces, surtout ceux d'origine aviaire. Cet article présente une étude complète du crâne de cette espèce, révise le diagnostic crânien et discute de ses similitudes avec ceux d'autres dromæosauridés et d'*Archaeopteryx*. Les caractéristiques crâniennes distinctives de *S. millenii* comprennent la présence d'une excavation profonde sur la bordure postéroventrale du prémaxillaire, un diasthème entre les dents prémaxillaires et maxillaires, un certain nombre de creux et de bosses sur la surface antérolatérale de la fosse antorbitale et un long processus postérolatéral du pariétal qui sont nettement dirigés vers l'arrière, une bordure de style colonne du processus ptérygoïde de l'os carré, une extrémité postérieure bifurquée du dentaire et un sillon distinctif en arrière de la carène antérieure sur la surface médiale des couronnes des dents prémaxillaires. La présente étude sur le crâne de *S. millenii* fournit de nouvelles informations sur l'anatomie crânienne peu connue des dinosaures dromæosauridés, révélant que les dromæosauridés partagent plus de points en communs avec *Archaeopteryx* qu'on ne le croyait antérieurement. Cette étude fournit également des évidences voulant que les formes précoces des dromæosauridés ressemblent plus à des oiseaux que les formes plus tardives et plus dérivées, contredisant ainsi les allégations que des dinosaures ressemblant plus à des oiseaux sont apparus plus tard dans les gisements fossilifères que les oiseaux les plus précoces.

[Traduit par la Rédaction]

Introduction

Dromaeosaurids are small to medium-sized cursorial carnivores with the foot showing an exceptional raptorial talon and a stiff tail with unique rod-like extensions of prezygapophyses and chevrons. Traditionally, they have been regarded as very agile animals, but slower than most other coelurosaurians (Ostrom 1969; Currie 1997). Dromaeosaurids have attracted particular attention since the description of *Deinonychus* (Ostrom 1969), due to its pivotal role in supporting a theropod origin of birds. They, either by themselves or together with troodontids (Gauthier 1986; Holtz 1994; Makovicky and Sues 1998; Xu et al. 1999; Sereno 1999), have been regarded as most closely related to birds. However, dromaeosaurids as a group were poorly characterized because previously known specimens are either disarticulated or incompletely preserved (Norell and Makovicky 1998), until recent discoveries of a number of well-preserved specimens

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(e.g., Norell and Makovicky 1997, 1998; Barsbold and Osmolska 1999; Xu et al. 1999; Burnham et al. 2000).

The holotype and only known specimen of S*inornithosaurus millenii* was collected by an expedition of the IVPP (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences) in the summer of 1998, from the lower part of the Lower Cretaceous Yixian Formation at the famous Sihetun site, Beipiao City, Liaoning Province, northeastern China. The discovery of *S. millenii* is significant for the following reasons: first, it represents one of the most complete dromaeosaurid specimens found to date and greatly increases our knowledge of Dromaeosauridae; second, *S. millenii* has not only many derived *Archaeopteryx*-like postcranial features (Xu et al. 1999), but many troodontid-like features as well (Xu and Wang 2000), which are especially important for our understanding of maniraptoran evolution; and third, it provides evidence for the presence of a filamentous integumentary covering in the group.

Sinornithosaurus millenii probably represents the earliest dromaeosaurid yet discovered. Previously, the stratigraphically oldest described dromaeosaurid species were known from the Barremian of North America (*Utahraptor*; Kirkland et al. 1993) although a few dromaeosaurid-like teeth have been collected from the Middle Jurassic of southern England (Evans and Milner 1994). The lower Yixian Formation has been dated as Barremian in age by some radiometric analyses (about 125 million years ago; Smith et al. 1995; Sweisher et al. 1999), but has been suggested to be Late Jurassic in age by some other analyses (about 145 million years ago; Lo et al. 1999). Paleontological evidence also remains contradictory as some suggests an Early Cretaceous age (Xu and Wang 1998), but others date a Late Jurassic age (Ji et al. 1999). The proposed age of the *Sinornithosaurus*-bearing beds ranges from 145 to 125 million years ago. As probably the oldest known dromaeosaurid species, *S. millenii* is important for understanding the temporal setting for character distribution among dromaeosaurids and maniraptorans. It shares more similarities with *Archaeopteryx* and other early birds than any temporally later dromaeosaurids. The contention that more bird-like dinosaurs appreared later in fossil record than the earliest birds (Feduccia 1999) is contradicted by the early age and more bird-like morphology of *S. millenii*.

In the present paper, we provide a detailed description of the cranial anatomy of *Sinornithosaurus millenii* and compare it with other dromaeosaurids and early birds. The study of the postcranial skeleton and a revision of the phylogenetic relationships of the species will be published elsewhere.

Material

The partially disarticulated skull of *Sinornithosaurus millenii* (IVPP V 12811) is nearly complete, preserving the premaxilla, maxilla, nasal, frontal, prefrontal, lacrimal, scleral plates, postorbital, parietal, quadrate, quadratojugal, parasphenoid, pterygoid, dentary, angular, surangular, splenial, hyoid, and possibly jugal, squamosal, palatine, and articular. Most elements of the palate and braincase are obscured by cracks and overlying bones.

Revised diagnosis (based only on cranial characters)

Sinornithosaurus millenii is diagnosized by the following autapomorphies: a deep excavation on the posteroventral margin of the premaxilla, a diastema between the premaxillary and maxillary teeth, a semicircular maxillary fenestra with a straight ventral margin, a large promaxillary fenestra, a number of pits and ridges on the anterolateral surface of the antorbital fossa, the posterolateral process of the parietal being long and sharply posteriorly directed, the column-like margin of the pterygoid process of the quadrate, a large excavation on the posterolateral surface of the parasphenoid process, the bifurcated posterior margin of the dentary, and a distinctive groove posterior to the anterior carina on the lingual surface of the premaxillary tooth crowns.

Description and comparison

The specimen represents an incomplete skeleton, with a nearly complete skull and mandible (Figs. 1, 2). The skull roof is preserved facing the opposite direction to the mandible and the rest of the skull. Most elements of the skull are disarticulated and preserved on an area of about 110 cm^2, but many elements of the palate and braincase are obscured by cracks and are overlain by other bones. Although most skull elements are disarticulated, they are well preserved, even with delicate processes and sharp edges being well preserved. These suggest that the skull bones were not fused together.

The skull is lightly built, with a shallow, about 75 mm long, snout and a large, dorsally inflated braincase (Figs. 3A, 3B). The articulated skull is estimated to be 152 mm long. The height of the skull is difficult to estimate due to crushing. The well-preserved right quadrate is 28 mm tall, making the quadrate-height/skull-length ratio = 0.18. In comparison, this ratio is 0.28 in *Dromaeosaurus*, 0.20 in *Bambiraptor,* 0.16 in *Velociraptor,* and 0.25 in *Archaeopteryx* (Elzanowski and Wellnhofer 1996). The skull/femur (estimated) ratio is 1.03, which is similar to 1.05 in *Bambiraptor* (Burnham et al. 2000). The snout is relatively short, with a pre-orbital/skull-length ratio of 0.49. It is similar to 0.52 in *Bambiraptor* (estimated from Burnham et al. 2000, fig. 1), 0.50 in *Dromaeosaurus,* and 0.49 in *Archaeopteryx* (estimated from Elzanowski and Wellnhofer 1996, figs. 7A, 7B), but less than 0.60 in *Velociraptor* (Barsbold and Osmolska 1999) and 0.62 in *Deinonychus* (estimated from Ostrom 1969, fig. 4). There are six openings visible on the left side: a probably oval-shaped external naris, a small rounded antorbital fenestra, a promaxillary fenestra, a maxillary fenestra, a large orbit, and a supratemporal fenestra (Figs. 1, 2).

Both premaxillae are preserved and exposed in medial view (Figs. 1, 2, 4A). They probably meet loosely at an acute angle, indicated by the flat and straight symphysial facet. The symphysis is only about 1 mm wide anteroposteriorly. Posterior to the symphysis, the rostral portion of the premaxilla is steep and slightly depressed. As in *Velociraptor* (Barsbold and Oslmoska 1999), the premaxilla forms a narrow palatal shelf only below the naris. This is suggested by a medial extension of the bone posterior to the second premaxillary tooth (Figs. 4A). The main body of the

Fig. 1. *Sinornithosaurus millenii* (IVPP V 12811). Photograph of skull and mandible in side view (skull roof in dorsal view).

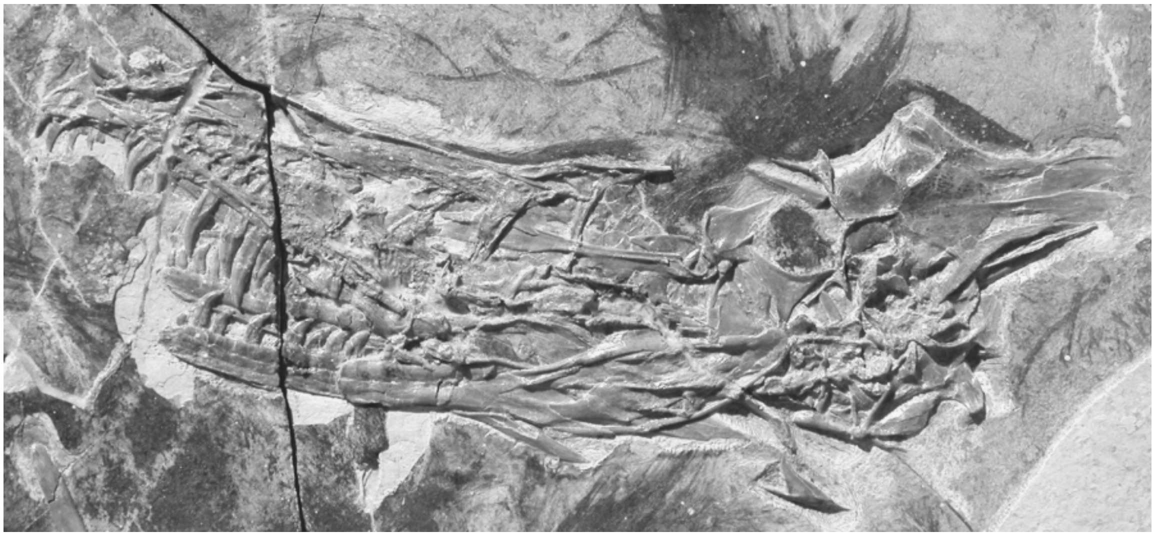
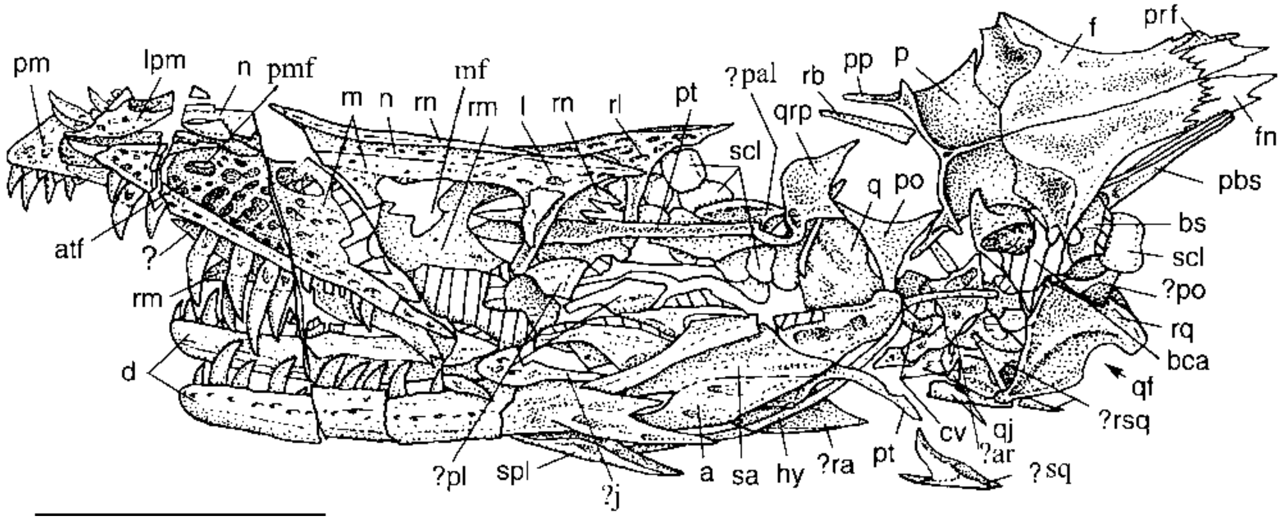
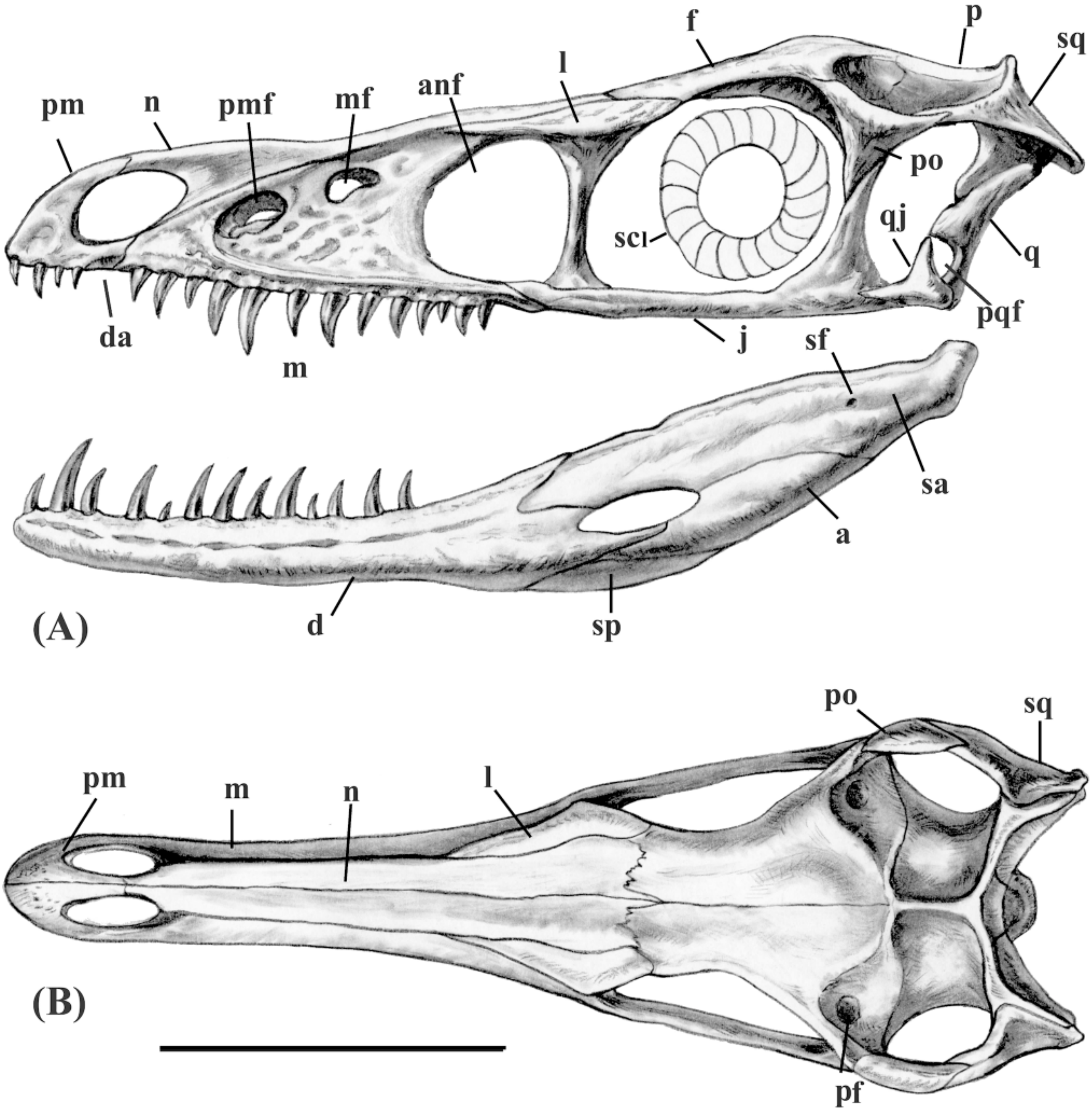


Fig. 2. *Sinornithosaurus millenii* (IVPP V 12811). Skull and mandible in side view (skull roof in dorsal view). a, angular; ?ar, ?articular; atf, antorbital fossa; bca, braincase; bs, basisphenoid; cv, elements of the diarticulated first and ?second cervical vertebrae; d, dentary; f, frontal; fn, facet for nasal; hy, hyoid; ?j, ?jugal; l, lacrimal; lpm, left premaxilla in medial view; m, maxilla; mf, maxillary fenestra; n, nasal; p, parietal; pbs, parabasisphenoid process; ?pal, palatine; ?pl, ?palatine; pm, right premaxilla in medial view; pmf, promaxillary fenestra; po, left postorbital; ?po, ?right postorbital; pp, posterolateral process of the parietal; prf, prefrontal; pt, pterygoid; q, quadrate; qf, fenestra between quadratojugal and quadrate; qj, quadratojugal; qrp, quadrate ramus of pterygoid; ?ra, ?right angular. rb, rib; rl, right lacrimal in medial view; rm, right maxilla in medial view; rn, right nasal; rq, right quadrate in anteromedial view; sa, surangular; scl, scleral bones; spl, splenial; ?sq, squamosal. (modified from fig. 3 in Xu et al. 1999). Scale bar = 50 mm.



premaxilla is much longer than high. It is about 17 mm long anteroposteriorly and 6 mm high dorsoventrally. The length/depth ratio of the main body of the premaxilla is 0.9 in *Deinonychus*, 1.64 in *Velociraptor*, 0.86 in *Dromaeosaurus*, 1.01 in *Utahraptor* (Kirkland et al. 1993), and about 1.5 in *Bambiraptor* (Burnham et al. 2000), all of these much smaller than 2.8 in *Sinornithosaurus*. The anterior margin slopes posterodorsally at an angle of about 45°. This angle is much smaller than about 85° in *Utahraptor*, 80° in *Deinonychus*, about 75° in *Velociraptor*, 74° in *Dromaeosaurus* (Kirkland et al. 1993), and about 85° in *Bambiraptor* (Burnham et al. 2000). The long main body and sharp anterior angle of the premaxilla also occur in *Archaeopteryx* (Wellnhofer 1992). As in *Velociraptor* (Barsbold and Osmolska 1999), the nasal process has a stout base. The posterior part of the premaxilla is unusual. Laterally, it is strongly excavated, forming a distinctive deep embayment with an open ventral margin (Fig. 4A). This excavation may separate the premaxilla and maxilla, interrupting the otherwise continuous alveolar margin. This excavation is medially walled. The medial surface of this wall has a triangular posterior articular surface, possibly for contact with the vomer (Fig. 4A). The posterior margin of the medial wall forms a wide concavity, possibly contacting the anteroventral process of the maxilla (Fig. 4A). It is not known whether there is a long maxillary process of the premaxilla, as in other dromaeosaurids (Currie

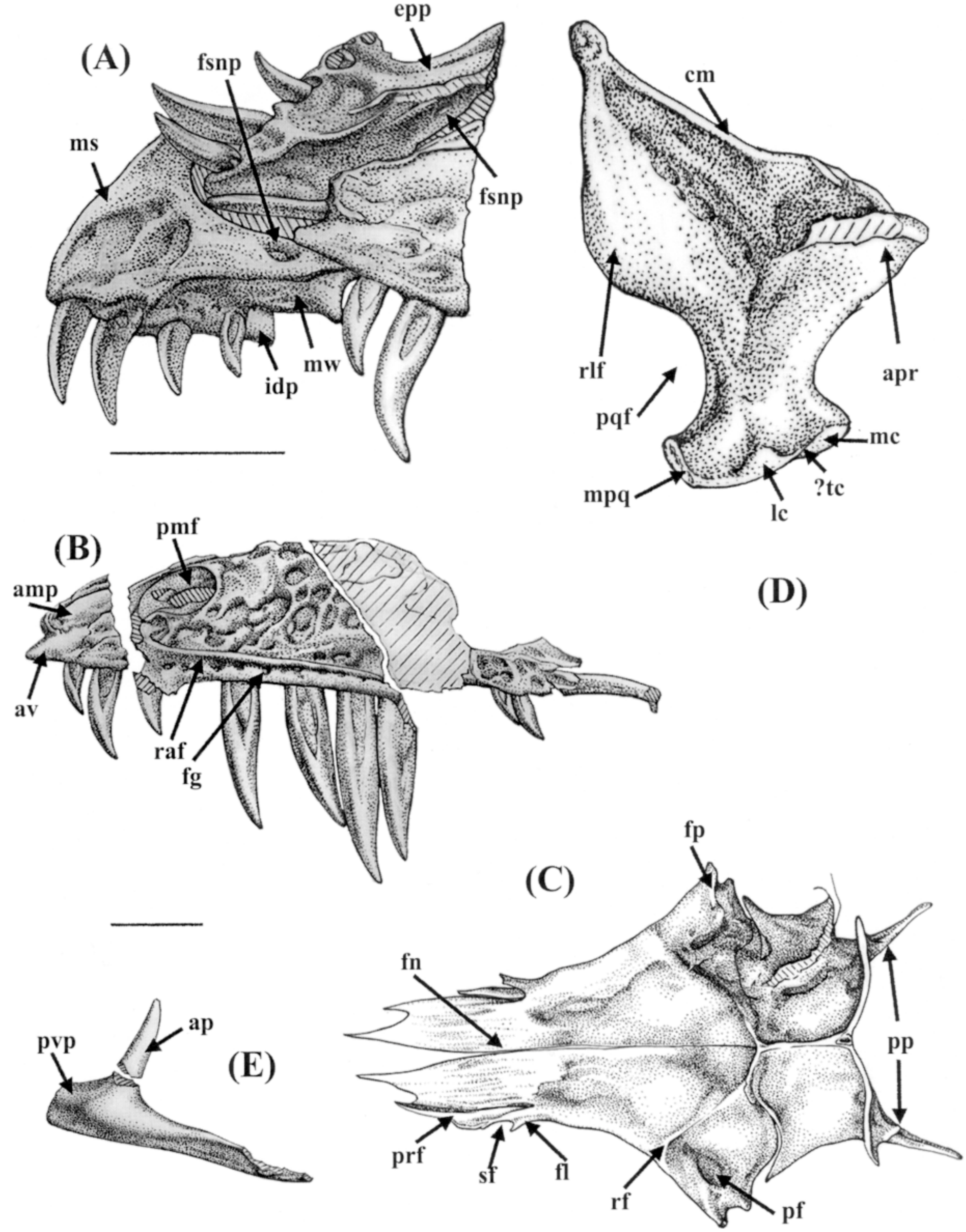
Fig. 3. Reconstruction of the skull and mandible of *Sinornithosaurus millenii* (IVPP V 12811) in lateral (A) and dorsal (B) views. a, angular; anf, antorbital fenestra; d, dentary; da, diastema; f, frontal; j, jugal; l, lacrimal; m, maxilla; mf, maxillary fenestra; n, nasal; p, parietal; pf, pit on frontal; pm, premaxilla; pmf, promaxillary fenestra; po, postorbital; pqf, prequdrate foramen; q, quadrate; qj, quadratojugal; sa, surangular; sf, surangular foramen; sp, splenial; sq, squamosal;. Scale bar = 50 mm.



1995). Judging from the shape of the posterior part of the main body, the premaxilla may not have had such a long maxillary process to exclude the maxilla from the posterior border of the external naris in *Sinornithosaurus*, as is commonly seen in troodontids, therizinosaurs, *Archaeopteryx*, and many other theropods (Barsbold and Osmolska 1999). The narial opening is located more ventrally than most other coelurosaurians due to the shallow main body of the premaxilla (Fig. 4A). In this feature, it is more similar to *Archaeopteryx* than to other dromaeosaurids. The narial opening may have been very large and elongate. The length of the premaxillary part of the narial opening is about 11 mm long, and the total length of the narial opening is estimated to be about 17 mm. Ventral to the narial opening is a foramen on the medial surface of the very shallow main body, which is similar to that in *Utahraptor* (Kirkland et al. 1993).

Both maxillae were partially damaged during excavation. The left is nearly complete and the right is mostly obscured by other bones (Figs. 1, 2). The maxilla is large and triangular in lateral view, with a maximum length of about 69 mm and a maximum height of about 28 mm (Fig. 4B). The angle between the anterodorsal margin and ventral margin is about

Fig. 4. *Sinornithosaurus millenii* (IVPP V 12811). Right and left premaxillae in medial view (A); left maxilla in lateral view (B); left prefrontal, frontals, and parietals in dorsal view (C); right quadrate in anterior view (D); right quadratojugal in lateral view (E). amp, anteromedial process of the maxilla; ap, ascending process of the quadratojugal; apr, apex of the pterygoid ramus of the quadrate; av, anteroventral end of the maxilla; cm, columnar margin of the pterygoid ramus; epp, excavation on the posterior premaxilla; fg, foramina in a groove; fl, facet for lacrimal; fn, facet for nasal; fp, facet for postorbital; fsnp, foramin below subnarial process; idp, interdental plate; lc, lateral condyle; mc, medial condyle; mpq, mandibular process of quadrate; ms, medial symphysis; mw, medial wall; pf, pit on frontal; pmf, promaxillary fenestra; pp, posterior process of parietal; pqf, prequdrate foramen; prf, prefrontal; pvp, posteroventral process of quadratojugal; raf, ridge below antorbital fossa; rf, ridge on frontal; rlf, rostrolateral flange of quadrate; sf, slot on frontal; ?tc, ?third condyle. Scale bar = 10 mm.



30°. The anterior extremity of the maxilla is somewhat pointed and directed slightly ventrally. Immediately dorsal to this extremity, there is a slightly medially directed process on the anterior margin. The antorbital fossa is subtriangular in outline, covering most of the lateral surface of the maxilla. The length of the antorbital fossa is about 54 mm, making up 78% the total length of the maxilla. There are three large openings in the antorbital fossa: an antorbital fenestra, a maxillary fenestra, and a promaxillary fenestra. The antorbital fenestra is probably round in outline, as indicated by its rounded anterior border. The antorbital fenestra is subtriangular in *Deinonychus* (Ostrom 1969) but rounded in outline in *Velociraptor* and *Bambiraptor*. Its precise size is not known, but it was apparently less than half the size of the antorbital fossa. Other dromaeosaurids also have a small antorbital fenestra compared to the orbit, but it is usually subequal to or larger than half of the antorbital fossa. The maxillary fenestra is positioned anterior to the antorbital fenestra and is semilunate in outline, with a straight ventral border. *Velociraptor* has a small teardrop-shaped maxillary fenestra, *Dromaeosaurus* a rounded one, and *Deinonychus* a semicircular one with a straight dorsal margin (Ostrom 1969). A similar maxillary fenestra is not known in other theropods. The promaxillary fenestra is well developed and even larger than the maxillary fenestra, with a long diameter of 9 mm, which has never been reported in other theropods. The promaxillary fenestra opens medially through a relatively wide, slit-like opening (Fig. 4B). The slit-like promaxillary fenestra is characteristic of velociraptorines (Sues 1978; Witmer and Maxwell 1996). The antorbital fossa has a better developed rim (Fig. 4B), in comparison to those in most other coelurosaurians, though not as developed as in oviraptorosaurians and therizinosauroids (Clark et al. 1994). In *Bambiraptor* and in the troodontid *Sinornithoides youngi* (IVPP V9612), the antorbital fossa also seems to have a distinct margin. The anterolateral surface of the antorbital fossa bears a number of pits and ridges, which are unusual. These pits and ridges are well marked and show no trace of pathological origin. We tentatively consider the presence of such ridges and pits as a diagnostic feature of this species. Ventral to the antorbital fossa is a prominent but narrow ridge (Fig. 4B) and, further ventral to this ridge, the maxilla is inset as a narrow and shallow groove, as in oviraptorosaurians, including *Caudipteryx* (Sereno 1999). A narrow ridge ventral to the antorbital fossa is also present in *Velociraptor* (Barsbold and Osmolska 1999) but not as distinct as in *Sinornithosaurus*. A row of neurovascular foramina is present within the groove. The maxillary alveolar border is straight in *Sinornithosaurus* but convex in *Deinonychus* and probably in *Dromaeosaurus* as well (Barsbold and Osmolska 1999).

Both nasals are preserved but crushed (Figs. 1, 2). Each is long and narrow (about 75 mm long), reaching about 50% of the total skull length. The nasal is L-shaped in cross-section. In dorsal view, the nasal is very narrow anteriorly and widens posteriorly. The nasal seems to be elevated at the level where it widens, thus leading to a depressed dorsal surface of the bone, as in *Velociraptor* (Barsbold and Osmolska 1999). Some irregularly spaced, small excavations were observed on the dorsal surface of the nasal. It is not known whether they are foramina or pits. In dorsal view, the maximum width of the nasal is about 7 mm, about 2.5 times as wide as the portion medial to the external naris. The posterior end of the nasal has three prongs that wedge into grooves on the dorsal surface of the frontal.

The left prefrontal (Fig. 4C) is a small bone, 13 mm in anteroposterior length and about 2 mm in maximum transverse width. As in the therizinosauroid *Erlikosaurus* (Clark et al. 1994), the prefrontal is triangular in dorsal view, with a very broad, almost straight medial base and a lateral apex, but its anterolateral edge is subequal to its posterolateral edge in length. Differing from most theropods, the prefrontal overlaps the anterolateral portion of the frontal and is posteriorly wedged into a groove on the dorsal surface of the latter rather than medially contacting the latter. Medially, it has a broad contact with the nasal. A separate prefrontal is present in *Deinonychus* and probably also *Dromaeosaurus* but is absent in *Velociraptor*, troodontids, and birds (Witmer and Maxwell 1996).

Both frontals are completely preserved (Fig. 4C). The frontal is very long, with a total length of 48 mm. It is about four times longer than wide across the orbital portion, as in *Bambiraptor* and *Velociraptor*, but differs in that the anterior end of the frontal in the latter two taxa is tapered (Barsbold and Osmolska 1999; Burnham et al. 2000). The frontal is three times longer than wide across the orbital portion in *Saurornitholestes* (Sues 1978) and *Deinonychus*, and twice as long as wide in *Dromaeosaurus* (Barsbold and Osmolska 1999). It is narrow anteriorly and broad posteriorly, somewhat triangular in dorsal view as in *Saurornitholestes*. Anteriorly, a sharply V-shaped gap is present between the two frontals, for the reception of the medial prongs of the nasals. Each frontal has three prongs anteriorly, the medial one of which is the longest. The articular surface of the frontal for the nasal is about 17 mm long, with a grooved posterior portion. A long nasal–frontal contact is also present in *Dromaeosaurus* and *Velociraptor* but the contact is short in *Saurornitholestes* (Barsbold and Oslmoska 1999). At the anterodorsal corner of the orbit the frontal is depressed ventrally and medially, indicating an articular surface for the lacrimal. Anterior to this articular surface, there is a very short slot. A slot-like frontal–lacrimal contact could be characteristic of Dromaeosauridae (Currie 1995), though there is no vertical slot on this contact in *Velociraptor* (Barsbold and Osmolska 1999). The frontal contributes to a long orbital rim as in *Troodon* (Currie 1987). Dorsal to the orbit, its lateral border is rugose and raised dorsally. Medial to this border, the frontal is depressed. The depression is separated from that of the other side by a low and wide crest that extends along the medial suture between the frontals. Posteriorly the frontals are convex, forming a somewhat anterior convex skull roof, but become concave further posteromedially near the midline. The posterior ends of the frontals together form a stout process and are sutured to the curved anterior margin of the parietals. The posterolateral portion of the frontal is depressed to form the anterior half of the supratemporal fossa. The anterior demarcation of the supratemporal fossa on the frontal is sinusoidal in outline, with a faint ridge as in *Saurornitholestes* (Sues 1978; Currie 1987), posterior to which is an associated deep pit, as in Velociraptorinae (Currie 1995). The postorbital process of the frontal is relatively short and stout, smoothly transiting from the orbital margin, as in *Bambiraptor* and most other theropods. Conversely, it diverges strongly from the rest of the orbital rim in most dromaeosaurids, particularly in *Dromaeosaurus* (Currie 1987). Its ventral margin is sharply concave.

Both parietals are complete. Together they are anteroposteriorly short, more or less square in dorsal view, and transversely wider than the interorbital region of the frontals (Fig. 4C), as in *Bambiraptor*, *Archaeopteryx* (Elzanowski and Wellnhofer 1996), and other birds. The lateral parietal is strongly depressed to form the majority of the supratemporal fossa. The depressed area of the parietal extends onto the posterodorsal surface of the frontal, but it is much larger here and, together with that of the frontal, forms an unusually large supratemporal fossa that occupies almost the entire posterior portion of the skull roof. Anteriorly, the sutures of the parietals with the frontals are sigmoid in dorsal view. Medially, the parietals form a sharp and very narrow sagittal crest along their median suture. The latter rises gradually towards its posterior end and is continuous with the raised posterodorsal borders of the parietals that form a nearly straight transverse crest. This transverse nuchal crest is nearly horizontal in posterior view. It forms the posterior border of the supratemporal fossa and broadens laterally to form a pointed extremity projecting into the supratemporal fenestra and slightly overhanging the lateral border of the parietal. In dorsal view, the supratemporal fenestra of *Sinornithosaurus* seems to be elongated as in *Deinonychus* and *Bambiraptor*, whereas it is subcircular in *Velociraptor* (Barsbold and Osmolska 1999). The posterolateral process of the parietal is 11 mm long and distinctly rod-like. It bears a relatively wide base that bears a groove on the lateral surface, which may be the facet for the parietal process of the squamosal. The elongate posterolateral process is unusual in that it is directed posteriorly and slightly laterally. A long posterolateral process is present in some primitive tetanuran theropods, such as *Sinraptor* (Currie and Zhao 1994). The occipital portion of the parietal faces posteroventrally and cannot be seen.

Both lacrimals are well preserved (Fig. 5A). As in most other dromaeosaurids (Currie 1995) and troodontids (Makovicky and Sues 1998), the lacrimal is T-shaped. In dorsal view, it appears triangular with a pointed lateral apex, although its dorsal surface is transversely narrower and its lateral apex is more posteriorly located in *Sinornithosaurus* than in most other dromaeosaurids. The rostral process of the lacrimal is long and narrow, with a groove on its dorsal surface to receive the nasal. *Deinonychus* has a much shorter rostral process, and *Velociraptor* and *Bambiraptor* have a longer one, but it is not as relatively long as in *Sinornithosaurus*. In this character, *Sinornithosaurus* is more similar to troodontids (Norell et al. 2000). The distal half of the rostral process is depressed slightly on dorsal surface, which also seems to be the case in troodontids (Currie 1985). The posterior process of the lacrimal is also longer and narrower than in other dromaeosaurids. It contacts the prefrontal and frontal medially and forms the anterodorsal border of the orbit. There is a fossa present on the medial surface of the posterior process. The descending process is nearly vertical and may have formed the entire antorbital bar.

Six scleral bones from the right side are preserved and most of them are scattered around the orbit (Figs. 1, 2). Most of the preserved scleral bones are subrectangular in outline, with sharp and thin edges. There seems to be a faint ridge on each scleral bone to demarcate the region overlapped by the adjacent sclerotic plate. The largest bone is about 9 mm long.

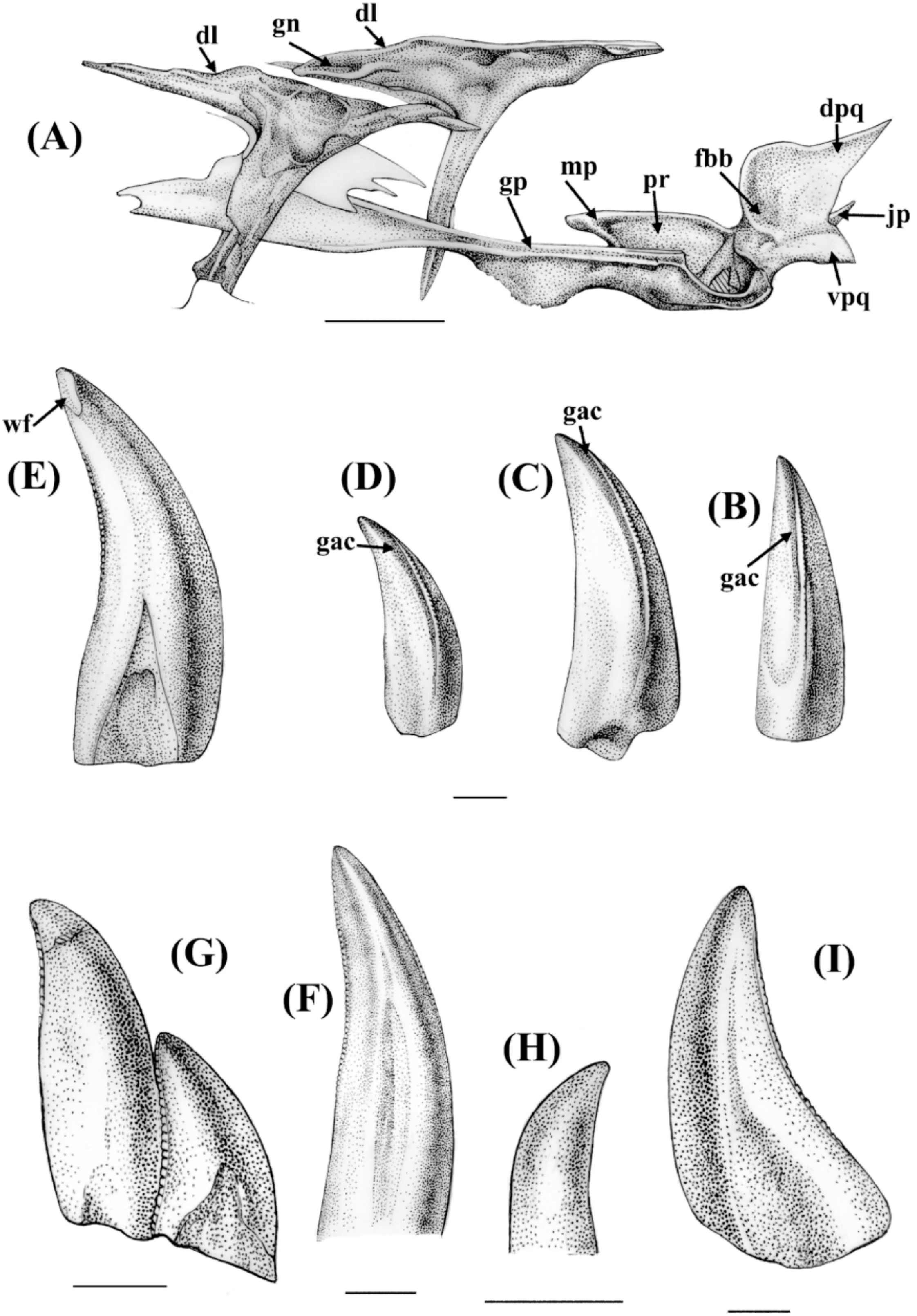
Both postorbitals are preserved, although disarticulated (Figs. 1, 2). Each is triradiate, with a narrow squamosal process and a somewhat more stout jugal process. As in some advanced maniraptorans (Sereno 1999), the squamosal process is long and subequal to the jugal process in length. The frontal process is slightly upturned, but is more strongly upturned in other dromaeosaurids. In *Deinonychus* and *Bambiraptor*, the frontal process forms a much larger angle to the jugal process (about 175°), and in *Velociraptor*, this angle is smaller (about 135°) but still much larger than in *Sinornithosaurus* (about 110°). The upturned frontal process of the postorbital has been cited as a diagnostic feature of Dromaeosauridae (Currie 1995). This feature has also occurred in a few other non-avian theropods, such as oviraptorids (Barsbold and Osmolska 1999) and *Caudipteryx* (IVPP V 12344) and in the basal bird *Confuciusornis* (Chiappe et al. 1999), but the angle between the frontal process and jugal process in these taxa is close to that seen in *Velociraptor*.

The right quadratojugal is preserved between the two quadrates (Figs. 1, 2, 4E). It has the inverted T-shape typical of dromaeosaurids (Paul 1988). The quadratojugal is very small relative to the quadrate, which is more similar to the condition in *Archaeopteryx* than in other dromaeosaurids. The ascending process of the quadratojugal is rod-like, much more slender and shorter (5 mm high) than in other non-avian theropods, suggesting the possible absence of a contact with the squamosal. In all dromaeosaurids, the posteroventral process is stouter than the ascending and jugal processes (Barsbold and Osmolska 1999), but, in *Sinornithosaurus*, the former is much stouter than the other processes and has a blunt end. The posteroventral process is also shorter than that in other dromaeosaurids, about only one third the length of the jugal process. In other dromaeosaurids, such as *Velociraptor*, *Deinonychus*, and *Bambiraptor*, the posteroventral process is apparently more than half the length of the jugal process. The jugal process of the quadratojugal is the longest among the three processes, with its distal end somewhat dorsoventrally flattened. The quadratojugal is generally similar to that of *Archaeopteryx* in having a long jugal process, a very short and slender ascending process, and a short and stout posteroventral process (Elzanowski and Wellnhofer 1996).

A long slender fragmentary bone was identified as left jugal (Figs. 1, 2). The exposed length is about 33 mm and maximum height is about 10 mm. Its anterior ramus is sheet-like and shallow (about 4 mm high). Posteriorly, it raises to form the postorbital process, the anterior margin of which is distinctively everted to form the posterior rim of the orbit. This seems to be comparable to the condition in *Bambiraptor* (Burnham et al. 2000, fig. 1). The rest of the bone, including most of the postorbital process, was broken off.

Both quadrates are preserved (Figs. 1, 2, 4D). The quadrate is about 28 mm tall dorsoventrally. Dorsally, it has a single rounded head for articulation with squamosal. Its pterygoid process is triangular in outline, with a ventrally located apex, but the ramus is relatively small when compared to those of

Fig. 5. *Sinornithosaurus millenii* (IVPP V 12811). Lacrimals, palatine, and pterygoid (A); first (B), second (C), third (D) preserved right premaxillary teeth in medial views; second (E), sixth (F), two posterior (G) preserved left maxillary teeth in lateral views; first (H) and third (I) preserved right dentary teeth in medial views. dl, depression on lacrimal; dpq, dorsal process of quadrate ramus; fbb, facet for basipterygoid process of basisphenoid; gac, groove posterior to anterior carina; gn, groove for nasal; gp, groove on pterygoid; jp, jugal process; mp, maxillary process; pr, palatine recess; vpq, ventral process of quadrate ramus; wf, wear facet. Scale bar = 10 mm in A, 2mm in B–E, and 1 mm in F–I.



most other theropods. Unusually, the pterygoid ramus has a thickened, round, and sharp margin for articulation with the quadrate ramus of the pterygoid. Ventral to the base of the pterygoid ramus and dorsal to the articular condyles, the quadrate constricts and forms a concavity on its medial side. Ventral to the dorsal head, the anterolateral edge of the quadrate shaft expands into a large, somewhat rounded triangular flange, directed rostrally and slightly medially, and opposes, together with the ascending process of the quadratojugal, the large quadratojugal foramen, as it does in other dromaeosaurids (Currie 1995). The large, triangular anterolateral flange is also seen in *Velociraptor*. In *Dromaeosaurus*, there is only a slight rostral extension of the lateral edge of the shaft; in *Saurornitholestes*, it is absent altogether (Barsbold and Osmolska 1999). The mandibular process of the quadrate is short and oriented obliquely at 30° to the saggital plane. The articular surface appears to have three condyles, as in *Erlikosaurus* (Clark et al. 1994). The lateral one is separated from the medial one by a shallow, obliquely oriented groove. The former is much larger than latter and bears a mediolaterally extended articular surface. The articular surface of the medial condyle is oriented obliquely (rostromedially–posterolaterally) to the long axis of the skull. The third condyle is located on the anterior margin between the two condyles and is very small, more or less ridge-like, and slightly expanded anteriorly.

The braincase is displaced and partially damaged, and its elements are partially obscured by the overlap of other bones (Figs. 1, 2). The braincase is large, as is indicated by the broadened parietals and dorsally convex posterior frontals. As suggested by broken surfaces, the braincase of *Sinornithosaurus* may have not been highly pneumatic.

The cultriform process of the basisphenoid–parasphenoid is well preserved (Figs. 1, 2). It is triangular in outline, with straight dorsal and ventral edges. It is about 26 mm long and about 4 mm high. Dorsally, the lamella-like lateral edges of both sides meet along the midline. The parasphenoid process is a hollow structure, as indicated by breakages on its lateral surface. Its cross-section appears to be triangular. A shallow groove is possibly developed on the lateral surface of the parasphenoid process. The parasphenoid process is very similar to that of *Archaeopteryx* (Elzanowski and Wellnhofer 1996), whereas those in other dromaeosaurids are curved anterodorsally (Burnham et al. 2000). Laterally, at the base of parasphenoid process, is a large rounded excavation. This feature has not been reported in other theropods. In *Velociraptor*, there are two small excavations in the same region (Barsbold and Osmolska 1999), and these may be homologous to the large excavation described here.

The almost complete right pterygoid and partial left pterygoid are preserved (Figs. 1, 2, 5A). The pterygoid is very thin and long (72 mm in anteroposterior length), less than half of the skull length. The anterior (palatine) ramus is a very thin, vertically oriented sheet (5 mm high), with a tapering anterior end. Its dorsal margin seems to be thinner than the ventral margin, but both are column-like. Posteriorly, the palatine ramus becomes narrower and then expands into a ventrally curved and somewhat laterally directed sheet-like lamina. There is a groove on the medial surface of the main shaft of the bone, which is deeper and narrower posteriorly. Further posteriorly, the main shaft curves ventrally to form a concavity. Posterior to this concavity is the quadrate ramus, which is broad, very thin, bifurcated, and generally similar to that of *Archaeopteryx* (Elzanowski and Wellnhofer 1996, fig. 11). The ventral process of the quadrate ramus is relatively thicker than the dorsal one, but the latter, with a slightly thickened dorsal margin, is larger than the former. At the base of the medial surface of the quadrate ramus is a shallow, concave facet facing ventrally and posteriorly. This is identified as the articular surface for the basipterygoid process of the basisphenoid. The basipterygoid facet is not as developed as in *Deinonychus* (Ostrom 1969).

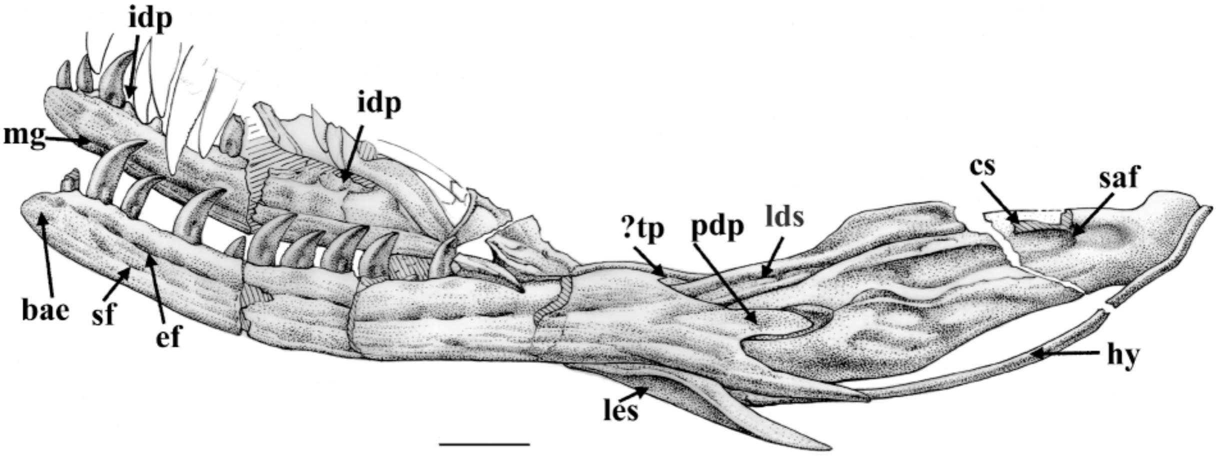
A bone underlying the right pterygoid is tentatively identified as the right palatine. This bone is comparatively smaller than that of other dromaeosaurids. It has a very short maxillary process and a relatively long jugal process. A triangular palatine recess, characteristic of velociraptorines (Witmer and Maxwell 1996), is present.

A hyoid element is exposed ventral to the left mandibular ramus (Figs. 1, 2, 6). It is curved, rod-like, and 53 mm long. Its anterior end seems to be compressed and more strap-like.

The mandible is well preserved, especially the left ramus, but the postdentary portion of the ramus was dislocated anteriorly to a certain degree (Figs. 1, 2, 6). Therefore, the recorded mandibular length of 125 mm in the previous study (Xu et al. 1999) is shorter than the actual length. The latter may approximately reach to 135 mm in length, apparently shorter than the skull length (152 mm). In birds, including *Archaeopteryx*, the skull is longer relative to the mandible. The dentary is shallow with a depth/length ratio of about one thirteenth. The external mandibular fenestra is probably shallow and oval, modest in size (probably less than one sixth of the total mandibular length). The mandibular ramus may not have had a hinge joint, because the bifurcated posterior margin of the dentary forms an interlocking joint with the postdentary bones, as it does in oviraptorosaurians, including *Caudipteryx* and some non-coelurosaurians, such as *Yangchuanosaurus* (Dong et al. 1978) and *Sinraptor* (Currie and Zhao 1994).

The dentary is long (91 mm) and surprisingly slender, with a length/depth ratio of about 13. Along most of its length, the dorsal (slightly concave) and ventral (convex) margins extend nearly parallel to each other, as in other dromaeosaurids (Fig. 6). In comparison, the ventral margin is convex in *Velociraptor* and *Bambiraptor*, weakly convex in *Saurornitholestes*, and straight in *Deinonychus* and *Dromaeosaurus* (Barsbold and Osmolska 1999). The anterior end of the dentary is relatively blunt as in other dromaeosaurids. Posteriorly, the dentary is bifurcated (Fig. 6), as in oviraptorosaurians, including *Caudipteryx* (Ji et al. 1998), *Confuciusornis* (Chiappe et al. 1999), and some primitive theropods, with a long ventral process and a shorter dorsal process. Anterodorsal to the dorsal process there is possibly a very short third process. The ventral process, particularly its pointed posterior end, is thick, and probably fits a shallow groove on the lateral surface of the angular. It comprises about half of the ventral margin of the external mandibular fenestra. The dorsal process is thin and sheet-like, underlying the surangular to form only a small part of the dorsal margin of the external mandibular fenestra. In lateral view, a row of elongated, oval-shaped foramina sit in a shallow groove below the tooth row. Ventral to the row of foramina is a

Fig. 6. *Sinornithosaurus millenii* (IVPP V 12811). Mandible. bae, blunt anterior end of dentary; crest on surangular; ef, elongated foramina; hy, hyoid; idp, interdental plate; lds, longitudinal depression on surangular; les, lateral exposure of splenial; mg, Meckelian groove; pdp, posterodoral process of dentary; saf, surangular foramina; sf, second row of foramina; ?tp, ?third process. Scale bar = 10 mm.



second row of less developed foramina (Fig. 6). Two rows of foramina on the lateral surface of the dentary also occur in other dromaeosaurids and troodontids (Currie 1995). In medial view, the mandibular symphysial surface is flat, suggesting a loose contact between the dentaries, which diverged posterolaterally at a very small angle. The Meckelian groove is deep and narrow (Fig. 6), extending to the mandibular symphysis and dividing the medial surface of the dentary into a strongly convex dorsal part and a narrow, ridge-like ventral part. This is also the case in *Archaeopteryx* (Elzanowski and Wellnhofer 1996). In other dromaeosaurids, this groove is wide and shallow (Currie 1995).

The left splenial is visible, and the exposed part is about 32 mm long (Figs. 1, 2, 6). The thickened ventral border of the splenial wraps around the ventral surface of the dentary and is exposed on the lateral surface of the mandibular ramus as a triangular feature between dentary and angular, as in other dromaeosaurids and troodontids (Currie 1995). The lateral exposure is 24 mm long and 3 mm high. Posteriorly, the splenial ends in a pointed extremity.

The left angular has its lateral surface exposed (Figs. 1, 2, 6) and is estimated to be 45 mm long. The angular is shallow below the external mandibular fenestra, deepening posteriorly and reaching its maximum depth immediately posterior to the external mandibular fenestra. It narrows again toward its posterior end. Its ventral margin arches dorsally just behind the fenestra. Dorsally, it overlaps the surangular.

The left surangular has much of its lateral surface exposed (Fig. 6). It may be 65 mm long, about 71% of the dentary length. As in *Dromaeosaurus* (Colbert and Russell 1969), the dorsal margin of the surangular is more convex, and the glenoid fossa is more ventrally located than those of other dromaeosaurids (Sues 1977). Anteroventrally, the bone forms the most of the dorsal border of the external mandibular fenestra. There is a longitudinal depression on the lateral surface of the anterior surangular. Posterodorsally, the surangular contributes the lateral portion of the glenoid fossa and then extends further posteriorly and overlaps the lateral surface of the retroarticular process. A small oval foramen is present on the lateral surface of the surangular anteroventral to the glenoid fossa, but whether there is a second one is uncertain due to cracks. Conversely, the surangular foramen is large in *Bambiraptor* and *Velociraptor* (Barsbold and Osmolska 1999). There is a prominent crest just ventral to the dorsal edge of the surangular, which extends along the posterior one-third of the bone and overhangs the region near the surangular foramen.

A stout bone immediately behind the left ramus of the mandible is tentatively identified as the left articular (Figs. 1, 2), with its medial surface visible. Its anterior margin is concave, with a stout dorsomedial process, which is probably the articular contact for the prearticular. If so, this process is much more developed than those of other dromaeosaurids (Ostrom 1969). Posterior to the dorsomedial process, a concavity probably represents the glenoid fossa. Further posteriorly, a moderate retroarticular process is present, the posteromedial extremity of which raises to form a vertically and slightly posteromedially directly process. This process is much shorter than that of other dromaeosaurids (Currie 1995).

There are four premaxillary teeth, at least 12 maxillary teeth, and at least 13 dentary teeth. Most preserved teeth are mediolaterally compressed, modestly recurved, and inclined posteriorly. Their serrations are mostly rectangular and some of anterior ones are triangular in outline. All serrations have their long axes perpendicular to the carinae. The posterior serrations are about twice as large as the anterior ones. The anterior carina is shorter than the posterior carina. These features also occur in other dromaeosaurids (Ostrom 1969; Currie 1995).

All of the preserved premaxillary teeth show their lingual surfaces, and most are partially displaced from their sockets. Each has a distinctive groove posterior to the anterior carina, which extends proximodistally along the lingual surface of its crown (Figs. 5B–5D). The premaxillary teeth do not bear serrations on both anterior and posterior carinae, except for the first tooth that has a few very faint denticles on the middle portion of its anterior carina. Among non-avian theropods, non-serrated premaxillary teeth have been reported in coelophysids (Colbert 1989), compsognathids (Ostrom 1978), and *Caudipteryx* (Ji et al. 1998). The first premaxillary tooth is slightly smaller than the second one. Its posteriorly facing lingual surface is flat and its anteriorly facing labial surface is significantly convex (Fig. 5B). The second tooth is significantly larger than the third and fourth teeth as in *Velociraptor* (Barsbold and Osmolska 1999), but it is not enlarged in *Deinonychus* and *Dromaeosaurus* (Witmer and Maxwell 1996). The posterior three teeth are similar to each other in having mediolaterally compressed crowns and flat lingual surfaces (Figs. 5C, 5D).

The left maxilla preserves at least nine teeth, all of which show their labial surfaces. The maxillary teeth have convex labial surfaces, and most of them are larger than the corresponding dentary teeth. The first maxillary tooth is small and seems to lack serrations on both anterior and posterior carinae. The second one seems to have no anterior serrations, but has 14 posterior serrations per millimeter. It has a posterior wear facet on its tip (Fig. 5E). The third tooth is small. It has no anterior serrations but 10 posterior serrations per millimeter. The fourth of the preserved teeth has 13 anterior serrations per millimeter, which are weak and short. The anterior serrations are apically distributed along the carina. The posterior serrations of the fourth tooth are relatively larger (10 serrations per millimeter) than the anterior serrations, as they are in other velociraptorines (Ostrom 1969; Currie 1995). The fifth of the preserved maxillary teeth has 11 anterior serrations per millimeter, but 8 posterior serrations per millimeter, and the former are less than half the height of the latter, similar to the situation seen in other velociraptorines (Ostrom 1969). The sixth (Fig. 5F) and seventh of the preserved teeth are similar to the fifth tooth, but both have 9 anterior and 8 posterior serrations per millimeter. The eighth and ninth preserved teeth represent posterior maxillary teeth (Fig. 5G). They are smaller in size than most of the other maxillary teeth, and their serrations are slightly hooked apically. The eighth tooth has 12 anterior, 9.5 posterior serrations per millimeter. The crown of the ninth maxillary tooth is less compressed than other maxillary teeth.

Three right and 11 left dentary teeth are preserved. Based on the preserved teeth and alveoli, there are least 13 dentary teeth. Generally, the dentary teeth are modestly recurved, mediolaterally compressed, and have convex labial and lingual surfaces. The first right dentary tooth is small and not serrated (Fig. 5H). The second right dentary tooth is much larger than the first one and also not serrated. The third right dentary tooth has no anterior but 13 posterior serrations per millimeter (Fig. 5I). These three anterior dentary teeth are procumbent. A weak groove is present on the lingual surface of the crown posterior to the anterior carinae in the first two dentary teeth. The first preserved left dentary tooth is strongly convex and seems to be not serrated. The second of the preserved left dentary teeth has 14 posterior serrations per millimeter but no anterior serrations. The fourth of the preserved left dentary teeth has 10 posterior serrations per millimeter but probably no anterior serrations. The fifth of the preserved left dentary teeth has 12 or 13 anterior, and 9 or 10 posterior, serrations per millimeter. The other preserved dentary teeth have about 10 anterior and 7 posterior serrations per millimeter.

The anterior denticles are smaller than posterior denticles. The size difference of the anterior and posterior denticles in *Sinornithosaurus* is, however, not as significant as in Velociraptorinae (Ostrom 1969; Sues 1978; Currie 1995; Barsbold and Osmolska 1999) but more significant than in *Utahraptor* (Kirkland et al. 1993). *Sinornithosaurus* has a DSDI (denticle size difference index; see Rauhut and Werner 1995) of about 1.35, which is less than over 1.5 in Velociraptorinae but larger than around 1 in most other theropods (Rauhut and Werner 1995).

Four unfused interdental plates are recognizable between the alveoli of the premaxilla (Fig. 4A). The first one is small and the second one much larger and seems fused with the premaxilla. The first two interdental plates are somewhat triangular in outline. The third (trapezoid) and fourth (subsquare) interdental plates are subequal in size and not fused to the premaxilla. The interdental plates of the dentary are well developed. The anterior dentary interdental plates are triangular in outline and ventrally fused to the bone, while the posterior dentary interdental plates are fused with one another, but the united plates are not fused to the bone. Troodontids and basal birds lack interdental plates. In this feature, *Sinornithosaurus* is plesiomorphically similar to most other theropods, as well as *Archaeopteryx* (Wellnhofer 1993).

Discussion

The skull anatomy of the Dromaeosauridae has been described, illustrated, or commented on by Osborn (1924), Colbert and Russell (1969), Sues (1977, 1978), Barsbold (1983), Paul (1988), Ostrom (1969, 1990), Currie (1995), Norell and Makovicky (1998), Xu et al. (1999), Barsbold and Osmolska (1999), and Burnham et al. (2000). However, much fewer cranial similarities have been recognized as shared between dromaeosaurids and early birds than have their postcranial resemblances. *Sinornithosaurus* represents a basal dromaeosaurid (Xu et al. 1999) and is important for our understanding the morphological transition from non-avian theropods to birds. Drawn from this study, a number of cranial similarities between *Sinornithosaurus* and *Archaeopteryx* (and other early birds) may have phylogenetic implications. They are discussed below.

(1) The mandible is relatively short relative to skull length. The skull of *Sinornithosaurus* reaches about 152 mm in length and its mandible is about 135 mm long, with a mandible/skull length ratio of less than 0.89 (Fig. 3A). This ratio is larger than 0.90 in most non-avian theropods: 0.91 in *Velociraptor*, 0.97 in *Bambiraptor*, 0.97 in *Deinonychus*, and 0.96 in *Sinornithoides*. *Archaeopteryx* (the seventh specimen) has a mandible/skull length ratio of 0.87 (Elzanowski and Wellnhofer 1996).

(2) The main body of the premaxilla is long and shallow. The main body of the premaxilla of *Sinornithosaurus* is very long and shallow, particularly below the narial opening (Fig. 3A). The premaxilla of *Archaeopteryx* has a long ramus anterior to the external naris but its main body is otherwise identical to that of *Sinornithosaurus* (Wellnhofer 1992). The main body of the premaxilla is much deeper in troodontids and other dromaeosaurids than in *Sinornithosaurus*. In some remotely related non-avian theropods, such as *Compsognathus* (Ostrom 1978) and some ornithomimids, the premaxilla has a long and shallow main body.

(3) Sharp premaxillary angle. The premaxillary angle in *Sinornithosaurus* is of about 45° (Fig. 3A). This is much smaller than those in most other theropods (Kirkland et al. 1993), including other dromaeosaurids

and troodontids. However, in birds, *Compsognathus* (Ostrom 1978), and some ornithomimids, the premaxillary angle is sharp.

(4) Position of ventral margin of narial opening. The ventral border of the narial opening of *Sinornithosaurus* is almost at the same level as the ventral border of the antorbital fossa (Fig. 3A). This is comparable to the condition seen in Avialae and *Compsognathus* (Ostrom 1978). In most theropods, including other dromaeosaurids and troodontids, the ventral border of the narial opening is apparently dorsal to the ventral border of the antorbital fossa. In oviraptorosaurians, including *Caudipteryx*, the narial opening is even more dorsally located (Sereno 1999).

(5) Relatively large narial opening. The narial opening is large relative to the antorbital (Fig. 3A), as in *Bambiraptor* (Burnham et al. 2000, fig. 1) and some troodontids. In Avialae and some oviraptorosaurians, including *Caudipteryx* (IVPP V 12344), the narial opening is even larger than the antorbital fenestra. Most other known non-avian theropods have a much smaller narial opening.

(6) Diastema between the premaxillary and maxillary teeth. It is inferred that the premaxillary and maxillary teeth were separated by a diastema based on the morphology of the posterior end of the premaxilla and anterior end of the maxilla in *Sinornithosaurus* (Fig. 3A). This feature is unusual among theropods and has been reported only in ceratosaurians (Rowe and Gauthier 1990) and *Compsognathus* (Ostrom 1978). Interestingly, it is also present in *Archaeopteryx* (Wellnhofer 1992, fig. 19).

(7) Posteroventral margin of the premaxilla excavated. The lateral surface of the posterior premaxilla of *Sinornithosaurus* is deeply excavated (Figs. 3A, 4A). The London specimen of *Archaeopteryx* appears to share this feature (Wellnhofer 1992, fig. 19).

(8) Wide parietal. As in *Bambiraptor* (Burnham et al. 2000) and *Archaeopteryx* (Elzanowski and Wellnhofer 1996), the parietal of *Sinornithosaurus* is wider than the interorbital portion of the frontals (Figs. 3B, 4C). Troodontids have a slightly narrower parietal, although it is wider than that in most other non-avian theropods. The wide parietal indicates an enlarged braincase.

(9) Short and blunt posteroventral process of quadratojugal. Dromaeosaurids have a diagnostic reversed T-shaped quadratojugal (Paul 1988) due to the development of the distinctive posteroventral process. *Archaeopteryx* shares this T-shaped quadratojugal (Elzanowski and Wellnhofer 1996, figs. 7B, 12). In this character, *Sinornithosaurus* is similar to *Archaeopteryx* in that the posteroventral process is very short and blunt (Figs. 3A, 4E), differing from the long and slender one in other dromaeosaurids. In most other non-avian theropods, the quadratojugal is L-shaped, without a distinctive posteroventral process.

(10) Reduced quadratojugal. The quadratojugal is much smaller in *Sinornithosaurus* than in most non-avian theropods. Its ascending process is particularly short, suggesting a lack of a quadratojugal–squamosal contact (Fig. 3A). The absence of a quadratojugal–squamosal contact is considered to be an autapomorphy of birds, including *Archaeopteryx* (Ji et al. 1998).

(11) Triangular pterygoid process of the quadrate with a ventrally located apex. In *Sinornithosaurus*, the pterygoid process of the quadrate is distinctively triangular in outline and bears a ventrally located apex (Fig. 4D). *Archaeopteryx* shares this feature (Walker 1985, fig. 5C). This apex is more dorsally located in other non-avian theropods that have such a structure (*Velociraptor*, *Bambiraptor*, and *Dromaeosaurus*).

(12) Bifurcated quadrate ramus of the pterygoid. The quadrate ramus of the pterygoid in *Sinornithosaurus* is bifurcated, which is not seen in other theropods. In *Archaeopteryx* the quadrate ramus of the pterygoid appears to be bifurcated as well (Elzanowski and Wellnhofer 1996, fig. 11).

(13) Very shallow dentary. The length/depth ratio of dentary is about 13 in *Sinornithosaurus*, which is larger than in most non-avian theropods (less than 10), including other dromaeosaurids. This ratio is close to 14 in *Archaeopteryx*.

(14) Bifurcated posterior margin of the dentary (Fig. 6). This feature is similarly present in the basal bird *Confuciusornis* (Chiappe et al. 1999), though it also occurs in oviraptorosaurians, including *Caudipteryx* (Ji et al. 1998), and some primitive theropods.

The above characters are shared by *Sinornithosaurus*, *Archaeopteryx*, and early birds, and provides additional evidence supporting a close relationship between dromaeosaurids and birds. The phylogenetic implications of these characters cannot be ascertained until a thorough phylogenetic analysis of all available data is made. Also noteworthy is the presence of a large number of similarities between *Sinornithosaurus* and other major maniraptoran groups, which suggest that the diversification of Maniraptora may have occurred quite rapidly.

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