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ARTICLE

THEROPOD TEETH FROM THE MIDDLE-UPPER JURASSIC SHISHUGOU FORMATION OF NORTHWEST XINJIANG, CHINA

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ABSTRACT—Sixteen isolated theropod teeth were discovered in two areas in the upper Middle–lower Upper Jurassic Shishugou Formation of the Xinjiang Uyghur Autonomous Region, northwest China. This sample can be divided on the basis of qualitative features and simple quantitative metrics into seven tooth morphotypes, each of which probably represents a distinct taxon. Three of the morphotypes may be attributable to theropods already known from the Shishugou Formation, namely the alvarezsauroid *Haplocheirus* and the basal tetanurans *Monolophosaurus* and *Sinraptor*. The other four morphotypes, however, appear to represent new taxa, taking the known theropod diversity of the Shishugou Formation from six species to at least ten. One of the new taxa is probably a dromaeosaurid. Another appears to represent a troodontid or a relative of the potentially troodontid-like *Paronychodon*, itself so far known only from isolated teeth. Of the remaining two taxa, one appears to be a basal tetanuran or tyrannosauroid, whereas the other either belongs to one of these same groups or represents a ceratosaur. The probable deinonychosaurian teeth in our sample are among the oldest fossils known for this clade, and highlight the diversity of coelurosaurs in the Shishugou Formation.

INTRODUCTION

The Junggar Basin in the Xinjiang Uyghur Autonomous Region of northwestern China is famous for its Jurassic and Early Cretaceous dinosaurs (Dong, 1992; Eberth et al., 2001). Among the dinosaur-bearing deposits is the Middle-Upper Jurassic Shishugou Formation, which forms richly fossiliferous outcrops in the Jiangjunmiao, Konglonggou, and Wucaiwan areas of the northeastern part of the basin. In addition to dinosaurs, the Shishugou Formation has previously yielded crocodylomorphs, turtles, and mammals (Clark et al., 2006).

Tuffs in the uppermost and middle parts of the formation have been dated at 158.7 ± 0.3 and 161.2 ± 0.2 Ma, respectively (Clark et al., 2006). The latter date is coincident with the Middle–Upper Jurassic boundary (Gradstein et al., 2004), although the boundary itself is dated only within ±4 million years (My). Because there is no apparent break in sedimentation within the formation, it is probable that the lower part of the formation dates to the late Middle Jurassic, whereas the upper part of the formation dates to the early Late Jurassic, and that the lower and upper parts respectively correlate with the Callovian and Oxfordian marine stages.

Theropods have been previously reported from two localities where the Shishugou Formation crops out, separated by approximately 90 km. At Jiangjunmiao, in the east, *Sinraptor dongi* (Currie and Zhao, 1994) was recovered from the upper part of the formation and *Monolophosaurus jiangi* (Zhao and Currie, 1994) from the lower part. In the Wucaiwan area, in the west, the basal tyrannosauroid *Guanlong wucaii* (Xu et al., 2006), the basal alvarezsauroid *Haplocheirus* (Choiniere, Xu, et al., 2010), the edentulous ceratosaur *Limusaurus* (Xu et al., 2009), the basal coelurosaur *Zulong* (Choiniere, Clark, et al., 2010), and a *Sinraptor*-like taxon represented by a large tooth (Xu and Clark, 2008) were found in the upper part of the Shishugou Formation.

The purpose of this paper is to describe, and identify as precisely as possible, 16 isolated theropod teeth that have recently been collected from the Shishugou Formation. All but one of these specimens were collected from the surface at various sites in the Wucaiwan area. The remaining tooth was collected by screen-washing at a site near the Konglonggou ('Dinosaur Gully' in Chinese) locality, approximately 25 km southeast of Wucaiwan and ENE of the town of Huoshaoshan. Only the lowest part of the Shishugou Formation is well exposed there, and fossils are mainly known from two specific sites: a quarry with abundant bones of subadults of the sauropod *Bellusaurus sui* (Dong, 1990), and the microvertebrate site where the mammaliaform *Klamelia zhaopengi* (Chow and Rich, 1984) was discovered. Screen-washing sediment from the latter site produced a diversity of microvertebrate fossils, including the theropod tooth. This specimen represents the first reported evidence of fossil theropods from the Konglonggou area.

Theropod teeth provide far less character information than other parts of the skeleton, and the diagnostic value of theropod teeth is limited in comparison to the teeth of mammals. Taxa established on the basis of tooth morphology alone often become *nomina dubia*. By the same token, it is often difficult to confidently assign isolated theropod teeth to existing species. Farlow et al. (1991) studied taxonomic variation in such parameters as crown basal length and width, crown height, and denticle density, and found that many theropod species overlap with respect to these variables and therefore cannot be easily distinguished on the basis of dental information. Conspicuous qualitative

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features do not always have a simple phylogenetic distribution: for example, enamel wrinkles have sometimes been considered diagnostic of carcharodontosaurid teeth (e.g., Canudo et al., 2006), but in fact are more widely distributed among basal tetanurans and tyrannosaurids (Brusatte et al., 2007). Nevertheless, teeth do contain morphological information of taxonomic value. Denticle size and shape vary widely among theropod taxa (Currie et al., 1990; Bakker and Bir, 2004), although denticle density often correlates with crown size and is therefore of limited utility as a character. Crown size itself can be informative in that very large tooth crowns can only be plausibly assigned to large taxa.

Accordingly, a number of workers have successfully used theropod tooth morphology for taxonomic purposes (Currie et al., 1990; Rauhut and Werner, 1995; Baszio, 1997; Sankey et al., 2002, 2005; Smith et al., 2005; Fanti and Therrien, 2007; Sankey, 2008). This research has established that some theropod clades have distinctive dental features that may allow their presence at a particular locality to be deduced on the basis of isolated teeth. From this perspective, the 16 teeth in our sample are of interest because they may reveal the existence of taxa in the Shishugou Formation that are not yet represented by more extensive skeletal material.

Unfortunately, the late Middle–early Late Jurassic of China represents a particularly difficult time and place from the point of view of assigning isolated theropod teeth to particular clades. A combination of direct fossil evidence and ghost lineage arguments suggests the presence of a wide range of theropod taxa: among major theropod clades possessing reasonably generalized dentitions, only the coelophysids can be readily eliminated on stratigraphic or biogeographic grounds when attempting to identify a particular tooth. Allosauroids, basal spinosauroids ('megalosauroids'), ceratosaurs, alvarezsauroids, and tyrannosauroids were certainly all present by the close of the early Late Jurassic (Oxfordian), and all except the basal spinosauroids are definitively known from Asia during the Middle–Late Jurassic (Weishampel et al., 2004; Xu et al., 2009; Choiniere, Xu, et al., 2010). The documented record of maniraptorans in the Jurassic of China is limited to an alvarezsauroid from Wucaiwan (Choiniere, Xu, et al., 2010) and a few paravian taxa from Middle to Upper Jurassic deposits in northeastern China whose precise age is disputed (Zhang et al., 2002; Xu and Zhang, 2005; Zhang et al., 2008; Hu et al., 2009).

However, the existence of these Chinese Jurassic paravians, and of *Archaeopteryx* from the Tithonian of Germany, implies that the diversification of the major maniraptoran clades took place by the early Late Jurassic at the latest. It is necessary to consider the possibility that some of the teeth collected in the Shishugou Formation may come from maniraptoran taxa such as dromaeosaurids or troodontids. The diversification of maniraptorans was presumably still a recent event when the Shishugou Formation was deposited, and even some major non-maniraptoran clades had probably diverged only recently from the stem theropodan lineage. Representatives of these clades in the Shishugou Formation might be early forms lacking dental specializations present in their more derived relatives (e.g., the D-shaped teeth of advanced tyrannosaurids), rendering the problem of identification even more difficult. Essentially, an isolated theropod tooth from the Middle–Upper Jurassic of Asia could conceivably belong to any major theropod clade other than Coelophysidae, without necessarily showing diagnostic features present in derived members of the clade to which it does belong.

In this study we sort the teeth in our sample into morphotypes, on the basis of both qualitative features such as the presence or absence of enamel wrinkles (Brusatte et al., 2007) and quantitative measures of tooth shape such as the length to width ratio of the crown. In most cases, all of the teeth assigned to a given morphotype were also found in close proximity to one another, but not to any teeth assigned to other morphotypes. Based on this spatial separation of morphotypes, as well as the large differences in shape and size that distinguish the various morphotypes in our sample, we consider it unlikely that any two morphotypes belong to a single taxon. Factors such as ontogeny, heterodonty, and intraspecific variation among individuals seem insufficient to account for the differences observed among morphotypes, especially given that heterodonty in theropod dentitions tends to be relatively minor apart from the distinctiveness of premaxillary teeth (e.g., Ostrom, 1969). Likewise, major ontogenetic changes in the dentition have not been reported in theropods, although the teeth may grow more robust throughout ontogeny (Carr, 1999; compare also juvenile and adult specimens of the tyrannosauroid *Guanlong*, IVPP V14531 and IVPP V14532, respectively).

We nevertheless acknowledge that theropod teeth do vary intraspecifically, and that future work might show that two or more of our morphotypes in fact represent a single taxon. However, our provisional interpretation is that each morphotype represents a different taxon, a working assumption that is both justified by the subtle nature of intraspecific variation in theropod dentitions and intrinsically more informative than the alternative of lumping vaguely similar morphotypes; even if two morphotypes in our sample turn out to belong to a single taxon, our diagnoses and descriptions will still pertain to distinct tooth types within a strongly heterodont dentition.

We have attached taxonomic identifications to our morphotypes only to the extent of trying to assign them to major theropod clades. In some cases distinctive characteristics made it possible to assign a given morphotype to a particular clade with reasonable confidence, although for other morphotypes multiple alternative identifications seemed possible.

Institutional Abbreviation—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology.

Anatomical Abbreviations—AL, apical length; **BW**, basal width; **CBL**, crown base length; **CBR**, crown base ratio; **CBW**, crown base width; **CH**, crown height; **CHR**, crown height ratio; **DAVG**, average denticle density on posterior (distal) margin of tooth; **DSDI**, denticle size difference index; **EW**, enamel wrinkles; **MAVG**, average denticle density on anterior (mesial) margin of tooth.

MATERIALS AND METHODS

Sixteen isolated theropod teeth were collected in the Wucaiwan and Konglonggou areas. V15849, the smallest tooth in the sample, was collected by screen-washing in the Konglonggou area. All of the other teeth were found on the surface in the Wucaiwan area (Table 1). All of the teeth are housed in the IVPP collections.

Dental Measurements

We follow the terminology of Smith et al. (2005) with respect to dental measurements. Crown shape was assessed in our study

TABLE 1. Theropod teeth from the Middle-Upper Jurassic Shishugou Formation, Xinjiang, China.

Occurrence	Specimens	Age
Upper part of Shishugou Formation, Wucaiwan	V15842–V15846; V15850; V15851–V15856; V15857; V15861	Oxfordian
Lower part of Shishugou Formation, Wucaiwan	V15848	Callovian
Lower part of Shishugou Formation, near Konglonggou	V15849	Callovian

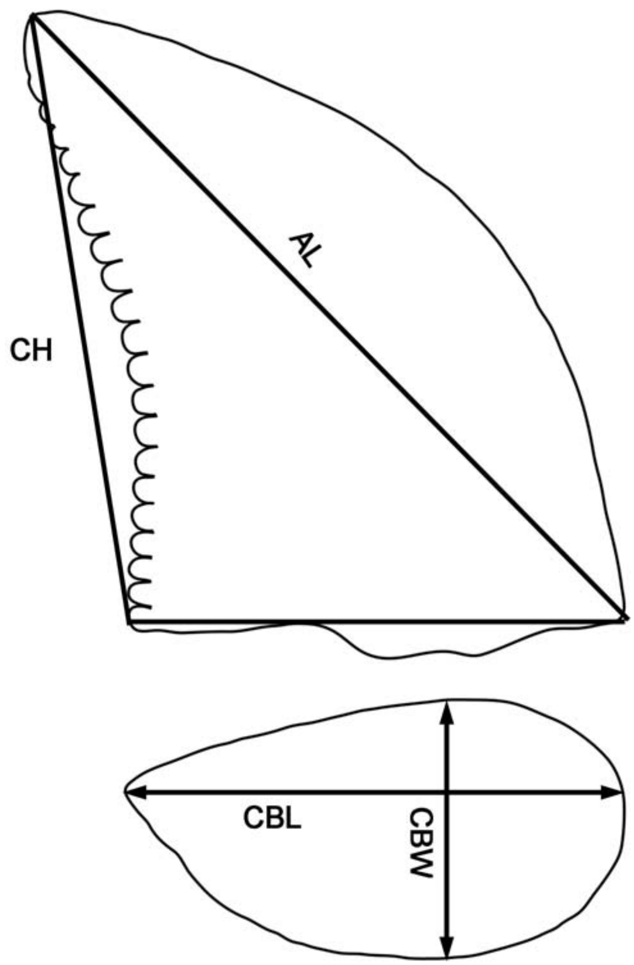

FIGURE 1. Theropod dental anatomy and variables used in this study.

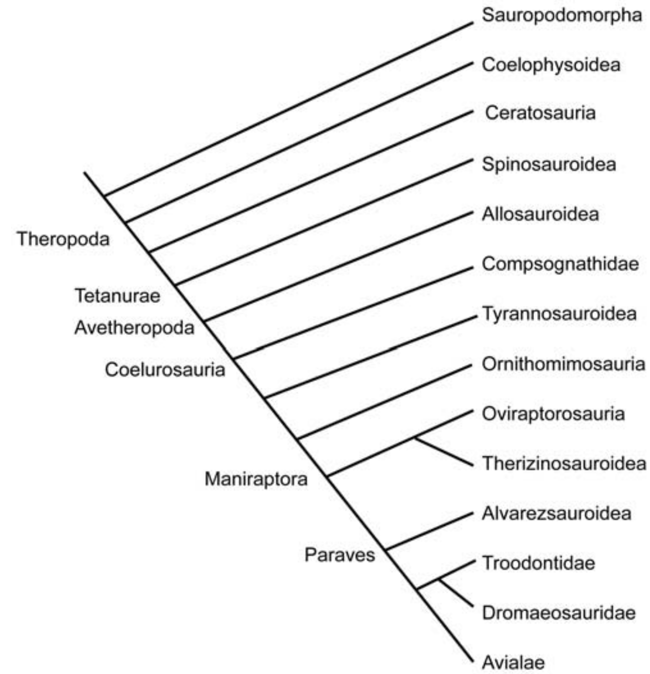

FIGURE 2. Cladogram of Theropoda used in this paper. Topology and nomenclature simplified from Holtz and Osmólska (2004) and Smith et al. (2007).

using CBL, CBW, CH, and AL (Fig. 1). Where possible, CBL was measured at the level of the basal end of the posterior carina, along the longitudinal axis of the tooth, whereas CBW was measured at the same level but perpendicular to the longitudinal axis in a horizontal plane. CBW is equivalent to BW of Farlow et al. (1991). CH was measured in a straight line from the tip of the tooth to the base of the crown on the posterior edge. CBR was calculated as CBW/CBL, and represents a descriptor of the cross-sectional shape of the crown base. CHR was calculated as CH/CBL. Not all measurements could be taken accurately on every tooth, owing to wear and breakage of some specimens in the sample. Values that had to be estimated for a particular tooth are identified clearly in the text and in the table of measurements given in Appendix 1.

Denticle size is an important character in theropod tooth identification. DAVG and MAVG express the average number of denticles per mm on the posterior (distal) and anterior (mesial) carinae, respectively. Where possible, these average values were computed by dividing the total number of denticles on the anterior or posterior carina by the total length over which the denticles occurred, measured along the curvature of the carina. DSDI is the ratio of MAVG to DAVG, and is a useful parameter for tooth identification (Rauhut and Werner, 1995). In this paper the length of a denticle is measured anteroposteriorly, whereas the width is measured apicobasally.

Theropod Systematics

Phylogenetic relationships among the major theropod taxa remain uncertain in many respects, and some taxa are defined differently by different authors. These discrepancies have little impact on our conclusions, but for clarity and ease of reference we adopt a theropod phylogeny following Holtz and Osmólska (2004) and Smith et al. (2007), as shown in Figure 2. We use the term 'basal tetanuran' to denote any tetanuran falling outside Coelurosauria.

DESCRIPTION

Morphotype 1

Referred Specimens—V15851–V15855 (Fig. 3).

Diagnosis—Crown large and compressed labiolingually, with CBR approximately 0.5; denticles present on posterior carina, variably present on anterior carina; anterior denticles narrow and not separated by intervening spaces; posterior denticles twice the length of anterior ones, when the latter are present; steeply inclined enamel wrinkles may occur near anterior or posterior carina over basal part of tooth.

Description—V15851–V15855 were recovered from the lower part of the Shishugou Formation in the Wucaiwan area. These five teeth were found in close association and are similar to one another in size and shape, which suggests that they may belong to one species and perhaps even to a single individual. Most of the teeth are badly damaged, with their tips broken away, but the crown heights of the intact teeth were probably close to 4 cm. The preserved crown height of one specimen (V15855) is significantly smaller, but cannot be precisely measured because the base of this tooth is missing. Where the base is intact, CBR values range from 0.45 to 0.48. However, these values may have been somewhat affected by distortion, because specimens V15851–V15854 all show signs of taphonomic compression. Sections of the enamel

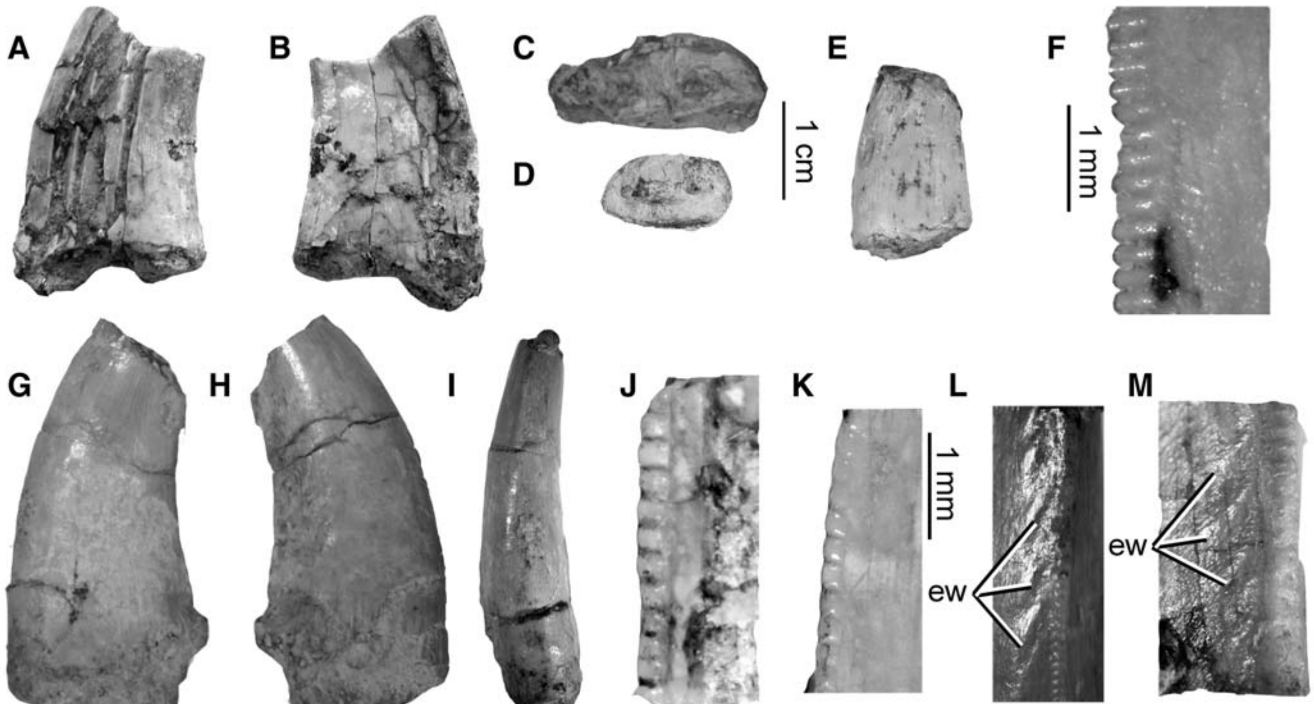

FIGURE 3. Theropod teeth of Morphotype 1 from the Middle-Upper Jurassic Shishugou Formation, Wucaiwan. **A**, crown of V15851 in labial view; **B**, crown of V15851 in lingual view; **C**, cross-section of V15851 near base; **D**, cross-section of V15855; **E**, crown of V15855 in labial view; **F**, posterior denticles of V15855 in lingual view; **G**, crown of V15852 in lingual view; **H**, crown of V15852 in labial view; **I**, Crown of V15852 in anterior view; **J**, posterior denticles of V15852 in labial view. **K**, anterior denticles of V15852 in lingual view; **L**, enamel wrinkles of V15852 along anterior carina in anterior view; **M**, enamel wrinkles of V15854 along posterior carina in posterior view.

surface of each tooth are depressed, and some teeth show open cracks along which these displacements have occurred.

Specimens V15852 and V15853 have denticles both anteriorly and posteriorly (Fig. 3J, V15852), whereas anterior denticles are absent in V15851 and V15855. The presence of anterior denticles in V15854 is uncertain as the anterior carina is damaged in this specimen. Where present, the anterior denticles are generally short, narrow, square, and closely packed, with no intervening spaces between adjacent denticles. They stop well short of the base of the crown in V15852. In V15853 they seem to approach the base more closely, but the situation is unclear because the basal part of the anterior carina is damaged. The posterior denticles are almost identical in width to the anterior ones, but are twice as long (Fig. 3J, K) and also somewhat wider in the case of V15852. V15852 and V15853 have DSDI values of 1.23 and 0.99, respectively. In V15855, a badly broken tooth (Fig. 3E), the posterior denticles are even longer, and indeed resemble the posterior denticles in V15858 (see Morphotype 5, below). However, we retain V15855 as part of Morphotype 1 because it was found together with the other teeth assigned to this morphotype, and because it resembles them in its size and overall structure.

In most Morphotype 1 teeth, the posterior carina is relatively straight and close to the midline of the tooth. In V15851, the basal part of the posterior carina is close to the lingual side of the tooth, and also angles lingually as it continues basally (Fig. 3A, B). In V15855 the posterior carina is also lingually displaced, but is nearly straight. The anterior carina is well defined apically but becomes progressively subdued basally (Fig. 3I, V15852). In cross-section, the lingual side of V15851 is linear, whereas the labial side is convex and reaches its maximum curvature close to the posterior edge of the tooth, and this nearly 'D'-shaped cross-section may indicate that V15851 is a premaxillary tooth. However, the other specimens included in this morphotype tend to have a more symmetrical cross-section (Fig. 3D).

Enamel wrinkles are clearly present, although weakly developed, in V15852 and V15854. In V15854, a parallel series of short, oblique ridges extend across the lingual surface from the posterior carina (Fig. 3M). The ridges diverge from the carina at an angle of about 45°, running anterobasally across the surface of the tooth. In V15852, the enamel wrinkles are adjacent to the anterior rather than the posterior carina, but are parallel and oblique as in the posterior enamel wrinkles of V15854. In V15852 the angle between the wrinkles and the anterior carina is about 30° (Fig. 3L).

Discussion—Morphotype 1 specimens display the gross characteristics of generalized theropod teeth, including recurvature, lateral compression, and denticulation. The combination of relatively prominent posterior denticles with small or absent anterior denticles is typical of a wide range of theropods, including the ceratosaurs *Masiakasaurus* (Carrano et al., 2002; Smith, 2007) and *Kryptops* (Sereno and Brusatte 2008), sinraptorids (Xu and Clark, 2008), compsognathids (Ostrom, 1978; Currie and Chen, 2001; Hwang, 2005), basal tyrannosauroids (Xu and Clark, 2008), velociraptorine dromaeosaurids (Lindgren et al., 2008), and some or most troodontids (Currie et al., 1990; Averianov and Sues, 2007). Although this is probably best regarded as the typical theropod condition, exceptions exist. In the ceratosaur *Majungasaurus* (Smith, 2007) and tyrannosaurids (Hwang, 2005; Samman et al., 2005), the anterior and posterior serrations tend to be subequal in size. In many spinosaurines (Hone et al., 2010), the ornithomimosaurs *Pelecanimimus* (Perez-Moreno et al., 1994), and *Shenzhousaurus* (Ji et al., 2003), some troodontids such as *Byronosaurus* (Makovicky et al., 2003), the enigmatic Cretaceous taxa *Paronychodon* and *Richardoestesia* (Currie et al., 1990; Sankey et al., 2002), the alvarezsaurids *Mononykus* and *Shuvuuia* (Longrich and Currie, 2009), and toothed birds (Sankey et al., 2002), anterior denticles are minute or entirely absent.

The enamel wrinkles present on V15852 and V15854 are more narrowly diagnostic. Although the distribution of these structures in theropods remains to be fully explored, enamel wrinkles occur in some basal tetanurans and some tyrannosauroids, but seem to be absent in other tetanurans (Brusatte et al., 2007). The carcharodontosaurids *Mapusaurus*, *Tyrannotitan*, and *Carcharodontosaurus inguidensis* (Brusatte et al., 2007) resemble V15852 and V15854 in having enamel wrinkles that are limited to the vicinity of the carinae, whereas in many other taxa the wrinkles extend as continuous bands across the lingual and/or labial surfaces of the crown. This might suggest that Morphotype 1 teeth are likely to represent a carcharodontosaurid, but enamel wrinkle patterns are still insufficiently well documented to provide a strong basis for identifying isolated teeth. In any case, the teeth of derived carcharodontosaurids differ from Morphotype 1 specimens in having very low CBR values (Smith et al., 2005; Coria and Currie, 2006) and reduced recurvature, although Morphotype 1 teeth could still belong to a basal member of the group. Carcharodontosaurids have a ghost lineage extending back to the Late Jurassic (Brusatte et al., 2008), so the presence of a basal carcharodontosaurid in the Shishugou Formation would not be biostratigraphically implausible.

The generalized morphology of Morphotype 1 teeth would not rule out either a basal tetanuran or a tyrannosauroid identification, although the truncated length of the anterior denticles implies that Morphotype 1 teeth are unlikely to belong to a tyrannosaurid. The largest of the Morphotype 1 teeth (V15853) probably had a crown height of approximately 4 cm when complete, falling well within the range of crown heights reported by Smith et al. (2005) for *Allosaurus* but considerably smaller than most of the teeth of the subadult *Sinraptor* described by Currie and Zhao (1994). By contrast, teeth of the basal tyrannosauroid *Guanlong* from the Upper Shishugou have crown heights not exceeding about 2 cm (Xu et al., 2006). In *Guanlong* the anterior carinae of the anterior teeth also spiral onto the lingual crown surface as they pass basally, a feature also characteristic of the entire dentition of *Dromaeosaurus* (Currie et al., 1990) and known to occur in some tyrannosaurid (Sankey et al., 2002) and allosauroid (Currie and Carpenter, 2000) teeth. A similar condition has been reported in isolated dromaeosaurid teeth from the Barremian of Uña, Spain (Rauhut, 2002). In the present sample, lingual spiraling is evident only in Morphotypes 6 and 7.

The average CBR of 0.51 for Morphotype 1 teeth is consistent with a basal tetanuran identification. Zinke (1998) found CBR values of approximately 0.5 in allosaurid teeth from the Upper Jurassic coal mine of Guimarota, and Smith et al. (2005) recorded broadly similar values for maxillary and posterior dentary teeth of both *Allosaurus* and *Acrocanthosaurus*. Similarly, the DSDI value of 0.99 for V15853 agrees with the values of approximately 1.0 that have been previously reported for allosaurids (Rauhut and Werner, 1995; Zinke, 1998) as well as for various other theropods, including *Coelophysis*, *Ceratosaurus*, *Dromaeosaurus*, and several tyrannosauroids (Rauhut and Werner, 1995). However, the DSDI of V15852 is considerably higher (1.23), although still smaller than the values of ca. 1.5–1.8 that characterize velociraptorine dromaeosaurids and the relatively basal tyrannosauroids *Dryptosaurus* (Rauhut and Werner, 1995) and *Eotyrannus* (Hutt et al., 2001). CBR values for basal tyrannosauroids have not been reported, but preliminary measurements of *Guanlong* (V14531) demonstrate that the maxillary teeth have a typical CBR of about 0.5 as in Morphotype 1. CBR values in tyrannosaurids tend to be considerably higher (see Smith et al., 2005).

Morphotype 1 teeth could conceivably belong to either a basal tyrannosauroid larger than *Guanlong*, or a basal tetanuran in the same approximate size range as *Allosaurus*. Known teeth of *Sinraptor* (Currie and Zhao, 1994) and *Monolophosaurus* (Zhao and Currie, 1994) from the Shishugou Formation are much larger than Morphotype 1 specimens, but have not been described in sufficient detail to rule out the possibility that Morphotype 1 teeth are attributable to a juvenile of one of these taxa.

Discriminating among the various possibilities would require more information on the dentitions of these relatively generalized theropods than is presently available. As with derived carcharodontosaurids, spinosaurids can be ruled out because of their specialized tooth morphology, but Morphotype 1 teeth could easily belong to an allosaurid, a sinraptorid, a basal spinosauroid, a basal carcharodontosaurid such as *Neovenator* (Brusatte et al., 2008), or a basal tetanuran falling outside any of these well-defined clades. Detailed descriptions of tooth morphology in such taxa as *Allosaurus*, *Sinraptor*, *Torvosaurus*, and *Guanlong*, including explicit discussion of heterodonty and (where possible) ontogenetic and individual variation in each case, would do much to facilitate the identification of isolated theropod teeth from the Jurassic.

Morphotype 2

Referred Specimen—V15848 (Fig. 4).

Diagnosis—Crown slightly recurved with subrectangular cross-section; CBR approximately 0.5; denticles round, blunt, and slightly inclined towards tip of the crown; enamel wrinkles present on basal portion of crown, adjacent to anterior carina.

Description—Morphotype 2 contains a single mid-sized tooth (estimated crown height 2 cm) from the lower part of the Shishugou Formation in the Wucaiwan area. The crown is apically damaged, missing perhaps one quarter of its total height (Fig. 4A), and moderately compressed labiolingually (CBR about 0.54; Fig. 4B). Both the lingual and labial surfaces are nearly flat, and in cross-section the tooth is subrectangular with a rounded anterior end. The posterior edge of the basal part of the tooth is damaged. The anterior carina forms a sharp edge but becomes less prominent as it approaches the base of the crown, as in Morphotype 1 specimens. In V15848 the tips of the posterior denticles are often damaged, but the intact ones taper to blunt, broad points and are approximately perpendicular to the apicobasal axis of the tooth crown (Fig. 4C). The posterior denticles are longer and sharper than those of most Morphotype 1 specimens, although they resemble the elongate posterior denticles of V15855 (Fig. 3F).

It is difficult to be certain whether or not anterior denticles are present in V15848, because the edge of the anterior carina is damaged. However, the anterior carina retains a sharp and rugose appearance, suggesting the presence of denticles. The anterior carina is situated along the midline of the tooth, whereas the basal part of the posterior carina curves lingually. The DAVG of this tooth is 3.7 denticles/mm, close to the average value for Morphotype 1 teeth (see Appendix 1). Enamel wrinkles are present along both sides of the anterior carina, as in V15852 (Fig. 3L). In V15848, however, the enamel wrinkles differ in form from those seen in Morphotype 1. Whereas Morphotype 1 enamel wrinkles are straight, basally sloping lines, the enamel wrinkles of V15848 are horizontal in overall orientation but are distinctly concave towards the apex of the tooth (Fig. 4D). As in Morphotype 1, however, the enamel wrinkles of V15848 are very short, being essentially restricted to a small area of enamel adjacent to the carina on either side.

Discussion—V15848, the only tooth assigned to Morphotype 2, is similar to Morphotype 1 specimens but can be distinguished from them by the horizontal orientation and apically concave curvature of its enamel wrinkles. The elongate, relatively sharp

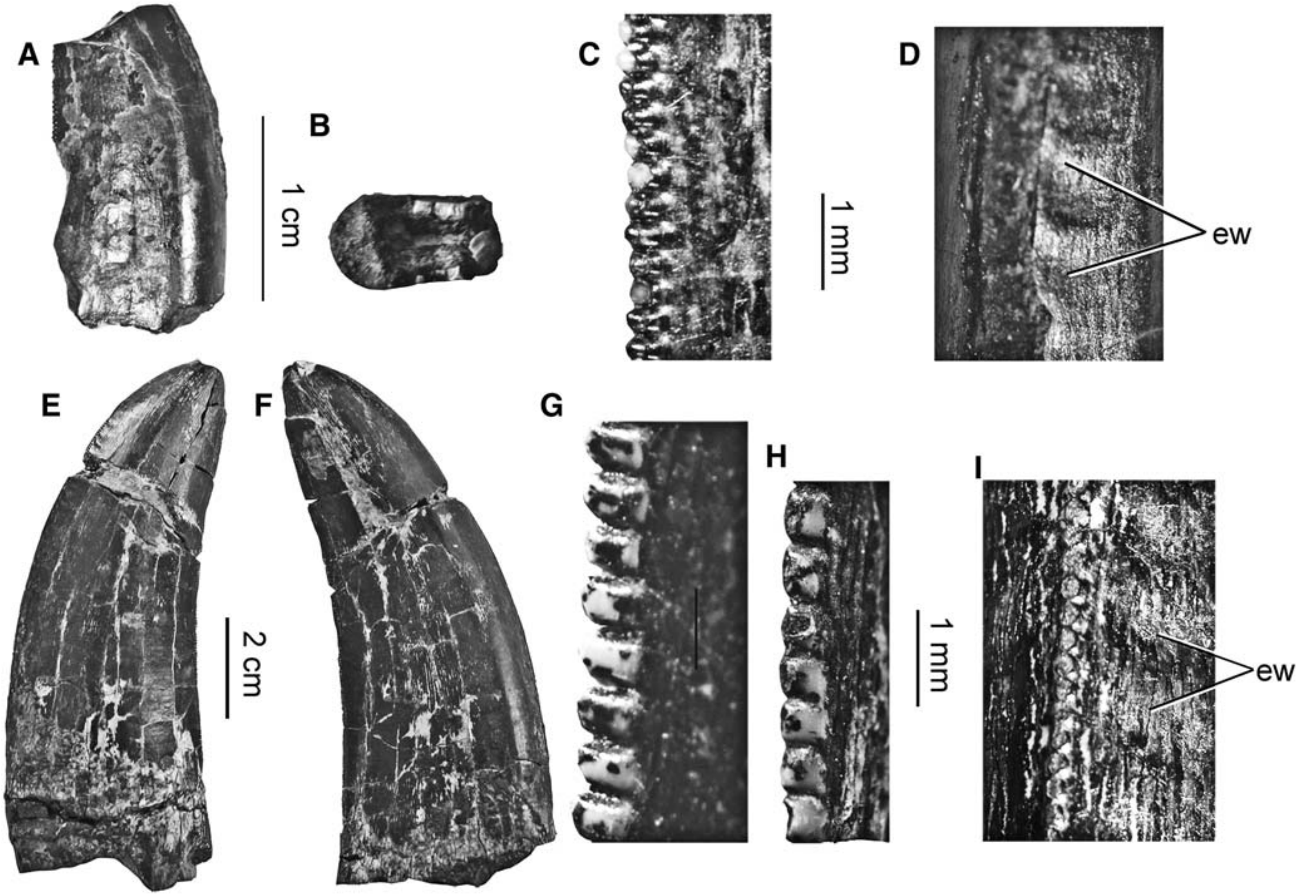

FIGURE 4. Theropod tooth of Morphotype 2 (V15848) from the Middle-Upper Jurassic Shishugou Formation, Wucaiwan, and comparable large tooth (V15310). **A**, crown of V15848 in labial view; **B**, cross-section of V15848 near base; **C**, posterior denticles of V15848 in lingual view; **D**, enamel wrinkles of V15848 along the anterior carina in anterior view; **E**, crown of V15310 in labial view; **F**, crown of V15310 in lingual view; **G**, posterior denticles of V15310 in lingual view (scale bar equals 1 mm as in **H** and **I**); **H**, anterior denticles of V15310 in labial view; **I**, enamel wrinkles of V15310 along the anterior carina in anterior view.

posterior denticles of V15848 also distinguish this specimen from most Morphotype 1 teeth, although not from V15855. V15848 is close to the lower end of the size range for Morphotype 1, with an estimated crown height of only approximately 2 cm.

As with Morphotype 1, the enamel wrinkles and generalized morphology of V15848 imply that this tooth belongs to a basal tetanuran or a tyrannosauroid. Although damage to the anterior carina does not permit the anterior denticles to be compared to the posterior ones, the small size and moderate rather than slight lateral compression of V15848 (CBR $\approx$ 0.54) imply that this tooth is unlikely to belong to a tyrannosaurid, although it could easily belong to basal tyrannosauroid. Distinguishing between the basal tetanuran and basal tyrannosauroid alternatives is again difficult. In either case, V15848 is likely to come from a smaller theropod than the Morphotype 1 taxon, and might have belonged to an animal only slightly larger than the basal tyrannosauroid *Guanlong*. However, it is unlikely that this tooth is referable to *Guanlong* itself, because enamel wrinkles are absent in the teeth of the *Guanlong* holotype (V14531) and referred specimen (V14532).

It is notable that V15848 bears some surprising resemblances to a much larger tooth (V15310; Fig. 4E, F) previously described by Xu and Clark (2008) from the upper part of Shishugou Formation near Wucaiwan. V15310 has a crown height of 9.2 cm (Xu and Clark 2008), but resembles V15848 in overall shape and particularly in the form of the enamel wrinkles. Although V15310 bears enamel wrinkles along both carinae, whereas the wrinkles of V15848 occur in association with the anterior carina only, the wrinkles of V15310 are similar to those of the smaller specimen in orientation and curvature. By contrast, the morphology of the posterior denticles differs between the two specimens, in that those of V15848 are straight, closely packed, and relatively sharply pointed (Fig. 4C), whereas those of V15310 display a slight apical curvature, have rounded tips, and are more widely spaced (Fig. 4G). Nevertheless, the similarity in the enamel wrinkles is suggestive. Xu and Clark (2008) identified V15310 as the tooth of a 'giant sinraptorid,' and it is possible that V15848 comes from a small or juvenile representative of the same clade. However, it might also belong to a representative of a different group of basal tetanurans, or to a basal tyrannosauroid. V15848 may even be attributable to a juvenile *Sinraptor* or *Monolophosaurus*.

Morphotype 3

Referred Specimen—V15858 (Fig. 5).

Diagnosis—Crown moderately compressed; anterior and posterior carinae both bear subrectangular denticles; anterior denticles nearly as long as posterior denticles, but less apicobasally broad.

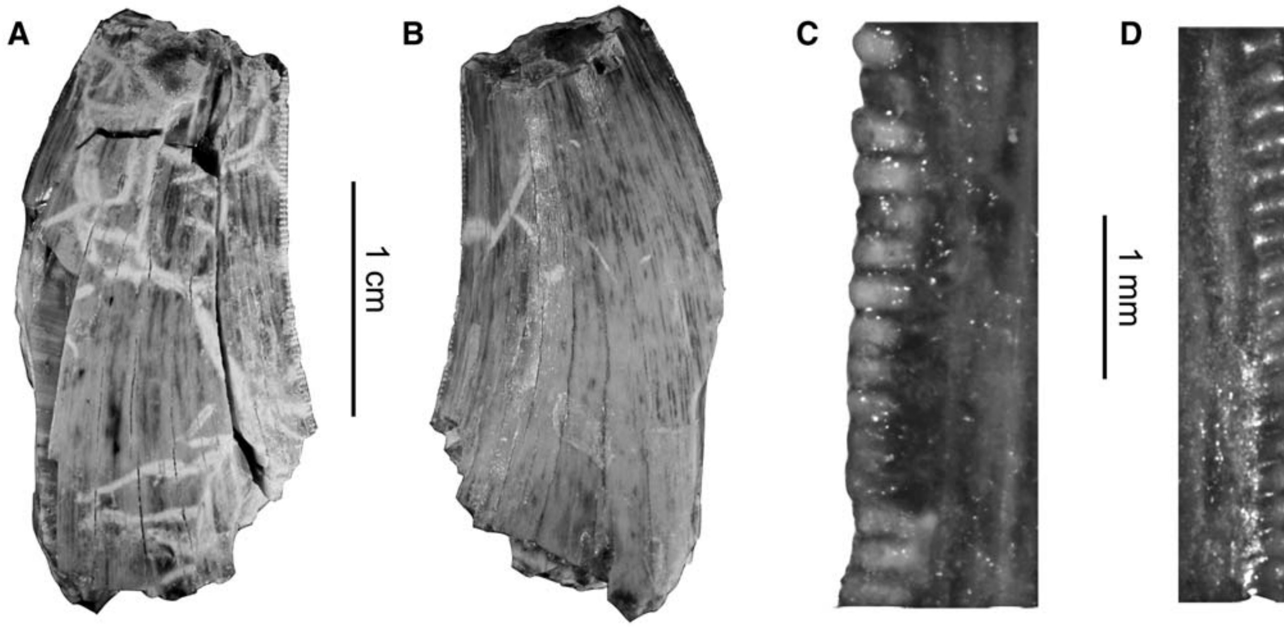

FIGURE 5. Theropod tooth of morphotype 3 from the Middle-Upper Jurassic Shishugou Formation, Wucaiwan. **A**, crown of V15858 in labial view; **B**, crown of V15858 in lingual view; **C**, posterior denticles of V15858 in lingual view; **D**, anterior denticles of V15858 in lingual view.

Description—Specimen V15858 was collected from the lower part of the Shishugou Formation at Wucaiwan, near the site that yielded specimens V15851–V15855 (see Morphotype 1, above). Specimen V15858 is badly damaged (Fig. 5A, B). The height of the intact crown may have been approximately 3.5 cm, but both the base and apex are now broken away. The crown expands lingually from the tip to the base, and its proportions suggest a fairly robust base with a CBR value probably exceeding 0.5. The posterior denticles are narrow and slender, and not inclined towards the tip of the tooth (Fig. 5C). The anterior denticles are even narrower (DSDI = 1.22), and the denticles of both carinae are closely packed without intervening spaces. The MAVG and DAVG of V15858 are 4.4 and 3.6, respectively, values close to those recorded for Morphotype 1 (see Appendix 1). The anterior denticles are approximately twice as anteroposteriorly long as they are apicobasally wide, whereas in the narrower posterior denticles the length/width ratio is approximately 3. Uniquely within the present sample, the anterior denticles of V15858 angle slightly towards the tip of the crown rather than being perpendicular to the anterior carina (Fig. 5D). Enamel wrinkles are absent.

Discussion—Despite severe damage, specimen V15858 can be distinguished from Morphotype 2 by its large size, and from Morphotype 1 by its slightly more robust proportions. Furthermore, the very high length/width ratio seen in the anterior denticles of V15858 is unparalleled in the present sample, although the even higher ratio in the posterior denticles is matched by one Morphotype 1 specimen (V15855). The anterior denticles of V15858 are almost as long as the posterior denticles, resembling the condition in tyrannosaurids (Samman et al., 2005) but in contrast to most theropods. Although the CBR of V15858 is difficult to estimate precisely, because of the damage to the base of the crown, this tooth appears to be more robust than Morphotype 1 specimens and possibly more robust than the single specimen assigned to Morphotype 2. However, V15858 is nevertheless more slender than the teeth of tyrannosaurids, and its CBR value is well within the ranges that are typical of basal tetanurans, basal tyrannosauroids, and even dromaeosaurids. The DSDI of V15858 (1.22) is intermediate between the relatively low values reported by Rauhut and Werner (1995) for tyrannosaurids (close to 1.0) and the higher values reported for dromaeosaurids and more basal tyrannosauroids by Rauhut and Werner (1995) and Hutt et al. (2001). The absence of enamel wrinkles is of little taxonomic value, because wrinkles are lacking in many individual tyrannosauroid and basal tetanuran taxa, even though they are broadly characteristic of these groups (Brusatte et al., 2007). However, V15858 is much larger than most dromaeosaurid teeth: even in *Deinonychus*, a relatively large dromaeosaurid, the teeth have crown heights not exceeding 1.5 cm (Smith et al., 2005). The large size, moderately low DSDI, and long anterior denticles of V15858 argue strongly against the dromaeosaurid interpretation.

Similarly, V15858 is too large to pertain to the Shishugou basal tyrannosauroid *Guanlong*, and is also distinguished from *Guanlong* teeth by its long anterior denticles. The long anterior denticles are a point of resemblance to tyrannosaurids, perhaps suggesting that V15858 belongs to a second Shishugou tyrannosauroid that is larger and more derived than *Guanlong*. However, the tooth could also belong to a basal tetanuran with unusually elongated anterior denticles. It could possibly represent a juvenile *Sinraptor* or *Monolophosaurus* tooth.

An additional, intriguing possibility is that V15858 might represent the tooth of a ceratosaur. The only ceratosaur presently known from the Shishugou formation is *Limusaurus*, which is edentulous at least at adult sizes (Xu et al., 2009), but the possibility that a toothed ceratosaur was also present in the ecosystem should not be dismissed. However, few ceratosaur teeth have been described in detail, and we are not aware of any ceratosaur whose teeth V15858 closely resembles. *Ceratosaurus* is characterized by a low DSDI value (1.0; Rauhut and Werner, 1995) in comparison to V15858, and *Ceratosaurus* teeth are quite strongly laterally compressed (posterior maxillary teeth with CBR <0.5; Smith et al., 2005). *Majungasaurus* has a more robust dentition (Smith et al., 2005), but the teeth of this taxon differ from V15858 in that their posterior edges are nearly straight rather

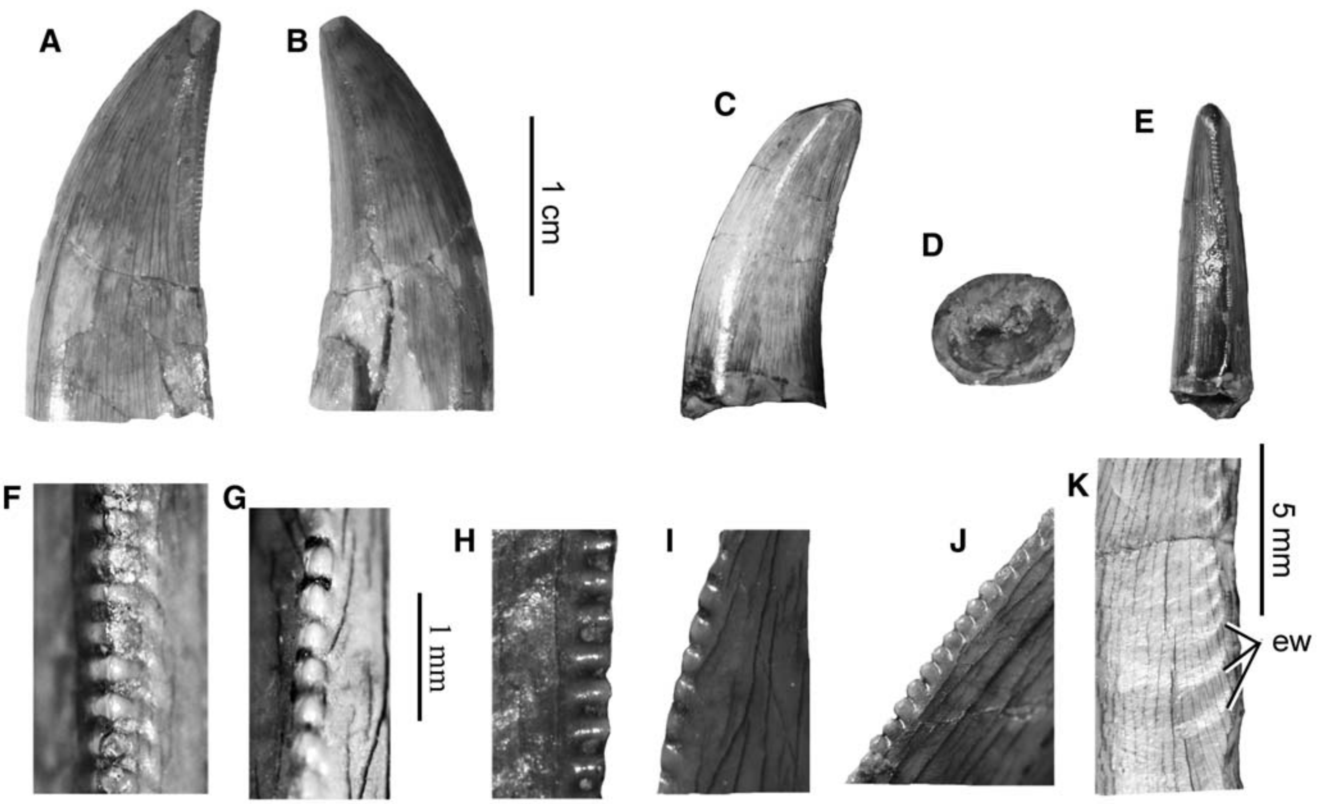

FIGURE 6. Theropod teeth of Morphotype 4 from the Middle-Upper Jurassic Shishugou Formation, Wucaiwan. **A**, crown of V15842 in labial view; **B**, crown of V15842 in lingual view; **C**, crown of V15844 in labial view; **D**, cross-section of V15844 at base; **E**, crown of V15844 in posterior view; **F**, posterior denticles of V15842 in posterior view; **G**, anterior denticles of V15842 in anterior view; **H**, posterior denticles of V15842 in labial view; **I**, anterior denticles of V15842 in labial view; **J**, anterior denticles of V15845 in labial or lingual view; **K**, enamel wrinkles of V15843 in lingual view.

than markedly recurved, and again have low DSDI values (Smith, 2007). Further research into ceratosaur dentitions will be helpful in evaluating the possibility that isolated Jurassic theropod teeth from Wucaiwan and elsewhere might pertain to this clade.

Morphotype 4

Referred Specimens—V15842–V15846, V15856 (Fig. 6).

Diagnosis—Crown slightly recurved, with elliptical cross-section; CBR about 0.6–0.7; denticles always present on posterior carina, variably present on anterior carina; posterior denticles subrectangular, not inclined in lateral view, and about twice as long as anterior denticles if the latter are present; enamel wrinkles present near posterior carina in some specimens.

Description—Specimens V15842–V15846 are similar to each other in both size and shape, and were found together in the Wucaiwan area in the upper part of the Shishugou Formation. V15856 is a slightly damaged tooth that was collected at Wucaiwan, close to the specimens assigned to Morphotype 1. Nevertheless, V15856 can be tentatively assigned to Morphotype 4 on the basis of its size and proportions. The longest tooth is missing a small part of the apex, but has an estimated CH of about 23 mm. Morphotype 4 teeth are slightly recurved and moderately laterally compressed, with CBR values ranging from 0.57 to 0.70 (mean = 0.65; see Appendix 1). In all specimens other than V15845, the anterior carina forms a sharp edge extending from the apex to the midpoint of the crown's height, but becomes progressively rounded towards the base. By contrast, V15845 is damaged at the base but appears to have a sharp anterior carina extending the entire length of the crown. The posterior carinae in Morphotype 4 teeth (Fig. 6E) are close to the midline near the apex, but as they descend towards the base the carinae angle initially towards the flatter side of the tooth, which we take to be lingual. Close to the base, the carinae either straighten or curve slightly back towards the labial side.

The MAVGs of specimens V15842 and V15845 are 4.0 denticles/mm and 4.6 denticles/mm, respectively. Their DAVGs are respectively 3.2 denticles/mm and 4.4 denticles/mm, showing that the posterior denticles are slightly greater in average apicobasal width (DSDIs = 1.24 and 1.03, respectively). The posterior denticles are perpendicular to the carina and slender, with a length/width ratio of approximately 2 (Fig. 6F, H). In overall form they resemble the posterior denticles seen in Morphotype 2, Morphotype 3, and specimen V15855 within Morphotype 1. In Morphotype 4 the posterior denticles are long and wide in the middle of the carina, and become smaller in both dimensions basally and apically. Any anterior denticles, by contrast, are small and subrectangular, with anteroposterior lengths less than or equal to their apicobasal widths. The posterior denticles are not only approximately twice as long as the anterior ones, but are also more sharply pointed (Fig. 6F–I). The anterior denticles are packed together closely, whereas small spaces separate adjacent posterior denticles (Fig. 6H, I). Specimens V15843, V15844, V15846, and 15856 lack denticles on the anterior carina, and have DAVG values ranging from 3.6 to 4.2.

Specimens V15842 and V15845 are damaged in such a way that the cross-sectional shape is unclear, whereas V15843, V15844, and V15846 are well preserved and have subrectangular cross-sections (Fig. 6D). Enamel wrinkles are visible on both sides of the posterior carina in V15843 (Fig. 6K), on the lingual side of the posterior carina in V15842, and on both sides of the anterior carina in V15845. Faint striations that may represent shallow enamel wrinkles are also present on the lingual side of the posterior carina of V15856. In V15842, the lingual side of V15843, one side of V15845 and apparently V15856, the wrinkles are best developed close to the carina, where they angle steeply towards the base of the tooth. However, they level off at a point further from the carina, and extend subhorizontally for a short distance. In the other morphotypes, by contrast, the subhorizontal part of each wrinkle is absent, so that the wrinkles terminate close to the carina and appear shorter, straighter, and quite steeply angled. In all cases the enamel wrinkles of Morphotype 4 teeth are significantly shallower than in Morphotype 2. In Morphotype 4 the enamel wrinkles are closely packed along the edge of the carina, but the spacing between adjacent wrinkles increases as they curve horizontally. This contrasts once again with Morphotype 2, in which the spacing between adjacent wrinkles tends to remain constant. The enamel wrinkles of Morphotype 4 are closer in structure to those occurring along the posterior carina of one of the Morphotype 1 teeth (V15854).

Discussion—The specimens assigned to Morphotype 4 have a suite of features common to most theropod teeth, including recurvature, reduction of the anterior denticles relative to the posterior ones, and a degree of lateral compression. However, the average CBR of 0.65 indicates that Morphotype 4 teeth are more robust than teeth assigned to Morphotypes 1 through 3, and Morphotype 4 also displays enamel wrinkles that differ in form from those seen in Morphotype 2. In Morphotype 3 enamel wrinkles are entirely absent. Morphotype 4 teeth are smaller than those of Morphotype 1, with only a slight overlap in size range, and the largest Morphotype 4 tooth is substantially smaller than the estimated size of the single tooth assigned to Morphotype 3. Finally, the short or absent anterior denticles of Morphotype 4 teeth also clearly distinguish them from the Morphotype 3 tooth.

However, Morphotype 4 specimens resemble those assigned to Morphotypes 1 and 2 in being relatively generalized theropod teeth, some of which bear enamel wrinkles. They are similar in size to teeth of the Shishugou tyrannosauroid *Guanlong*. Enamel wrinkles are not visible in the dentition of *Guanlong*, but this could be the result of wear. However, anterior teeth of *Guanlong* show lingual spiraling of the anterior carina, a feature not seen in Morphotype 4, and posterior *Guanlong* teeth tend to be more laterally compressed than Morphotype 4 specimens. The robust build of Morphotype 4 teeth is reminiscent of more derived tyrannosauroids (i.e., tyrannosaurids), but the size discrepancy between the anterior and posterior denticles differs from the tyrannosaurid condition (Samman et al., 2005) and resembles velociraptorine dromaeosaurids (Lindgren et al., 2008) and some basal tetanurans. The presence of enamel wrinkles in some Morphotype 4 teeth argues against a dromaeosaurid identification, but it is possible that the teeth belong to a small tyrannosauroid with the unusual combination of robust tooth crowns and proportionally short anterior denticles.

We know of no individual basal tetanuran taxon that has teeth closely resembling those assigned to Morphotype 4. These teeth are small in comparison to adult teeth of *Allosaurus*, *Sinraptor*, and many other basal tetanurans, and lack the respective specializations of spinosaurids and derived carcharodontosaurids. However, it is difficult to dismiss the possibility that Morphotype 4 specimens belong to a small, generalized taxon within the basal tetanuran evolutionary grade, or to a juvenile.

For example, Smith (2005) found CBR values ranging from 0.46 to 0.75 in maxillary and posterior dentary *Allosaurus* teeth from North America, encompassing the range seen in Morphotype 4. The DSDI value of 1.0 given by Rauhut and Werner (1995) for *Allosaurus* is close to that calculated for V15845 (1.03), although it is smaller than that of V15842 (1.24). However, allosaurid teeth from the Morrison Formation typically have denticles that incline towards the tip of the crown, in contrast to Morphotype 4 (Bakker and Bir, 2004). Similarly, allosaurid teeth from the Upper Jurassic of Guimarota, Portugal (Zinke, 1998), differ from Morphotype 4 specimens in having CBR values averaging about 0.5 and in bearing on the lingual surface a well-developed ridge flanked by two longitudinal grooves.

Given the variation that exists in allosaurid teeth, Morphotype 4 could represent a small or juvenile allosaurid despite differing in some features from the Morrison and Guimarota examples. Assignment to another clade of basal Tetanurae (particularly Sinraptoridae) is also plausible. As with previous morphotypes, there is nothing to rule out the possibility that Morphotype 4 teeth belong to a juvenile specimen of *Monolophosaurus* or *Sinraptor*. Accordingly, a basal tetanuran identification must be considered as an alternative to the basal tyrannosauroid identification suggested above.

Morphotype 5

Referred Specimen—V15857 (Fig. 7).

Diagnosis—Crown slightly recurved, with elliptical cross-section; labial and lingual surfaces smooth, lacking enamel wrinkles or longitudinal ridging; crown base protrudes posteriorly so that posterior margin of tooth appears sinuous in labial or lingual view; anterior carina sharp and lingually spiraling; anterior denticles absent; lingual and labial depressions occur between bases of adjacent posterior denticles.

Description—V15857 is a well-preserved specimen from the upper part of the Shishugou Formation in the Wucaiwan area (Fig. 7A, C), with a CH of 0.71 cm and a CBR of 0.57. The cross-section is elliptical (Fig. 7B), and the tooth is symmetrical in anterior or posterior outline (Fig. 7D, E). The anterior carina is sharp near the apex of the crown, but becomes subdued towards the base (Fig. 7E). The anterior carina also spirals lingually as it passes basally, although a separate branch of the carina diverges in a labial direction. In contrast, the posterior carina is straight and vertical in posterior view, lacking the deflection or curvature seen in Morphotypes 1 and 4 (Fig. 7D). Denticles are absent on the anterior carina. The posterior denticles are wide in proportion to their length, particularly near the midpoint of the carina and for some distance further apically. Over the basal half of the carina the denticles are somewhat narrower. The DAVG of the tooth is 5.7, and small, rounded depressions occur between the bases of adjacent denticles on the labial side of the tooth (Fig. 7F). V15857 is the only tooth in our sample in which such depressions are evident. Another unusual character is that the base of the tooth expands posteriorly, so that the posterior margin has a sinuous appearance in labial or lingual view (Fig. 7A, C). Enamel wrinkles and longitudinal ridging are absent.

Discussion—The lingual spiraling of the anterior carina seen in V15857 also occurs in the dromaeosaurid *Dromaeosaurus* and in the anterior teeth of a few other taxa, including the Shishugou basal tyrannosauroid *Guanlong* (see Morphotype 1, above). In *Dromaeosaurus* and *Guanlong*, the labial deflection of the anterior carina begins almost at the apex of the crown, whereas in V15857 and isolated dromaeosaurid teeth from the Barremian of Spain (Rauhut, 2002), the anterior carina does not begin to spiral labially until it has descended a short distance towards the crown base. A Spanish tooth illustrated by Rauhut (2002:fig. 2F) even shows a diverging labial branch of the anterior carina, as in V15857. This condition is reminiscent of the 'split carinae' observed in some tyrannosaurid teeth by Erickson (1995), who tentatively attributed the phenomenon to a genetic anomaly.

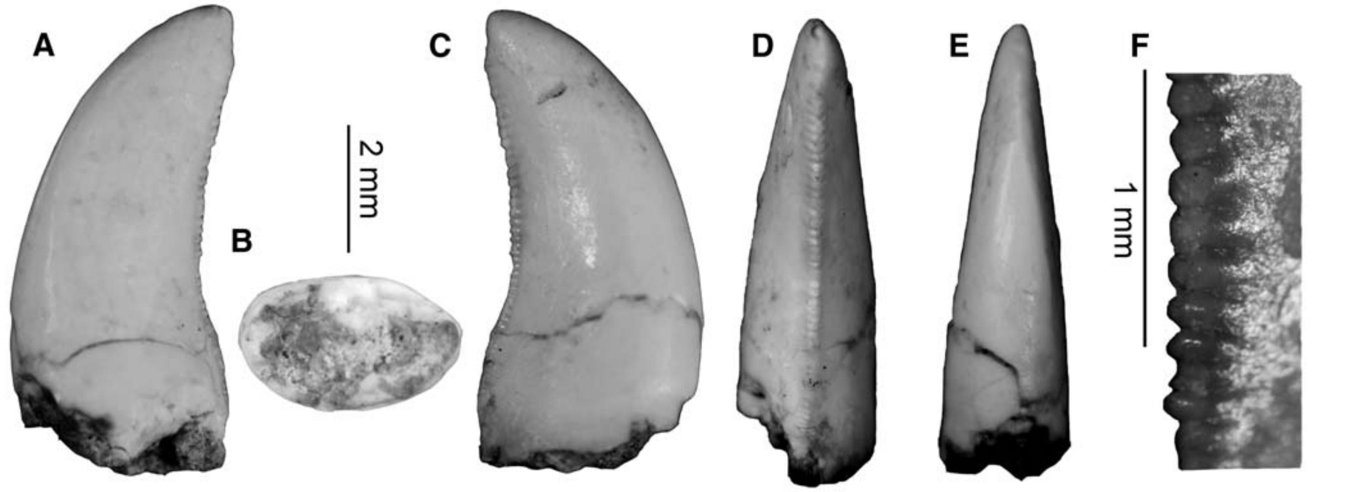

FIGURE 7. Theropod tooth of Morphotype 5 from the Middle-Upper Jurassic Shishugou Formation, Wucaiwan. **A**, crown of V15857 in labial or lingual view; **B**, cross-section of V15857 taken near base; **C**, crown of V15857 in lingual or labial view; **D**, posterior view of V15857 showing straight posterior carina; **E**, anterior view of V15857 showing anterior carina; **F**, posterior denticles of V15857 in labial view, showing depressions near denticle bases.

By contrast, V15857 differs from both the Spanish teeth and *Dromaeosaurus* in lacking anterior denticles. This feature is reminiscent of velociraptorine dromaeosaurids (sensu Lindgren et al., 2008), in which the anterior denticles are typically small or reduced in most of the teeth. The relatively small size of the tooth and moderate degree of lateral compression are also consistent with dromaeosaurid affinities: the crown height of V15857 (7.1 mm) is too small for *Deinonychus* or *Dromaeosaurus*, too large for *Bambiraptor*, and near the upper end of the range for *Velociraptor*, whereas its CBR of 0.57 is higher than values given by Smith et al. (2005) for the posterior maxillary and dentary teeth of *Velociraptor* and *Deinonychus* but within the ranges for *Dromaeosaurus* and *Bambiraptor*.

The small size of V15857 and the complete absence of anterior denticles would be unusual in a ceratosaur, basal tetanuran, or tyrannosauroid tooth, and to our knowledge no ceratosaur has been shown to possess a spiraling anterior carina. Similarly, the spiraling carina and the evident lack of a constriction between the crown and the root would be surprising in a troodontid tooth, whereas the small posterior denticles and the high, gently recurved form of the crown would at least qualify as unusual features for a troodontid. It seems most probable that V15857 is a dromaeosaurid tooth, but with an unusual combination of dromaeosaurine (sensu Currie et al., 1990) and velociraptorine features. The depressions between adjacent posterior denticles, and the sinuous shape of the posterior crown margin, are unusual features that deserve further investigation.

Morphotype 6

Referred Specimen—V15849 (Fig. 8).

Diagnosis—Crown extremely small and strongly curved; base wide, with teardrop cross-section; CBR 0.57; denticles present on posterior carina only; denticles short and subrectangular; no enamel wrinkles on crown surface.

Description—Specimen V15849 is a very small isolated tooth, with a crown height of 2.8 mm, from the lower part of the

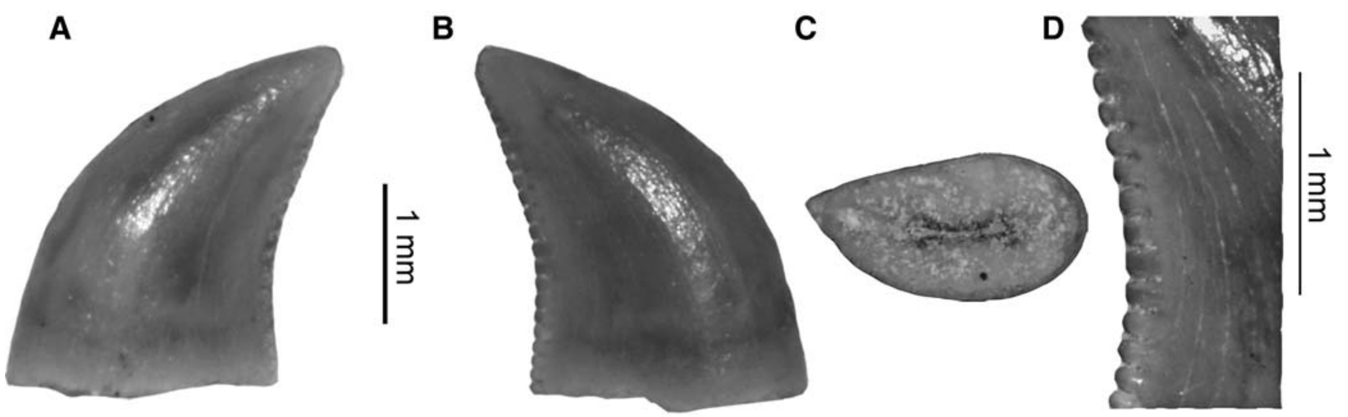

FIGURE 8. Theropod tooth of Morphotype 6 from the Middle-Upper Jurassic Shishugou Formation near Konglonggou. **A**, crown of V15849 in labial view; **B**, crown of V15849 in lingual view; **C**, cross-section of V15849 near base; **D**, posterior denticles of V15849 in labial view.

Shishugou Formation near Konglonggou. The crown is relatively robust (CBR = 0.57) and sufficiently recurved that the tip of the crown extends to a point posterior to the level of the tooth base (Fig. 8A, B). The posterior part of the tooth is particularly labiolingually compressed, resulting in a teardrop-shaped cross-section (Fig. 8C). There are 22 denticles on the posterior edge of the tooth, but denticles are lacking on the anterior edge. The DAVG is 8, much higher than in any other tooth in the present sample. The posterior denticles are wide, relatively short and bluntly rounded, and they decrease in prominence from the middle of the carina towards the apex (Fig. 8D).

Discussion—The diminutive size of this tooth, in addition to its unusual cross-sectional shape, high DAVG value, and great proportional anteroposterior length, immediately distinguish it from the morphotypes described above. Teeth as small as V15849 have only rarely been reported in adult theropods, although those of the small Early Cretaceous dromaeosaurid *Microraptor zhaoianus* (Xu et al., 2000) are even smaller. V15849 is likely to have come from a juvenile animal, and even then must represent a small taxon. Theropods that may have possessed teeth of this size as juveniles include dromaeosaurids (Osborn, 1924a; Xu et al., 2000; Norell et al., 2006), compsognathids (Currie and Chen, 2001), troodontids (Sankey et al., 2002), basal ornithomimosaurs such as *Pelecanimimus* (Perez-Moreno et al., 1994), and primitive alvarezsauroids (Choiniere, Xu, et al., 2010).

Despite its diminutive size and unusual, posteriorly compressed morphology, V15849 possesses some of the dromaeosaurid traits discussed previously. The lack of anterior denticles, high posterior denticle density, and posterior displacement of the crown tip resulting from strong recurvature are all features present in the teeth of dromaeosaurids. *Microraptor zhaoianus* is especially relevant as a point of comparison because of its very small teeth, which are slightly smaller (CH about 2.0 mm) than V15849. The posterior dentary teeth of *M. zhaoianus* resemble V15849 in lacking anterior denticles and to some extent in overall labial or lingual outline, but differ from this specimen in having a round cross-section and a constriction between the crown and root (Xu et al., 2000). Furthermore, the anteroposteriorly long, unevenly compressed overall shape of V15849 differs strikingly from most dromaeosaurid teeth, although occasional examples (e.g., Currie et al., 1990:fig. 8.2S; Lindgren et al., 2008:fig. 3) that approach the anteroposterior length of V15849 do exist. Nevertheless, the proportions of this specimen seem to preclude a dromaeosaurid identification.

Although compsognathids resemble V15849 in having teeth that bear denticles only on the posterior carina, the teeth of these taxa differ from V15849 in being slender and sharply recurved (Ostrom, 1978; Currie and Chen, 2001; Hwang, 2005; Peyer, 2006). The unserrated, basally constricted teeth of the basal ornithomimosaurs *Pelecanimimus* (Perez-Moreno et al., 1994) and *Shenzhousaurus* (Ji et al., 2003) are even more strikingly distinct from V15849. It is highly unlikely that this tooth pertains to an ornithomimosaur.

Troodontids present a more complex comparison, largely because of the considerable morphological variability within this group. For example, the teeth of *Troodon* (Currie et al., 1990) often have anteroposteriorly broad proportions not greatly dissimilar to V15849, but are less recurved and have large posterior (and often anterior) denticles. The posterior denticles also appear to be much larger in *Saurornithoides* (Osborn, 1924b) than in V15849. By contrast, the teeth of *Byronosaurus* (Makovicky et al., 2003), *Mei* (Xu and Norell, 2004), *Urbacodon* (Averianov and Sues, 2007), and *Anchiornis* (Hu et al., 2009) differ from those of V15849 in lacking denticles entirely. A constriction between the crown and the root occurs in most of these taxa. Although V15849 falls within the troodontid range of variation in many respects, and indeed bears a gross resemblance to some individual troodontid teeth (e.g., Averianov and Sues 2007:fig. 7M–O), there are no compelling features to link the specimen to this clade.

The basal alvarezsauroid *Haplocheirus* (Choiniere, Xu, et al., 2010; V15988) from the upper part of the Shishugou Formation of Wucaiwan has maxillary and posterior dentary teeth that are similar in size and in some aspects of their shape to V15849. These teeth are laterally compressed and recurved. Denticles are lacking on the anterior carina, but well developed on the posterior carina. In contrast to these points of resemblance, however, the teeth of the new alvarezsauroid each bear multiple vertical ridges on the labial surface of the crown, whereas both sides of the crown in V15849 are smooth. However, the specimen may be attributable to *Haplocheirus* or a close relative, particularly if the lack of labial ridging can be interpreted as a juvenile feature. Alternatively, V15849 may represent a small dromaeosaurid tooth that is unusually broadened posteriorly, or even a troodontid tooth with an unusual combination of features.

Morphotype 7

Referred Specimen—V15850 (Fig. 9).

Diagnosis—Crown strongly recurved; several longitudinal ridges on labial surface; cross-section strongly asymmetric, with basal part of crown labially convex; distinct constriction occurs between the crown and the root; denticles present on both anterior and posterior carinae; posterior denticles slightly inclined towards apex, and larger than anterior denticles; no enamel wrinkles on crown surface.

Description—Specimen V15850 was discovered in the upper part of the Shishugou Formation at Wucaiwan. It is a small tooth, with a CH of only 4.8 mm, and may represent a juvenile. This possibility is reinforced by the undeveloped condition of the anterior denticles, which form small tubercles along the anterior carina. Poorly developed denticles are characteristic of juvenile theropod teeth (Currie et al., 1990). The tooth is relatively robust, with a CBR of 0.64. The base of the crown is labially convex but almost flat on the lingual side (Fig. 9A, B), producing a somewhat D-shaped cross-section. The crown is recurved (Fig. 9A, B), and the apex is deflected lingually at an angle of about 45° to the vertical. The root is slightly damaged, but the preserved portion is approximately the same size as the crown. Uniquely in the present sample, a distinct constriction occurs between the crown and the root. There are three low but distinct longitudinal ridges positioned near the center of the labial surface of the crown, forming two clear longitudinal grooves, but there are no apparent longitudinal ridges on the lingual face of the tooth. The specimen has small denticles on both the anterior and posterior carinae, but the denticles do not extend to either the base or the apex of the crown (Fig. 9C, D). There are only five posterior denticles, and four anterior ones. The posterior denticles are small, rounded, and slightly inclined towards the tip of the crown, and the apical-most and basal-most members of the series are even smaller than the others. On the anterior carina, the denticles are poorly defined and are joined together to form an uneven ridge. The anterior carina spirals onto the lingual surface of the tooth as it descends from the apex.

Among other teeth in the present sample, lingual spiraling is only observed in Morphotype 5, which differs from V15850 in lacking anterior denticles and possessing a split anterior carina. V15850 is also readily distinguishable from the other specimens described in this paper on the basis of its constricted crown-base and ridged labial surface.

Discussion—In some features, specimen V15850 resembles previously described teeth of *Troodon* (Currie, 1987; Currie et al., 1990). The posterior denticles of V15850 incline towards the apex, as do both the anterior and posterior denticles of *Troodon*, and V15850 also shares with *Troodon* teeth a conspicuous constriction between the crown and the root. The denticles are much

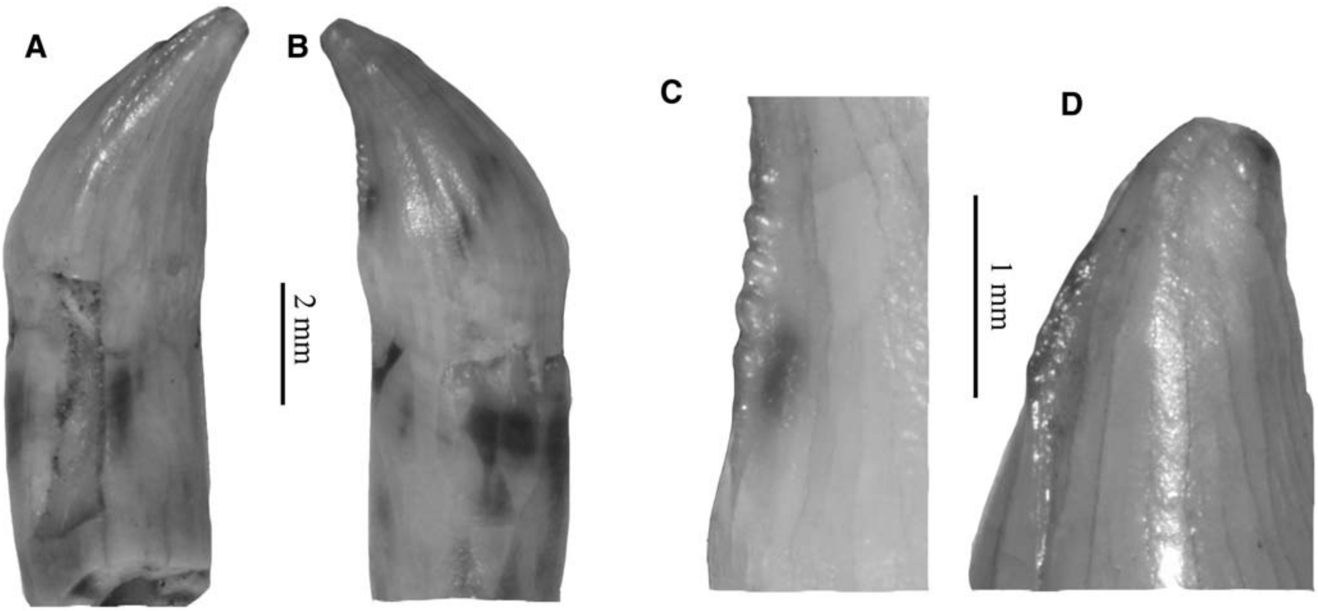

FIGURE 9. Theropod tooth of morphotype 7 from the Middle-Upper Jurassic Shishugou Formation, Wucaiwan. **A**, crown and root of V15850 in lingual view; **B**, crown and root of V15850 in labial view; **C**, posterior denticles of V15850 in labial view; **D**, anterior denticles of V15850 in lingual view.

smaller in V15850 than in typical specimens of *Troodon*, but denticle size is variable both ontogenetically and taxonomically within Troodontidae. As noted above (see Morphotype 6), a number of troodontids either have relatively small serrations or lack them entirely. V15850 also differs from *Troodon* and resembles *Mei*, *Byronosaurus*, and *Sinornithoides* (Currie and Dong, 2001) in having a relatively recurved crown. Although we are not aware of any previously described troodontid teeth that closely resemble V15850, the basal constriction of the tooth and the apical inclination of the posterior denticles are common troodontid features, and the size of the denticles and degree of crown recurvature fall well within the ranges previously reported for troodontids. Similarly, the CBR value of 0.64 is too high for *Troodon*, but would be within the range reported for *Saurornithoides* (Smith et al., 2005). However, the lingual spiraling of the anterior carina is an unusual feature that to our knowledge has not been reported in any troodontid. The longitudinal ridges seen on the labial surface of V15850 also lack any known counterpart in troodontids.

V15850 also shares some features with *Paronychodon lacustris* teeth from the Campanian Judith River Group of Alberta. Currie et al. (1990) diagnosed teeth of this taxon as unserrated, with one surface flat and usually bearing three or more longitudinal ridges. Sankey et al. (2002) divided *Paronychodon* into two morphotypes, designated A and B, and V15850 resembles Morphotype B in being small and recurved with a convex anterior margin. However, V15850 has only three longitudinal ridges, a minimal number for *P. lacustris*, and differs from this taxon in having small denticles both anteriorly and posteriorly.

In overall shape, V15850 is broadly similar both to *Paronychodon* and to some troodontid teeth, and unlike other the teeth of other theropods. The longitudinal ridges present in this specimen are typical of *Paronychodon*, but to our knowledge have not been reported in troodontids. By contrast, some troodontid teeth bear denticles, whereas *Paronychodon* is restricted by definition (Currie et al., 1990) to unserrated teeth. The lingually spiraling anterior carina of V15850 represents an unusual feature not seen in either *Paronychodon* or troodontids. It seems possible that V15850 might be either an unusual troodontid tooth or the tooth of a relative of *Paronychodon*, and indeed *Paronychodon* may be phylogenetically close to troodontids in any case (Zinke and Rauhut, 1994). Because teeth comparable to *Paronychodon* have been reported from the Barremian of Spain (Rauhut, 2002), as well as from the Upper Cretaceous of North America, the temporal gap between V15850 and known occurrences of *Paronychodon*-like specimens does not seem prohibitively large.

DISCUSSION

As noted in the Introduction, six theropod species have previously been described from the Shishugou Formation (Currie and Zhao, 1994; Zhao and Currie, 1994; Xu et al., 2006; Xu et al., 2009; Choiniere, Xu, et al., 2010; Choiniere, Clark, et al., 2010). A large isolated tooth from the upper part of the Shishugou Formation (Xu and Clark, 2008) may belong either to a large individual of *Sinraptor* or to a different sinraptorid. Although these finds have established that a variety of taxonomically and morphologically disparate theropods are present in the Shishugou Formation, the isolated teeth described in the present study provide evidence that the diversity of the theropod fauna was even greater, especially at the lower end of the size range. The seven distinct dental morphotypes present in our sample can each be tentatively regarded as a separate taxon. Although some of these taxa may be identical to ones that have already been described from the Shishugou Formation, others are almost certainly distinct from previous finds.

Table 2 summarizes the identifications presented above for the morphotypes covered in this study, and considers possible matches between each morphotype and taxa previously described from the Shishugou Formation. Morphotypes 1 through 4 each seem likely to represent either a basal tetanuran or a basal tyrannosauroid, although there is also a possibility that Morphotype 3 (in which enamel wrinkles are lacking) might pertain to a ceratosaur. The only basal tyrannosauroid known from the Shishugou Formation is *Guanlong*, and its teeth differ morphologically from Morphotypes 1 through 4 as well as being too small

TABLE 2. Identifications of seven theropod teeth morphotypes from the Shishugou Formation.

Morphotype	Possible identifications	Possible matches to Shishugou taxa
1	Basal tetanuran, basal tyrannosauroid	Juvenile *Sinraptor* or *Monolophosaurus*?
2	Basal tetanuran, basal tyrannosauroid	Juvenile *Sinraptor* or *Monolophosaurus*?
3	Basal tyrannosauroid, basal tetanuran, ceratosaur	Juvenile *Sinraptor* or *Monolophosaurus*?
4	Basal tetanuran, tyrannosauroid	Juvenile *Sinraptor* or *Monolophosaurus*?
5	Dromaeosaurid	—
6	Dromaeosaurid, troodontid, basal alvarezsauroid	*Haplocheirus* (Choiniere, Xu, et al., 2010)?
7	Troodontid, *Paronychodon*-like form	—

to correspond to Morphotype 1 or 3. In contrast, Morphotype 1 through 4 specimens are smaller than adult teeth of *Sinraptor* and *Monolophosaurus*, but the possibility remains that any of these morphotypes might belong to a juvenile specimen of one taxon or the other. It is difficult to rigorously evaluate this possibility at present because the teeth of *Sinraptor* and *Monolophosaurus* have never been described in detail, and unfortunately the holotype specimens are mounted in a way that makes study of the dentition difficult. However, Morphotypes 1 through 4 are distinct enough that they likely belong to separate taxa. Given the substantial differences in size and morphology among these four morphotypes, it is unlikely that any two of them belong to a single species with a heterodont dentition, although of course the possibility of extreme heterodonty cannot be ruled out completely. Even if two of these morphotypes turn out to be attributable to *Sinraptor* and *Monolophosaurus*, the others are likely to represent novel basal tyrannosauroid or basal tetanuran taxa. Morphotype 3 might also pertain to a ceratosaur, which would necessarily be different from the edentulous *Limusaurus*.

The smaller teeth assigned to Morphotypes 5 through 7 are not referable to tyrannosauroids or basal tetanurans. Morphotype 5 is most likely to represent a dromaeosaurid, and this may be true of Morphotype 6 as well. Dromaeosaurid, or at least conspicuously dromaeosaurid-like, teeth have been previously reported from the Kimmeridgian of Oker, Germany (van der Lubbe et al., 2009), and Guimarota, Portugal (Zinke, 1998). Furthermore, the recovery of the troodontid *Anchiornis* from the Jurassic Tiaojishan Formation of China (Hu et al., 2009) implies that dromaeosaurids and troodontids had diverged from one another by the time the Tiaojishan was deposited. Unfortunately, the exact dating of the Tiaojishan is still unclear (Hu et al., 2009), with estimates ranging from 161 Ma (near the Callovian-Oxfordian boundary) to 151 Ma (near the Kimmeridgian-Tithonian boundary). Morphotype 6 is from the Lower (Callovian) part of the Shishugou Formation, whereas Morphotype 5 is from the Upper (Oxfordian) part. If either of these morphotypes can be conclusively shown on the basis of more complete material to belong to a dromaeosaurid, it will represent the oldest known fossil evidence of this clade. However, the occurrence of a dromaeosaurid in the Callovian-Oxfordian of China would not be particularly surprising in light of *Anchiornis* and the two European occurrences of dromaeosaurid teeth in Upper Jurassic strata.

Another possibility for Morphotype 6 is that the single specimen assigned to this morphotype is a troodontid tooth, and this seems even more likely for Morphotype 7. The latter morphotype also has points of resemblance to the enigmatic North American taxon *Paronychodon*, as noted above, but *Paronychodon* may be a close troodontid relative in any case. A Shishugou Formation troodontid would rival *Anchiornis* as the oldest known representative of the clade, and might turn out to be definitively older following more secure dating of the Tiaojishan Formation. Again, the occurrence of a troodontid even in the Callovian lower part of the Shishugou Formation would be far from implausible. The presence of small denticles in both Morphotypes 6 and 7 contrasts with the unserrated teeth of *Anchiornis* (Hu et al., 2009) and of the relatively basal troodontid *Mei* (Xu and Norell, 2004). However, *Sinovenator* emerged as the most basal troodontid in the phylogenetic analysis of Hu et al. (2009), and this taxon resembles Morphotypes 6 and 7 in possessing small denticles (Xu et al., 2002). Nevertheless, Morphotype 6 may simply represent an isolated tooth of the Shishugou taxon *Haplocheirus* (Choiniere, Xu, et al., 2010).

A conservative interpretation of the sample of isolated teeth considered in this paper implies that at least 10 theropods, including the six already known on the basis of skeletal remains, are present in the Shishugou Formation. If the identifications presented above are correct, the four additional taxa must include (1) one dromaeosaurid (Morphotype 5); (2) one troodontid or *Paronychodon*-like form (Morphotype 7); (3) one additional basal tetanuran or tyrannosauroid (any of Morphotypes 1–4); (4) one additional basal tetanuran, tyrannosauroid, or ceratosaur (any of Morphotypes 1–4). At the other extreme, it is possible that all seven morphotypes described in this paper might represent new taxa, if the 'matches' presented in Table 2 all turn out to be spurious. Accordingly, the currently known theropod diversity of the Shishugou Formation can be estimated at 10–13 taxa. Although this number may appear high, it is comparable to other well-known theropod faunas from the Jurassic and Cretaceous such as the Morrison Formation (Late Jurassic, U.S.A), the Dinosaur Park Formation (Late Cretaceous, Canada), and the Nemegt Formation (Late Cretaceous, Mongolia), among others (see Weishampel et al., 2004).

Comparisons to the Theropod Fauna of the Shaximiao Formation, Sichuan Province

Within China, a fauna similar to that of the Shishugou is present in the Lower and Upper parts of the Shaximiao Formation of the Sichuan Basin, which are probably both Middle Jurassic in age (Chen et al., 2006). Three very similar species of large theropod, *Yangchuanosaurus magnus* (Yong, 1942), *Y. shangyouensis* (Dong et al., 1978), and *Sinraptor hepingensis* (Gao, 1992), are present in the Upper Shaximiao Formation. These taxa are remarkably similar to *Sinraptor dongi* from the upper part of Shishugou Formation (Currie and Zhao, 1994), and are accordingly regarded as sinraptorids. The Lower Shaximiao Formation has produced three basal tetanurans, *Xuanhanosaurus qilixiaensis* (Dong, 1984), *Gasosaurus constructus* (Dong and Tang, 1985), and "*Szechuanosaurus*" *zigongensis* (Gao, 1993). Teeth were referred to both *Gasosaurus* and "*S.*" *zigongensis*, but were not described in detail. Despite this diversity, no coelurosaurs have been reported from either part of the Shaximiao Formation, in contrast to the presence of extensive skeletal material from at least three coelurosaurs (*Guanlong*, *Haplocheirus*, *Zuolong*) in the Upper Shishugou. The isolated teeth described in the present study provide evidence for an even greater diversity of coelurosaurian species, suggesting that the prevalence of coelurosaurs in the upper part of Shishugou Formation is a major difference from the Shaximiao fauna. This may point to a diversification of coelurosaurs in the Late Jurassic.

CONCLUSIONS

Based on qualitative features and simple measurements, seven morphotypes can be identified within our sample of 16 isolated theropod teeth from the Shishugou Formation. Three of these morphotypes may be referable to taxa that have already been described from the Shishugou, but the other four appear novel. Our results increase the known theropod diversity of the Shishugou fauna from six taxa to anywhere from 10 to 13. The new taxa include at least one dromaeosaurid, at least one probable troodontid (or taxon similar to *Paronychodon*, which may be a close troodontid relative in any case), at least one basal tetanuran or tyrannosauroid, and possibly a ceratosaur. The presence of deinonychosaurian teeth is particularly interesting, because these specimens would constitute the first evidence of this clade from the Shishugou Formation and would be among the oldest known deinonychosaurian fossils. The deinonychosaurian teeth also highlight the diversity of coelurosaurs in the Shishugou Formation, in contrast to their absence from the nearly contemporary Shaximiao Formation of Sichuan Province.

The teeth in our sample could be identified only to the extent of placing them within major theropod clades, or in some cases within the basal tetanuran grade of organization. Theropod teeth, in comparison to those of mammals, are simple in structure and are endowed with relatively little morphological information of taxonomic value. Nevertheless, more precise identifications of isolated theropod teeth would likely be possible if the dentitions of more taxa were known in detail, providing a wider and more informative basis for comparisons. Our study demonstrates the need for more descriptions of ceratosaur, basal tetanuran, and basal tyrannosauroid dentitions, in particular. Discriminant functional analysis (DFA) is a promising technique that has been recently brought to bear on the study of theropod teeth by Smith et al. (2005), and this method may prove useful in the future for refining identifications of isolated specimens from the Shishugou Formation. Furthermore, incorporation of more Jurassic theropod taxa into the predominantly Cretaceous data set established by Smith et al. (2005) might broaden the utility of the DFA approach.

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APPENDIX 1. Morphometric measurements from sixteen theropod teeth from the Shishugou Formation, Xinjiang, China. Italics indicate estimated values; underlining indicates measured values that are uncertain because of wear or minor damage.

Specimens	CBL (mm)	CBW (mm)	CH (mm)	AL (mm)	MAVG	DAVG	CBR	CHR
Morphotype 1								
IVPP V15851	18.5	8.3	*40*	—	—	3.92	0.45	*2.2*
IVPP V15852	19.9	9.0	*40*	—	4.00	3.26	0.45	*2.0*
IVPP V15853	16.9	8.1	*40*	—	3.93	3.96	0.48	*2.4*
IVPP V15854	21.2	7.3	*25*	—	—	3.93	0.34	*2.1*
IVPP V15855	13.3	7.8	*25*	—	—	3.62	0.59	*1.9*
Morphotype 2								
IVPP V15848	*10*	5.4	*20*	23.9	—	3.65	0.54	*2.0*
Morphotype 3								
IVPP V15858	*15*	8.0	*35*	—	4.37	3.59	0.53	2.3
Morphotype 4								
IVPP V15842	10.1	5.8	21.2	21.6	3.97	3.20	0.57	2.1
IVPP V15843	9.3	6.1	*23*	—	—	4.19	0.66	*2.5*
IVPP V15844	8.1	5.7	17.4	21.1	—	3.69	0.70	2.2
IVPP V15845	7.9	—	17.0	17.5	4.55	4.41	—	2.2
IVPP V15846	7.0	4.6	15.4	16.3	—	4.07	0.66	2.2
IVPP V15856	8.8	5.4	*19*	—	—	3.66	0.61	*2.2*
Morphotype 5								
IVPP V15857	3.7	2.1	7.1	7.4	—	5.73	0.57	1.9
Morphotype 6								
IVPP V15849	2.1	1.2	2.8	4.0	—	8.03	0.57	1.3
Morphotype 7								
IVPP V15850	3.9	2.5	4.8	6.2	4.49	4.20	0.64	1.23