

TAPHONOMY AND AGE PROFILE OF A LATEST CRETACEOUS DINOSAUR BONE BED IN FAR EASTERN RUSSIA

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ABSTRACT

A large dinosaur bone bed has been investigated in the Udurchukan Formation (?late Maastrichtian) at Blagoveschensk, Far Eastern Russia. The observed mixture of unstratified fine and coarse sediments in the bone bed is typical for sediment-gravity-flow deposits. It is postulated that sediment gravity flows, originating from the uplifted areas at the borders of the Zeya-Bureya Basin, reworked the dinosaur bones and teeth as a monodominant bone bed. Fossils of the lambeosaurine *Amurosaurus riabinini* form >90% of the recovered material. The low number of associated skeletal elements at Blagoveschensk indicates that the carcasses were disarticulated well before reworking. Although shed theropod teeth have been found in the bone bed, <2% of the bones exhibit potential tooth marks; scavenging activity was therefore limited, or scavengers had an abundance of prey at hand and did not have to actively seek out bones for nutrients. Perthotoxic features are very rare on the bones, implying that they were not exposed subaerially for any significant length of time before reworking and burial. The underrepresentation of light skeletal elements, the dislocation of the dental batteries, and the numerous fractured long bones suggest that most of the fossils were reworked. The random orientation of the elements might indicate a sudden end to transport before stability could be reached. The size-frequency distributions of the femur, tibia, humerus, and dentary elements reveal an overrepresentation of late juveniles and small sub-adult specimens, indicative of an attritional death profile for the *Amurosaurus* fossil assemblage. It is tentatively postulated that the absence of fossils attributable to nestling or early juvenile individuals indicates that younger animals were segregated from adults and could join the herd only when they reached half of the adult size.

INTRODUCTION

Four dinosaur localities have been discovered in the Amur-Heilongjiang region in eastern Asia (Fig. 1): Jiayin (Riabinin, 1930; Godefroit et al., 2001) and Wulaga (Hai, 2004) in the Yuliangze Formation of northern Heilongjiang Province (China), and Blagoveschensk (Bolotsky and Kurzanov, 1991; Godefroit et al., 2004) and Kundur (Godefroit et al., 2003; Van Itterbeeck et al., 2005) in the Udurchukan Formation of the southern Amur Region (Russia). Bugdaeva (2001) showed that the Yuliangze and Udurchukan Formations are synchronous and Maastrichtian in age. At all four sites, the elements form large bone beds extending over several hundred square meters, and the dinosaur fauna is largely dominated by lambeosaurine hadrosaurids (Godefroit et al., 2000, 2003, 2004).

The Blagoveschensk dinosaur locality (BDL) was discovered in 1981 and, until 1989, a surface of about 200 m² had been excavated (Moiseenko et al., 1997). About 1,000 elements were recovered from this locality during this period. The lambeosaurine dinosaur *Amurosaurus riabinini*

Bolotsky and Kurzanov, 1991 is the dominant dinosaur at BDL (Godefroit et al., 2004), but the locality has also yielded isolated bones of the hadrosaurine *Kerberosaurus manakini* (Bolotsky and Godefroit, 2004), isolated teeth of theropods (Alifanov and Bolotsky, 2002), caudal vertebrae and teeth of sauropods, and turtle fragments (Danilov et al., 2002).

In 2005 and 2006, the Amur Complex Integrated Research Institute of the Far Eastern Branch of the Russian Academy of Sciences (KNII) and the Royal Belgian Institute of Natural Sciences organized new excavations at Blagoveschensk. A surface of about 200 m² was excavated, yielding more than 500 bones. The main purpose of these new excavations was to collect more data on the stratigraphy, sedimentology, and taphonomy of this locality.

The aims of this paper are to (1) clarify the taphonomy of the BDL and (2) study the age profile of the *Amurosaurus riabinini* population, the most common dinosaur from the Blagoveschensk site. The taphonomic interpretations are mainly based on information collected during field work in 2005. Each bone was measured, and its precise position and orientation noted on a map. The demographic profile of the *Amurosaurus* population is based primarily on specimens collected during the 1981–1989 excavations. All the fossils collected during the different field campaigns are housed in the Amur Natural History Museum, Blagoveschensk (AEHM). Additional specimens are housed in the American Museum of Natural History, New York (AMNH), and the Palaeontological Institute of the Russian Academy of Sciences, Moscow (PIN).

GEOLOGIC SETTING AND AGE OF THE BLAGOVESCHENSK LOCALITY

The Zeya-Bureya Basin is located in the southern and southeastern part of the Amur Province of Far Eastern Russia. The basin formed during Late Jurassic time as a series of north-south trending grabens (Kirillova et al., 1997). Rift infill is composed of Upper Jurassic–Lower Cretaceous volcano-sedimentary deposits, and plate infill composed of Upper Cretaceous and Cenozoic sediments (for an overview, see Crosdale et al., 2002, fig. 2). The Amur-Mamyn uplift divides the Zeya-Bureya Basin into two parts: the northwestern Amur-Zeya depression and the southeastern Lower Zeya depression (Akhmetiev et al., 2003, p. 12). Both the Blagoveschensk and Kundur sites are situated in the Lower Zeya depression near the border of adjacent uplifted areas—the Lesser Khingang Mountains and the Turan uplift (Moiseenko et al., 1997).

The BDL is located on a hillside along the upper part of Nagornaia Street, west of Blagoveschensk City (N50°15'06.8'', E127°28'49.4''). These sediments belong to the Udurchukan Formation, in the lower part of the Tsagayan Group. According to previous authors (Markevich and Bugdaeva, 1997; Bugdaeva, 2001), the dinosaurs from the Udurchukan Formation lived in relatively open habitats, with denser vegetation along the banks of lakes and rivers, under a warm-temperate and relatively arid climate. The sediments of the Udurchukan and Yuliangze Formations belong to the *Wodehouseia spinata*–*Aquilapollenites subtilis* palynozone, as defined by Markevich (1994, 1995). Although the three sites belong to the same palynozone, Bugdaeva (2001) and Akhmetiev et al. (2003)

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FIGURE 1—Map of the Amur-Heilongjiang Region (modified from Kirillova, 2003) indicating the main dinosaur sites (▲); Blagoveschensk locality indicated by an arrow.

date Kundur and Jiayin as early Maastrichtian but Blagoveschensk as middle Maastrichtian, based mainly on comparisons with neighboring basins (Markevich, 1994). Godefroit et al. (2004) compared the Blagoveschensk palynological assemblage with assemblages from well-dated vertebrate localities of western North America (Leffingwell, 1970; Srivastava, 1970; Nichols et al., 1986; Lerbekmo et al., 1987; Newman, 1987; Nichols and Sweet, 1993; Braman and Sweet, 1999; Nichols, 2002) and suggested a late Maastrichtian age for Blagoveschensk and Kundur, based on the presence of *W. spinata*, together with at least six other species characteristic of the North American *W. spinata* Assemblage (Nichols and Sweet, 1993; Nichols, 2002). Further research that includes independent calibrations with the Asian palynozones, however, is necessary to completely resolve these differences.

SEDIMENTOLOGY

Because of the location of the fossil site within the outskirts of the city, the exposure is limited both vertically and laterally. The dinosaur-bearing sediments cover a surface of at least 5000 m², and the total exposed thickness of Cretaceous rocks in outcrop is estimated as no more than 5 m. The fossil beds unconformably overlie metamorphic rocks that are locally weathered at the top and form the basement of the Amur-Zeya Basin. The weathered zone is distinguished from underlying metamorphic rocks by its friable and clay-rich nature.

The dinosaur-bearing sediments are green-to-brown massive claystones with a considerable number of dispersed granules. These diamicts can be divided into two stratigraphic units with a very similar appearance (Fig. 2). Both consist dominantly of massive, clast-poor diamicts but have a

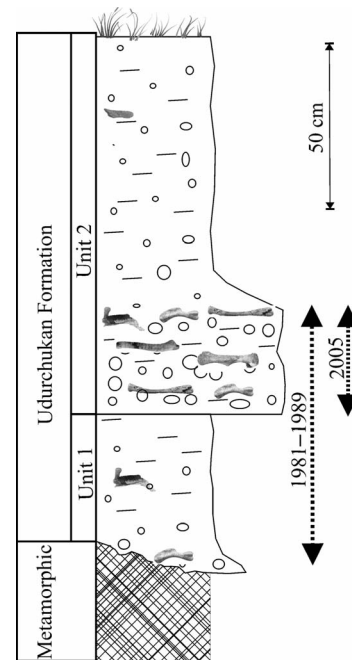


FIGURE 2—Stratigraphic column of the Blagoveschensk section. Arrows indicate levels excavated during different field seasons. Clast size in both units is ≤ 5 cm. Clast lithologies observed in unit 1 include light-gray-to-dark-blue quartzite, green mica schist, gneiss, altered volcanic rock, and rare fragmentary dinosaur elements.

coarser, clast-rich base. A basal pebble lag with a maximum clast size of 20 cm occurs locally at the base of unit 1, at the contact with the weathered gneiss below. At the base of unit 2, a coarser-grained, clast-rich level occurs 0.4–0.75 m above the basement, with clast size being ≤ 16 cm. Although dominantly matrix supported, thin lenses (a few cm) of clast-supported conglomerates have been observed within this unit. Although dinosaur elements have been found throughout the lower 75 cm of the Udurchukan Formation, they are particularly concentrated at the base of the second unit. The recognition of these two units is the only indication of stratification within the Upper Cretaceous deposits at Blagoveschensk.

The clays are dominantly smectite with some illite and kaolinite. No bioturbation or paleosol development beyond inceptisols has been observed; the massive fabric with a mixture of unstratified fine and coarse material seems to be primary and not the result of postdepositional processes. Tabular beds of massive diamictites are typical for debris-flow deposits (Dasgupta, 2003, and references therein), and the presence of two units at the BDL indicates at least two flow events. In the limited outcrops at this site, however, ultimate proof for a sediment-gravity-flow origin of the sediments—that is, intercalation of the diamictites with pervasively stratified beds—is missing. At Kundur, the sediment-gravity-flow origin of the dinosaur-bearing deposits in the Udurchukan Formation has been proven (Van Itterbeeck et al., 2005), and the observed flow deposits have the characteristics of both debris flows and hyperconcentrated flows (Dasgupta, 2003). Based on the similarities of the deposits from both sites, the units at Blagoveschensk are treated as debris-flow deposits until proved otherwise. Indeed, the high mudstone content and the matrix-supported clasts indicate that the flow was cohesive, as is typical for debris flows (Dasgupta, 2003, fig. 1). The concentration of dinosaur elements and larger clasts at the base of each unit and the predominantly horizontal orientation of the elements, however, indicate a transition to more hyperconcentrated flows (Dasgupta, 2003, fig. 1).

The dinosaur sites of the Zeya-Bureya Basin are all located close to the basin edges, and the Kundur and Wulaga bone beds probably have a debris-flow origin as well (Van Itterbeeck et al., 2005; P. Godefroit, personal communication, April 2007). Today, the Lesser Khingang Mountains are 60 km from the Blagoveschensk site, along the western borders

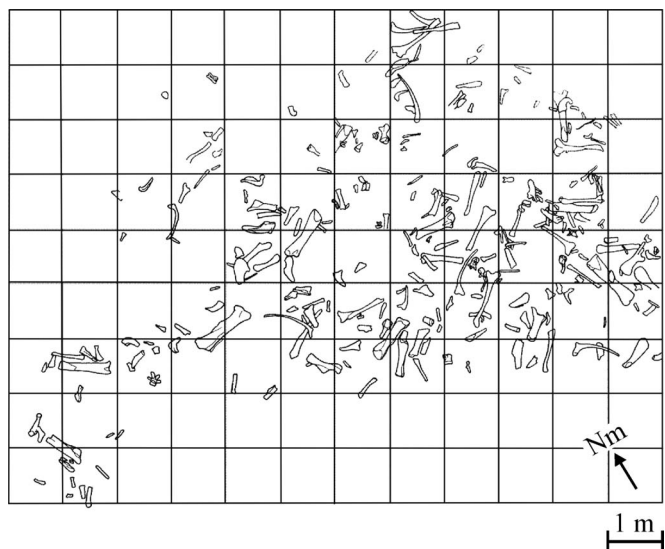


FIGURE 3—Map of the Blagoveschensk bone bed made during 2005 field work; Nm = magnetic north.

of the Lower Zeya depression. Therefore, the paleo-Khingang Mountains are good potential source regions for such debris flows at the end of the Cretaceous. The sediments at the BDL are slightly coarser than those observed at Kundur (Van Itterbeeck et al., 2005), perhaps due to the more proximal setting of BDL in relation to the basin margin.

In addition to relief, several other factors influence the occurrence of sediment gravity flows. They can be triggered by seismic events or intense rainfalls after a dry period. Because the Upper Cretaceous deposits represent plate infill—that is, sediments deposited after the main tectonic events—the former trigger seems unlikely. Based on the suggested paleoclimate during the Maastrichtian in the Zeya-Bureya Basin (Bugdaeva, 2001), intense rainfalls after dry periods are a more likely trigger.

The occurrence of dinosaur fossils within debris flows is not limited to these sites in the Zeya-Bureya Basin. Similar dinosaur-bearing deposits have been described from the Lower Cretaceous of Utah (Eberth et al., 2006) and the Upper Cretaceous of Madagascar (Rogers, 2005). Upper Cretaceous deposits from Mongolia described by Loope et al. (1998) were deposited in more arid, aeolian-influenced environments and differ in that aspect from the deposits in the Zeya-Bureya Basin.

TAPHONOMY

The various taphonomic parameters observed at the BDL—degree of skeletal articulation, spatial distribution, size distribution of the elements, hydraulic sorting, orientation of the bones, and bone modification features—provide important information for determining the geologic and biological processes that led to the formation of the dinosaur bone bed.

Taphonomic Mode

Taphonomic modes can be defined as recurring preservational and taphonomic features and geologic associations among fossils from a particular stratigraphic interval that reflect postmortem influences, as well as basin-scale controls on sediment budget and accommodation (Behrens-meyer, 1991; Eberth and Currie, 2005). The classification of taphonomic modes followed in this paper is that developed by Eberth and Currie (2005).

The BDL consists of an accumulation of elements belonging to numerous individuals of different sizes. The fossils discovered during the 2005 campaign come from a single horizon at the base of unit 2, probably the same that provided most of the numerous fossils discovered between 1981 and 1989 (Fig. 2). In this layer, the elements are usually completely

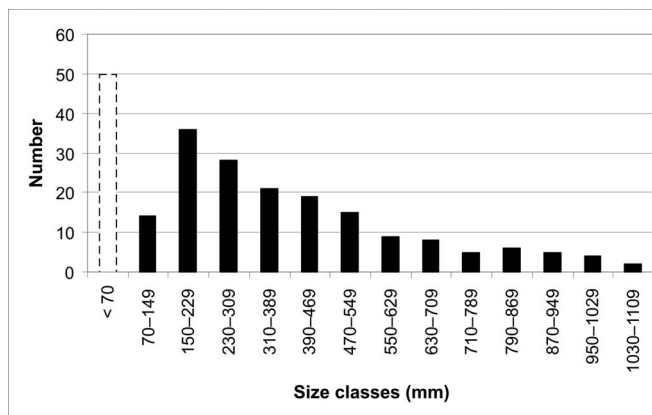


FIGURE 4—Size distribution of the elements collected during 2005. White bar is an estimate of the number of bones <70 mm, not all of which were collected.

mixed together, and articulated elements are rare (Fig. 3). The only elements found in articulation during the 2005 excavations were a tibia and a fibula and a sacrum and two ischia.

Figure 4 represents the size distribution (maximum dimension) of fossil specimens in the sample collected during 2005. Although the number of small fragmentary specimens is probably slightly undervalued, due to excavation biases, it can be observed that medium-sized bones (15–55 cm) dominate the BDL bone bed. The average size of the bones is around 40 cm. The largest specimens are over 1 m, which is approximately the maximum size for complete hadrosaurid femora and tibiae. In contrast, small specimens (<7 cm) represent only about 15 % of the recovered elements. Therefore, the BDL layer can be regarded as a macrofossil bone bed (Mode D; *sensu* Eberth and Currie, 2005), which is defined as concentrations of disarticulated remains dominated by elements >5 cm in maximum dimension. Such bone beds are interpreted as consisting of elements secondarily concentrated after having been dispersed during decomposition and disarticulation (Eberth and Currie, 2005).

Lambeosaurine elements referred to *Amurosaurus riabinini* represent ~90% of the diagnostic elements, dominating the BDL. So far, there is no evidence that more than a single lambeosaurine species lived in the Blagoveschensk region during latest Cretaceous time (Godefroit et al., 2004). Remains of other taxa at this locality include only a dozen hadrosaurine bones, three sauropod caudal vertebrae and one tooth, and ~30 shed theropod teeth. Turtle and crocodile remains are also relatively rare. Therefore, the BDL can be regarded as a monodominant bone bed (mode D2; *sensu* Eberth and Currie, 2005), that is, a bone bed consisting of the remains of more than one taxon but overwhelmingly dominated (>50%) by skeletal elements from one species. Monodominant bone beds are common in the geologic record, and the category includes, for example, all the known ceratopsian bone beds at the Dinosaur Provincial Park in Alberta, Canada (Eberth and Getty, 2005). Monodominant bone beds are usually regarded as having been formed, in part, by some degree of social interactivity or gregariousness in the taxa that are most abundant in the assemblage (Currie and Dodson, 1984; Rogers, 1990; Eberth and Getty, 2005). They are often interpreted as resulting from a catastrophic (i.e., nonselective) event that quickly killed all the members of the death assemblage in a given area, and postmortem transport and concentration of carcasses are often regarded as limited. Bone beds, however, also consist of accumulations of elements of animals that died at different times and in different places and were subsequently concentrated. The formation of these latter assemblages potentially reflects little about the life behavior of members of the death assemblage. Therefore, it may also be postulated that *Amurosaurus riabinini* dominates the BDL simply because this taxon was overwhelmingly more abundant than other macrovertebrates in the area.

Above the main bone-bed horizon, isolated elements are rarely found

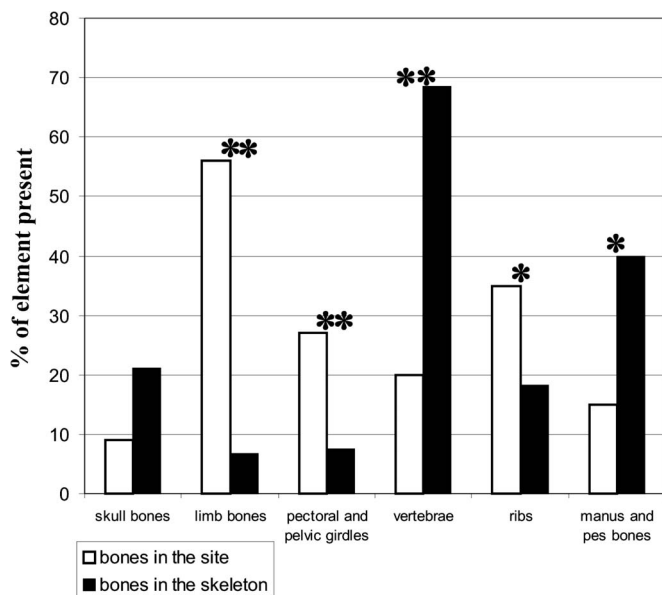


FIGURE 5—Frequencies of bones from 2005 field work. White columns show absolute frequencies of bones recovered; black columns show relative frequencies from an ideal *Amurosaurus* skeleton. Bones are divided into sorting groups based on Voorhies (1969). Significance: * $p < 0.01$; ** $p < 0.001$.

at the BDL. They can be interpreted as elements that were deposited during the same event as that recorded in the main bone bed (Koster et al., 1987) or as elements deposited independently and as an attritional assemblage after the main depositional event.

Hydraulic Sorting

Hydraulic transportation of disarticulated skeletal remains usually leads to some sorting of the elements, according to their size and density. Light elements are reworked over larger distances than heavier bones (Voorhies, 1969). Therefore, comparison of the relative frequencies of the different skeletal elements in the bone bed is usually regarded as a good method for estimating whether fossil assemblages are autochthonous or reworked (see, e.g., Eberth and Getty, 2005; Gates, 2005). In autochthonous or parautochthonous assemblages, the relative frequencies of the recovered bones do not significantly differ from the theoretical frequency of the skeletal elements in a complete skeleton. This is usually not the case when the elements have been transported over some distance by flows. Voorhies (1969) distinguishes two main hydraulic sorting groups: bones that are immediately removed, transported by saltation or flotation in the flow (ribs, vertebrae, sacrum, pectoral girdle, and phalanges), and bones that are gradually removed and transported by traction (limb bones, pelvic girdle, and skull bones). Because he studied mammals, Voorhies (1969) also distinguished a third group for fused skulls. In contrast to mammals, hadrosaurid skulls typically do not exhibit fusion outside the braincase (Gates, 2005). Therefore, hadrosaurid skull bones are here regarded as dense skeletal elements (Voorhies' Group 2), following Gates (2005).

Figure 5 compares the number of bones recovered from the 2005 excavations with the relative frequencies of bones expected to occur within a complete lambeosaurine skeleton (estimations are from Lull and Wright, 1942; Horner et al., 2004). The frequencies of the skeletal elements in the theoretical lambeosaurine skeleton were adjusted so that the total number of bones is identical to the number of bones from the fossil sample (modified from %MAU [minimum animal units] in Lyman, 1994). The chi-square test indicates that the proportions of skeletal elements between the fossil sample and the ideal theoretical skeleton are significantly different, except for the skull bones. Girdle and limb bones, which are typical heavy elements (Voorhies' group 2) are significantly overrepresented in the BDL. In contrast, lighter elements of the skeleton, such

as vertebrae, manus, and pes bones (Voorhies' group 1), are underrepresented in the bone bed. The significant overrepresentation of ribs, which, according to Voorhies (1969), can be regarded as lighter elements, is a bit puzzling but may be explained by the greater massiveness of these elements in large, herbivorous dinosaurs compared to modern herbivorous mammals. Overall, however, the underrepresentation of light skeletal elements and the paucity of associated elements suggest that the BDL is a hydraulically accumulated lag deposit and that the disarticulation of the carcasses preceded the reworking of skeletal elements.

Orientation of Elements

The majority of the bones lie horizontally within the bone bed. Only a few elements of small size are inclined, mainly because they lie on larger specimens. In some cases, hydraulic reworking also leads to a preferential orientation of the skeletal elements. The degree of alignment depends on the stream velocity and depth, but it also depends on the size and shape of the bones. Voorhies (1969) noticed the tendency of linear elements to align parallel to flow direction if the elements are submerged but perpendicular if partially emergent. Long bones and complete pelvis bones appear to be the most reliable mammalian skeletal elements for deducing the direction and sense of stream flow (Voorhies, 1969). Figure 6 illustrates the distribution of the orientations of the bones collected at BDL during 2005, using all bones (Fig. 6A) or just limb, girdle, and unidentified limb bones longer than 30 cm (Fig. 6B).

At first glance there seems to be a tendency for elements to line up with the NW-SE or NE-SW axis. A nonparametric Rayleigh test was performed in order to determine whether these apparent preferential directions are significant or whether the bones are randomly oriented (null hypothesis: uniform circular distribution). In both cases, a Rayleigh test shows that the null hypothesis of a uniformly distributed dataset cannot be rejected at $p = 0.05$ ($Z = 0.02$ when all the bones are included in the analysis, $p > 0.5$; $Z = 0.7$, when only long bones are included, $0.2 < p < 0.5$). Therefore the bones are considered randomly oriented in the Blagoveschensk bone bed, contrary to earlier results (Godefroit et al., 2004). Although an interpretation of randomness appears to contradict an hypothesis of hydraulic reworking, Wnuk and Pfefferkorn (1987) observed that random orientations are diagnostic of many reworked plant assemblages, presumably the result of interference patterns caused by the high density of elements, and Toots (1965) has shown that nonpreferred orientations of modern bones in flowing water may result from disruption of the flow by obstacles or chaotic flow conditions (e.g., debris flows). Based on bone-modification features (see below), we consider a secondary randomizing process—for example, trampling (Fiorillo, 1987)—as unlikely.

Bone Modification

Bone modification processes can provide valuable clues to the taphonomic history of the bones at a fossil site. Reviews by Lyman (1994) and Behrensmeyer (1991) were used to help interpret bone-modification data.

The absence of teeth in the dentary battery can be regarded as a good indicator for reworking of hadrosaurid fossils. In hadrosaurids, the dental battery is concealed by a very thin wall of bone on the medial side of the dentary. This parapet is usually destroyed after the death of the animal, even in well-preserved, articulated specimens. Consequently, teeth can easily be removed from the dentary during reworking. In the fossil material collected at Kundur, the dental battery is partially or completely preserved in more than half of the recovered specimens. Thirty-seven well-preserved lambeosaurine dentaries were recovered from the BDL between 1981 and 1989. From this collection, the dental battery is preserved in only one specimen, the holotype of *Amurosaurus riabinini* (Fig. 7A); teeth are completely absent in all the other specimens (Fig. 7B). It must also be noted that isolated and rolled coronoid processes are very abundant in the Blagoveschensk collection, represented by more than 20

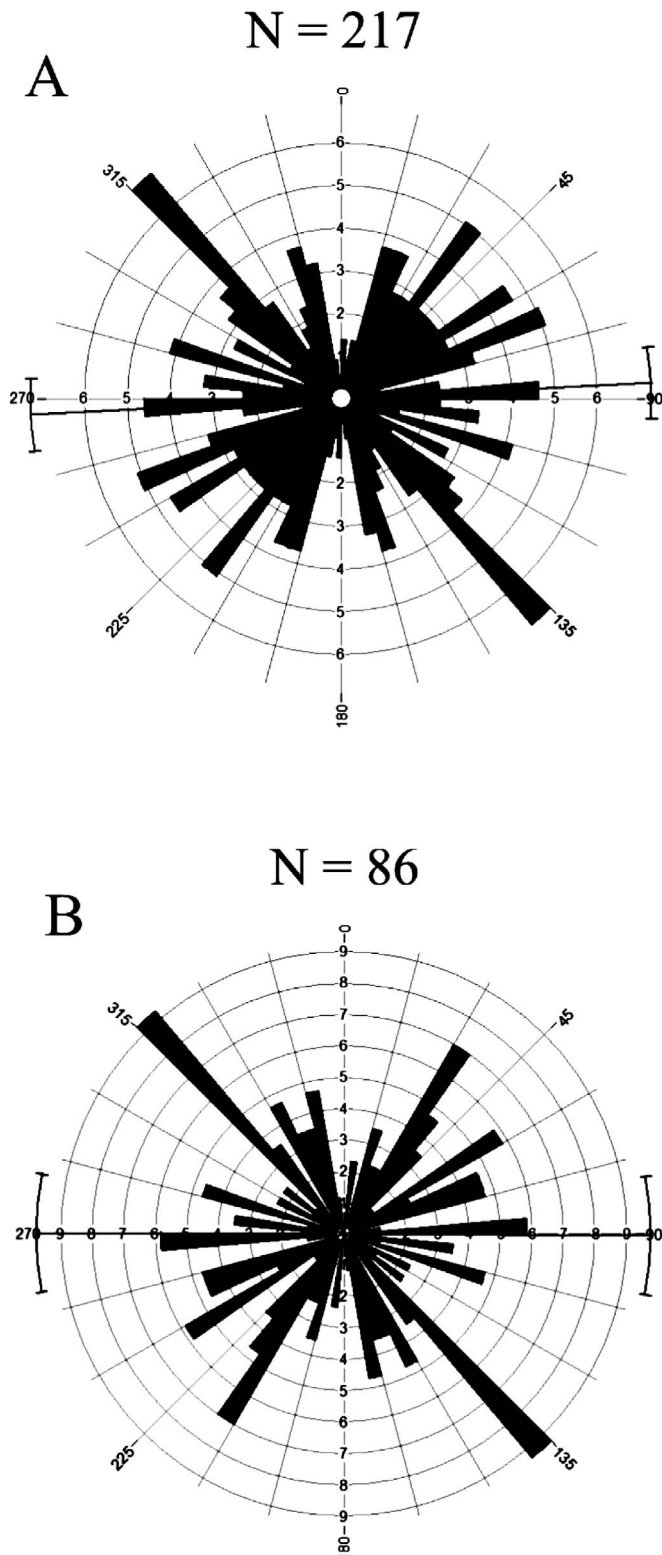


FIGURE 6—Mirror rose diagrams with 5° petals for bones recovered at Blagoveschensk in 2005. A) All bones recovered; B) Limb, girdle, and unidentified bones >30 cm. Statistical analyses show that the null hypothesis of a uniformly distributed data set cannot be rejected; Rayleigh test, A: $z = 0.020739$, $p > 0.05$; B: $z = 0.701737$, $p > 0.05$.

specimens (Fig. 7C), suggesting that reworking was probably a more important influence at Blagoveschensk than at Kundur. Loss of teeth may also result from gravity, trampling, or scavenging; however, such interpretations are not supported by our study of perthotaxic features and predation marks (see below).

Postmortem fractures of long bones are very common in the BDL (Fig. 8). Of 13 femora collected during 2005, at least 10 are broken off at both ends, and the fractured edge is always quite rounded (abrasion levels 2–3; see Fiorillo, 1988). This feature also indicates that the femora were significantly reworked after being broken (Fiorillo, 1988). Behrensmeier (1988, 1991) observed that fresh limb bones from large mammals often showed no evidence of breakage during vigorous hydraulic reworking. According to Ryan et al. (2001) and Eberth and Getty (2005), large numbers of broken limb bones indicate a destructive history prior to or during final reworking. Thus, it is more likely that many limb elements discovered at BDL experienced an earlier taphonomic episode, such as the breakdown of trabecular bone and collagen (Eberth and Getty, 2005), that weakened the specimens and increased their susceptibility to hydraulically induced breakage. As noted below, it is unrealistic to assume that the high incidence of damage to the ends of the limb bones is due to biological mechanisms (scavenging or trampling).

Perthotaxic features (bone modification processes active on the land surface; see Clark et al., 1967) are very rare on the bones inspected during this survey. Less than 2% of the bones exhibit weathering features (flaking and cracking), and those observed are indicative of early stage weathering. Most of the bones from BDL show that they were not exposed subaerially for any significant length of time before or after reworking. We also have not recognized trample marks in this material. These are characterized by shallow, subparallel scratch marks on the bone surfaces (see, e.g., Behrensmeier et al., 1986; Fiorillo, 1984, 1987). Thus, perthotaxic features suggest that the dinosaur elements at BDL were quickly buried or reworked after soft tissue decay.

Carnivorous tooth marks on bone surfaces can be identified as grooves that are V-shaped in cross section and often several millimeters deep or as isolated punctures (Fiorillo, 1991b). On the lambeosaurine bones collected at BDL from 1981 to 1989, less than 2% of the fossils exhibit potential tooth marks (Fig. 9). Tooth marks on dinosaur bones are usually attributed to scavenging and prey carcass utilization (Fiorillo, 1988, 1991a, 1991b). The relatively small number of tooth-marked bones at BDL, compared to the number of shed theropod teeth discovered (~30), may reflect a low incidence of scavenging. Alternatively it may also be hypothesized that prey were particularly numerous or that scavengers only ate the fleshy parts of carcasses (Eberth and Getty, 2005). Fiorillo (1991b) observed that tooth-marked bones are uncommon in most dinosaur localities and that theropod dinosaurs did not routinely chew bones during prey carcass utilization.

DEATH PROFILE OF THE *AMUROSOSAURUS* FOSSIL ASSEMBLAGE

Age-frequency distributions are useful for interpreting the origins of vertebrate assemblages. The observed profile at BDL can be compared with two theoretical endpoints representing catastrophic and attritional distributions (Lyman, 1994). In a catastrophic profile (resulting from a nonselective mass mortality; see Varricchio and Horner, 1993), the relative size of age-classes matches those of the living population, with the difference between adjacent classes being equivalent to attritional mortality during the transition from one class to the next (Fig. 10A). In an ideal attritional profile, the relative size of age-classes reflects the attritional mortality during the transition from one class to the next (Lyman, 1994). The profile shows peaks that correspond to ages in which mortality rates are the highest, usually among the very young and, to a lesser extent, the very old (Fig. 10B). In this case, the age profile of the fossil assemblage is distinctly different from the age profile of the living population, and younger and older individuals are overrepresented. Intermediate

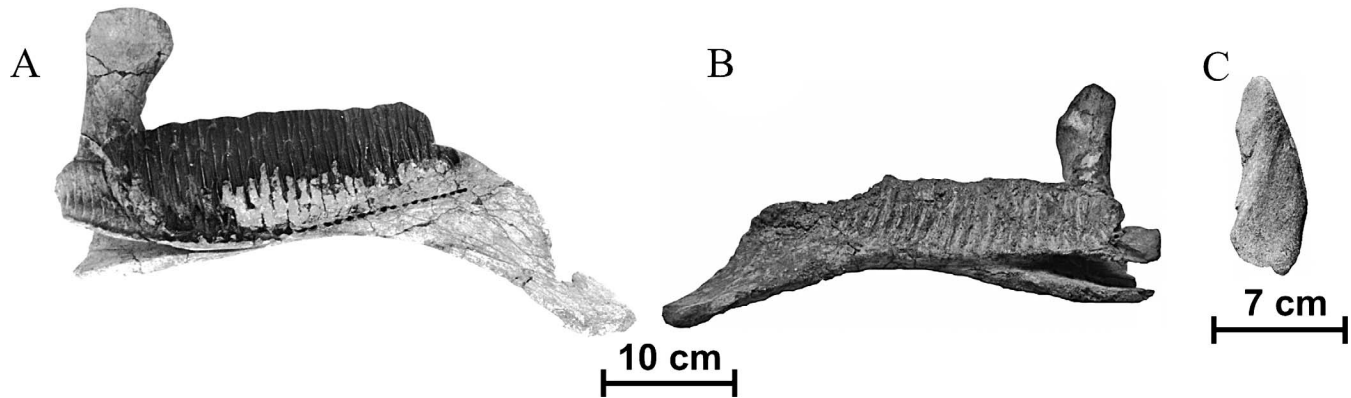


FIGURE 7—Dentaries of *Amurosaurus riabinini* from Blagoveschensk, displaying different types of preservation. A) Complete dentary with preserved dental battery; AEHM 1/12. B) Incomplete dentary without teeth; AEHM 1/382. C) Isolated and rolled coronoid process; AEHM 1/1487.

profiles reflect selective mortality or preservation bias (Varricchio and Horner, 1993).

Because the BDL is clearly a reworked assemblage, we hypothesized that the age profile of the *Amurosaurus* population, as deduced from the size-frequency distribution of the bones recovered from the bone bed, was biased and that smaller and younger individuals were underrepresented. In order to test this hypothesis, we compared the size-frequency distribution of four elements from different size categories, as follows: femora (5–113 cm; Fig. 11A), tibiae (40–95 cm; Fig. 11B), humeri (23–62 cm; Fig. 11C), and dentaries (14–44 cm; Fig. 11D). These elements represent the best-preserved specimens in the BDL samples collected from 1981 to 1989, and all belong to a single transportability group (Voorhies, 1969, group 2). Although we anticipated underrepresentation of small femora and tibiae (mean length of 40–60 cm) compared to large humeri and dentaries, our data show that the size-frequency distributions of large and small elements are similar (Fig. 11). Furthermore, because the abundance of these elements, regardless of their size range, is greatest in the smallest size categories, there is clearly an overrepresentation of young animals in this deposit. These results indicate that hydraulic sorting did not significantly influence the size-frequency distribution of different skeletal elements and that the age profile is probably a reliable reflection of the pattern of death within the original population of *Amurosaurus*. Our observation that element size is not biased is also consistent with the hypothesis that the BDL was deposited by a debris flow, which would have had the capacity to carry clasts of varying sizes (Eberth et al., 2006). The BDL assemblage may therefore be regarded as significantly density sorted, but poorly size sorted.

Size Distribution and Age Classes

It is difficult to correlate size-frequency distribution and age profile in nonmammalian vertebrates, especially in fossil taxa, when little is known

about the growth rate. Recent advances in techniques for determining age at death by using skeletal growth-line counts, coupled with developmental size estimates, now make quantitative growth-curve reconstructions for dinosaurs feasible (Erickson et al., 2001, 2004). Horner et al. (2000) studied ontogenetic changes in the bone histology of the femur of the hadrosaurid *Maiasaura peeblesorum*. They distinguished six relatively distinct but gradational growth stages: early and late nestling, early and late juvenile, subadult, and adult. These stages are distinguished by relative size and by changes in the histological patterns of bone at each stage.

We have tentatively extrapolated the results obtained by Horner et al. (2000) to the *Amurosaurus* femora recovered at Blagoveschensk. This extrapolation is based on the assumption that *Maiasaura* and *Amurosaurus* had similar growth rates and adult sizes. Figure 11A shows that of 12 complete or subcomplete femora discovered at BDL, 11 can be identified as belonging to late juvenile or small subadult specimens (femur length 520.5–610 mm). According to Anderson et al.'s (1985) formula for bipedal dinosaurs, these femur lengths correspond to small-to-medium-sized animals, weighing 343–627 kg (Table 1). Only one specimen, with a femur length of 1120 mm, can be identified as belonging to an adult individual. This femur belonged to an individual weighing ~2975 kg (Anderson et al., 1985).

The femur length of four other lambeosaurine specimens known from mostly complete skeletons and representing different growth stages (Table 2) is also included in Figure 11A: *Olorotitan arharensis* (AEHM 2/845), *Procheneosaurus convincens* (PIN 2230), *Tetragonosaurus* cf. *erectofrons* (AMNH 5461, a young *Corythosaurus* specimen, according to Dodson, 1975, and Evans et al., 2005), and *T. praeceps* (AMNH 5340, a young *Lambeosaurus* specimen, according to Dodson, 1975).

According to Horner et al. (2000), *T. cf. erectofrons* and *P. convincens* can be regarded as late juveniles, *T. praeceps* as a large late juvenile or

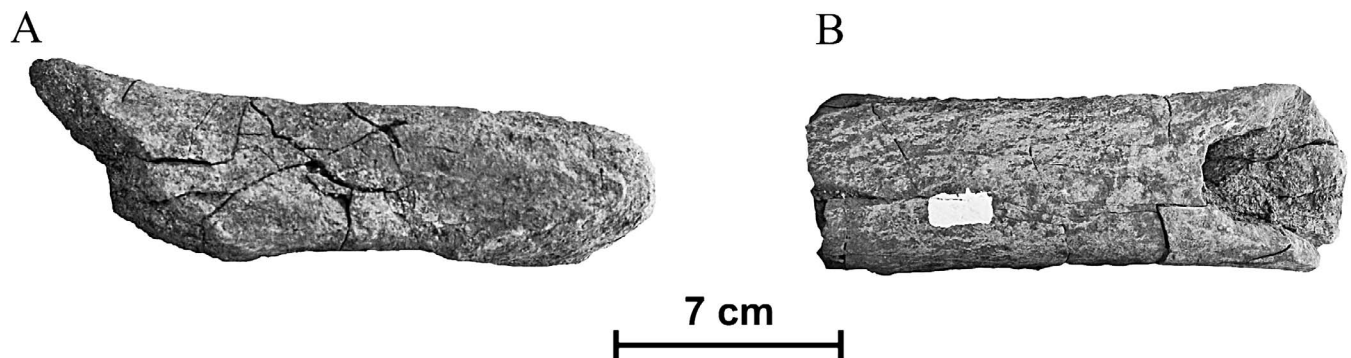


FIGURE 8—Long bones from the Blagoveschensk collection with different types of fractures. A) Metatarsal displaying oblique fracture (proximal end) and abrasion (distal end); AEHM 1/1488. B) Unidentified long bone displaying transverse fracture (left) and oblique fracture (right); AEHM 1/1489.

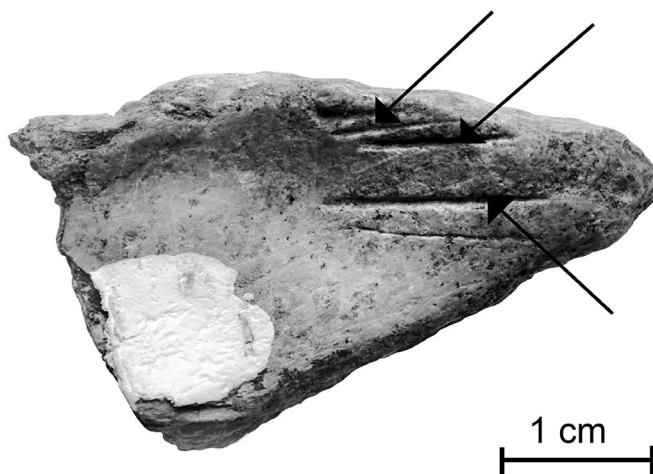


FIGURE 9—Dentary fragment displaying subparallel grooves, interpreted as predator or scavenger tooth marks; AEHM 1/1490.

a small subadult, and *O. arharensis* as an adult. These four skeletons are used as standards for the interpretation of the size-frequency distribution of the tibia, humerus, and dentary (Figs. 11B–D). The size-frequency distribution of these three elements indicates that the fossil assemblage from BDL is largely dominated by specimens smaller than, or of comparable size to, *T. cf. erectofrons*, *T. praeceps*, and *Procheneosaurus convincens*. In other words, the size-frequency distribution confirms that most of the elements discovered at BDL belong to late juvenile or small subadult *Amurosaurus* specimens.

Adult *Amurosaurus* specimens, which reach the same size as the holotype of *O. arharensis*, are rare at BDL. Such size-frequency distributions, with a strong overrepresentation of smaller specimens, suggest an attritional death profile, with a strongly selective mortality of younger, weaker individuals (cf. Fig. 10). These results indicate that the BDL may be interpreted as a local accumulation of animals that died at different times and that the size-frequency distribution reflects the high mortality rate among young animals rather than the demographic profile of a living population. The formation of the BDL is apparently not the result of a single catastrophic event, which would have indiscriminately killed all members of the *Amurosaurus* group, regardless of age, size, or robustness of the animals. Instead, the sediment gravity flow seems to have concentrated an attritional assemblage of elements accumulated in different places upstream from the site of deposition, and this assemblage clearly represents individuals that died at different times. Of course, the causes of death cannot be determined and are probably multiple. Moreover, we cannot exclude the possibility that the BDL is a mixing of attritional and mass kill material.

Age Segregation in Hadrosaurid Dinosaurs

Very small individuals (nestling and young juvenile age classes) are completely absent in the BDL. In a catastrophic mortality model, the absence of individuals that are less than one year old could be explained by seasonal and synchronous reproduction in association with rapid growth (Varricchio and Horner, 1993). Debris-flow deposits, by their nature, tend to be seasonal. If a catastrophic event occurred just before the reproduction season, or if the debris flow was itself the catastrophic event, the absence of very young age classes could be considered normal. In an attritional mortality model, however, as we propose to explain the death profile of the BDL, very young individuals are usually overrepresented because they are the most vulnerable individuals of the population. Thus, the absence of the very smallest individuals at BDL represents either (1) their absence in the death assemblage or (2) an artifact of preservation. Because our data show that very small elements from older individuals are well represented (Fig. 4), we regard the absence of late nestling and



FIGURE 10—Two basic types of mortality profiles. A) Catastrophic age profile. Light gray bars represent age structure of a hypothetical population of large vertebrates in which females give birth to one offspring each year; dark gray bars represent the number dying in each age class in order to maintain the population's age structure. B) Dark gray bars show a model attritional age profile for this population (after Lyman, 1994).

early juvenile individuals as a true reflection of their absence in the death assemblage and, thus, their likely absence, via age segregation, in the living population from this area.

Matthew (1915) was the first to suggest that young and adult hadrosaurids lived in different habitats. He believed that adult hadrosaurids lived in lowland habitats and migrated upland to their ancestral habitat to nest. The young then remained for a time after hatching before returning to the lowlands. Recent discoveries from the Judith River Formation in Montana (Clouse and Horner, 1993; Horner, 1999), however, contradict the hypothesis that nesting was restricted to upland environments. Carpenter (1999) considered that the formation of the famous *Maiasaura* (Horner and Makela, 1979) and *Hypacrosaurus* (Horner and Currie, 1994) baby bone beds in Montana and Alberta might be explained by age segregation in hadrosaurids. In these localities, none of the specimens directly associated with the nesting horizons is larger than 1 m in length (Horner, 1994; Horner and Currie, 1994). This hypothesis is not completely convincing, however, because such concentrations of baby dinosaur skeletons may also be explained by predation or different natural phenomena that would have preferentially killed the most vulnerable individuals, sparing the adults.

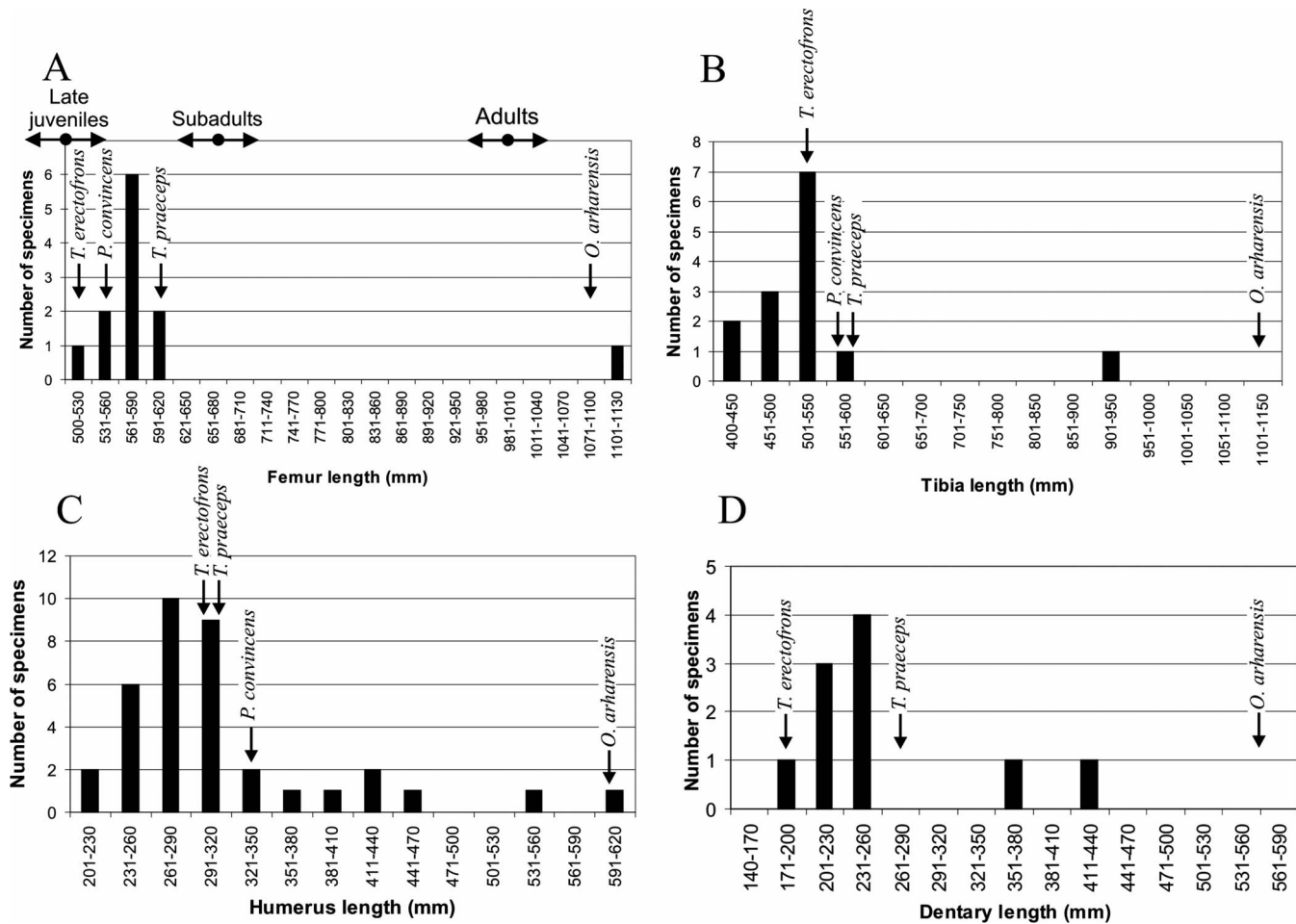


FIGURE 11—Size-frequency diagrams of different types of bones in the *Amurosaurus riabinini* collection recovered at Blagoveschensk. A) Maximal femur length; age classes (late juveniles, subadults, adults) defined according to Horner et al. (2000). B) Maximal tibia length. C) Maximal humerus length. D) Maximal dentary length. Arrows indicate the corresponding sizes for four mostly complete specimens used as standards: *Tetragonosaurus* cf. *erectofrons* (AMNH 5461, late juvenile), *Procheneosaurus convincens* (PIN 2230, late juvenile), *T. praeceps* (AMNH 5340, large late juvenile or small subadult), and *Olorotitan arharensis* (AEHM 2/845, adult).

Studies of dinosaur footprints provide stronger evidence for age segregation in dinosaurs generally and hadrosaurids more specifically. Carpenter (1992) shows that although tracks of hatchling hadrosaurids are known, these do not occur with adult prints; instead, the smallest prints found with adults are about one half of adult size (Currie, 1983; Lockley et al., 1983). The apparent segregation of the young from adults is also

TABLE 1—Estimated weight of *Amurosaurus riabinini* specimens, calculated from the circumference of the femur, according to Anderson et al.'s (1985) formula. AEHM = specimens from the Amur Natural History Museum, Blagoveschensk.

AEHM	Femur circumference (mm)	Weight estimation (kg)
1/981	252	581
1/982	208	343
1/983	229	443
1/966	260	627
1/967	253	583
1/937	239	498
1/984	244	531
1/985	247	546
1/986	265	665
1/987	297	908
m1	237	487
m2	242	517
1/265	460	2975

seen in small ornithischian tracks from Australia (Thulborn and Wade, 1984), interpreted as those of juveniles (Carpenter, 1999).

The same phenomenon can, in fact, be observed in the composition of dinosaur bone beds. Carpenter (1999) compiled smallest and largest femur lengths from different dinosaur bone beds: *Camptosaurus* (Quarry 13, Como Bluff, Wyoming), 25.8 cm versus 59.2 cm; *Coelophysis* (Ghost Ranch, New Mexico), 11.8 cm versus 20.9 cm; *Syntarsus* (Zimbabwe), 14.2 cm versus 20.8 cm; and *Allosaurus* (Cleveland-Lloyd Quarry, Utah), 43.5 cm versus 91 cm. (T. Gates, personal communication, August 2006, reports that the smallest femur from Cleveland-Lloyd Quarry is ~25 cm.) In these examples, the smallest individuals are almost half the largest adult size. Carpenter (1999) hypothesized that, at least in several taxa, baby dinosaurs apparently stayed together and did not join adults until they were about half grown. He explained the apparent segregation by the fact that the adults were far ranging and that the short legs of the young would have prevented them from keeping up with adults. Moreover, because of their important size disparity, the diet of young and adult individuals was probably very different. Nevertheless, drought-induced mass deaths have been postulated for the formation of Ghost Ranch and Cleveland-Lloyd Quarry dinosaur assemblages (Schwartz and Gillette, 1994; Gates, 2005). As discussed above, it is also possible that those catastrophic events, which by their nature tend to be seasonal, occurred just before the reproduction season and that no very young age classes may have existed at that time.

In the case of the BDL, the smallest and largest femur lengths are 52

TABLE 2—Measurements of lambeosaurine taxa used as standards in this paper.

	<i>Tetragonosaurus cf. erectofrons</i>	<i>Procheneosaurus convincens</i>	<i>Tetragonosaurus praeceps</i>	<i>Olorotitan arharensis</i>
Dentary length (mm)	184.6	unknown	273	561
Humerus length (mm)	295	330	305	596
Femur length (mm)	522	560	591	1100
Tibia length (mm)	510	590	550	1143

cm and 112 cm, respectively (Fig. 11), which fits Carpenter's (1999) model well. Considering this fossil assemblage as an attritional accumulation without significant size sorting and formed of elements from dinosaurs that died at different times, we regard age segregation as a plausible hypothesis to explain the complete absence of very young age classes. It is hypothesized that hatchling and young juvenile *Amurosaurus* perhaps lived elsewhere and joined the adult community when they were half the adult size.

CONCLUSION: PROPOSED SCENARIO FOR THE FORMATION OF THE BLAGOVESCHENSK BONE BED

By the Maastrichtian (probably late Maastrichtian), several vertebrate groups were living in the Blagoveschensk area: lambeosaurines, hadrosaurines, theropods, sauropods, crocodiles, and turtles. They lived in relatively open habitats, with denser vegetation along the banks of lakes and rivers. The climate was warm to temperate and relatively arid, with occasional but intense rainfalls. The lambeosaurine *Amurosaurus riabini*, a fairly large herbivorous dinosaur, dominated the terrestrial fauna. The *Amurosaurus* population was formed by half-grown-to-adult individuals. Hatchlings and young juveniles were apparently segregated from the adults and are not represented in the Blagoveschensk locality. There is no indication for a catastrophic (i.e., nonselective) mass mortality for the *Amurosaurus* population. The size-frequency distribution of the bones, however, is typical for an attritional death profile, with a strongly selective mortality of younger and presumably weaker individuals. The carcasses of the dead animals were not exposed subaerially for a long time, and scavengers were either not very active in the area or had an abundance of suitable food sources available. A sediment gravity flow, originating from the uplifted areas at the borders of the Zeya-Bureya Basin, swept away the dinosaur elements and carcasses, at different stages of alteration, and reworked them as a bone bed further in the basin. The relative underrepresentation of less dense elements, the dislocation of the dental batteries, and the numerous fractured long bones are indices of transportation. Some fragile elements are exquisitely preserved, however, indicating that they did not travel over long distances. The random orientation of the bones within the bone bed can be explained by their abundance or by their sudden deposition.

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