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Oviraptorosaur anatomy, diversity and ecology in the Nemegt Basin

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ABSTRACT

The interfingering Baruungoyot and Nemegt Formations of Mongolia host an exceptional diversity of oviraptorosaurs that is unique in including members of all three Late Cretaceous families (avimimids, caenagnathids, and oviraptorids). The oviraptorosaurs from the Baruungoyot and Nemegt Formations are reviewed, with a description of a new species of *Avimimus*. Emended diagnoses are provided for each taxon, including the first diagnosis of *Rinchenia mongoliensis*. The anatomy of these oviraptorosaurs is updated, taking into account data from recent discoveries. Avimimids and caenagnathids may be monotaxic in the Nemegt Formation, but oviraptorids are represented by at least four genera, with one additional undescribed genus. Oviraptorosaur ecology is examined by incorporating them into a dataset of nearly 500 dinosaur occurrences throughout the Nemegt Region. Oviraptorosaurs compose a small but constant part of Nemegt faunas. Oviraptorid species each occur at a single locality, which may be an artifact of sampling. Alternatively, it may indicate that they were spatially partitioned, or that species turned over rapidly. The occurrence of avimimids and caenagnathids throughout the Nemegt Formation and their absence in the Baruungoyot Formation suggests that they preferred mesic habitats. In contrast, oviraptorids were successful in both xeric and mesic environments, but are relatively more abundant in the former. The coexistence of these families can be explained through dietary niche partitioning. Oviraptorosaurs probably had an Asian origin, but rapidly spread to North America and interchanged between continents several times in the Late Cretaceous.

1. Introduction

The Baruungoyot and Nemegt Formations of Mongolia are home to a remarkable diversity of theropod dinosaurs, especially oviraptorosaurs. To date, seven oviraptorosaur genera have been named from the Baruungoyot or Nemegt Formations (Fig. 1), and at least one new genus from Guriliin Tsav has yet to be described (Funston et al., in prep). The discovery of new oviraptorosaur material in Canada, China, Mongolia, and the United States has increased our understanding of intra- and inter-specific variation in oviraptorosaurs. Consequently, it is important to reexamine older holotypes to determine whether they still represent valid taxa. This abundant fossil record also offers ecological clues to the lifestyles of oviraptorosaurs. Although there is some work on the diet of oviraptorosaurs (Osborn, 1924; Barsbold, 1977, 1986; Smith, 1992; Currie et al., 1993; Funston et al., 2014), no study has yet attempted to understand their ecological roles. The Nemegt Formation in the western Gobi desert is unique in that it is home to three groups of oviraptorosaurs—avimimids, caenagnathids, and oviraptorids—and is the only place where the latter two coexist. Previous work (Currie et al., 1993; Tsuihiji et al., 2016) has suggested that caenagnathids and oviraptorids rarely coexist because they are adapted for different environments—mesic and arid, respectively. Their anatomy and distribution in the Baruungoyot and Nemegt Formations are therefore crucial for understanding their behaviour and ecology.

New insights on stratigraphy and sedimentology suggest that parts of the Baruungoyot and Nemegt Formations overlap temporally, and may represent a single ecosystem with different subenvironments and patterns of sedimentation through time (Eberth et al., 2009; Fanti et al., 2012; Eberth, 2017, this volume; Fanti et al., 2017, this volume). These Formations outcrop extensively in the Nemegt Basin, but most prominently at Altan Uul, Bugiin Tsav, Hermiin Tsav, and Nemegt. Correlation of the strata (Eberth, 2017, this volume) suggests that these localities form a transect of the Baruungoyot and Nemegt Formations, decreasing in age from Hermiin Tsav through Nemegt and Altan Uul, to the youngest deposits at Bugiin Tsav. Previous work on stratigraphy (Gradziński, 1970; Gradziński et al., 1977) allows other localities from the Nemegt Basin to be incorporated into this stratigraphic sequence. The collection of Global Positioning System (GPS) data of sites in the

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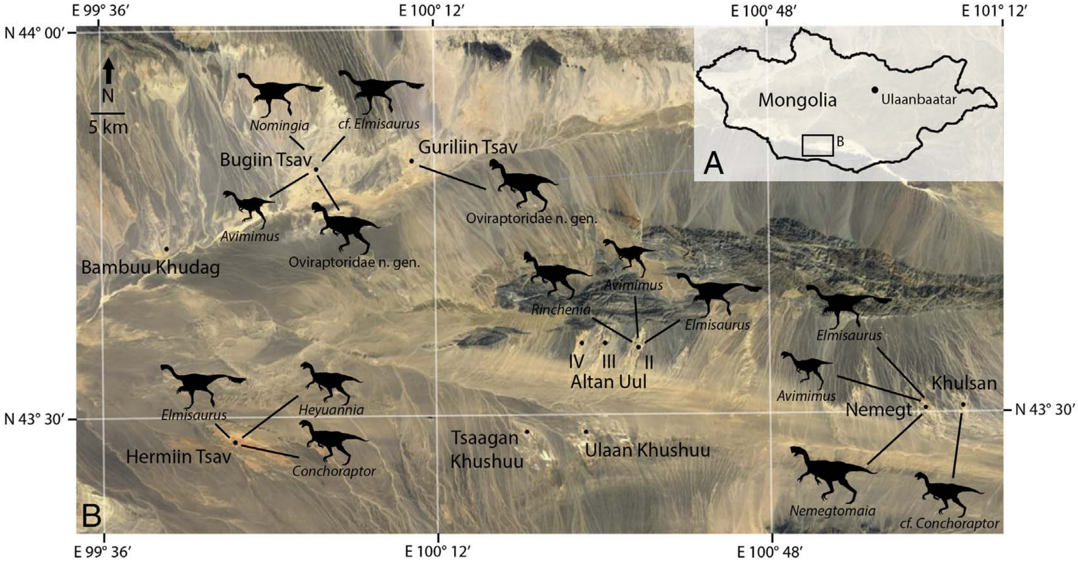

Fig. 1. Map of fossil localities and oviraptorosaur occurrences in the Nemegt Basin. Satellite image from Google Earth.
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Nemegt Basin over the course of two decades has revealed the distribution of dinosaur skeletons. Combined with information from the literature, this allows nearly 500 dinosaur skeletons to be incorporated into a community data set spanning the Nemegt interval (see Supplementary Tables 1–2 in Funston et al. (in prep)). Oviraptorosaur diversity and distribution can thus be compared to the overall patterns of community composition in the Nemegt Formation (see Supplementary Information).

Here, the diversity of Nemegt Basin oviraptorosaurs is reevaluated through anatomical and ecological perspectives. Reexamination of material from the *Avimimus* bonebed (Funston et al., 2016b) indicates it is a new species. Updated diagnoses are provided for *Elmisaurus rarus*, *Nemegtomaia barsboldi*, and *Rinchenia mongoliensis*. The holotype specimens of *Heyuannia* (= *Ajancingenia*) *yanshini* and *Conchoraptor gracilis* from Hermiin Tsav are redescribed taking into account new insights on oviraptorid anatomy. Although its presence is noted and it is used in the ecological analysis, a new Guriliin Tsav oviraptorid will be described elsewhere (Funston et al., submitted). These anatomical data are used to assess previous taxonomic frameworks and functional morphology of Nemegt Basin oviraptorosaurs, while the community data are used to understand their diversity, niche partitioning, and ecological roles.

2. Institutional abbreviations

MPC-KID, Korean International Dinosaur Expedition, specimens housed at the Institute of Paleontology and Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; MPC, Institute of Paleontology and Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; MPC-NEE, Nemegt Educational Expedition field number, specimens housed at the Institute of Paleontology and Geology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; RSM, Royal Saskatchewan Museum, Regina, Saskatchewan, Canada; UALVP, University of Alberta Laboratory of Vertebrate Paleontology, Edmonton, Alberta, Canada; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

3. Methods

3.1. Data collection

Map data for plotting geographic distribution (see Supplementary File 1 of Funston et al. (submitted)) was gathered over the course of decades by the third author on expeditions organized by Nomadic Expeditions, the Korean-Mongolian International Dinosaur Project, and the MPC. Latitude, longitude, and altitude measurements were taken using a handheld Garmin Global Positioning System (GPS) unit for each site. Each site corresponds to a skeleton, which varies in completeness from partial to complete, and is at least associated, although the majority are articulated. A total of 358 sites were included in the map, each of which was identifiable at least to the superfamily level, and most to the species level. Two assemblage datasets were created with each locality as a separate sample: species occurrences and superfamily occurrences (see Supplementary Tables 1–2 in Funston et al. (submitted)). Assemblage composition data was generated from the Google Earth map as well as from reports in the published literature that were not included in the map (Kielan-Jaworowska, 1968, 1969, 1971, 1972, 1974, 1975, 1977, 1979, 1981, 1984; Ishii et al., 2000, 2004; Weishampel et al., 2008; Tsubamoto, 2010; Arbour et al., 2014; Currie, 2016; Tsuihiji et al., 2016). The sample was thereby improved from 364 identifiable occurrences (Currie, 2016) to 472 (species-level) or 476 (superfamily-level) occurrences. Although the duration of deposition at each locality is not known, each represents only a small portion of the ~350 m thick Baruungoyot-Nemegt interval. Furthermore, because the assemblages are time-averaged, the sample at each locality is probably reflective of broad-scale community structure at that site (Kidwell and Flessa, 1995; Kidwell, 2001). Locality assemblages are therefore regarded here as communities. Sites where multiple individuals of a single taxon occur, like the 'Dragon's Tomb' of *Saurolophus angustirostris* (Bell et al., 2017, this volume) and the *Avimimus* bonebed (Funston et al., 2016b), are taphonomic exceptions and, because they are not time-averaged, were counted as single occurrences. Counts were generated for 11 localities: Altan Uul II, Altan Uul III, Altan Uul IV, Bambuu Khudag, Bugiin Tsav, Guriliin Tsav, Hermiin Tsav, Khulsan, Nemegt, Tsagaan Khushuu, and Ulaan Khushuu.

3.2. Taphonomic considerations

Taphonomic biases were not accounted for in the raw counts of the data, to maximize available data. It is likely that taphonomic processes influenced the relative proportions of taxa preserved between each formation, and that these influences differed between the Baruungoyot and Nemegt Formations, but it is unlikely that there was significant variation within each formation. There is, however, some evidence that

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