

SOCIAL BEHAVIOUR AND MASS MORTALITY IN THE BASAL CERATOPSID DINOSAUR *PSITTACOSAURUS* (EARLY CRETACEOUS, PEOPLE'S REPUBLIC OF CHINA)

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Abstract: An exceptionally preserved herd of the ceratopsian dinosaur *Psittacosaurus* was recovered from the Lujiatun Beds of the Lower Cretaceous Yixian Formation, Liaoning Province, north-east China. This specimen provides the earliest direct evidence of post-nestling gregarious behaviour in this important dinosaur clade. The sediment in which the skeletons occur represents a lahar (volcanic mudflow), indicating that the six individuals present were entombed simultaneously during a catastrophic mass mortality event. Reconstruction of the herd age profile shows it was com-

posed of offspring from at least two clutches, revealing that group fidelity in these dinosaurs extended beyond time spent together in the nest. This demonstrates that sociality appeared much earlier in ceratopsian evolution than is generally acknowledged and that such behaviour preceded the evolution of the elaborate horns and frills seen in derived ceratopsids.

Key words: Yixian Formation, Early Cretaceous, *Psittacosaurus*, social behaviour, lahar.

LATE Cretaceous ceratopsid dinosaurs, such as *Chasmosaurus* and *Triceratops*, are characterized by elaborate cranial ornamentation, including the presence of nasal and/or supraorbital horns, an expansive parietosquamosal frill and varying numbers of epoccipital ossifications that are fused to the frill margins (e.g. Dodson *et al.* 2004). These structures are generally regarded as analogous to the horns and antlers of living mammals and are thought to have functioned similarly, as either visual signals for species-recognition and/or display, or as defensive weapons (e.g. Farlow and Dodson 1975; Sampson *et al.* 1997; Sampson 2001). Such features provide circumstantial evidence for complex social organization among advanced horned dinosaurs, an inference supported by bone-bed data that indicate at least some ceratopsids lived in large, multi-generational herds (Currie and Dodson 1984; Ryan *et al.* 2001). Social behaviour is not well documented among basal ceratopsians, however, as the latter generally lack the well-developed cranial display structures of ceratopsids: horns are completely absent in these animals and the parietosquamosal frills (where present) are relatively small and lack marginal ornamentation (You and

Dodson 2004). In addition, bone-bed assemblages of basal ceratopsians have not been found to date (You and Dodson 2004). As a result, the origin and evolution of social behaviour in derived ceratopsids is poorly understood and it has not been possible to establish if the visual display structures present in these animals are a prerequisite for, or a direct consequence of, sociality.

The Lower Cretaceous Yixian Formation of Liaoning Province, People's Republic of China, has yielded an exceptionally preserved terrestrial/freshwater biota, which includes a rich assemblage of plant, invertebrate and vertebrate taxa, some of which are known from material that exhibits spectacular preservation of soft tissues, gut contents and colour banding (reviewed in Chang *et al.* 2003; Zhou *et al.* 2003). The most famous specimens to be recovered from this unit are undoubtedly the feather-bearing non-avian dinosaurs, such as *Sinosauropteryx*, *Caudipteryx*, *Microraptor* and *Sinornithosaurus* (Norell and Xu 2005). However, a variety of other dinosaur taxa was also present in this biome, including the basal ceratopsians *Psittacosaurus*, *Hongshanosaurus* and *Liaoceratops* (Xu and Norell 2006). Here, we describe an

exceptionally preserved group of *Psittacosaurus* (IVPP V14341), which provides an unprecedented opportunity to test whether the advent of ceratopsian herding behaviour preceded the appearance of horns, frills and other display structures. In addition, it has been proposed that many of the accumulations of vertebrate material from the Yixian Formation resulted from mass mortality events mediated by nearby volcanic centres (e.g. Wang *et al.* 2000*a, b*; Wang and Zhou 2003). Analysis of the host matrix encasing IVPP V14341 allows rigorous testing of this taphonomic hypothesis.

On the basis of sedimentological and petrological evidence we demonstrate that the individuals comprising IVPP V14341 were preserved together *in situ* and that this assemblage did not result from post-mortem transport of the skeletons into the same area. The specimens appear to have been overcome by a lahar (volcanic debris flow). Developmental evidence indicates that the individuals preserved within the group represent two distinct age classes, suggesting that offspring from different clutches were living together in the same social unit. These two lines of evidence lead us to conclude that IVPP V14341

represents a small herd of *Psittacosaurus* and that habitual group-living in basal ceratopsian dinosaurs preceded the evolution of the impressive cranial ornamentation associated with sociality in derived ceratopsians.

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DESCRIPTION

IVPP V14341 was collected from the Lujiatun Beds of the Yixian Formation in the vicinity of Lui Tai village, near Yixian, Liaoning Province. Radiometric analyses of tuff samples from the main fossiliferous horizon have provided a mean weighted $^{40}\text{Ar}/^{39}\text{Ar}$ date of 123.2 ± 1.0 Ma (He *et al.* 2006), placing this unit within the late Early Cretaceous (lower Aptian: Gradstein *et al.* 2004). The specimen comprises a single block that includes six complete and fully articulated *Psittacosaurus* individuals in close association (Text-fig. 1). The skeletons in the group are all orientated in the same general direction, covering an



TEXT-FIG. 1. A herd of juvenile *Psittacosaurus* from the Lujiatun Beds of the Yixian Formation (lower Aptian: Lower Cretaceous), near Liu Tai village, Yixian, Liaoning Province, China (IVPP 14341). Letters refer to each of the six individuals present. Scale bar represents 100 mm.

area of approximately 0.26 m². Although the individuals partially overlap each other there is no mixing of elements between adjacent skeletons. This observation indicates that this accumulation was not a time-averaged, attritional assemblage, but was entombed rapidly before decomposition, erosion or scavenging could permit mixing of elements among the different carcasses. Moreover, the complete articulation and excellent preservation of the skeletons (which are not abraded, weathered or otherwise damaged) is also consistent with rapid burial.

Each individual in IVPP 14341 exhibits numerous autapomorphies of the Psittacosauridae, including: an elevated external narial opening; an extremely broad caudolateral premaxillary process; convergence of the premaxillary, maxillary, lachrymal and jugal sutures to a single point on the snout; and an open canal on the lateral surface of the lachrymal (You *et al.* 2003; You and Dodson 2004; You and Xu 2005). The specimens differ from the recently reported psittacosaurid *Hongshanosaurus* (You and Dodson 2004; You and Xu 2005) in possessing a shorter snout, more rounded external nares and an infratemporal fenestra whose long axis is less posteriorly inclined. However, the morphology of the individuals in IVPP 14341 is entirely consistent with referral to *Psittacosaurus* (e.g. Sereno *et al.* 1988a, b; Xu 1997; You *et al.* 2003; You and Dodson 2004; You and Xu 2005; Zhou *et al.* 2006).

Around 10–12 species of *Psittacosaurus* are recognized currently (You and Dodson 2004), but taxonomic revision of the genus is overdue and it is probable that the true number of diagnosable species is much lower. Pending such revisions, we provisionally assign IVPP V14341 to the recently erected species *P. lujiatunensis* (Zhou *et al.* 2006) as these specimens share an apparently unique combination of cranial character states, including narrow prefrontals, a depression on the jugal and a strongly developed, posteriorly offset jugal boss. In addition, individuals in IVPP 14341 display a few unique features that may prove to have taxonomic utility, such as the apparent absence of manual digits IV and V. One of us (ZQ) is currently studying the specimens in detail to determine whether erection of a new species is justified.

VOLCANICLASTIC PRESERVATION

The Lujiatun Beds form the basal member of the Yixian Formation and consist predominantly of unstructured tuffaceous conglomerates, silty mudstones and sandstones (Wang *et al.* 2000a, b; Wang and Zhou 2003). Vertebrate material from the Lujiatun Beds lacks the soft-tissue preservation present in specimens from other members of the Yixian Formation (the Jianshangou and Dawangzhangzi beds): however, this is compensated for by the fact that specimens from the Lujiatun Beds are often

fully articulated and three-dimensionally preserved (Zhou 2006). This contrasts with specimens from the Jianshangou and Dawangzhangzi beds, which are two-dimensionally preserved (Zhou 2006). In addition, some of the dinosaur specimens from the Lujiatun Beds record rarely obtainable behavioural information, such as evidence of an avian-like sleeping posture in the troodontid theropod *Mei* (Xu and Norell 2004) and parental care in the basal ceratopsian *Psittacosaurus* (Meng *et al.* 2004). It has been suggested that the Lujiatun Beds record a single catastrophic mass mortality event, though no detailed sedimentological evidence has been provided to support this scenario (e.g. Wang *et al.* 2000a, b; Wang and Zhou 2003). In order to test the mass mortality hypothesis, the matrix containing IVPP V14341 was examined petrologically, petrographically and by X-ray diffraction (XRD), allowing determination of the taphonomic and palaeo-environmental conditions that prevailed during burial.

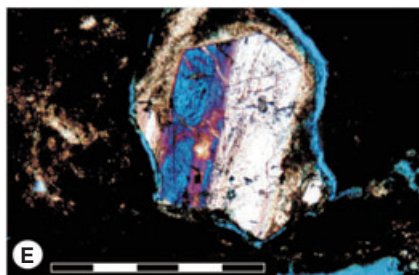
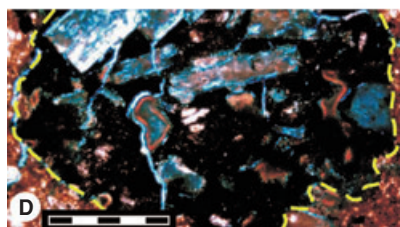
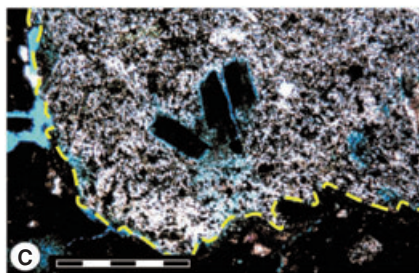
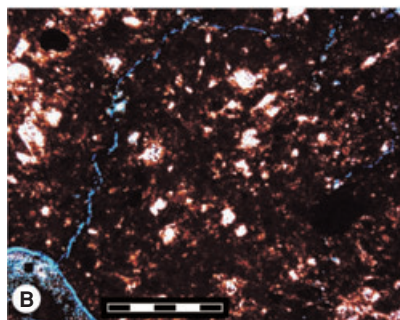
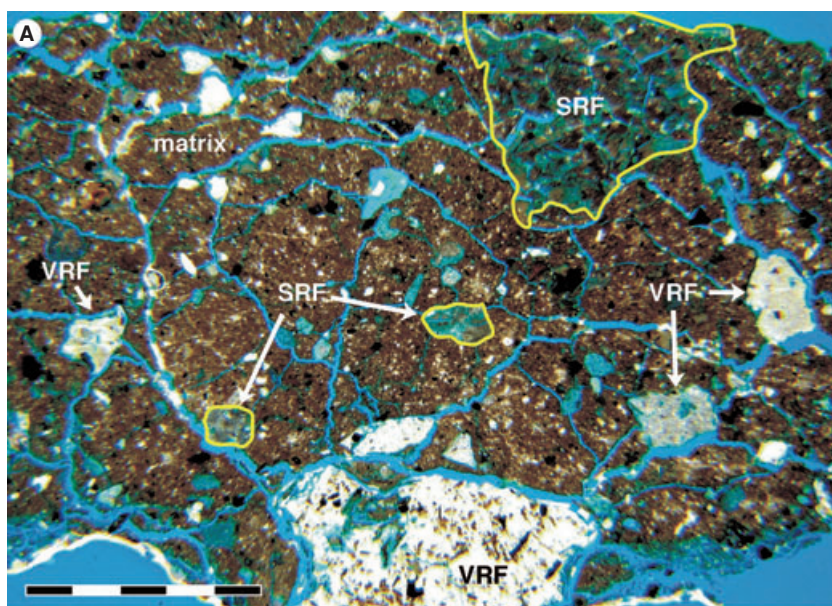
The sediment consists of massive, reddish brown (iron oxide-rich), sandy to pebbly mudstone matrix (Text-fig. 2A–B). Grains, granules and pebbles in the mudstone are matrix-supported and consist primarily of volcanic rock fragments (VRF) composed of quartz, plagioclase, volcanic glass and mica (Text-fig. 2A, C), with secondary sedimentary rock fragments (SRF) containing large proportions of VRF and fresh to corroded euhedral grains of plagioclase, quartz and biotite (Text-fig. 2A, D). The VRF and SRF also comprise the largest clasts and are up to 5 mm in maximum diameter. Silt to sand-sized grains (0.05–1.00 mm) of euhedral to subangular, fresh to corroded quartz, plagioclase, potassium feldspar and biotite are also present throughout the matrix (Text-fig. 2E). These are identical to those that occur in the VRFs and SRFs, suggesting an origin from the breakdown of intraclasts. The matrix exhibits a wholly massive texture with no evidence of grading or sorting (Text-fig. 2A). Iron oxide rinds or halos are absent around grains and there is no evidence of invertebrate bioturbation or plant roots. XRD analysis of the bulk sample revealed the following pattern of mineralogical abundances (in descending order by weight): 39 per cent quartz, 27 per cent plagioclase, 15 per cent potassium feldspar, 12 per cent smectite and 8 per cent pyrite. The clay fraction (< 5 µm) consists (by weight) of 84 per cent smectite, 13 per cent illite and 3 per cent quartz. Further details of results from the XRD analyses are in supplementary files, which can be downloaded from the Palaeontological Association website (<http://www.palass.org>).

The high percentage of silica, aluminosilicates and smectitic clays in both the bulk and the clay-smear samples coupled with the abundance of volcanic phenocrysts and VRF indicates that the host sediment is a reworked dacite or rhyolite (e.g. Deer *et al.* 1966; Moorhouse 1970; Fisher and Schmincke 1984). In addition, the co-occurrence of VRF and SRF, iron-oxide-rich smectitic clays

and fresh to highly weathered VRF and volcanic mineral grains (e.g. volcanic glass, deeply corroded potassium feldspar and euhedral plagioclase) indicate that there must have been a significant degree of reworking and mixing of volcanic debris. Furthermore, the massive texture, matrix-supported grains and pebbles, very poor size sorting, mixture of fresh and weathered grains, and absence of evidence for bioturbation all indicate that the host matrix was deposited by massive flows that were very likely cohesive and possibly of high density (Lowe 1979; Major 2003, 1997; Leeder 1999). This interpretation clearly excludes an origin from suspension or turbulent flows (hydraulic or aeolian) and suggests, instead, that this matrix was deposited as a lahar, either during the eruptive phase of a nearby volcanic centre, or during a non-eruptive debris flow event that reworked previously

deposited volcanic material (Fisher and Schmincke 1984). Dinosaur material has been collected from lahar deposits elsewhere, although examples are rare (Fastovsky *et al.* 1995; Schmitt *et al.* 1998). IVPP V14341 provides the first direct sedimentological evidence for the action of such a preservational mechanism in the Yixian Formation in general and the Lujiatun Beds in particular, supporting the hypothesis that volcanically induced mass mortality events were responsible for at least some of the vertebrate accumulations in this unit (e.g. Wang *et al.* 2000a, b; Wang and Zhou 2003).

A lahar interpretation is fully compatible with the high-quality *in situ* preservation of the psittacosaur specimens. As demonstrated by Fisher and Schmincke (1984, pp. 302–303), it is common for lahars to bury sedimentary surfaces and organic remains across low-gradient



TEXT-FIG. 2. Photomicrographs of thin sectioned matrix from IVPP V14341. A, general fabric of the matrix. Note the variable size and irregular edges of the intraclasts, and the 'floating grains' texture, indicating a nearby source and rapid deposition. B, iron oxide-rich, reddish brown smectite-rich matrix with 100- μ m or smaller grains. C, volcanic rock fragment (bounded by broken yellow line) with glassy (quartz-rich) matrix and volcanic phenocrysts. D, sedimentary rock fragment (bounded by broken yellow line) with very dark, oxide-stained clays and volcanic phenocrysts. E, fresh, volcanic-plagioclase phenocryst. Abbreviations: VRF, volcanic rock fragment; SRF, sedimentary rock fragment. Scale bars represent 5 mm (A) and 0.5 mm (B–E).

slopes (< 10 degrees) without erosion, transport or other modification, even when travelling over distances of up to 80 km. Consequently, although little is known about the precise palaeogeography of the Lujiatun psittacosaur locality, we can reasonably conclude that the site was located a significant distance downslope from a volcanic centre where the gradient was 10 degrees or less.

AGE PROFILE

Previous work on a population of the congeneric taxon *Psittacosaurus mongoliensis* used histological data and information on body masses to construct an empirically derived logistic growth curve for this species (Erickson and Tumanova 2000). Counting the annually deposited Lines of Arrested Growth present in sectioned limb-bones provided age estimates for individuals within this population and mass estimates were calculated using Developmental Mass Extrapolation (DME: Erickson and Tumanova 2000). In DME the body mass of the largest individual in a population is calculated from femoral dimensions using a standard allometric growth equation (Anderson *et al.* 1985). As femoral length is known to scale isometrically with body mass in extant archosaurs, it is then possible to extrapolate body masses from the femoral dimensions of other (smaller) individuals as a proportion of the body mass of the largest adult (Erickson and Tumanova 2000). Histological data are not available for IVPP V14341; however, we were able to use DME to investigate the structure of the age profile in this group.

It is possible that species-level or anagenetic evolutionary differences may preclude exact comparisons between the growth dynamics of the *Psittacosaurus mongoliensis* (Aptian–Albian) population studied by Erickson and Tumanova (2000) and our *P. lujiatunensis* (lower Aptian) sample (IVPP V14341). However, as these taxa are congeneric, such differences (if any) are likely to be minor. For the purposes of this study, it was assumed that the growth patterns exhibited by *P. lujiatunensis* would be identical to those documented for *P. mongoliensis* (Erickson and Tumanova 2000). It was also assumed that the two species would exhibit similar adult size ranges, thereby allowing the body mass estimate of the largest *P. mongoliensis* individual in the previous study (*c.* 20 kg; Erickson and Tumanova 2000) to be used as a basis for estimating the body masses of the specimens in IVPP 14341. The largest skeleton in IVPP 14341 is equivalent in size to the smallest individual used in the previous study (femoral lengths of *c.* 75 mm: see Erickson and Tumanova 2000 and Table 1) and much larger specimens of *Psittacosaurus* than those present in IVPP 14341 are known from the Lujiatun Beds (e.g. Zhou *et al.* 2006), demonstrating considerable overlap in the size ranges of these two species.

TABLE 1. Femoral dimensions, body mass estimates and age estimates for five of the individuals in IVPP V14341 (letters refer to the individuals labelled in Text-fig. 1: it was not possible to obtain femoral lengths for individual F). Body mass estimates were obtained by Developmental Mass Extrapolation and age estimates were obtained by substituting body masses into the logistic growth equation obtained for *Psittacosaurus mongoliensis* (Erickson and Tumanova 2000: see text for further details). Unfortunately, it is not currently possible to confirm the ages of these specimens histologically. Error margins were calculated on the basis of possible uncertainty in femoral measurements (± 0.5 mm), which led to a possible range of body mass estimates that consistently varied as ± 0.02 kg in each case.

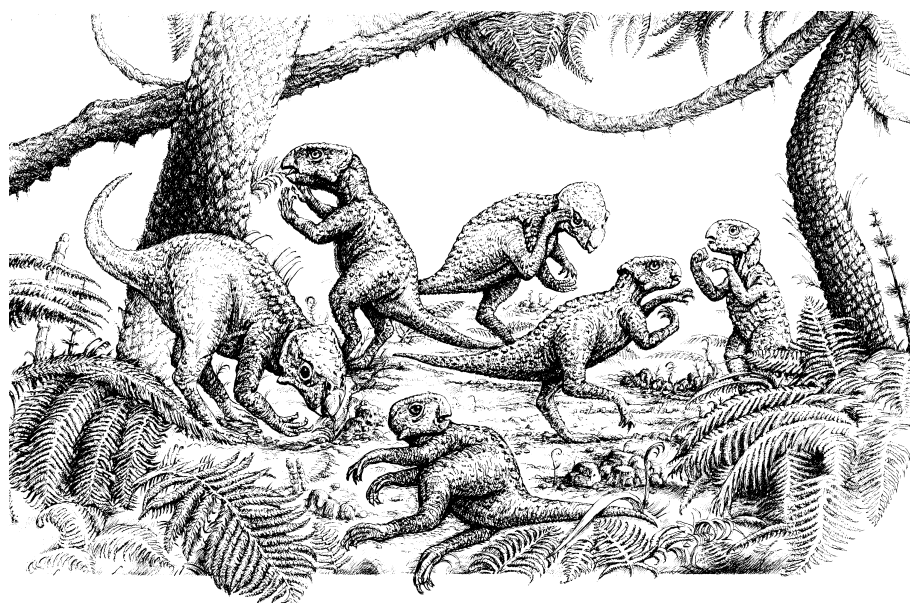
Individual	Femur length (mm)	Body mass (kg)	Age (years)
A	53	0.32	1.45 \pm 0.09
B	68	0.68	2.49 \pm 0.04
C	62	0.52	2.11 \pm 0.04
D	72	0.97	2.98 \pm 0.03
E	57	0.40	1.75 \pm 0.07

Femoral lengths were taken from five of the skeletons in IVPP V14341 (Table 1) and body masses were calculated as a proportion of the weight of the largest individual of *Psittacosaurus mongoliensis* using DME. These body masses were then incorporated into a rearranged version of the logistic growth equation previously derived for *P. mongoliensis*, which describes age as a function of body mass (Erickson and Tumanova 2000). Thus, the original equation $\text{Mass} = 25.2/1 + e^{-0.74(\text{Age}-7.33)}$ becomes $\text{Age} = 7.33 - 1.35\ln(25.2/\text{mass} - 1)$.

Using this method, the largest (= oldest) individual in IVPP V14341 was calculated to be 2.98 years old at the time of death, while the smallest (= youngest) member of the group was 1.45 years old (see Table 1). However, these apparently precise age estimates should be regarded with some caution as they are derived directly from the logistic growth equation. Nevertheless, conservative interpretation of these results indicates that the largest and smallest individuals in the group were separated in age by approximately 1.5 years (Table 1). This age profile indicates that offspring from at least two different clutches were preserved together in IVPP V14341.

CONCLUSIONS

Sedimentological, petrological and taphonomic evidence all indicate that the *Psittacosaurus* specimens in IVPP V14341 perished together as they were engulfed by a lahar and that their co-occurrence did not result from post-mortem transport of the individuals into the same area. Consequently, the six individuals in this assemblage



TEXT-FIG. 3. Life reconstruction of the *Psittacosaurus* herd preserved in IVPP V14341 (courtesy of Robert Laws).

probably represent a small herd that was overcome during a mass mortality event. As this herd contains a mixture of different-aged individuals, spanning 1.5 years in age, we propose that more than one clutch is represented, suggesting in turn that *Psittacosaurus* lived in small, potentially stable herds that habitually incorporated more than one age class (Text-fig. 3). IVPP V14341 therefore represents the first direct evidence for post-nestling gregarious behaviour in a basal ceratopsian dinosaur. Many extant archosaurs (birds and crocodylians) produce clutches on an annual or semi-annual basis (e.g. Carpenter 1999), which accords with the interval between clutches that occurs within the *Psittacosaurus* herd. Together with evidence for post-hatching parental care in *Psittacosaurus* (Meng *et al.* 2004), this demonstrates that complex social behaviours emerged early in ceratopsian evolutionary history and preceded the appearance of the flamboyant cranial ornamentation that characterizes more derived neoceratopsians.

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