

Juvenile-only clusters and behaviour of the Early Cretaceous dinosaur *Psittacosaurus*

QI ZHAO, MICHAEL J. BENTON, XING XU, and P. MARTIN SANDER



Zhao, Q., Benton, M.J., Xu, X., and Sander, P.M. 2014. Juvenile-only clusters and behaviour of the Early Cretaceous dinosaur *Psittacosaurus*. *Acta Palaeontologica Polonica* 59 (4): 827–833.

It has hitherto been hard to prove that any association of juvenile dinosaurs represents original behaviour rather than sedimentary accumulation, and it has been hard also to determine the ages of such juveniles. A previously described specimen, which consists of an “adult” *Psittacosaurus* with 34 fully articulated juveniles, turns out to be a composite: the “adult” skull probably has been added, and in any case it is below breeding age. Other juvenile-only clusters have been reported, but the best examples that likely reflect behaviour rather than sedimentary accumulation are specimens from the Early Cretaceous Lujiatun beds in NE China, which were entombed beneath pyroclastic flow deposits. A remarkable juvenile-only cluster of *Psittacosaurus* shows clear evidence of different ages (five 2-year olds and one 3-year old) based on bone histological analysis. These juveniles may have associated together as a close-knit, mixed-age herd either for protection, to enhance their foraging, or as putative helpers at the parental nest.

Key words: Dinosauria, Ceratopsia, juvenile-only, mixed-age, bone histology, Cretaceous.

Qi Zhao [zhaoqi@ivpp.ac.cn], School of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK and Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing 100044, China;

Michael J. Benton [Mike.Benton@bristol.ac.uk], School of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK; *Xing Xu* [xuxing@ivpp.ac.cn], Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, PO Box 643, Beijing 100044, China;

P. Martin Sander [martin.sander@uni-bonn.de], Division of Paleontology, Steinmann Institute, Rheinische Friedrich-Wilhelms-Universität Bonn, Nussallee 8, D-53115 Bonn, Germany.

Received 29 November 2012, accepted 13 May 2013, available online 15 May 2013.

Copyright © 2014 Q. Zhao et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Gregarious behaviour is beneficial to animals because it provides protection in numbers and gives each individual a better opportunity for survival (Alexander 1974). Advantages of living in a flock or herd include a decreased risk of predation and increased foraging efficiency, and these may outweigh disadvantages such as increased competition for resources and increased transmission of diseases and parasites (Alexander 1974). Gregarious behaviour has been identified in many modern animal groups, such as birds, crocodiles, fishes, and arthropods.

Some animals show specialized kinds of gregarious behaviour in which species form groups according to gender, especially where there is marked sexual dimorphism, or by age (Ruckstuhl and Neuhaus 2000, 2001). Juvenile-only clusters may reflect particular aspects of reproductive cycles, population size, resource distribution, or environmental conditions that favour segregation of adults from their young

(Main and Coblenz 1996). Care of the young can be costly for many modern species, especially of birds and mammals, and so those species that do not care for their young after hatching gain by conserving energy that would otherwise have been required to defend and provision their offspring (Isles 2009). Juveniles that are abandoned after hatching or birth, as is commonly the case in groups other than birds and mammals, then gain the advantages already noted by aggregating in clusters. At small size, the main threat to life is predation, and clusters of juveniles, while running the risk of attracting attention by their very existence, can aid individuals in escaping predation by scattering randomly when threatened. In some cases, the juvenile cluster might assist the individuals to master a food supply that would otherwise be out of reach.

Juvenile-only aggregation is uncommon in extant archosaurs such as crocodylians and birds (Isles 2009). In modern birds like ostriches and ravens, while adults are preoccupied with breeding, nesting, and the care of eggs and hatchlings,

nonbreeding juveniles and adults may congregate elsewhere in social groups of mixed age (Varricchio et al. 2008). Further, in species of birds and mammals where there are complex breeding rituals, and especially where single dominant males may build harems, the unmated juveniles or subadult males live safely in non-breeding herds, separate from the mated adults.

Numerous examples of gregarious behaviour of juvenile dinosaurs also have been noted (Forster 1990a; Varricchio and Horner 1993; Kobayashi and Lu 2003; Varricchio et al. 2008). For example, Horner and Makela (1979) first described 11 young hadrosaurs jumbled together in a nest-like structure from the Two Medicine Formation (Upper Cretaceous) near Choteau, Teton County, Montana. However, the identification of this hadrosaur “nest” has been questioned and considered to be a secondary sedimentary mound (Isles 2009)

Juvenile dinosaurs were unusual among terrestrial vertebrates for aggregating into what appear to have been exclusive herds or groups for an extended period of time, and with no sign of adult supervision. Juvenile clusters have been reported for all major dinosaur groups, except Pachycephalosauria, namely Sauropodomorpha (Myers and Fiorillo 2009), Theropoda (*Megapnosaurus rhodesiensis* [Raath 1990]; *Albertosaurus sarcophagus* [Currie 1998], and *Sinornithomimus dongi* [Kobayashi and Lu 2003; Varricchio et al. 2008]), Ornithopoda (*Iguanodon* [Norman 1987] and *Tenontosaurus* [Forster 1990b]), Thyreophora (stegosaur *Stegosaurus* [Galton 1982]; ankylosaurs *Gastonia bergei* [McWhinney et al. 2004] and *Pinacosaurus* [Currie 1989]), Ceratopsia (*Protoceratops* [Weishampel et al. 2000] and *Triceratops* [Mathews et al. 2009]). The skeletons in these bone-beds (except *Tenontosaurus* and *Protoceratops*) seem to have been transported to their final position by floodwaters, and so it cannot be demonstrated that the associations of numerous juvenile skeletons could not have been produced in some cases at least by sedimentary sorting and winnowing of similar-sized carcasses.

One exceptional juvenile dinosaurian assemblage is that of the ornithomimosaur theropod *Sinornithomimus dongi* (Kobayashi and Lu 2003; Varricchio et al. 2008), preserved on the floor of a small dried-up lake. The uniform preservation, close proximity on a single bedding plane, and sub-parallel alignment of skeletons supports a catastrophic mass mortality of a group rather than the attritional death of individuals (Varricchio et al. 2008). It cannot be entirely excluded that the individuals came together at the drying lake from different sources, in search of water as the landscape dried up, and so perhaps did not live together. This bonebed site emphasizes the important role of drought in the fossil record both as an agent of mortality and as a mechanism driving vertebrates into depositional settings where preservation can occur (Shipman 1975; Rogers 1990).

In this paper, we present what may be the first convincing example of a mixed-age juvenile group from the fossil record, an assemblage of six juvenile skeletons of the ceratopsian dinosaur *Psittacosaurus lujiatunensis* from the Early Cretaceous of NE China. We explore possible reasons for

such a mixed-age cluster without adults, whether it indicates a group seeking to find food or avoid predation, or, perhaps a hint of helpers at the (dinosaur) nest. First, we consider previously reported examples of juvenile-only clusters of dinosaurs, and find that the evidence of biological, rather than geological, association is often weak.

Institutional abbreviations.—DNHM, Dalian Natural History Museum, Dalian, Liaoning, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

Other abbreviations.—LAG, line of arrested growth.

Methods

Bone histological thin sections were made using standard techniques. Based on earlier studies on dinosaur long-bone histology and general principles of bone growth, the middle of the shaft is recognized as the best place to obtain the most complete growth record (Erickson and Tumanova 2000; Horner et al. 2000; Sander 2000). This is owing to the predominantly appositional growth of the shaft and the location of the neutral zone in this region (Sander 2000). Before making the diaphyseal transverse thin-sections for each long bone, we used resin to embed the specimen. Then we used diamond circular saws fitted with a diamond-tipped wafering blade for cutting resin-embedded specimens to obtain bone sections. After that, we used a wheel grinder/polisher to polish bone sections. Then we used grinding powder (600 grit) to grind the bone sections manually to get the ideal smooth surface for gluing to a glass slide. After gluing, we used diamond circular saws to cut the bone section again to obtain a thin section, and then we used grinding powder to get the desired thickness (50–80 µm) and ideal surface. The slides were then placed in a water-filled ultrasonic cleaner to remove microscopic grit. Finally, we glued the cover slip to the bone surface slide.

Previous report of parental care in *Psittacosaurus*

Some of the most widely discussed examples of clusters of juveniles are those of the Early Cretaceous basal ceratopsian *Psittacosaurus*. A remarkable cluster of 34 juveniles was reported from the Lujiatun site in Liaoning Province, China, apparently associated with the skull of an adult (Meng et al. 2004), but we question whether this is a true association. The only additional information comes from Meng et al. (2004), in which they state that the specimen comes from a small outcrop of variegated mudstone, with root traces and gradational contacts, from the lowest portion of the formation near Shangyuan in western Liaoning. Our close inspection of this cluster of 34 juveniles (DNHM D2156) shows that the “adult” skull has been added with glue, and so maybe not part of the original specimen; there is no sedimentary connection

to the main slab below, and the skull rests loosely on top of that slab, and is not in any way part of the sedimentary layer in which the juveniles all occur, intertwined with each other. The evidence is that the “adult” skeleton just contains a few postcranial bones without any articulation, and the skull position is much higher than the juvenile bone-bed plane. The juveniles all seem to belong together because they are preserved at one level in the rock, and their limbs and tails overlap each other in complex ways.

Even if the larger skull was truly associated with the cluster of juveniles in this specimen, it is unlikely that this was the “mother” of those juveniles, for two reasons. First, it is unlikely that a female could produce a clutch of such size, based on wider comparison of female sizes and clutch sizes across archosaurs (Isles 2009). The 34 juveniles have femora 30–34 mm long, and so these individuals might have been 1 year old, based on comparisons with our histologically aged specimens in IVPP V14341 (femora 53–65 mm long in 2-year-olds; see below). Second, the dimensions of the “adult” skull (about 125 mm) suggest it came from a 6-year old animal, still too young to breed (the breeding age for *Psittacosaurus* is about 10 years old). This is based on studies of series of juvenile to adult skeletons and bone histological analysis of *Psittacosaurus mongoliensis* (Erickson and Tumanova 2000) and *P. lujiatunensis* (Erickson et al. 2009), which show that sexual maturity began no later than the tenth year of life. The isometric growth line (Fig. 1) of *Psittacosaurus lujiatunensis* shows the relationship between skull length and age (more detailed statistical analysis in Supplementary Online Material, SOM available at http://app.pan.pl/SOM/app59-Zhao_et_al_SOM.pdf).

The Dalian specimen then does not show a mother and her young, as first suggested, but a subadult skull probably artificially associated with a genuine cluster of 34 yearlings.

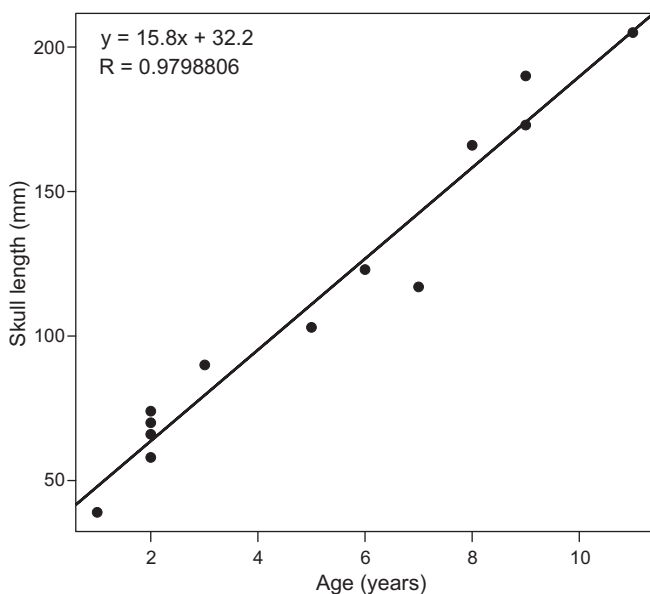


Fig. 1. Isometric growth in *Psittacosaurus lujiatunensis*. Skull length (y-axis) increases linearly with estimated age, in years (x-axis). The plot is based on measurements of 13 specimens (see SOM).

Such a large juvenile-only cluster is in itself important evidence about dinosaurian behaviour, and is in line with other evidence of juvenile-only clusters.

Mixed-age juvenile group of *Psittacosaurus*

In our new specimen, IVPP V14341, a cluster of six juvenile skeletons, we show that these vary in age—one is three years old, the others two, based on their bone histology. We have to demonstrate first that this is a natural cluster, and not the result of sedimentary accumulation, and then that we have a reliable method of age determination. These topics are discussed in turn. It should be noted that we do not claim that *Psittacosaurus* juveniles always occur in juvenile-only clusters. Other specimens from Lujiatun consist of individuals of mixed ages, and others were single specimens representing various developmental stages, but juvenile-only clusters are common.

Biological association, not sedimentary accumulation.—As noted by Zhao et al. (2007), the six skeletons come from the Lujiatun locality in Liaoning. The geology of the site shows that the fossils are preserved within pyroclastic flow deposits (Jiang and Sha 2007; Zhao et al. 2007; Eberth et al. 2010; Jiang et al. 2011, 2012). By examining the matrix through petrology, petrography and X-ray diffraction, the sediment in which the skeletons occur was identified as representing a lahar (volcanic mudflow), indicating that the six individuals present were entombed simultaneously during a catastrophic mass mortality event. This interpretation clearly excludes an origin from suspension or turbulent flows (hydraulic or aeolian) and suggests, instead, that the matrix containing the *Psittacosaurus* skeletons 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).

A lahar interpretation is fully compatible with the high-quality in situ preservation of the psittacosaur specimens. And this is a most unusual mode of preservation for dinosaur fossils. In most cases (Dodson et al. 1980; Norman 1980, 1987; Roach and Brinkman 2007), dinosaur bones are preserved in ancient river sediments, sometimes in channel lags or channel bars, in which case numerous carcasses may have accumulated over a long time span, extending to months or even years. The carcasses might all be equally well articulated, and in apparently identical physical condition of preservation, but nonetheless they might have accumulated through a series of annual flood events, and so represent a time-averaged assemblage. In such a case, it could not be assumed that the association says anything about the original life habitat or the original putative gregarious behaviour of the dinosaurs.

Age determination from bone histology.—There is extensive evidence that dinosaurs grew episodically. Although they had high metabolic rates, and so laid down primarily

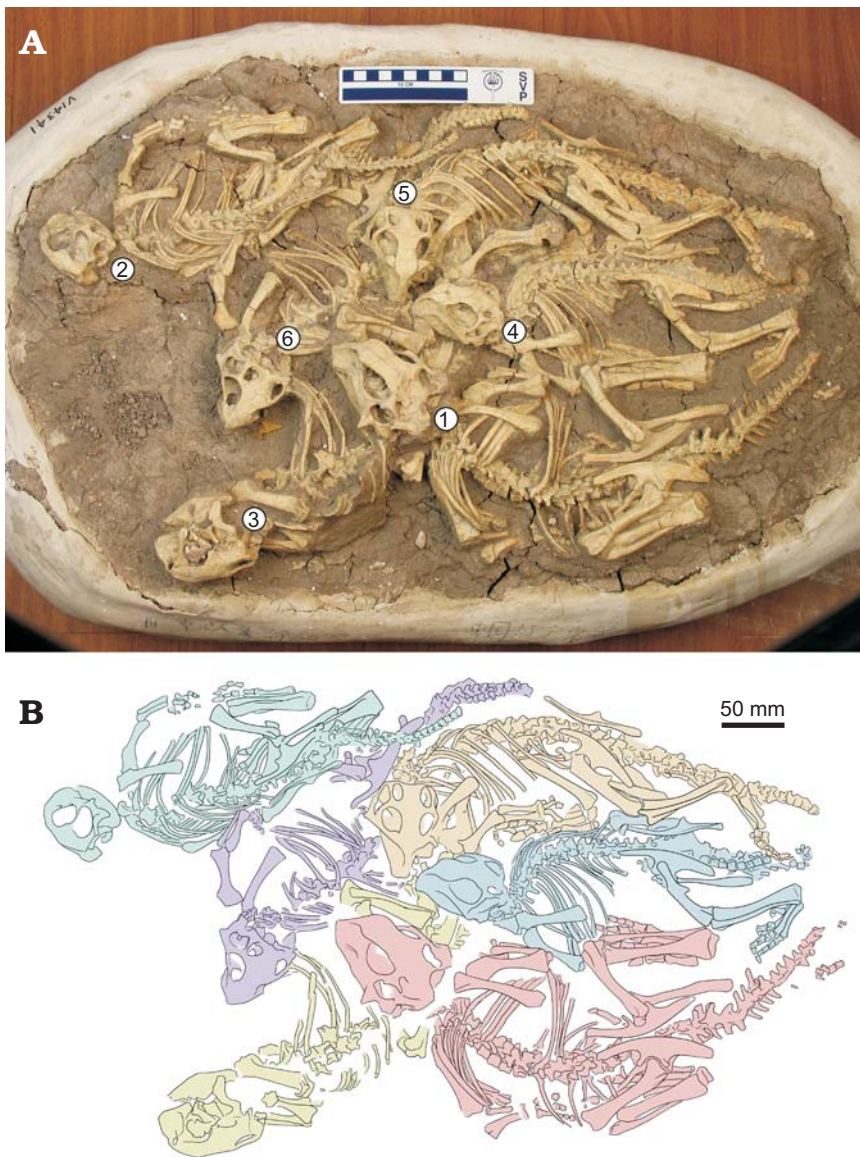


Fig. 2. Cluster of six juvenile ceratopsian dinosaurs *Psittacosaurus* (IVPP V14341) from the Early Cretaceous of Lujiatun, Liaoning Province, China. The specimen, illustrated as a photograph (A) and interpretive drawing (B), shows six aligned juvenile specimens, of which specimens 2–6 are estimated to have been two years old at death, and specimen 1 was three years old, based on bone histological analysis.

fibro-lamellar bone, indicating high growth rate (Amprino 1947), they all seem to show one episode each year when growth rates slowed and a dense layer was deposited in the bone, termed a line of arrested growth (LAG) (Chinsamy-Turan 2005). Such LAGs could represent numerous episodes of slow growth, mainly resulting from food shortage or low precipitation events rather than sudden cooling (Kohler et al. 2012) each year, but there are no reports of only one LAG formed every two years, which supports the deduction that LAGs in fossil vertebrates are more than likely annual (Chinsamy-Turan 2005). Seasonality appears to be the main factor for the cyclical growth pattern in bones of reptiles (Peabody 1961). However, the occurrence of LAGs in bones of extant reptiles and amphibians living in non-seasonal environments (Chinsamy et al. 2005) indicates that the cyclical variations in osteogenesis and growth are the result of an inherent (genetic) rhythm that becomes synchronized with and reinforced by seasonal cycles (Castanet et al. 1993).

If LAGs represent annual markers in the bone (Kohler et al. 2012), then individual dinosaur skeletons can be aged, and growth curves can be compiled. Such growth curves for a wide range of dinosaurs (Erickson et al. 2001), such as *Psittacosaurus mongoliensis*, show classic sigmoid growth curves, with an early phase of slow growth in years 1–2, a burst of rapid growth in years 5–10, and a slowing of growth in years 10–15 (Erickson and Tumanova 2000). As growth slows, comparison with growth curves for living vertebrates suggest that this marks the attainment of sexual maturity and adult size. Studies of series of juvenile to adult skeletons and bone histological analysis of *Psittacosaurus lujiatunensis* (Erickson et al. 2009) show that sexual maturity began no later than the tenth year of life.

Evidence from bone histology for a mixed-age juvenile group in IVPP V14341.—The largest individual in this cluster is IVPP V14341.1 (Fig. 2). Thin sections show three LAGs in the humerus, femur and fibula, but just two LAGs

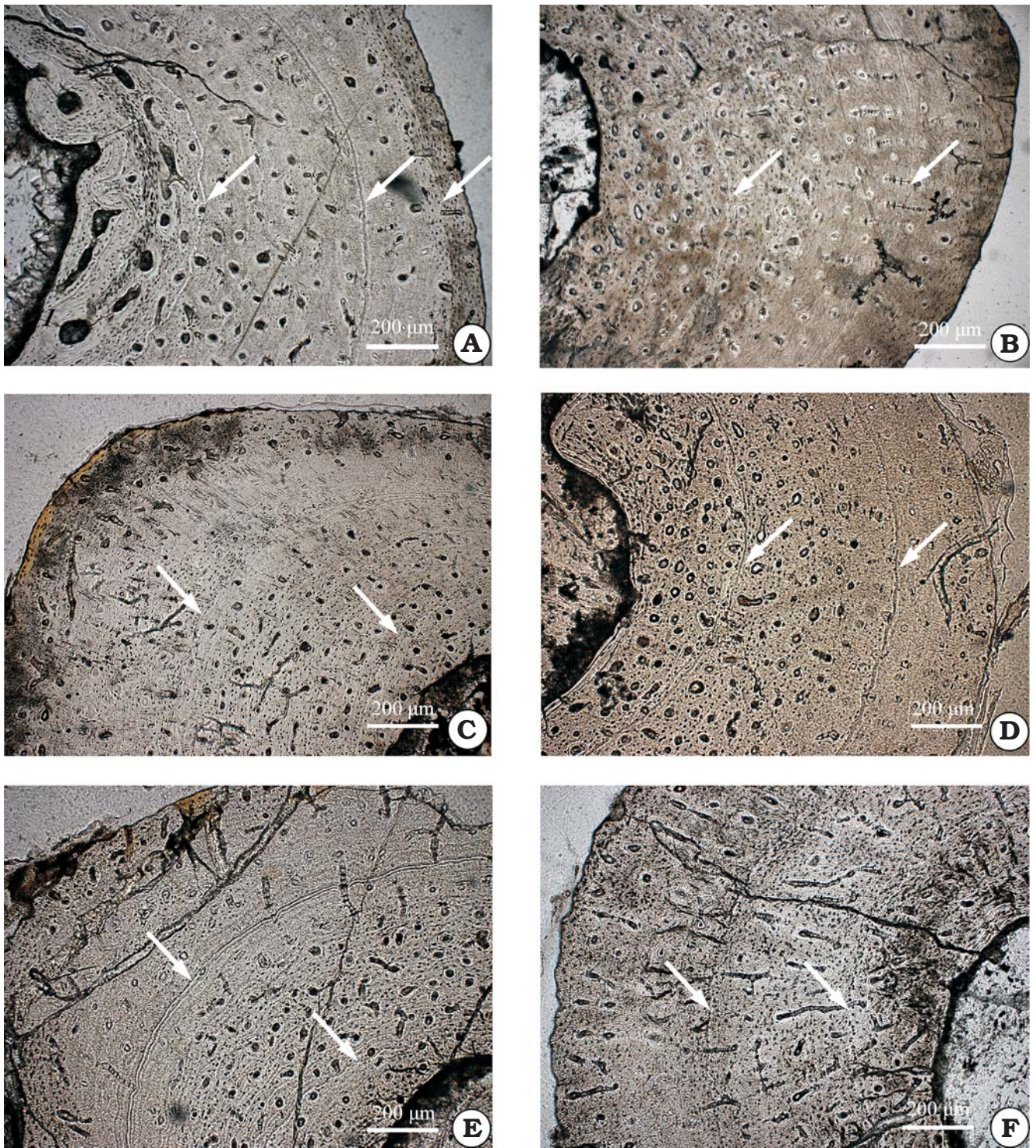


Fig. 3. Bone histological evidence for growth and age in ceratopsian dinosaur *Psittacosaurus lujiatunensis* Zhou, Gao, Fox, and Chen, 2006 from the Early Cretaceous of Lujiatun, Liaoning Province, China. Mid-diaphyseal transverse sections of fibulae: IVPP V14341.1 (A), IVPP V14341.2 (B), IVPP V14341.3 (C), IVPP V14341.4 (D), and IVPP V14341.5 (E); radius: IVPP V14341.6 (F). White arrows indicate lines of arrested growth (LAGs).

in the tibia. Medullary cavity expansion may have obliterated the first-year LAG in this tibia. We studied four tibial thin sections from different individuals of the same cluster. There are just two LAGs in each thin section. Using a camera lucida, we drew each section including the LAGs under the microscope and then superimposed the drawings. We found

the medullary cavity of the tibia of IVPP V14341.1 to be much larger than in the others, and its size overlaps with the first-year LAG in the other tibiae (IVPP V14341.2–5).

To test this, we sampled five fibulae and one radius thin sections from different individuals of IVPP V14341. The mid-diaphyseal transverse sections of the fibulae showed

three LAGs in IVPP V14341.1 (Fig. 3A), and two LAGs in the other four individuals (Fig. 3C–E). The thin sections of the radius from IVPP V14341.6 also just showed two LAGs. This is consistent with the LAG count for the tibiae of the smaller specimens and the resorption of one LAG in the tibia of the larger specimen.

All the thin sections from this cluster thus indicate that the offspring came from two different clutches, separated by about one year.

Descriptions of the thin sections.—The cortex of the fibular diaphysis of IVPP V14341 is fibro-lamellar bone with predominantly longitudinal vascular canals and very few simple reticular vascular canals. The degree of vascularization is high, and only primary osteons can be observed in the thin sections. The degree of vascularization at age 2 is relatively higher than it is at age 3. No external fundamental system of closely packed peripheral growth lines was found in these thin sections.

The presence of fibro-lamellar bone tissue shows a very fast grow rate. This kind of bone tissue is usually found in juvenile or sub-adult individuals (Chinsamy 1995). The absence of secondary osteons suggests that the observed tissue had not been remodeled (Xu et al. 2012). All this evidence suggests that these individuals are juveniles.

Discussion

Juvenile-only clusters in *Psittacosaurus*, ranging from six to 34 individuals, and with evidence for a variety of ages in at least one specimen (IVPP V14341) suggests some unique juvenile-only behaviour. Perhaps *Psittacosaurus* juveniles congregated for protection, for a specialized diet, or for helping at the nest. Today, juvenile-only flocks or herds of birds and mammals may exist for protection (Pelletier and Festa-Bianchet 2004) and this may have been the same for dinosaurs after they had hatched and become self-sufficient (Myers and Fiorillo 2009). Erickson et al. (2009) suggested that *Psittacosaurus lujiatunensis* appears to have reached threshold sizes somewhere between 3 and 4 years old, as these animals were entering the transition to the exponential stage of growth when they would have explosively increased in body mass. It is expected that under 4 years old, young *Psittacosaurus* still needed to gather together to protect each other. Indeed, direct fossil evidence (Hu et al. 2005) shows that the triconodont mammal *Repenomamus* ate juvenile *Psittacosaurus* on occasion, and small herds of juveniles might have existed for their own protection from predators.

In addition, there is some circumstantial evidence for a change in diet during ontogeny of *Psittacosaurus*: the presence of numerous large gastroliths in adult *Psittacosaurus* suggests a high-fibre, nut-eating diet (Serenio 2010). Gastroliths have not been found in any juvenile psittacosaurus, and so they may have eaten a less fibrous diet. Different diets between juveniles and adults would indicate different loca-

tions and modes of foraging for food, and the likelihood that juveniles and adults might be found in age-specific clusters in different locations. Such a dietary switch has been hypothesized in many dinosaur groups (Codron et al. 2012), and in each case might have been associated with a major change of behaviour during ontogeny.

The third suggestion, that *Psittacosaurus* juveniles may have acted as “helpers at the nest”, is even more circumstantial. Among modern birds, juveniles in many clades stay around their parents and their nests and may help the parents bring up subsequent broods; this is interpreted as a way in which the non-breeding juveniles may increase their genetic fitness until they are of breeding age themselves (Skutch 1961; Hamilton 1963; Hatchwell 2009). It is also a reason that juveniles from different year classes, assuming an annual breeding regime, might be found associating together, and would imply that all juveniles, of whatever age, might have been siblings.

Acknowledgements

We thank Shoji Hayashi for helping and training in thin section preparation, and Qinqin Shi for helping in preparing illustrations. We thank Peter Dodson (University of Pennsylvania, Pittsburgh, USA) and Greg Erickson (Florida State University, Tallahassee, USA) for their very helpful reviews. This study was supported by a Ph.D. grant to QZ from BIS (Department for Business Innovation & Skills) and CSC (China Scholarship Council), as well as travel grants from the Bob Savage Memorial Fund and LESV (Key Laboratory of Evolutionary Systematics of Vertebrates, Chinese Academy of Sciences), and Chinese National Infrastructure for Science and Technology-National Infrastructure of Mineral, Rock and Fossil Specimen Resources. This study was also supported by grants from the National Natural Science Foundation of China (to XX) and the German Research Foundation (to PMS).

References

- Alexander, R.D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5: 325–383.
- Amprino, R. 1947. La structure du tissu osseux envisagée comme expression de différences dans la vitesse de l'accroissement. *Archives de Biologie* 58: 315–330.
- Castanet, J., Francillon-Vieillot, H., Meunier, F.J., and Ricqlès, A. de 1993. Bone and individual aging. In: B.K. Hall (ed.), *Bone. Volume 7: Bone Growth B*, 245–283. CRC Press, Boca Raton.
- Chinsamy, A. 1995. Ontogenetic changes in the bone histology of the Late Jurassic ornithomimid *Dryosaurus lettowvorbecki*. *Journal of Vertebrate Paleontology* 15: 96–104.
- Chinsamy, A., Hanrahan, S.A., Neto, R.M., and Seely, M. 1995. Skeletochronological assessment of age in *Angolosaurus skoogi*, a cordylid lizard living in an aseasonal environment. *Journal of Herpetology* 29: 457–460.
- Chinsamy-Turan, A. 2005. *The Microstructure of Dinosaur Bone: Deciphering Biology with Fine-Scale Techniques*. 195 pp. The Johns Hopkins University Press, Baltimore.
- Codron, D., Carbone, C., Müller, D.W.H., and Clauss, M. 2012. Ontogenetic niche shifts in dinosaurs influenced size, diversity and extinction in terrestrial vertebrates. *Biology Letters* 8: 620–623.

- Currie, P.J. 1989. Long-distance dinosaurs. *Natural History* 6: 60–65.
- Currie, P.J. 1998. Possible evidence of gregarious behavior in tyrannosaurids. *Gaia* 15: 271–277.
- Dodson, P., Behrensmeyer, A.K., Bakker, R.T., and Mcintosh, J.S. 1980. Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. *Paleobiology* 6: 208–232.
- Eberth, D.A., Xing, X., and Clark, J.M. 2010. Dinosaur death pits from the Jurassic of China. *Palaios* 25: 112–125.
- Erickson, G.M. and Tumanova, T.A. 2000. Growth curve of *Psittacosaurus mongoliensis* Osborn (Ceratopsia: Psittacosauridae) inferred from long bone histology. *Zoological Journal of the Linnean Society* 130: 551–566.
- Erickson, G.M., Makovicky, P.J., Inouye, B.D., Zhou, C.F., and Gao, K.Q. 2009. A life table for *Psittacosaurus lujiatunensis*: initial insights into ornithischian dinosaur population biology. *The Anatomical Record* 292: 1684–1684.
- Erickson, G.M., Rogers, K.C., and Yerby, S.A. 2001. Dinosaurian growth patterns and rapid avian growth rates. *Nature* 412: 429–433.
- Fisher, R.V. and Schmincke, H.-U. 1984. *Pyroclastic rocks*. 472 pp. Springer, Berlin.
- Forster, C.A. 1990a. Evidence for juvenile groups in the ornithomimid dinosaur *Tenontosaurus tilletti* Ostrom. *Journal of Paleontology* 64: 164–165.
- Forster, C.A. 1990b. The postcranial skeleton of the ornithomimid dinosaur *Tenontosaurus tilletti*. *Journal of Vertebrate Paleontology* 10: 273–294.
- Galton, P.M. 1982. Juveniles of the stegosaurian dinosaur *Stegosaurus* from the Upper Jurassic of North America. *Journal of Vertebrate Paleontology* 2: 47–62.
- Hamilton, W.D. 1963. The evolution of altruistic behavior. *American Naturalist* 97: 354–356.
- Hatchwell, B.J. 2009. The evolution of cooperative breeding in birds: kinship, dispersal and life history. *Philosophical Transactions of the Royal Society B* 364: 3217–3227.
- Horner, J.R. and Makela, R. 1979. Nest of juveniles provides evidence of family-structure among dinosaurs. *Nature* 282: 296–298.
- Horner, J.R., de Ricqlès, A., and Padian, K. 2000. Long bone histology of the hadrosaurid dinosaur *Maiasaura peeblesorum*: Growth dynamics and physiology based on an ontogenetic series of skeletal elements. *Journal of Vertebrate Paleontology* 20: 115–129.
- Hu, Y.M., Meng, J., Wang, Y.Q., and Li, C.K. 2005. Large Mesozoic mammals fed on young dinosaurs. *Nature* 433: 149–152.
- Isles, T.E. 2009. The socio-sexual behaviour of extant archosaurs: implications for understanding dinosaur behaviour. *Historical Biology* 21: 139–214.
- Jiang, B.Y. and Sha, J.G. 2007. Preliminary analysis of the depositional environments of the Lower Cretaceous Yixian Formation in the Sihetun area, western Liaoning, China. *Cretaceous Research* 28: 183–193.
- Jiang, B.Y., Fursich, F.T., and Hethke, M. 2012. Depositional evolution of the Early Cretaceous Sihetun Lake and implications for regional climatic and volcanic history in western Liaoning, NE China. *Sedimentary Geology* 257: 31–44.
- Jiang, B.Y., Fursich, F.T., Sha, J.G., Wang, B., and Niu, Y.Z. 2011. Early Cretaceous volcanism and its impact on fossil preservation in Western Liaoning, NE China. *Palaeogeography Palaeoclimatology Palaeoecology* 302: 255–269.
- Kobayashi, Y. and Lu, J.C. 2003. A new ornithomimid dinosaur with gregarious habits from the Late Cretaceous of China. *Acta Palaeontologica Polonica* 48: 235–259.
- Kohler, M., Marin-Moratalla, N., Jordana, X., and Aanes, R. 2012. Seasonal bone growth and physiology in endotherms shed light on dinosaur physiology. *Nature* 487: 358–361.
- Main, M.B. and Coblenz, B.E. 1996. Sexual segregation in Rocky Mountain mule deer. *Journal of Wildlife Management* 60: 497–507.
- Mathews, J.C., Brusatte, S.L., Williams, S.A., and Henderson, M.D. 2009. The first *Triceratops* bonebed and its implications for gregarious behavior. *Journal of Vertebrate Paleontology* 29: 286–290.
- McWhinney, L., Matthias, A., and Carpenter, K. 2004. Corticated pressure erosions, or “pitting,” in osteodermal ankylosaur armor. *Journal of Vertebrate Paleontology* 24: 92A.
- Meng, Q., Liu, J., Varricchio, D.J., Huang, T., and Gao, C. 2004. Palaeontology: parental care in an ornithischian dinosaur. *Nature* 431: 145–146.
- Myers, T.S. and Fiorillo, A.R. 2009. Evidence for gregarious behavior and age segregation in sauropod dinosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology* 274: 96–104.
- Norman, D.B. 1980. On the ornithischian dinosaur *Iguanodon bernissartensis* from the Lower Cretaceous of Bernissart (Belgium). *Institut Royal des Sciences Naturelles de Belgique, Mémoires* 178: 1–103.
- Norman, D.B. 1987. A mass-accumulation of vertebrates from the Lower Cretaceous of Nehden (Sauerland), West-Germany. *Proceedings of the Royal Society of London Series B* 230: 215–255.
- Peabody, F.E. 1961. Annual growth zones in living and fossil vertebrates. *Journal of Morphology* 108: 11–62.
- Pelletier, F. and Festa-Bianchet, M. 2004. Effects of body mass, age, dominance and parasite load on foraging time of bighorn rams, *Ovis canadensis*. *Behavioral Ecology and Sociobiology* 56: 546–551.
- Raath, M.A. 1990. Morphological variation in small theropods and its meaning in systematics: evidence from *Syntarsus rhodensis*. In: K. Carpenter and P.J. Currie (eds.), *Dinosaur Systematics: Approaches and Perspectives*, 92–105. Cambridge University Press, Cambridge.
- Roach, B.T. and Brinkman, D.L. 2007. A reevaluation of cooperative pack hunting and gregariousness in *Deinonychus antirrhopus* and other nonavian theropod dinosaurs. *Bulletin of the Peabody Museum of Natural History* 48: 103–138.
- Rogers, R.R. 1990. Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of Northwestern Montana: Evidence for drought-related mortality. *Palaios* 5: 394–413.
- Ruckstuhl, K.E. and Neuhaus, P. 2000. Causes of sexual segregation in ungulates: a new approach. *Behavior* 137: 361–377.
- Ruckstuhl, K.E. and Neuhaus, P. 2001. Behavioral synchrony in ibex groups: Effects of age, sex and habitat. *Behaviour* 138: 1033–1046.
- Sander, P.M. 2000. Longbone histology of the Tendaguru sauropods: implications for growth and biology. *Paleobiology* 26: 466–488.
- Sereno, P.C. 2010. Taxonomy, cranial morphology, and relationships of parrot-beaked dinosaurs (Ceratopsia: *Psittacosaurus*). In: M.J. Ryan, B.J. Chinnery, and D.A. Eberth (eds.), *New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*, 21–58. Indiana University Press, Bloomington.
- Shipman, P. 1975. Implications of drought for vertebrate fossil assemblages. *Nature* 257: 667–668.
- Skutch, A.F. 1961. Helpers among birds. *Condor* 63: 198–226.
- Varricchio, D.J. and Horner, J.R. 1993. Hadrosaurid and lambeosaurid bone beds from the Upper Cretaceous Two Medicine Formation of Montana: taphonomic and biologic implications. *Canadian Journal of Earth Sciences* 30: 997–1006.
- Varricchio, D.J., Sereno, P.C., Zhao, X.J., Lin, T., Wilson, J.A., and Lyon, G.H. 2008. Mud-trapped herd captures evidence of distinctive dinosaur sociality. *Acta Palaeontologica Polonica* 53: 567–578.
- Weishampel, D.B., Fastovsky, D.E., Watabe, M., Barsbold, R., and Tsogtbaatar, K. 2000. New embryonic and hatchling dinosaur remains from the Late Cretaceous of Mongolia. *Journal of Vertebrate Paleontology* 20: 78A.
- Xu, X., Zhao, Q., Sullivan, C., Tan, Q.W., Sander, P.M., and Ma, Q.Y. 2012. The taxonomy of the troodontid IVPP V10597 reconsidered. *Vertebrata Palasiatica* 50: 140–150.
- Zhao, Q., Barrett, P.M., and Eberth, D.A. 2007. Social behaviour and mass mortality in the basal ceratopsian dinosaur *Psittacosaurus* (Early Cretaceous, People’s Republic of China). *Palaeontology* 50: 1023–1029.
- Zhou, C.F., Gao, K.Q., Fox, R.C., and Chen, S.H. 2006. A new species of *Psittacosaurus* (Dinosauria: Ceratopsia) from the Early Cretaceous Yixian Formation, Liaoning, China. *Palaeoworld* 15: 100–114.