RESEARCH ARTICLE

GEOSCIENCES

Dinosaur-associated Poaceae epidermis and phytoliths from the Early Cretaceous of China

Yan Wu[1,2,3], Hai-Lu You[1,2,3,*] and Xiao-Qiang Li[1,2,3]

ABSTRACT

Grasses (Poaceae) are human's most important crop plants and among the most important extant clades of vascular plants. However, the origin and early evolution of grasses are controversial, with estimated ages from molecular dating ranging between 59 and 129 Ma (million years ago). Here we report the discovery of basalmost grasses from the late Early Cretaceous (Albian, 113-101 Ma) of China based on microfossils (silicified epidermal pieces and phytoliths) extracted from a special structure along the dentition of a basal hadrosauroid (duck-billed dinosaur). Thus, this discovery represents the earliest known grass fossils, and is congruent with previous estimations on grass origin and early evolution calibrated by oldest known fossil grasses, highlighting the role of fossils in molecular dating. This discovery also indicates deep-diverging grasses probably gained broad distribution across both Laurasian and Gondwanan continents during the Barremian (129-125 Ma).

Keywords: Poaceae, dinosaur, phytolith, epidermis, Early Cretaceous

[1]Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China; [2]CAS Center for Excellence in Life and Paleoenvironment, Beijing 100044, China and [3]College of Earth Sciences, University of Chinese Academy of Sciences, Beijing 100049, China

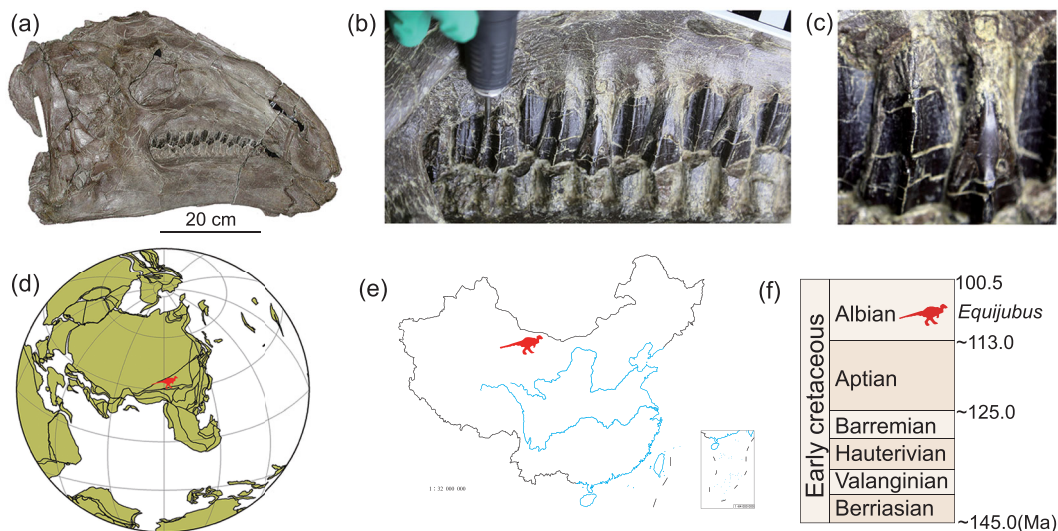*Corresponding author. E-mail: youhailu@ivpp.ac.cn

INTRODUCTION

Grasses (Poaceae or Gramineae) include human's most important crop plants (e.g. rice, corn, cereals). They are among the most important extant clades of vascular plants, inhabit all major landmasses, occupy warm and cold deserts to rainforests and range from herbs to the tree-like bamboos [1]. Recent molecular and morphological studies place the ∼12 000 extant species into 12 subfamilies and, among them, the APP group (including Anomochlooideae, Pharoideae and Puelioideae) forms the earliest diverging lineages leading to the split between the BOP (including Bambusoideae, Oryzoideae and Pooideae) and the PACMAD (including Panicoideae, Aristidoideae, Arundinoideae, Micraioideae, Danthonioideae and Chloridoideae) clades [2]. However, the origin and early evolution of grasses are uncertain, with estimated ages ranging from 59 to 129 Ma [3,4]. The accuracy of molecular-dating methods depends on both an adequate underlying model and the appropriate implementation of fossil evidence as calibration points [5]. Currently known earliest grass fossils are rare, and limited to the Maastrichtian (72–66 Ma) macrofossils, pollens and phytoliths from India [6] and the

Cenomanian (101–94 Ma) spikelet and phytoliths contained in Myanmar ambers [7–9]. Implementing these Late Cretaceous grass fossils as calibration points, the divergence times are estimated to be 74–82 Ma for the core grasses (the BOP+PACMAD clade) [5], 99 Ma for the spikelet clade (grasses except for the basalmost lineage Anomochlooideae) [10] and 129 Ma for the root of grasses [4]. In order to test these results and further inquire into the origin and early evolution of grasses, we use silicified epidermal pieces and phytoliths as tools to trace the evolution of early grasses. Moreover, these microfossils are extracted from a basal hadrosauroid dinosaur (*Equijubus normani*) recovered in the late Early Cretaceous (Albian, 113–101 Ma) Zhonggou Formation of Gongpoquan Basin, Mazongshan area, Gansu Province in north-western China [11] (Fig. 1), therefore potentially revealing the earliest history of grasses and the dietary structure of duck-billed dinosaurs.

Silicified epidermal pieces and phytoliths have helped to close vast gaps in the fossil record of grasses, due to their strong resistance to decay especially in the well-oxidized sediment types that are often devoid of pollen and macrofossils [1,12]. They are also taxonomically diagnostic [13] and

Figure 1. Basal hadrosauroid *Equijubus normani*. (a) Cranium in right lateral view. (b) Right dentition with needle pointing to where samples were taken. (c) Close-up of two maxillary teeth showing the special structure covering the basal portion of the enamel surface. Note the special structure is light dark with yellowish sedimentary matrix on it and the matrix has been largely removed during previous preparation. (d, e) Locations of *Equijubus normani* in 110 Ma and present. (d) is downloaded from www.odsn.de. (f) Age of *Equijubus*.

provide powerful tools for taxonomy and phylogeny. This is especially helpful for grasses because their pollen morphology is uniform and their macrofossils are rare. Electronic Microprobe analysis was performed for samples from both this special structure and the sedimentary matrix around it (see 'Methods' section).

RESULTS
Silicified epidermal pieces and phytoliths analysis

Two pieces of silicified epidermis were extracted from the special structure. One piece preserves four rows of epidermal cells in surface view (Fig. 2a). The upper row preserves a single short cell intervening long cells, the second row preserves two low-domed stomata intervening long cells, the third row shows a short-cell pair intervening long cells and the bottom row preserves one stoma and a partial long cell. The other piece preserves a short-cell pair intervening two partial long cells in a row, and another two partial long cells bounding them respectively on both sides (Fig. 2b). The single short cell is not lobed, defining a pentangle boundary with a large circular spot inside. In the short-cell pairs, one is much smaller than the other, and the large cell shows a crescent shape, with its concave margin receiving the small elliptical one. Three isolated slightly bilobate phytoliths (Fig. 2c, g and h) were extracted. Two of them (Fig. 2c, g) possess slightly convex ends, while

the third one (Fig. 2h) has flat ends and more constrained lateral sides. Another 10 variously shaped isolated phytoliths were also extracted (see Supplementary Figs S2 and S3 (see online supplementary material)).

EMP (Electronic Microprobe) analysis

EMP analysis shows a similar composition of two samples (N2 and N3) from the special structure of two maxillary teeth, but with striking contrast to that from the sedimentary matrix (N1) (see 'Methods' section). N2 and N3 possess high values of P_2O_5 and CaO, as well as BaO, while N1 is composed of muscovite (N1-2), hornblende (N1-3) and others, indicating its tuff origin. In both N2 and N3, CaO and P_2O_5 values are more than 51% and 36%, respectively, while those in N1 are less than 7% and 0.7%, respectively (Table 1). This result highly indicates a biological-related process for the formation of the special structure.

DISCUSSION

Dinosaur teeth typically consist of three hard parts: dentine, enamel and cementum. Recent study shows that, in hadrosauroids, cementum never covers the enamel but meet each other at the apex of each tooth, with cementum mainly on the lingual surfaces of the maxillary tooth [14]; therefore, the special structure cannot be a portion of the cementum. Besides, in our specimen, this special
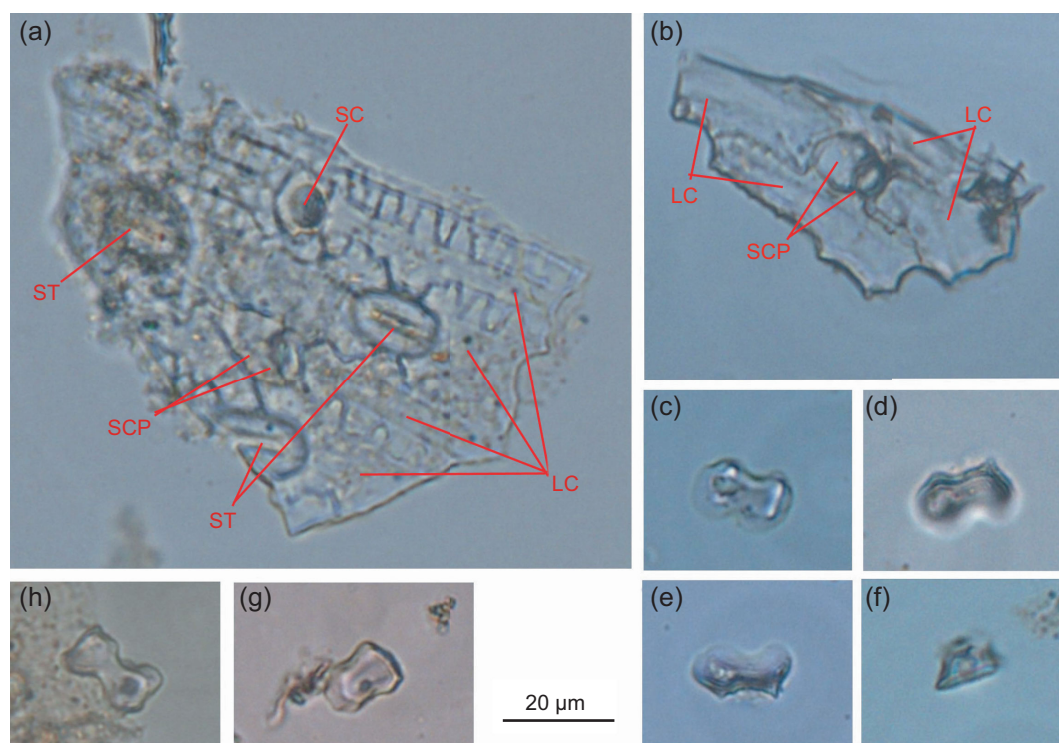
Figure 2. Silicified epidermal pieces and phytoliths extracted from the special structure of the Early Cretaceous (Albian) hadrosauroid dinosaur (*Equijubus normani*). (a, b) Silicified epidermal pieces. (c-h) Three slightly bilobate phytoliths with (c–f) representing one phytolith in four different views. LC, long cell; SC, short cell; SCP, short-cell pair; ST, stoma.

Table 1. Results of Electronic Microprobe analysis showing mineral compositions of the special structure and the sedimentary matrix around it.

	F	Na$_2$O	MgO	Al$_2$O$_3$	SiO$_2$	P$_2$O$_5$	SO$_3$	K$_2$O	CaO	TiO$_2$	MnO	FeO	CoO	SrO	BaO	Total
N1-1		0.40	6.78	16.01	39.78	0.33	0.29	3.54	3.71	1.11	0.32	7.19	0.09	0.55		80.10
N1-2		0.39	6.37	14.00	37.38	0.02		8.12	0.17	4.01	0.20	24.18	0.11	0.19		95.14
N1-3		1.01	9.14	16.84	42.91	0.70	0.21	2.13	7.02	0.56	0.47	8.58	0.20	0.49		90.26
N2-1	1.08	0.31		0.03	0.06	0.08	35.32		0.19	1.29		0.08		1.35	60.90	100.69
N2-2	4.48	2.67	0.55		0.37	36.61	2.08		52.82			0.03		1.95	0.21	101.77
N2-3	4.67	0.89	0.51	0.04	0.44	37.22	1.81		54.00	0.07		0.06	0.17	1.76		101.64
N3-1	1.35	0.16			0.09		35.97			1.20	0.13			0.40	61.82	101.12
N3-2	4.72	0.80	0.47	0.15	0.47	36.09	2.11		51.43	0.08		1.38	0.04	1.73	0.11	99.58
N3-3	0.21	0.26	0.66	0.45	1.08	0.14		0.05	53.25		1.77	0.53	0.00	0.05		58.45

N1 is from sedimentary matrix; N2 is from the special structure of covering a posterior maxillary tooth; N3 is from the special structure of covering a middle maxillary tooth (wt%).

structure is only known in one other basal hadrosauroid among dinosaurs (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences: IVPP V22529, an unnamed isolated partial right maxilla from the Early Cretaceous of Nei Mongol, China) [15]. Under laser-stimulated fluorescence analysis, this special structure in IVPP V22529 shows similar green fluorescence colors to maxillary bone and dentine, but different from the orange color of the enamel, and is labeled as a cementum 'jacket' that wraps the base of the tooth crown, although its identification as either cementum or ossified ligament cannot be supported [15]. The special structure may be similar to dental calculus (tartar, or calcified dental plaque)—a complex, mineralized bacterial biofilm formed on the surfaces of teeth. Its mineral composition is similar to that of bone and dentine, and is composed of multiple calcium phosphates. During the process of biomineral maturation, a few dietary microfossils, such as phytoliths and starch granules, could become incorporated into dental calculus [16]. However, no dental calculus has been reported in dinosaurs or even fossil reptiles to our knowledge,

and the exact nature of the special structure needs to be investigated further. Nevertheless, microfossils extracted from this special structure were probably obtained during the life of the animal.

The long–short dimorphic epidermal patterning is a unique feature shared by Poaceae and its close relative Joinvilleaceae [13,17]. The two silicified epidermal pieces clearly show the presence of short cell intervening between long cells, demonstrating its affinity with the Joinvilleaceae+Poaceae clade. Furthermore, short-cell pairs first appear in Anomochlooideae and are absent in grass relatives including Joinvilleaceae, and their formation is considered as a synapomorphy of Poaceae [13], strongly supporting the Poaceae affinity of these two pieces.

Unlobed, especially equidimensional-unlobed, costal phytoliths likely represent the ancestral condition in grasses [13]. Among the extant deep-diverging APP groups, Anomochlooideae is the basalmost family with two genera: *Anomochloa* and *Streptochaeta*. In *Anomochloa marantoides*, unlobed phytoliths exist in costal regions over the veins, while crescentic phytoliths are present in one of a pair of short cells in intercostal regions [13], resembling the condition in our two pieces. Furthermore, equidimensional phytoliths are characteristic for Anomochloa, which is also evidenced by the short cell in one piece of our specimens (Fig. 2a). However, in our specimens, the costal short cell is an isolated one with a pentangle outline and one cell is much smaller than the other in the short-cell pairs, unlike the condition in *Anomochloa marantoides* possessing rows of three or four short cells with orbicular outlines in the costal regions and similar-sized short-cell pairs [13]. Therefore, although potentially with the closest relationship with Anomochloa among extent APP members, our specimens cannot be assigned to it.

Costal unlobed or bilobate phytoliths are arranged either transversely (in *Streptochaeta* and Puelioideae except for *Guaduella*) or axially (in Pharoideae) [13]. Unfortunately, it is impossible to know the orientation of the three isolated slightly lobed phytoliths (Fig. 2c, g and h). Molecular analysis estimates the divergence times of extant Anomochlooideae at 69 Ma and Pharoideae at 40 Ma [10]; therefore, the three isolated phytoliths could not be assigned to any extant APP taxa, but probably derived from stem members of them or even more deep-diverging relatives of basalmost grasses.

The existence of long-short epidermal patterning, short-cell pairs, equidimensional-unlobed and slightly lobed phytoliths strongly indicates our specimens are derived from crown group grasses. Because the shapes of the isolated phytoliths are different from those in the two silicified epidermal pieces, there are probably more than one taxa represented. Here we emphasize the significance of the presence of basalmost Poaceae rather than define the exact taxonomy of these specimens and infer how derived they are (Fig. 3).

The age of the Mazongshan grasses is late Early Cretaceous (Albian), while that of the Indian grasses is late Late Cretaceous (Maastrichtian). Because Indo-Madagascar became separated from Antarctica, and therefore all other continents, at approximately 119 Ma (the beginning of late Aptian) [18], the ancestors of the Indian grasses must have existed there before late Aptian, and it is impossible for its origin as migration from Asia after their connection in Cenozoic. During early Aptian (125–119 Ma), land connection between Indo-Madagascar and South America was possible via Antarctica and Africa was still connected to South America until their final separation during latest Albian; therefore, it was possible for Gondwanan grasses to have a wide spread during this period. However, Africa-Europe (therefore Gondwana-Laurasia) biotic interchange was prevented from early Aptian to at least Campanian and Maastrichtian [19], indicating the common ancestor of Asian (Albian Mazongshan and Cenomanian Myanmar) and Gondwanan grasses must exist before early Aptian. During the early part of the Early Cretaceous (Berriasian–Barremian; 145–125 Ma), the Apulian Route created a series of microplates lying between northern Africa and southern Europe at a time of sea-level lowstand, making the land connection between Africa and Europe possible [19]; therefore, grasses could have gained broad distribution in Gondwana and Europe during this period. Considering the oldest estimated age for the origin of grasses is 129 Ma [4] and the age of the basalmost Mazongshan grasses is Albian, a Barremian (129–125 Ma) origin for grasses is reasonable. Interestingly, Asia was isolated from Europe and all other continents during late Berriasian–early Hauterivian (142–131 Ma) due to marine connection between the Boreal and Tethys Oceans in the Russian Basin/Turgai region and reconnected to Europe during late Hauterivian to Aptian (131–113) [19,20], suggesting grasses could have originated and gained broad distribution during Barremian. Despite their birthplace, deep-diverging grasses could have quickly gained worldwide distribution during Barremian, except for North America, which was isolated during Barremian–early Aptian but connected to Asia during the rest of the Early Cretaceous.

Equijubus is a basal member of Hadrosauroidea, the dominant herbivorous vertebrate clade in many Cretaceous ecosystems. The success of this
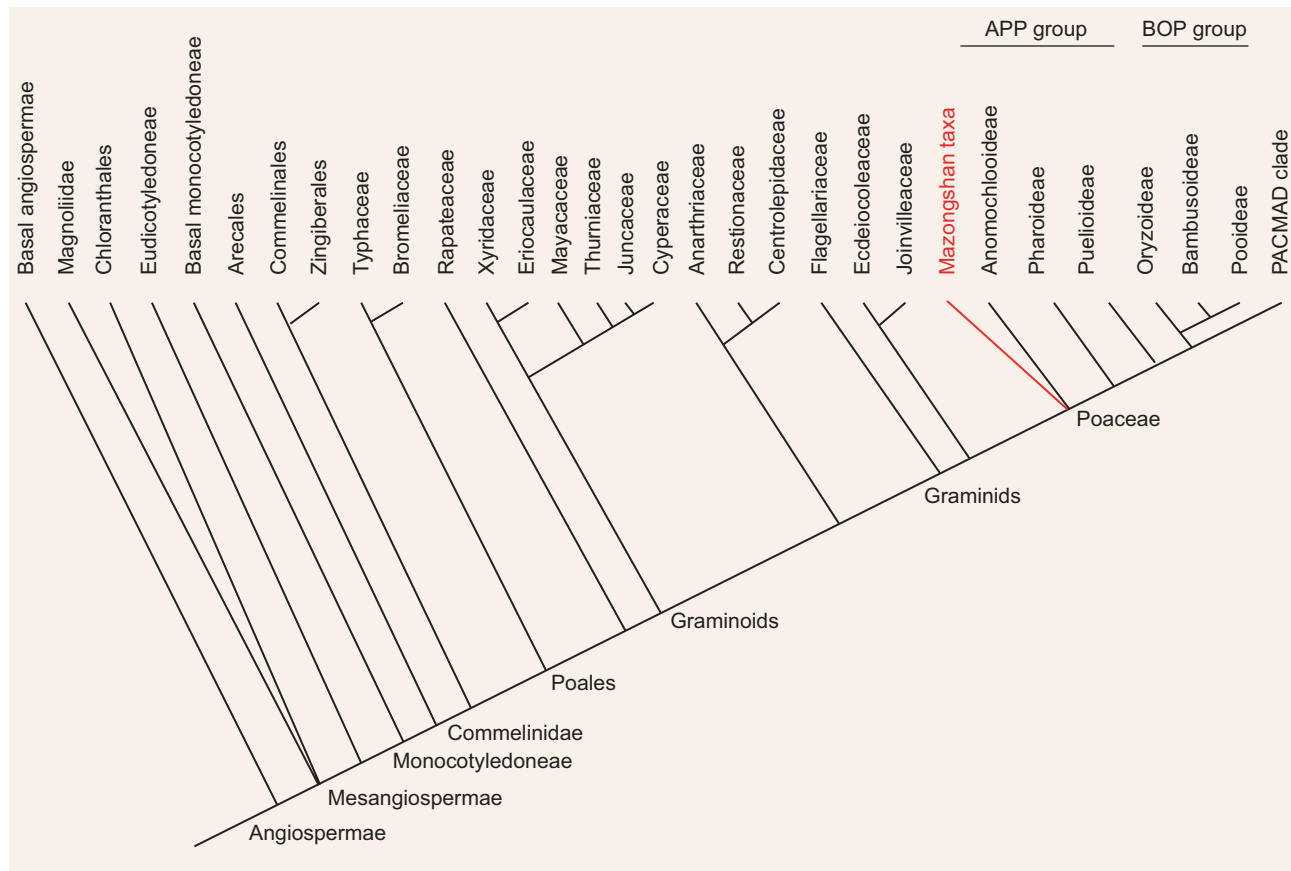
Figure 3. Phylogenetic position of silicified epidermal and phytolith-based taxa from the late Early Cretaceous (Albian) of the Mazongshan area in north-west China, highlighting its basalmost Poaceae status. Cladogram is modified from [2,3].

high-fiber herbivore clade is generally attributed to their sophisticated cranial and dental adaptations that rivaled those of living mammals. These adaptations include batteries of interlocking teeth, high tooth-replacement rates and complex jaw mechanisms involving a unique form of intracranial flexibility (pleurokinesis) [21,22]. Recent work shows in derived hadrosauroids, such as *Edmontosaurus*, that the teeth are composed of complicated tissue types [23], and scratched microwear fabrics dominated the wear facets of the functional surfaces of teeth, suggesting that *Edmontosaurus* was a grazer [24]. However, with very little evidence of the earliest grasses in the latest Cretaceous, grasses have not been considered as part of hadrosauroid diets [24]. The existence of grass epidermis and phytoliths in the special structure along the dentition of *Equijubus* strongly indicates basal grasses were in its diet; this opens up the possibility that grasses may have been in the diet of some other duck-billed dinosaurs as well.

The coevolution of dinosaurs and angiosperms has long been proposed, postulating a shift from Late Jurassic canopy-browsing (sauropods) to Early Cretaceous ground-level-feeding (ornithischians,

including hadrosauroids) closely tracking the newly appearing angiosperms [25]. However, this idea is treated as an 'elegant thought experiment' due to lack of supporting fossil evidence [26]. The prevailing thought is that angiosperms originated in the Early Cretaceous and did not become ecologically abundant and were probably not major components of dinosaur diet until the early Late Cretaceous, which implies a significant time lag of more than 10 million years [26]. Our discovery shows that basal grasses were at least food sources of hadrosauroids in the Albian. Recent molecular dating predicted a pronounced increase in the emergence of angiosperm orders that include phytolith-rich taxa during the Albian [3,27], and the nine various-shaped phytolith morphotypes extracted from the same special structure (see Supplementary Fig. S3 (see online supplementary material)) may be derived from some of these deep-diverging members of basal angiosperms, basal monocots or basal eudicots. However, a clear timeframe for events of active silica accumulation in plants still needs to be investigated [28]. Palynological analysis at the same geological level close to the *Equijubus* quarry indicates angiosperms composed 4% of the palynoflora and, among them,

Magnolipollis occupied about 75% [29]. Magnoliidae is rich in containing phytoliths [28,30], but their phytoliths are not extracted from the special structure, although this could not preclude their inclusion in *Equijubus*'s diet. Our discovery suggests grasses and other phytolith-bearing plants were likely a part of its diet. Newly evolving basal grasses and other angiosperms possibly provided food sources for numerous newly evolving animals, especially insects and birds during the beginning of the Cretaceous Terrestrial Revolution, which marked a crucial turning point in the history of life on Earth, when life on land became more diverse than life in the sea and the origins of many organisms with which we are familiar today (flowering plants, pollinating insects, leaf-eating flies, lizards, snakes, crocodilians, basal placental mammals, new birds, and the horned and duck-billed dinosaurs) [31,32].

METHODS

Extraction process for samples

The phytoliths analysed in this paper are accessible from the authors' affiliation (IVPP). Our sampling process was performed in a small office with the door closed. Technicians from IVPP wore lab clothing, gloves and masks, and the drilling tools were also cleaned up beforehand. Before extracting samples, the surface of the specimens was thoroughly cleaned by blower and acetone (see Supplementary Fig. S1a–d (see online supplementary material)). Subsequently, we scraped the sedimentary matrix on the surface of the special structure and saved them in a tube (see Supplementary Fig. S1e–h (see online supplementary material)). Following this, fresh samples of the special structure were taken and saved in two tubes (one for phytolith analysis and the other for EMP analysis). This process was applied on two maxillary teeth: one in the middle and the other on the posterior part of the dentition.

Extraction process for silicified epidermis and phytolith

The process of silicified epidermis and phytolith extraction followed the slightly modified methods outlined by several authors [33–38]. Approximately 3 grams of material was taken and dried ground into powder. The dry residue was placed in 10% hydrochloric acid to remove carbonates, and then 30% hydrogen peroxide was added to each sample to remove organic matter. To concentrate phytoliths, heavy liquid flotation was carried out using a ZnBr2 solution at a density of 2.3. Heavy liquid flotation was repeated again to ensure concentrate phytoliths.

The residue was washed with distilled water by centrifuging at 3000 rpm for 10 minutes. The residue was performed through the examination in Canada Balsam using a light microscope.

SEM–EDS analysis of characteristic morphology

In addition to identifying all phytoliths in plain polarized light, which were found to have the physical properties of opal phytoliths, SEM–EDS was used to identify characteristic morphology in elements present in the sample. All SEM–EDS values given were taken from a JSM-6610 LA scanning electron microscope with EDS. The characteristic x-rays were detected under 1.0 nA and the measuring time was 30–70 seconds. SEM -EDS analysis shows that the main element present in the phytolith is silicon (Fig. S3 (see online supplementary material)). Combining both optical and morphological characteristics, it can be determined that phytoliths exist in the samples.

EMP (Electronic Microprobe) analysis

This quantitative analysis was conducted at the EMP laboratory of China University of Geosciences (Beijing), China, with both line and area analyses under a 15-kV accelerating voltage, a 10-nA beam current and a 1-μm beam size. Each of the three samples was polished into a probe slide and observed under an optical microscope in order to locate three target areas for EMP analysis (Supplementary Figs S4–S7 (see online supplementary material)).

SUPPLEMENTARY DATA

Supplementary data are available at *NSR* online.

Conflict of interest statement. None declared.

REFERENCES

1. Strömberg CAE. Evolution of grasses and grassland ecosystems. *Annu Rev Earth Planet Sci* 2011; **39**: 517–44.

2. Soreng RJ, Peterson PM and Romaschenko K *et al.* A worldwide phylogenetic classification of the Poaceae (Gramineae). *J Syst Evol* 2015; **53**: 117–37.

3. Magallón S, Gómez-Acevedo S and Sánchez-Reyes LL *et al.* A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytol* 2015; **207**: 437–53.

4. Prasad V, Strömberg C and Leaché A *et al.* Late Cretaceous origin of the rice tribe provides evidence for early diversification in Poaceae. *Nat Commun* 2011; **2**: 1–8.

5. Christin P-A, Spriggs E and Osborne CP *et al.* Molecular dating, evolutionary rates, and the age of the grasses. *Syst Biol* 2014; **63**: 153–65.

6. Prasad V, Strömberg CAE and Alimohammadian H *et al.* Dinosaur coprolites and the early evolution of grasses and grazers. *Science* 2005; **310**: 1177–80.

7. Poinar G, Alderman S and Wunderlich J. One hundred million year old ergot: psychotropic compounds in the Cretaceous. Palaeodiversity 2015; **8**: 13–19.

8. Poinar G. Silica bodies in the Early Cretaceous Programinis laminatus (Angiospermae: Poales). *Palaeodiversity* 2011; **4**: 1–6.

9. Shi G, Grimaldi DA and Harlow GE *et al.* Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Res* 2012; **37**: 155–63.

10. Burke SV, Lin C-S and Wysocki WP *et al.* Phylogenomics and plastome evolution of tropical forest grasses (Leptaspis, Streptochaeta: Poaceae). *Front Plant Sci* 2016; **7**: 1–12.

11. You H-L, Luo Z-X and Shubin NH *et al.* The earliest-known duck-billed dinosaur from deposits of late Early Cretaceous age in northwest China and hadrosaur evolution. *Cretaceous Res* 2003; **24**: 347–55.

12. Strömberg CAE. Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proc Natl Acad Sci USA* 2005; **102**: 11980–4.

13. Rudall P, Prychid C and Gregory T. Epidermal patterning and silica phytoliths in grasses: an evolutionary history. *Bot Rev* 2014; **80**: 59–71.

14. LeBlanc ARH, Reisz RR and Evans DC *et al.* Ontogeny reveals function and evolution of the hadrosaurid dinosaur dental battery. *BMC Evol Biol* 2016; **16**: 1–13.

15. Pittman M, Xu X and Ali JR *et al.* Insights into iguanodontian dental architecture from an Early Cretaceous Chinese basal hadrosauriform maxilla (Ornithischia: Iguanodontia). *PeerJ PrePrints* 2015; **3**: e1636. doi: 10.7287/peerj.preprints.1329v1.

16. Warinner C, Speller C and Collins MJ. A new era in palaeomicrobiology: prospects for ancient dental calculus as a long-term record of the human oral microbiome. *Philos T Roy Soc B* 2015; **370**: doi: 10.1098/rstb.2013.0376.

17. Kellogg EA. The grasses: a case study in macroevolution. *Annu Rev Ecol Syst* 2000; **31**: 217–38.

18. Ali JR and Krause DW. Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: refutation of the Gunnerus Ridge causeway hypothesis. *J Biogeogr* 2011; **38**: 1855–72.

19. Ezcurra MD and Agnolín FL. A new global palaeobiogeographical model for the late mesozoic and early tertiary. *Syst Biol* 2012; **61**: 553–66.

20. Poropat SF, Mannion PD and Upchurch P *et al.* New Australian sauropods shed light on Cretaceous dinosaur palaeobiogeography. *Sci Rep* 2016; **6**: 34467. doi: 10.1038/srep34467.

21. Norman DB. On the cranial morphology and evolution of ornithopod dinosaurs. *Symposium of the Zoological Society of London* 1984; **52**: 521–47.

22. Weishampel DB. Evolution of jaw mechanisms in ornithopod dinosaurs. *Adv Anat Embryol Cell Biol* 1984; **87**: 1–109.

23. Erickson GM, Krick BA and Hamilton M *et al.* Complex dental structure and wear biomechanics in hadrosaurid dinosaurs. *Science* 2012; **338**: 98–101.

24. Williams VS, Barrett PM and Purnell MA. Quantitative analysis of dental microwear in hadrosaurid dinosaurs, and the implications for hypotheses of jaw mechanics and feeding. *Proc Natl Acad Sci USA* 2009; **106**: 11194–9.

25. Bakker R. Dinosaur feeding behaviour and the origin of flowering plants. *Nature* 1978; **274**: 661–3.

26. Barrett PM. Paleobiology of herbivorous dinosaurs. *Annu Rev Earth Planet Sci* 2014; **42**: 207–30.

27. Katz O. Silica phytoliths in angiosperms: phylogeny and early evolutionary history. *New Phytol* 2015; **208**: 642–6.

28. Strömberg CA, Di Stilio VS and Song Z. Functions of phytoliths in vascular plants: an evolutionary perspective. *Funct Ecol* 2016; **30**: 1286–97.

29. Tang F, Luo Z-X and Zhou Z-H *et al.* Biostratigraphy and palaeoenvironment of the dinosaur-bearing sediments in Lower Cretaceous of Mazongshan area, Gansu Province, China. *Cretaceous Res* 2001; **22**: 115–29.

30. Trembath-Reichert E, Wilson JP and McGlynn SE *et al.* Four hundred million years of silica biomineralization in land plants. *Proc Natl Acad Sci USA* 2015; **112**: 5449–54.

31. Lloyd GT, Davis KE and Pisani D *et al.* Dinosaurs and the cretaceous terrestrial revolution. *P Roy Soc B-Biol Sci* 2008; **275**: 2483–90.

32. Benton MJ. The origins of modern biodiversity on land. *Philos T Roy Soc B* 2010; **365**: 3667–79.

33. Pearsall DM. *Paleoethnobotany: A Handbook of Procedures.* 2nd edn. San Diego: Academic Press, Inc., 2000.

34. Piperno DR. *Phytoliths: A Comprehensive Guide for Archaeologists and Paleoecologists.* Lanham, MD: Alta Mira Press, 2006.

35. Zhao Z-J. The Middle Yangtze region in China is one place where rice was domesticated: phytolith evidence from the Diaotonghuan Cave, Northern Jiangxi. *Antiquity* 1998; **72**: 885–97.

36. Jenkins E. Phytolith taphonomy: a comparison of dry ashing and acid extraction on the breakdown of conjoined phytoliths formed in Triticum durum. *J Archaeolog Sci* 2009; **36**: 2402–7.

37. Parr JF, Lentfer CJ and Boyd WE. A comparative analysis of wet and dry ashing techniques for the extraction of phytoliths from plant material. *J Archaeolog Sci* 2001; **28**: 875–86.

38. Sun X-P, Wu Y and Wang C-S *et al.* Comparing dry ashing and wet oxidation methods: the case of the rice husk (Oryza sativa L.). *Microsc Res Tech* 2012; **75**: 1272–6.