An exceptionally well-preserved herbaceous eudicot from the Early Cretaceous (late Aptian–early Albian) of Northwest China

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ABSTRACT

A fossil eudicot, Gansufructus saligna gen. et sp. nov., is reported from the Early Cretaceous (late Aptian–early Albian) of the Gansu Province, Northwest China, based on numerous well-preserved axes with attached leaves and infructescences. The leaves are alternate, short petiolate and linear-lanceolate with low rank pinnate to reticulate venation. The infructescences are loose panicles bearing fruits in different stages of maturity, each containing four partly free carpels borne in a whorled arrangement. Each carpel has three to five seeds borne along its ventral margin. The nature of the leaves and axes indicates a terrestrial, herbaceous habit. In general organization, Gansufructus is closely similar to the fruit-bearing axes of Sinocarpus decussatus from the Early Cretaceous Jehol Biota, as well as other more or less contemporaneous angiosperms from the Far East, which together provide evidence of diverse eudicot angiosperms of low stature colonizing areas close to environments of deposition.

Keywords: eudicot, Early Cretaceous, Northwest China, Jehol Biota, Gansufructus, paleoecology

INTRODUCTION

Angiosperms (flowering plants) represent the largest and most successful clade of vascular plants, with >350,000 extant species distributed all over the world [1,2], but their origin, evolution, early diversification, as well as the habitat preferences and ecology of early forms, are still poorly understood [3–5]. Some molecular studies suggest a pre-Cretaceous origin for angiosperms, perhaps Late Triassic [5–7], but there are no reliable fossil angiosperms in Triassic or Jurassic deposits [8,9], and the rise of angiosperms during the Early and mid-Cretaceous has been regarded as a trigger for the Cretaceous Terrestrial Revolution (KTR) [10,11]. Rapid diversification of angiosperms in habit, morphology, anatomy, physiology and reproductive biology, may have been important in promoting the diversification of insects, amphibians, mammals, ferns and many other terrestrial organisms [12–15].

The Early Cretaceous terrestrial Jehol Biota is widely distributed in East Asia (northern China, southeastern Mongolia, Siberia, Korea and Japan), and is characterized by the Eosesthesia-Ephemeropsis-Lycoptera assemblage [16]. Well-preserved and informative Jehol Biota fossils are particularly abundant in western Liaoning, eastern Heilongjiang, northern Hebei and southeastern Inner Mongolia, and include crucial specimens of feathered dinosaurs, early birds, eutherian mammals and early flowering plants [17–19]. Lower Cretaceous strata are also widely distributed in Northwest China, especially in the western part of Gansu Province, where numerous fossils document a rich Jehol fauna and flora [20] that includes fishes [21], turtles [22], insects [23], birds [24], dinosaurs [25] and plants [26–28], although no angiosperms have been described. Here, we report an early angiosperm from the late Early Cretaceous (late Aptian–early Albian, 115–112 Ma) [20,23,29–31] Zhonggou Formation of the Jiuquan Basin in Northwest China (Fig. 1). The fossil specimens are assigned to the eudicots clade based on the morphology of both vegetative and reproductive organs.
**SYSTEMATIC PALEONTOLOGY**

**Angiospermae**

**Eudicots**

**Icertae sedis**

*Gansufructus* B. Du gen. nov.

**Etymology:** *Gansu,* after the region where the specimens were found, and *fructus,* Latin for fruit.

**Generic diagnosis:** Plant herbaceous, erect. Main axis slender, straight or slightly curved with alternating secondary axes. Leaves simple, elongated oval, lanceolate or ovoid-lanceolate shaped and alternately arranged on the branches. Leaf margin entire. Leaf apex acute. Leaf base decurrent and estipulate with short petiole. Leaf venation poorly organized, with pinnate lateral veins and reticulate tertiary veins. Infructescence open and paniculate. Ultimate branches bearing one to three terminal fruits. Gynoecium superior, basally syncarpous with four carpels fused or appressed proximally along their ventral surface for about half of their length. Carpels whorled, each in the axil of a small persistent tepal. Each carpel enclosing three to five anatropous ovules/seeds borne on linear placentae along the ventral suture. Seed oval or reniform.

*Gansufructus* is closely similar to *Sinocarpus* Leng et Friis, especially in the organization of the fruits that have four carpels united basally and arranged in a whorl. The two taxa are distinguished mainly by arrangement of leaves and twigs, size of the carpels and number of seeds. Carpels of *Gansufructus* are generally shorter, and each contains three to five seeds, whereas carpels of *Sinocarpus* typically contain ~10–20 seeds. Branching of *Gansufructus* is alternate, whereas it is decussate in *Sinocarpus.* The general organization of the infructescences in *Hyrcahtha* Krassilov et Vachrameev is very similar to *Gansufructus,* but *Hyrcahtha* is distinguished from both *Gansufructus* and *Sinocarpus* by the apocarpous gynoecium.

**Plant Fossil Names Registry Number:** PFN001823 (for new genus)

*Gansufructus saligna* B. Du gen. et sp. nov.

**Figures 2–4**

**Holotype:** JQ-2018-01(A, B) (Fig. 2A and B)

**Paratypes:** JQ-2017-01(A, B), JQ-2018-02(A, B), JQ-2018-03(A, B), JQ-2019-01(A, B), JQ-2020-01 and JQ-2020-02 (Fig. 2C and D and Fig. 3)
Figure 2. Infructescence axes bearing leaves of *G. saligna* gen. et sp. nov. (A and B) Part and counterpart of holotype of *G. saligna* gen. et sp. nov. showing leafy axes with infructescences and lanceolate leaves. Specimen JQ-2018-01(A and B). (C and D) Part and counterpart showing axes with alternate arranged branches and lanceolate leaves, as well as terminal fruits in different stages of maturity. Specimen JQ-2018-02(A and B). Scale bars: 1.0 cm.

**Etymology:** *saligna*, from the willow-shaped leaves (*saligna*, Latin for 'willow')

**Locality and horizon:** Laojumiao of Jiuquan City, western Gansu Province, Northwest China, uppermost part of the Zhonggou Formation, Hanxia Section; Early Cretaceous (late APTIAN–early ALBIAN)

**Plant Fossil Names Registry Number:** PFN001822 (for new species)

**Specific diagnosis:** As for the genus

**Description:** The plant was fossilized at fruiting stage and preserves the terminal part of a simple or more complex infructescence with attached leaves (Figs 2 and 3A–F). Plant erect, herbaceous, three to four times branched. Branches alternate and are predominantly at angles of 30–45° (Figs 2 and 3A–H). The main axis is slender and lightly striated, ~2–4 mm wide, with longitudinal grooves or ribs on the surface (Fig. 3G and H); secondary branches are ~1–1.2 mm wide, and tertiary branches are ~0.5 mm wide (Figs 2, 3A and B). Ultimate branches bear one to three terminal fruits (Figs 2 and 3A–F). Leaves are simple, symmetrical, deciduous or persistent and alternately arranged. They vary in size, typically being ~1–2.5 cm long and 0.2–0.4 cm wide, but are larger toward the base of the plant (Fig. 2). Leaves are narrow-ovate, lanceolate or ovoid-lanceolate in shape (Figs 2 and 3I). Leaf apex is acute, and the leaf margin is entire (Figs 2 and 3I–K). Leaf base is decurrent with a short petiole (Fig. 3I).

Leaf venation is poorly organized, pinnate to reticulate (Fig. 3I). The primary vein is prominent and straight, or slightly curved, and extends from the leaf base to the apex (Fig. 3I–K). Secondary veins are pinnate, arcuate and arise from the mid-vein alternately, each at an angle of 30–45°, but do not reach the leaf margin (Fig. 3J–L). Inter-secondary veins are shorter than secondary veins, extend from the mid-vein, and often fuse with the vein loops formed by the secondary veins. Tertiary veins are reticulate and oblique to the main course of the secondary veins (Fig. 3L).

The infructescence is open, paniculate and determinate, bearing terminal fruits at the apex of an elongated pedicel (Figs 2, 3A–F, 4A–D and G). Pedicels are slender, ~3.5–5.5 mm long, and 0.5–0.6 mm wide (Figs 3A–F, 4C, D and G). The gynoecium is basally syncarpous, and the ovary is superior (Figs 2, 3A–F and 4A–G). The fruits consist of four carpels arranged in a whorl on a convex receptacle (Fig. 4A–D). Receptacles are distinct and slightly expanded, up to ~2 mm long and 1.8 mm wide (Fig. 4C and D). A small and persistent tepal subtends each carpel (Fig. 4A–C). There are no other remains of either perianth or stamens, and it is unknown whether the flowers were unisexual or bisexual.

Prior to dehiscence, the closed fruits are elliptic or subglobose in shape, ~2–3 mm long and 2–3 mm wide (Fig. 4A). After dehiscence along the ventral suture, the fruits are ~4–5.5 mm long and 3–4.5 mm wide (Fig. 4A–G). In most fruits, the carpels are fused basally for about half or more of their length (Fig. 4A–D). Some are completely dehisced, and the elongated elliptic-shaped carpels are arranged in a whorl (Fig. 4E and G). The carpels are asymmetric with mucronate apices, ~4.5–5.5 mm long and 2–2.5 mm wide (Fig. 4B–D, F and G), and dehisce along the ventral side (Fig. 4E). Each carpel contains ~3–5 ovules/seeds arranged longitudinally on linear placentae along the ventral suture of the carpel, both in the free and fused portion of the fruit (Fig. 4F).

Seeds are tightly packed in the carpels with their margins sometimes overlapping (Fig. 4F–I). Seeds vary in size and morphology. They are ~1.5–1.8 mm long and 0.8–1.1 mm wide, asymmetrical and oval.
to elongated ovoid or reniform in shape (Fig. 4F–I), slightly pointed in the hilar region and rounded to truncate in the chalaza region (Fig. 4F–I). Seeds are anatropous, with chalaza opposite to the funiculus, and the micropyle situated at the base of the funiculus (Fig. 4H and I).

Epidermal cells on the carpels are irregular, polygonal or elongated rectangular, ∼50 μm long and 15–20 μm wide (Fig. 5A). Two epidermal layers are visible on the seeds. The inner layer is formed by pentagonal and hexagonal cells arranged in longitudinal rows that radiate from the chalaza towards the micropylar end of the seed (Fig. 5B and C). The cells become larger near the micropylar area, being ∼80–110 μm long and 50–80 μm wide, and narrowly elongated towards the chalaza part of the seeds (Fig. 5B–E, H and I). The cells of the outer layer are elongated (Fig. 5D and E), with irregularly curved anticlinal walls (Fig. 5D, E and H–J), and transverse ribs and grooves on the periclinal walls (Fig. 5I–K).

**DISCUSSION**

*Gansufructus saligna* gen. et sp. nov. is reconstructed as a small, slender plant with flexible stems, delicate leaves and paniculate infructescences (Fig. 6A). The pinnate-reticulate low rank leaf venation (Fig. 6B) together with partly syncarpous gynoecium and several completely enclosed seeds (Fig. 6C and D) securely place this ancient plant within the angiosperms. In addition, general morphological features of *G. saligna*, including alternate phyllotaxis, pinnate-reticulate leaf venation, partly apocarpous gynoecium and fruit with four carpels arranged in a whorl, indicate an affinity among the eudicots.

Eudicots appeared early in the diversification of angiosperms, as evidenced by worldwide discoveries of tricolpate pollen grains as well as fossil flowers, fruits and leaves from late Barremian and early Albian strata [5, 6, 32–34]. However, few macro-fossils of eudicots have been reported from Albian or earlier rocks, and very few are known from both vegetative and reproductive organs. Among the several fossil records (Table 1), the infructescence of *Sagara cilentana* is dichasium, and fruits are cup-shaped, composed of at least three follicles, and leaves are lobate [35]. *Achaenocarpites capitellatus* is characterized by stipulate, basically ternate, pinnatisect or three-lobed leaves and the reproductive structure is preserved as a head of achenes consisting of ∼16 radially spreading achenes. *Ternicarpites floribundus* possesses pinnatisect leaves and an apocarpous gynoecium of two to five, usually three, follicular carpels [36, 37]. *Leefructus mirus* is characterized by three-lobed leaves, and its fruit have five pseudo-syncarpous elongated carpels [17]. The fossil specimens described in this paper are distinguished from all these fossils by their simple and lanceolate leaves, paniculate and determinate infructescence with dehiscent fruits composed of four basally syncarpous carpels, each enclosing three to five oval ovules/seeds.

*Gansufructus* closely resembles *Sinocarpus* and *Hyrcantha* in gross morphology (Table 1), as well as in the paniculate infructescence and polycarpous fruits. They may be closely related despite showing different branching types and leaf characteristics. *Sinocarpus decussatus* differs from *G. saligna* by its decussate phyllotaxis, ovate or narrow-ovate
leaves with serrated margin, and its greater number of seeds per carpel (10–20 ovules/seeds in Sinocarpus versus ~3–5 in Gansufructus) [38,39]. Hrycantha karatscheensis is distinguished by its apocarpous gynoecium, and the terminal fruiting units that consist of three or five carpels [40].

Among many extant families of eudicots, the combined characteristics of Gansufructus, such as simple, lanceolate and alternately arranged leaves with entire margins and pinnate-reticulate venation, as well as subglobose and polycarpous fruits, suggest a systematic position among the basal grade of eudicots or the basal core eudicots as also suggested for Sinocarpus [38,39]. In particular, there are similarities to extant Ranunculaceae, Myrothamnaceae and Buxaceae, but Gansufructus differs from all of these families. Ranunculaceae is characterized by spiral phylloaxis, simple to compound leaves and apocarpous gynoecium [41]. Myrothamnaceae is distinguished by decussate phyllotaxis, sessile leaves and catkin-like inflorescences [42]. Buxaceae is distinct in having fruits with two to three carpels, each of which always carries only two ovules [43].

Palynological preparations made from the fossil specimens failed to provide pollen associated with Gansufructus. However, poorly preserved tricolpate pollen grains, typical of eudicots, do occur in the fossil-bearing strata, and the pollen assemblage is mainly dominated by grains assignable to the extinct pollen genus Retitricolpites (Fig. 5F and G). Previous palynological analyses have suggested a relatively temperate and humid climate in the study area during the early Albian, with an increase of xerophytic vegetation in palynological flora indicating obvious later aridification [31], which is also supported by the discovery of Cheirolepidiaceae macro-fossils from the uppermost Zhonggou Formation [27].

The slender, flexible and upright stems of Gansufructus are not lignified, and the longitudinal grooves or ribs on the stem surface probably represent vascular bundles of a herbaceous plant [40,44]. The numerous narrow-lanceolate and alternate leaves attached to the axes and panicule-like infructescence with numerous fruits terminally at the leafy axes would have required stable support and a sufficient vascular system. Gansufructus saligna was probably a herbaceous or scarcely woody plant growing in a terrestrial environment. The association with riparian Equisetum [28] and fishes suggest a locally wet and lowland environment. Therefore, Gansufructus is supposed to be a terrestrial herb colonizing lowland areas, probably growing in the mud or floodplains along lakeshores in a humid environ-
Figure 5. Cuticular structure of *G. saligna* gen. et sp. nov. and eudicot pollen grains from the fossil bearing strata. (A) Surface of carpel under stereo microscopy, showing the polygonal or elongated rectangular-shaped cells. (B and C) Cuticular structures of seeds under stereo microscopy, showing the pentagonal- and hexagonal-shaped cells. (D and E) Cuticles of seeds under light microscopy, showing two cuticular layers. (F and G) Eudicot pollen grains from the fossil bearing horizon of uppermost Zhonggou Formation, Hanxia Section. (H–K) Cuticular structures of seeds under scanning electron microscopy, showing pentagonal- and hexagonal-shaped cells and irregularly curved anticlinal walls, as well as transverse parallel ribs and grooves on the periclinal walls. Scale bars: (A–C) 0.5 mm; (D and E) 200 μm; (F and G) 20 μm; (H and I) 100 μm; (J) 20 μm; (K) 10 μm.

Figure 6. Reconstruction of *G. saligna* gen. et sp. nov. (A) Overview of *G. saligna* gen. et sp. nov. (B) Line diagram of a leaf showing lanceolate shape, short petiole, acute apex, entire margin and poorly organized venation. (C) Line diagram of fossil specimen JQ-2019-01(B), showing the basally syncarpous carpels enclosing three to five anatropous seeds. (D) Line diagram of fossil specimen JQ-2018-03(B), showing the dehiscent fruits with carpels arranged in a whorl (diagram by Mingchen Zhang).

MATERIALS AND METHODS

All the fossil specimens were collected from the uppermost Zhonggou Formation of Hanxia Section (39° 50' N, 97° 15' E), about ~40 km west of Laojunmiao County, Jiayuguan City, Gansu Province (Fig. 1). The fossils were photographed using a SONY Alpha 7 II EOS digital camera coupled with a SONY 50 mm FE macro lens and a stereo microscope (Zeiss, Oberkochen, Germany). The cuticle remains that were removed from the fossil specimens were firstly treated with 10% HCl (hydrogen chloride), and then 50% HF (hydrogen fluoride) subsequently. Some of them were treated with saturated NaClO (sodium hypochlorite), stained in a safranine solution, mounted on slides, embedded in a glycerine jelly, sealed with Canada balsam and then observed under an Axio Scope A1 light microscope and a Stemi508 fluorescence microscope (Zeiss, Oberkochen, Germany) at the Key Laboratory of Petroleum Resources, Gansu Province, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou, China.
| Characters | Sagaria cilentana | Achaenocarpites capitellatus | Ternicarpites floribundus | Leefructus minus | Sinocarpus decassatus | Hyrantha karatschenensis | Gansufructus aligna |
|------------|------------------|----------------------------|--------------------------|-----------------|----------------------|-------------------------|-------------------|
| Infructescence type | Dichasium | Head of achenes | Unknown | Single fruit and axillary | Paniculate and determinate | Paniculate | Paniculate and determinate |
| Fruit Size | 11 mm long and 6 mm wide | 3.6–3.9 mm in diameter | 6–8 mm long | 6 mm long and 4 mm wide | 13–15 mm long and 6–8 mm wide | 7 mm long and 3 mm wide | 4–5.5 mm long and 3–4.5 mm wide |
| Shape | Polycarpous, cup-shaped receptacle, basally fused, and dehiscent at the top | Globose | Polycarpous, ternate folliculum, and completely dehiscent | Elongated tips, and loosely fused at its basal two-thirds, with a flattened receptacle | Polycarpous, basically united, and upper-middle part dehiscent | Ascidial | Polycarpous, elliptic or subglobose, basically united, and upper-middle part dehiscent |
| Carpel or achene Size | 11 mm long and 3 mm wide | 1.5–1.8 mm long | 6–8 mm long and 2–3 mm wide | 6 mm long and 0.5 mm wide | 9–12.5 mm long and 1.5–3 mm wide | 7 mm long and 3 mm wide | 4.5–5.5 mm long and 2–2.5 mm wide |
| Number | ≥3 | ≥16 | 2 to 5, mostly 3 | 5 | 2 to 4 | 3 or 5 | 4 |
| Shape | Fused at its basal three-quarters, and distal tips mucronate | Obovate and minutely mucronate | Elongated | Elongated tips, and loosely fused at its basal two-thirds | Elongated elliptic | Ascidial | Elongated elliptic and asymmetric |
| Arrangement | Basally syncarpous and whorled | Radially spreading | Apocarpous and whorled | Pseudo-syncarpous | Basally syncarpous and whorled | Apocarpous and whorled | Basally syncarpous and whorled |
| Seed Size | Unknown | ~1 mm long | Unknown | Unknown | 2 mm long and 1 mm wide | Unknown | 1.5–1.8 mm long and 0.8–1.1 mm wide |
| Number per carpel | Unknown | 1 | Unknown | Unknown | 10–20, in two rows | Unknown | Oval to elongated ovoid or reniform, asymmetric |
| Shape | Unknown | Ovate | Elliptical | Unknown | Orate and asymmetric | Unknown | Anatropous, along the ventral suture |
| Arrangement | Unknown | Anatropous | In rows along the abaxial suture | Unknown | Anatropous, along linear placenta | Unknown | Anatropous, along linear placenta |
| Leaf Shape | Lobed and petiolate | Basically ternate, pinnatisect or three-lobed | Pinnatisect of opposite decurrent lobes | Simple and deeply trilobate | Orate or narrowly ovate, acute apex, rounded base and serrate leaf margin | Pinnately compound and ternate | Simple and lanceolate, acute apex, decurrent base, and entire margin |
| Arrangement | Alternate or helical | Opposite | Unknown | Clustered | Unknown | Unknown | Alternate |
| Place | Southern Italy | Eastern Russia | Eastern Russia | Southern Italy | Northeastern China | Western Kazakhstan | Northwestern China |
| Age | Middle Albian | Early-Middle Albian | Early-Middle Albian | Middle Albian | Late Barremian | Middle Albian | Late Aptian-Early Albian |
| Reference | [35] | [36,37] | [36,37] | [17] | [38,39,44] | [40] | This paper |
Other preparations were mounted on stubs, coated with gold and examined under a JSM-6510 scanning electron microscope (JEOL, Japan) at Lanzhou University, China. All the specimens (specimen no: JQ-2017-01(A, B), JQ-2018-01(A, B), JQ-2018-02(A, B), JQ-2018-03(A, B), JQ-2019-01(A, B), JQ-2020-01 and JQ-2020-02) as well as cuticular slides, were deposited in the Palaeontological Laboratory of the School of Earth Sciences, Lanzhou University, China.

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AUTHOR CONTRIBUTIONS
Baoxia Du and Bainian Sun designed the project; Baoxia Du, Mingzhen Zhang, Aijing Li and Jing Zhang joined the field sampling and performed the analyses and experiments; Baoxia Du and Mingzhen Zhang wrote the manuscript and prepared photographs and line drawings; Defei Yan, Sanping Xie and Jingyu Wu discussed the results and modified the manuscript. All authors read and approved the final manuscript.

Conflict of interest statement. None declared.

REFERENCES
1. The Plant List, Royal Botanic Gardens, Kew and Missouri Botanical Garden. The Plant List: A Working List of All Plant Species: http://www.thepantlist.org/ (20 April 2021, date last accessed).
2. Yang YZ, Sun PC and Lv LK et al. Prickly waterlily and rigid hornwort genomes shed light on early angiosperm evolution. Nat Plants 2020; 6: 215–22.
3. Li HT, Yi TS and Gao LM et al. Origin of angiosperms and the puzzle of the Jurassic gap. Nat Plants 2019; 5: 461–70.
4. Lee AP, Upchurch G and Murchie EH et al. Leaf energy balance modelling as a tool to infer habitat preference in the early angiosperms. Proc R Soc B 2015; 282: 20143052.
5. Jud NA. Fossil evidence for a herbaceous diversification of early eudicot angiosperms during the Early Cretaceous. Proc R Soc B 2015; 282: 20151045.
6. Smith SA, Beauleieu JM and Donoghue MJ. An uncorrected relaxed-clock analysis suggests an earlier origin for flowering plants. Proc Natl Acad Sci USA 2010; 107: 5897–902.
7. Zheng L, Zhang Q and Sun R et al. Resolution of deep angiosperm phylogeny using conserved nuclear genes and estimates of early divergence times. Nat Commun 2014; 5: 4956.
8. Herendeen PS, Friis EM and Pedersen KR et al. Palaeobotanical redux: revisiting the age of the angiosperms. Nat Plants 2017; 3: 17015.
9. Ciero M, Doyle JA and Hilton J. How deep is the conflict between molecular and fossil evidence on the age of angiosperms? New Phytol 2019; 223: 83–99.
10. Wang W, Lin L and Xiang XG et al. The rise of angiosperm-dominated herbaceous floras: insights from Ranunculaceae. Sci Rep 2016; 6: 27259.
11. Barba-Montoya J, dos Reis M and Schneider H et al. Constraining uncertainty in the timescale of angiosperm evolution and the veracity of a Cretaceous Terrestrial Revolution. New Phytol 2018; 218: 819–34.
12. Diao TP, Shih CK and Ren D. Insects—in the spotlight. In: Ren D, Shih CK and Gao TP et al. (eds). Rhythms of Insect Evolution: Evidence from the Jurassic and Cretaceous in Northern China. Chichester: John Wiley & Sons Ltd., 2019, 31–40.
13. Roelants K, Gower DJ and Wilkinson M et al. Global patterns of diversification in the history of modern amphibians. Proc Natl Acad Sci USA 2007; 104: 887–92.
14. Bininda-Emonds ORP, Cardillo M and Jones KE et al. The delayed rise of present-day mammals. Nature 2007; 446: 507–12.
15. Schneider H, Schuettpelz E and Pryer KM et al. Ferns diversified in the shadow of angiosperms. Nature 2004; 428: 553–7.
16. Jiang BY, Harlow GE and Wohletz K et al. New evidence suggests pyroclastic flows are responsible for the remarkable preservation of the Jehol Biota. Nat Commun 2014; 5: 3151.
17. Sun G, Dilcher DL and Wang HS et al. A eudicot from the Early Cretaceous of China. Nature 2011; 471: 625–8.
18. Zhou ZH, Barnett PM and Milton J. An exceptionally preserved Lower Cretaceous ecosystem. Nature 2003; 421: 807–14.
19. Xu X, Zhou ZH and Wang Y et al. Study on the Jehol Biota: recent advances and future prospects. Sci China Earth Sci 2020; 63: 757–73.
20. Zheng DR, Wang H and Li S et al. Synthesis of a chrono- and biostratigraphical framework for the Lower Cretaceous of Jiuquan, NW China: implications for major evolutionary events. Earth-Sci Rev 2021; 213: 103474.
21. Murray AM, You HL and Peng C. A new Cretaceous oosteglosomorph fish from Gansu Province, China. J Vertebr Paleontol 2010; 30: 322–32.
22. Brinkman DB, Yuan CX and Ji Q et al. A new turtle from the Xiangou Formation (Early Cretaceous) of Changma Basin, Gansu Province, P. R. China. Palaeobiodivers Palaeoenviron 2013; 93: 367–82.
23. Zheng DR, Zhang HC and Zhang Q et al. The discovery of an Early Cretaceous dragonfly Hemeroscopus baissicus Pritykina, 1977 (Hemeroscoptidae) in Jiuquan, Northwest China, and its stratigraphic implications. Cretaceous Res 2015; 52: 316–22.
24. You HL, Lamanna MC and Harris JD et al. A nearly modern amphibian from the Early Cretaceous of northwestern China. Science 2006; 312: 1640–3.
25. Tang F, Luo ZX and Zhou ZH 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.

26. Deng SH, Yang XJ and Lu YZ. Pseudofrenelopsis (Cheirolepidiaceae) from the Lower Cretaceous of Jiuquan, Gansu, northwestern China. *Acta Palaeontol Sin* 2005; 44: 505–16.

27. Du BX, Sun BN and Ferguson DK et al. Two Brachyphyllum species from the Lower Cretaceous of Jiuquan Basin, Gansu Province, NW China and their affinities and palaeoenvironmental implications. *Cretaceous Res* 2013; 41: 242–55.

28. Sun BN, Du BX and Ferguson DK et al. Fossil Equisetum from the Lower Cretaceous in Jiuquan Basin, Gansu, Northwest China and its paleoclimatic significance. *Palaeogeogr Palaeoclimatol Palaeoecol* 2013; 385: 202–12.

29. Kuang HW, Liu Y and Liu Y et al. Stratigraphy and depositional palaeogeography of the Early Cretaceous basins in Da Hinggan Mountains-Mongolia orogenic belt and its neighbouring areas (in Chinese). *Geo Bull China* 2013; 32: 1063–84.

30. Li XH, Xu WL and Liu WH et al. Climatic and environmental indications of carbon and oxygen isotopes from the Lower Cretaceous calcareous and lacustrine carbonates in Southeast and Northwest China. *Palaeogeogr Palaeoclimatol Palaeoecol* 2013; 385: 171–89.

31. Zhang MZ, Ji LM and Du BX et al. Palynology of the Early Cretaceous Hanxia Section in the Jiuquan Basin, Northwest China: the discovery of diverse early angiosperm pollen and palaeoclimatic significance. *Palaeogeogr Palaeoclimatol Palaeoecol* 2015; 440: 297–306.

32. Furness CA, Magallón S and Rudall PJ. Evolution of endoapertures in early-divergent eudicots, with particular reference to pollen morphology in Sabiaceae. *Plant Syst Evol* 2007; 263: 77–92.

33. Barral A, Gómez B and Feild TS et al. Leaf architecture and ecophysiology of an early basal eudicot from the Early Cretaceous of Spain. *Bot J Linn Soc* 2013; 173: 594–605.

34. Friis EM, Mendes MM and Pedersen KR. Paisia, an Early Cretaceous eudicot angiosperm flower with pantoporate pollen from Portugal. *Grana* 2017; 57: 1–15.

35. Bravi S, Rosaria MBL and James EM. Sagaria cilentana gen. et sp. nov. - a new angiosperm fructification from the middle Albian of southern Italy. *Cretaceous Res* 2010; 31: 285–90.

36. Krassilov V and Voynets Y. Weedy Albian angiosperms. *Acta Palaeobotanica* 2008; 48: 151–69.

37. Golovneva L, Alekseev P and Bugdaeva E et al. An angiosperm dominated herbaceous community from the early-middle Albian of Primorye, far East of Russia. *Fossil Imprint* 2018; 74: 165–78.

38. Leng Q and Friis EM. Sinocarpus decussatus gen. et sp. nov., a new angiosperm with basally syncarpous fruits from the Yixian Formation of Northeast China. *Plant Syst Evol* 2003; 241: 77–88.

39. Leng Q and Friis EM. Angiosperm leaves associated with Sinocarpus infructescences from the Yixian Formation (mid-Early Cretaceous) of NE China. *Plant Syst Evol* 2006; 262: 173–87.

40. Krassilov VA, Shilin PV and Vachrameev VA. Cretaceous flowers from Kazakhstan. *Rev Palaeobot Palynol* 1983; 40: 91–113.

41. Simpson MG. Diversity and classification of flowering plants: eudicots. In Simpson MG (ed.). *Plant Systematics*. London: Academic Press, 2019, 288–9.

42. Kubitzki K. Myrothamnaceae. In: Kubitzki K, Rohwer JG and Bittrich V (eds.). *Flowering Plants. Dicotyledons. The Families and Genera of Vascular Plants*, Vol. 2. Berlin, Heidelberg: Springer, 1993, 468–9.

43. von Balthazar M and Endress PK. Reproductive structures and systematics of Buxaceae. *Botanical J Linnian Soc* 2002; 140: 193–228.

44. Dilcher DL, Sun G and Ji Q et al. An early infructescence Hycrantha decussata (comb. nov.) from the Yixian Formation in northeastern China. *Proc Natl Acad Sci USA* 2007; 104: 9370–4.