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Research Article

The First Sign of the Complication of Angiosperm-Related Ecosystem

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Abstract

Angiosperms and insects are two most diverse groups of macroscopic organisms, and their relationship plays an important role in the current ecosystem. An angiosperm is usually attacked by multiple insects in the current ecosystem, which is a proxy of the complication of the ecosystem. However, such a complicate relationship appears lacking in the ecosystem for early angiosperms, which are usually attacked by only one type of insects. Therefore, when the complicate angiosperm-related ecosystem emerged is an important unanswered question. Here we document a new platanaceous species, *Arthollia dayangshuensis* gen. et sp. nov from the Nenjiang Formation (late Santonian-early Campanian, Late Cretaceous) with three different kinds of damages, suggesting that the ecological relationship between angiosperms and insects was already complicate in the Santonian. This surprising discovery implies that angiosperm-related ecosystem has already existed in the Late Cretaceous. To this date, this is the first sign of such a complicating process.

Keywords: Insects; angiosperms; ecosystem; late cretaceous; China

Introduction

As the top two most diverse groups of macroscopic organisms in the current world, angiosperms and insects as well as their mutual interplays define the complexity the Earth ecosystem. Although the interactions between insects and plants have been dated back to the Palaeozoic [1], and the interaction between angiosperms and insects has been documented at least back to the beginning of the Late Cretaceous [2], the interplay between insects and angiosperms remains simple and monotonous [2], unlike in the complicate current ecosystem. When and how the ecosystem became complex are important questions that demand answers. Here we report a new angiosperm fossil that signifies the first complication in angiosperms-related ecosystem by its multiple types of damage on a single leaf. We hope this fossil and ensuing studies will open a window on the complicating process of the current angiosperms-centered ecosystem.

Materials and Methods

The Nenjiang Formation is widely distributed in northeastern China, and previous works as well as recent isotopic dating results suggest that the age of the formation is late Santonian-early Campanian [3], a conclusion favored by the latest palynological analysis [4]. The associated estherian species, *Halysestheria yui* (Chang) Li, places the plant-fossil-bearing strata within the first member of the Nenjiang Formation (83.4-85.7 Ma) [5,6]. Angiosperm pollen in the palynoflora include *Retitricolpites* sp., *Liquidambarpollenites* sp., *Borealipollis yaojianica*, *B. songliaoensis*, *B.* sp., *Callistopollenites tumidoporus*, *Lythraites giganteus*, *Consoliduspollenites songliaoensis*, *Pentapollenites asymmetricus*, and *Euphorbiacites majorporus* [4].

The specimen of *Arthollia dayangshuensis* sp. nov is a leaf impression, 93 mm long and 48 mm wide, preserved on a yellowish gray siltstone slab. The slab was recovered from an outcrop of the Nenjiang Formation near the 4th Team, Ganhe Farm, Hulunbeier, Inner Mongolia, China (N49°20′36.39″, E124°39′32.69″, Figure 1), with default permit from Ganhe Farm. The age of the formation is 83.4-85.7 Ma [3]. The specimen was photographed using a Nikon D300S digital camera, a Nikon SMZ1500 stereomicroscope with a Nikon DS-Fi1 digital camera. All figures were organized using a Photoshop 7.0 software. The specimen (ZZB-P001) is deposited in the Natural History Museum, Weihai Ziguang Shi Yan School. For comparison, leaves of *Platanus occidentalis* Linn. (Voucher ID 222789) deposited in the Herbarium of the Institute of Botany, Nanjing were photographed. The study complies with relevant institutional, national, and international guidelines and legislation.

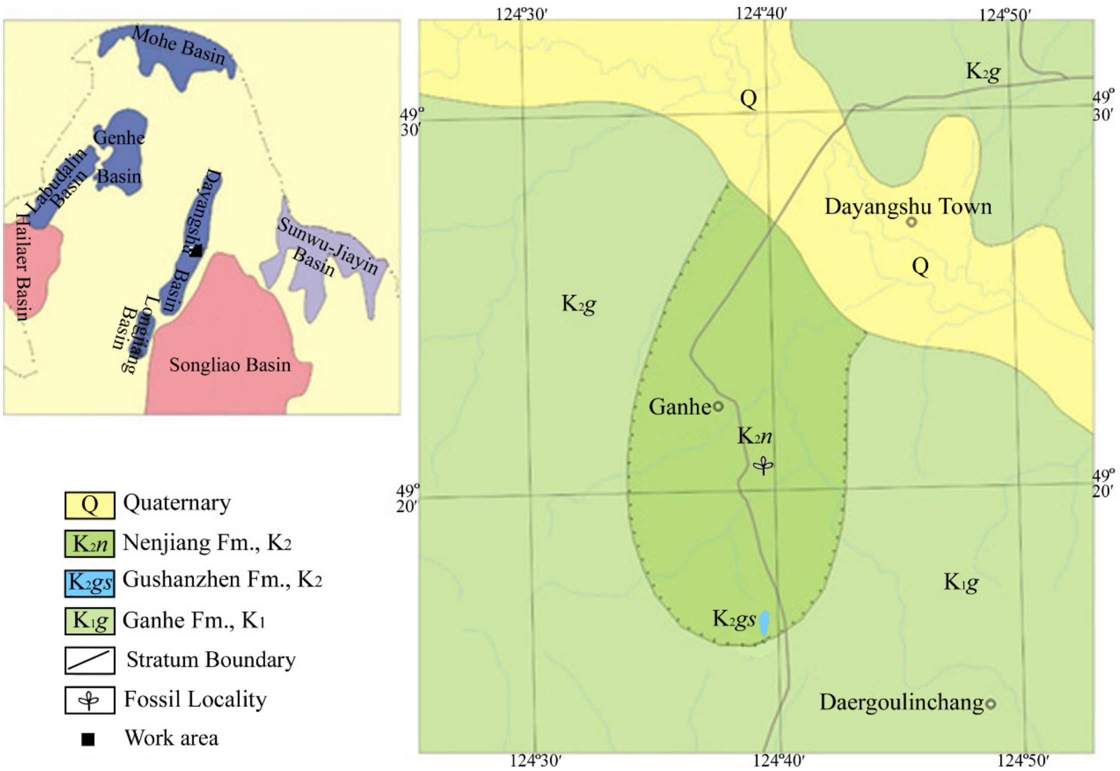

Figure1: Geographical position of the fossil locality for *Arthollia dayangshuensis* sp. nov in north Inner Mongolia, China. Upper-left shows portion of northeast China, the work area (square) is showed in detail in the main map. Our fossil was collected from a Late Cretaceous fossil locality near Ganhe Farm. Modified from Zhang et al. (2020), with permission.

Results

Arthollia dayangshuensis sp. nov. (Figure 2)

Specific diagnosis

Leaf simple. Petiole basally enlarged. Lamina elliptic in shape, coarsely serrate, widest in middle. Leaf base obtuse-decurrent, and leaf apex missing. Venation pinnate, with 4 orders of veins. Midrib rigid, percurrent. Five pairs of secondary veins opposite, craspedodromous, parallel, forming an angle of 30-35° with midrib, tapering distally, rarely furcating near lamina margin, running to teeth on lamina margins. Each basalmost secondary vein giving rise to up to 4 exmedial veins. Tertiary veins percurrent, alternate, almost perpendicular to secondary veins. Quaternary veins perpendicular to tertiary veins, forming polygonal meshes. Simple veinlet in some areoles.

Description

The leaf is simple, approximately 93 mm long and 48 mm wide, including a petiole and an almost completely preserved lamina (Figure 2a). The petiole is 20 mm long, basally 3.3 mm wide, tapering slightly into only 1.3 mm at the base of the lamina, slightly enlarged at the base (Figures 2a, 2b, 2e). The lamina is 73 mm long and 48 mm wide, elliptic in shape, coarsely serrate, widest in the middle (Figures 2a, 2g, 2h). The leaf base is obtuse-decurrent, while the leaf apex is missing (Figures 2a, 2g). The venation is pinnate, with 4 orders of veins (Figures 2a, 2c, 2f-2i). The midrib runs almost percurrent, rigid, 1.2 mm wide near the base, slightly tapering and curving (Figure 2a). Five pairs of secondary veins are opposite, craspedodromous, parallel, forming an angle of 30-35° with the midrib, 0.3-0.6 mm wide, tapering distally, rarely furcating near the lamina margin, running to teeth on the lamina margins (Figures 2a, 2c, 2h). Each of the basalmost secondary veins gives rise to up to 4 exmedial veins, each of which joins branches of superadjacent exmedial vein to form loops before reaching to the leaf margin (Figure 2a). The tertiary veins are alternately arranged on and almost perpendicular to the secondary veins, forming a scalariform pattern, 75-380μm wide, connecting the neighboring secondary and thus forming meshes 0.3-0.9 x 0.4-1.3 mm (Figures 2a, 2c), while some tertiary veins may connect the secondary with the tertiary and forming acute angles (Fig. 2f). The quaternary veins are orthogonally reticulate, almost perpendicular to the tertiary veins, forming polygonal meshes (Figures 2a, 2c, 2i). Simple veinlets are observed in some areoles (Figures 2c, 2i).

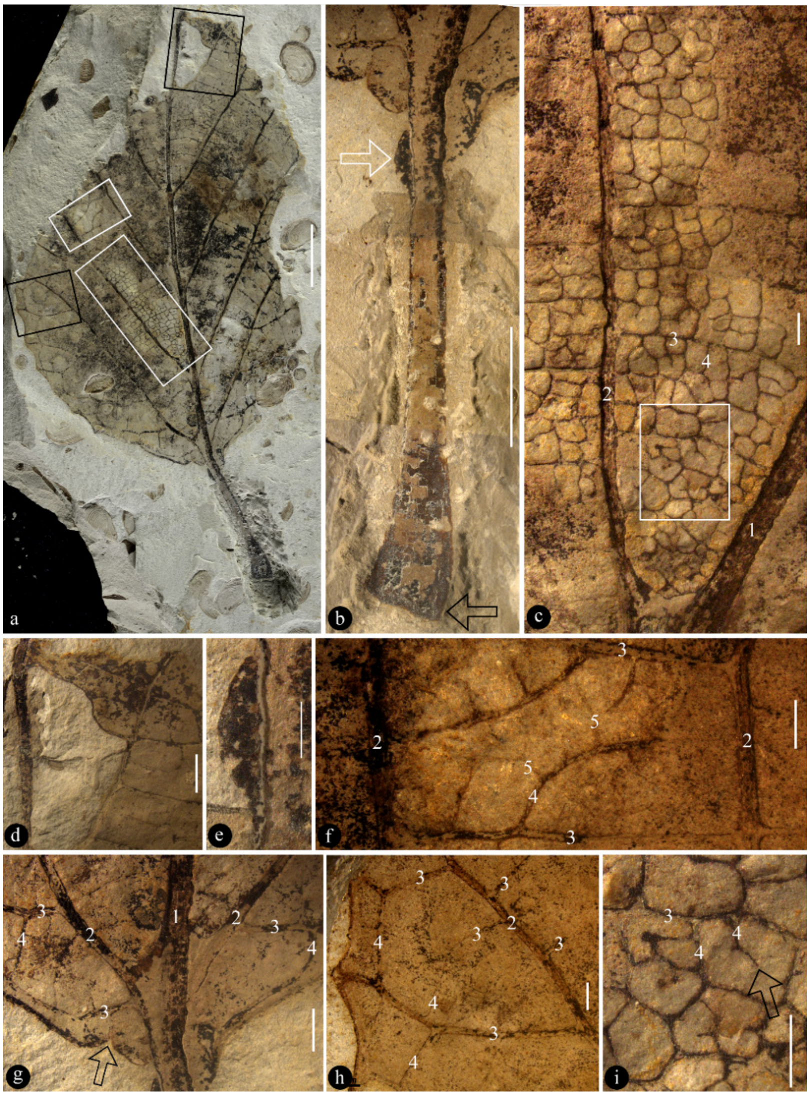

Figure 2: *Arthollia dayangshuensis* sp. nov and its details. The order of the veins are marked with corresponding numbers.

(a) General view of the leaf. The rectangular regions are detailed in later figures. Holotype. ZZB-P001. Bar = 1 cm. (b) Detailed view of the petiole of the leaf. Note the enlarged base and lamina remains (arrow) on the lateral of the petiole. Bar = 5 mm. (c) Detailed view of the bigger white rectangular region in (a), showing conspicuous venation after skeletonization (DT16). Bar = 1 mm. (d) Detailed view of the upper black rectangular region in (a), showing the removal of leaf tissues on both sides of the midrib (DT63). Bar = 2 mm. (e) Detailed view of the lamina remains after insect damage along the lateral of the petiole, refer to (b). Bar = 1 mm. (f) Detailed view of the smaller white rectangular region in (a), showing areoles and several orders of veins between two secondary veins. Bar = 1 mm. (g) Detailed view of basal portion of the lamina, showing several orders of veins and damaged lamina base (arrow, compared with the intact right side). Bar = 2 mm. (h) Detailed view of the lower black rectangular region in (a), showing crenate margin and veins. Bar =1 mm. (i) Detailed view of rectangular region in (c), showing areoles, several orders of veins, and simple linear veinlet (arrow). Bar =1 mm.

There are three types of insect damages (Figures 2a, 2c, 2d, 2g, 2i). The first type is hole feeding (DT 57) [7] with the trapped trace at the divergence of the secondary vein from the midvein (Figures 2a, d). The second type is margin feeding (DT12, DT14) [7] (Figure 2g). DT12 is characterized by the circular, shallow to deep excisions from the leaf margin and with no more than 180 degrees of arc (Figure 2g), and DT14 by the excision of leaf to the midvein (Figures 2a, d) [7]. The third type is skeletonization (DT16) (5), in which all the tissues except vascular bundles are consumed and reaction rim is poorly developed (Figures 2a, c, i). The skeletonization is situated in the central region of left half-lamina and is in direct contact with the midvein and major secondary veins (Figures. 2a, c, i).

Remarks

The new species is very similar to *Arthollia insignis* (Plate 3, Figures 1-5 [8]) in terms of the venation and leaf shape, but differs from the latter in strictly opposite arrangement of the secondary veins. This difference, in addition to its geographical distribution, justifies a new species, *A. dayangshuensis* sp. nov.

Etymology

dayangshu-, for Dayangshu, the name of the basin from which the fossil was collected.

Holotype: ZZB-P001 (Figure 2a).

Type locality:

Ganhe Farm, Hulunbeier, Inner Mongolia, China (N49°20′36.39″, E124°39′32.69″).

Stratigraphic horizon:

The Nenjiang Formation, Santonian-early Campanian, Upper Cretaceous (83.4-85.7 Ma).

Depository

Natural History Museum, Weihai Ziguang Shi Yan School.

Discussions

The basal position of the Platanaceae in Eudicots makes the family very important in the systematics of Eudicots [9-12]. The extant Platanaceae includes only one genus, *Platanus*, with 7-9 species scattered in the temperate to tropical regions of North America, Europe as well as southeastern Asia [12,13]. The diversity of the family used to be much greater than today [14-17]. Their fossil record starts from the Early Cretaceous, and is widely distributed in Greenland, Europe, North America, and Asia [10,11,13,15-35]. The oldest record goes back to the Aptian [36], but the records become abundant since the Albian [9,17,22,23,29-33,35,37]. The ubiquitous presence of the Platanaceae in the Early-Middle Cretaceous floras is in line with its basal position in Eudicots. Sometimes platanaceous leaves may constitute the dominant species in some megafloras of the Dakota Formation [35].

The new fossil leaf reported here is comparable to *Arthollia*, a platanaceous fossil leaf genus recognized in northeast Russia [8] in general leaf shape and venation. The leaf margins of extant *Platanus* species vary from entire to serrate [15]. *Arthollia dayangshuensis* is similar to the basal leaf of extant *Platanus* (especially *P. occidentalis*, Figure 3) in its unlobed lamina, general leaf shape, straight secondary veins almost reaching lamina margin, regular tertiary veins forming meshes, and enlarged petiole base, but differs in coarsely serrate lamina margin and poorly-developed teeth, and thus different from well-toothed *Platanus* of North America, Greenland, and Asia [15]. The enlarged petiole base is a feature shared among *Arthollia dayangshuensis, P. fraxinifolia* and *P. neptuni* [15], suggestive of the presence of intrapetiolar axillary bud in these taxa. This feature is a proxy of deciduous habit and seasonal climate [35]. Fossil leaves of nymphaealean affinity (in progress) associated with *Arthollia dayangshuensis* suggest that *Arthollia dayangshuensis* may be a tree living in a niche not far away from water body, which may be common in this region at that time, a landscape quite different from the current prairie.

The latest palynological study indicated that angiosperms played a minor role in the Nenjiang Flora, accounting for less than 1% of diversity in the palynoflora [4]. This is in stark contrast to the frequent occurrence of angiosperm leaves in the megaflora, on which further investigation is on-going. The occurrence of *Arthollia dayangshuensis* in north China, plus previous reports of platanaceous fossil records in USA, China, Russia, and Greenland, favors the circumboreal dispersal of the family, just like the Hamamelidae, proposed by Kvacek et al. [15]. The congeneric occurrence of *Arthollia* in north China and northeast Russia implies the geographical and ecological similarities shared between these regions. Three types of insect damages are recognized in this single specimen. The insect damages are hole feeding, margin feeding, and skeletonization (Figures 2a, 2c, 2d, 2g, 2i). These feeding damages are all due to external foliage feedings caused by mandibulate insects [7]. The hole feeding and margin feeding generally remove tissues and/or veins (Figure 2g), unlike skeletonization which is reluctant to chew the vein with nutritional barriers, such as lowness in nutrition (Figure 2c) [38-40], structure in sclerosis [39,41]. The most diverse leaf-chewing insects are mainly Coleoptera (beetles), but other major groups include Orthoptera, Phasmida, and Lepidoptera [42]. Skeletonization tends to be formed by holometabolous insects such as Coleoptera, Hymenoptera, Diptera, and Lepidoptera [39,43-45]. Due to the non-distinctive and non-recognizable damage pattern of external feedings, and considering no insect records in the Nenjiang Formation of Inner Mongolia, China, it is difficult to figure out the specific feeders now.

The varied damage types (Figures 2c, 2d, 2g) suggest that there were at least two chewing mouthpart types and at least three different insects were feeding on the leaf of *Arthollia dayangshuensis*. Checking out the previous record of insect damage on angiosperm leaves [2], it is clear that there is only one type of insect damage on each leaf, suggesting either that there is already host specificity at the beginning of the Late Cretaceous, or the ecological relationship between angiosperms and insects is primary and not diversified yet. The contrast between the present fossil material and previous record indicates that, at least by the Late Santonian, *Arthollia* (Platanaceae, Eudicots, Angiosperms) already has become the food resources for three different insects. This indicates that the Santonian ecosystem is already more complicated than that of the early angiosperms in term of food web and energy flow.

Figure 3: Leaves of *Platanus occidentalis* Linn. 222789, Herbarium of the Institute of Botany, Nanjing.
(a) General view of the specimen, showing variable leaf shapes in a single specimen. Bar = 2 cm.
(b) Detailed view of the basalmost leaf in Figure 3a, with an enlarged leaf petiole. Bar = 2 cm.

Conclusion

Arthollia dayangshuensis is a new fossil leaf recovered from the Nenjiang Formation (late Santonian-early Campanian) of Inner Mongolia. This fossil, together with previous data, adds evidence on the palaeogeography, history as well as ecology of the Platanaceae during the Late Cretaceous. The relationship between fossil angiosperms and insects has become complicated by the end of the Santonian, suggesting that, far before the eve of the Cenozoic, the angiosperms-related palaeoecosystem had started its complication and reached certain complexity.

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