Paleoguía 01
Paleonturology 22 award edition
Advanced level

Paleonturología

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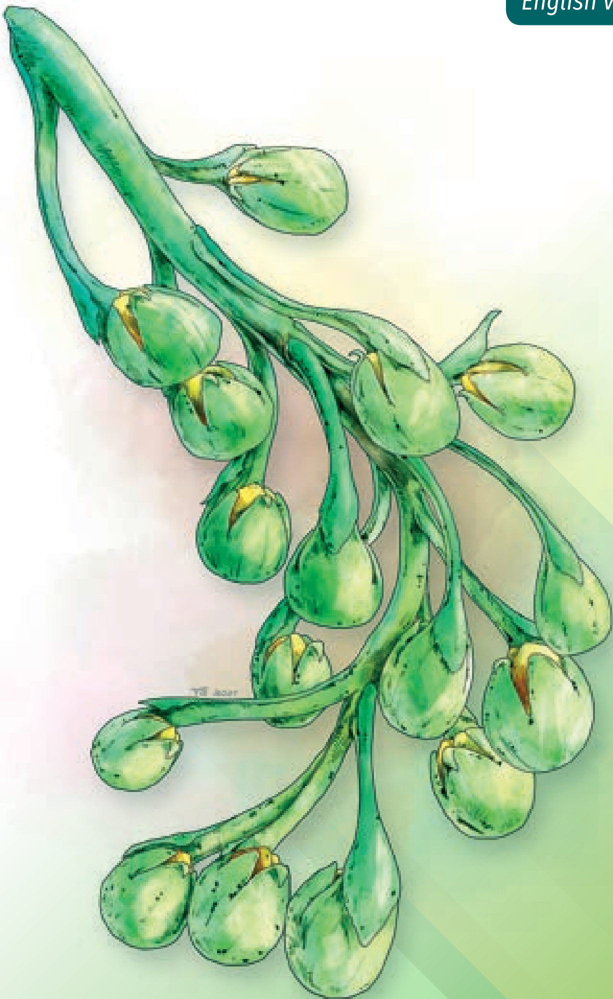

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Paleoguía collection

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Flowers and cupules:

shedding light into Darwin's "abominable mystery" concerning the origin of angiosperms

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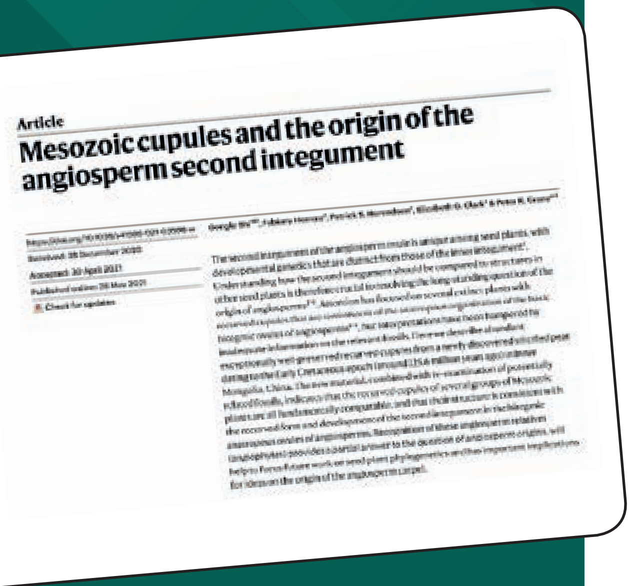
Article

Mesozoic cupules and the origin of the angiosperm second integument

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Introduction to flowering plants

Flowering plants (angiosperms) are the most diverse group of plants living on land and dominate almost all terrestrial ecosystems. Through the process of photosynthesis they provide most of the chemical energy that sustains terrestrial biodiversity and on which all of us also depend. Angiosperms provide not only food, but also timber, fiber, oils and medicine. In addition, they are also central in the planetary natural systems that cleanse the water, replenish the soils, and regulate the global climate.

For all these reasons the origin of angiosperms, and how they rose to vegetational dominance, has been of broad interest since Darwin considered their "sudden" appearance in the fossil record as an "abominable mystery" for science, and since the first ideas about the evolution of plants were formulated. Over the last few decades there have been major advances in understanding the timing and pattern of early angiosperm evolution through the Early Cretaceous between 130 and 100 million years ago. However, knowledge of how angiosperms arose and what their closest fossil relatives might be remains very uncertain.

Flowers (Fig. 1) are one of the distinctive innovations of angiosperms that almost certainly contributed to their early diversification. However, flowers are very varied and have diverse morphologies, so it is essential to understand how their different parts evolved to clarify their origin and how angiosperms could be related to other types of plants. For this reason, the unusual seeds that they present and the fruits that they develop are of special interest.

Fig. 1. Variety of types of angiosperms in greenhouse.

Angiosperm seed and the issue of the two layers

In gymnosperms (e.g., conifers, ginkgoales and cycads), and also in angiosperms, the structures from which the seeds develop are the ovules. The typical structure of a gymnosperm ovule is that there is one protective layer (integument) that surrounds the embryo early in its development (Fig. 2A). In contrast, the typical structure of an angiosperm ovule is that there are two integuments (Fig. 2B), of which the inner integument is thought to correspond to the single integument of gymnosperms. Therefore, understanding how the second (outer) integument arose is critical for understanding the evolutionary origin of angiosperms and to which group of extinct gymnosperms they might be related.

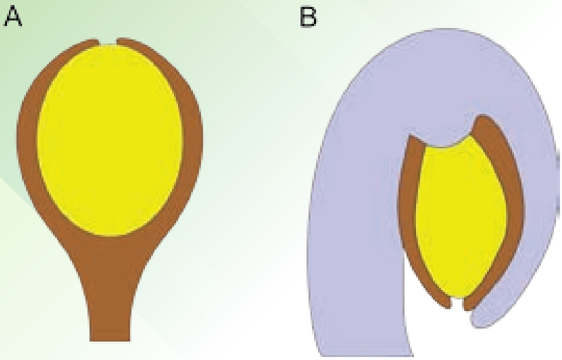

Fig. 2. Interpretative diagrams of ovules. A. Gymnosperms ovule with one integument (brown) surrounding the embryo. B. Recurved angiosperm ovule with two integuments.

The fossil record shows that several groups of extinct gymnosperms had a reflexed cup-like structure (cupule) that encloses the seed or seeds (e.g., *Caytonia*, Fig. 3). These cupules have been suggested to perhaps be the precursors of the angiosperm second integument. However, carefully assessment of this possibility has been hampered by inadequate knowledge of the relevant fossils and uncertainty about how the various cupules known among Mesozoic plants should be compared. Many of the fossil cupules reported in the fossil record are known only from impression or compression fossils, the detailed morphology and anatomy of which is not well preserved and therefore not well understood.

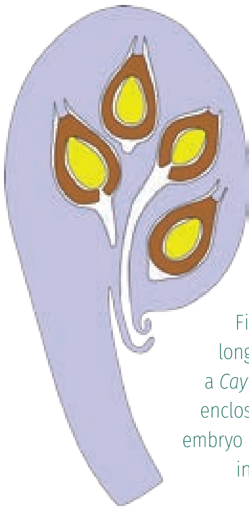

Fig. 3. Reconstructed longitudinal section of a *Caytonia* cupule (grey) enclosing the seeds with embryo (yellow) and single integument (brown).

A new Early Cretaceous exceptional fossil site

In 2017, a new silicified peat –chert- was discovered at an opencast coal mine in Jarud, eastern Inner Mongolia, northeastern China (Fig. 4).

Fig. 4. Geographical location of the fossil site containing the studied fossils.

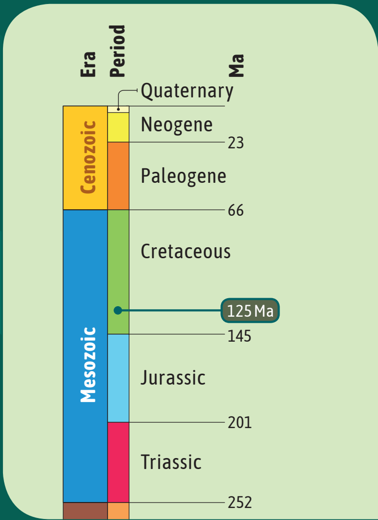

Fig. 5. Chronostratigraphic chart indicating the age of the cupules.

Fig. 6. A mineralized cupule exposed on the chert surface.

This fossil site that contains a silicified mass of well-preserved plant parts preserved in an silicified old deposit of peat named as chert. Dating using isotopic methods shows that the peat is of Early Cretaceous age and about 125 million years old (Fig. 5).

At the locality the fossil plants are preserved in silica, which infiltrated and petrified the plant tissues before they had decomposed. The preservation, which extends to the level of individual cells within the plant tissues, is exquisite. This allows the fossils to be described in great detail and enables careful comparison to other fossils as well as living plants. Especially common in these silicified deposits are the seed-bearing cupules of a new kind of extinct seed plant (Fig. 6).

Preparation and investigation of the new fossils

Blocks of chert collected from the Inner Mongolia locality were sawn into slabs with a diamond-blade saw. The polished surfaces of the slabs (Fig. 7) were etched with hydrofluoric acid and peels of the acid resistant plant cell walls were made using cellulose acetate sheets partially dissolved in acetone. Once dry, and carefully pulled away from the rock, the peels were examined under a microscope to reveal the individual cells making up the different tissues (Fig. 8).

The fossil seed-bearing structure, which is named as *Jarudia zhoui*, is lax seed cone consisting of flexible central axis bearing helically arranged, recurved cupules, each arising in the axil of a bract (Fig. 7), and each containing two three-angled seeds (Fig. 8).

The cupules were also scanned using X-ray micro–computed tomography to produce computer files from which the three dimensional structure of the fossils could be reconstructed (Fig.9).

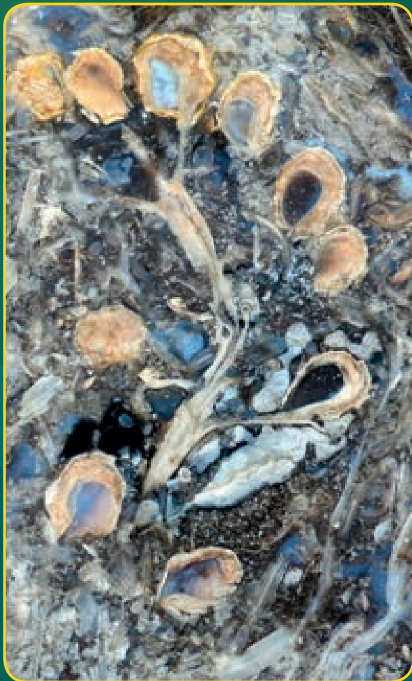

Fig. 7. Silicified seed cone of *Jarudia zhoui*.

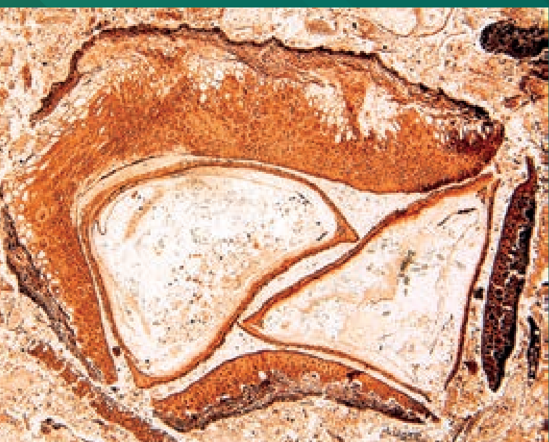

Fig. 8. Peel of cross section of a cupule enclosing two seeds.

Fig. 9. Three-dimensional reconstructions of the seed cone of *Jarudia zhoui* from Micro-CT data.

Implications for angiosperm origins

Detailed analysis of the new silicified cupules from Inner Mongolia (Fig. 10A), together with reexamination of previously described fossil cupules and careful comparisons, suggests that the recurved cupules found in several groups of extinct seed plants from the Mesozoic are all fundamentally the same.

Extinct seed plants with these kinds of cupules enclosing the ovules first appear in Late Permian 255 million years ago. The manner in which they are recurved is very similar to the curvature seen in most angiosperm ovules (Fig. 10B). In living angiosperms this curvature is also intimately connected, both developmentally and structurally, to the presence of the (second) outer integument.

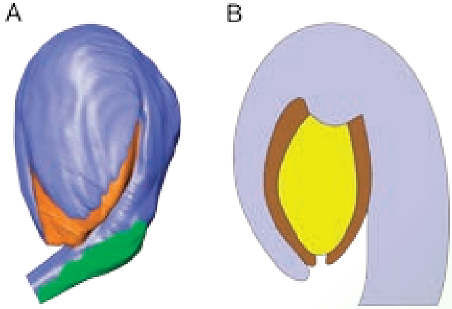

Fig. 10. Comparison of cupule of *Jarudia zhoui* (A) and angiosperm ovule (B).

Recognition that the recurved cupule of *Jarudia zhoui* surrounding the two seeds may be directly equivalent to the second integument in angiosperms (Fig. 10), one of their most distinctive features, provides a partial answer to the question of flowering plant origins. It suggests that *Jarudia zhoui* (Fig. 11) and similar cupulate seed plants are a key link in the evolutionary chain that connects early seed plants to flowering plants. It also indicates the recurved structure seen in the young ovules of flowering plants is a hold-over from an earlier pre-angiosperm phase of evolution. It also has important implications for understanding the relationships between angiosperms and other extinct seed plants, which is critical for ideas on the origin of the carpel, the structure that encloses the seed and forms the fruit wall and plays a critical role in flowering plant reproduction.

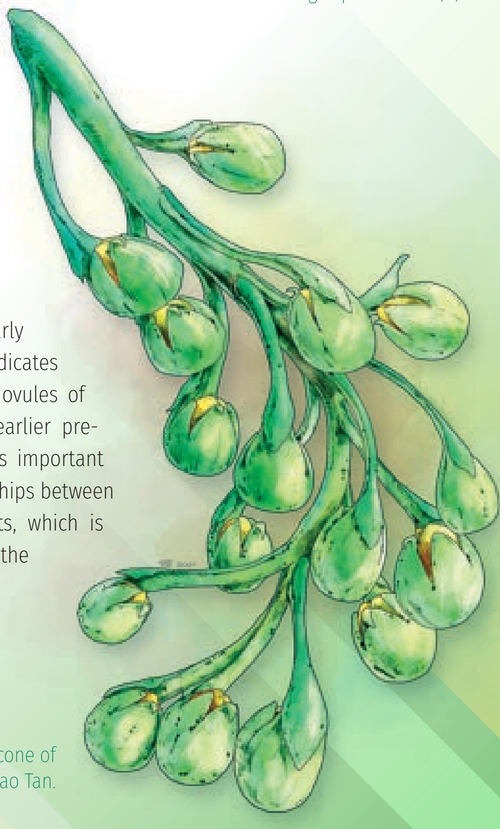

Fig. 11. Restoration of seed cone of *Jarudia zhoui* by Chao Tan.

Two views of the site in eastern Inner Mongolia (China) where the fossils of the studied cupules were found, together with the field team and researchers who discovered the locality in the summer of 2017.

Spanish version

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