millions of copies to be printed on expensive, cutting-edge silicon wafers. We can therefore expect the semiconductor industry to redouble its interest in replicating the authors' work, and to pursue a host of similar applications throughout the chip-design process.

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The author declares no competing interests.

Evolution

Seed for thought

Douglas E. Soltis

The origin and rapid diversification of flowering plants is a long-standing "abominable mystery", as Charles Darwin put it. Part of the puzzle – the origin of the protective covering of flowering-plant seeds – is nearing resolution. **See p.223**

One of the landmark events in evolution is the appearance of flowering plants, termed angiosperms. On page 223, Shi *et al.*[1] describe fossil evidence that sheds light on a long-standing mystery about seed evolution.

A number of botanical innovations accompanied the appearance of flowering plants and contributed to the organisms' rapid rise to worldwide dominance of terrestrial and many aquatic ecosystems. Such innovations include floral organs and a special nutritive tissue for the plant embryo – endosperm. In addition, flowering plants and another plant group, gymnosperms, produce seeds, which provide a protective layer around the developing embryo. This enabled seed plants to truly conquer the terrestrial environment, overtaking other land plants such as mosses and ferns, which do not produce seeds. Seeds have also had a central role in enabling human survival by providing an important food source.

Flowering plants arose from an ancestor in the gymnosperms[2,3]. The fossil record contains many clades of now-extinct gymnosperms, and it is not clear which group gave rise to the angiosperms, although it is definitely not one of the living groups of gymnosperms – plants such as conifers, ginkgo (*Ginkgo biloba*) or cycads[2,3].

All gymnosperms have just one protective layer, termed an integument, that surrounds their seeds, whereas flowering plants have two such layers. In a letter[4] to the botanist J. D. Hooker, Charles Darwin described the origin of flowering plants as an "abominable mystery". An enigma embedded in this mystery is how the second (outer) protective layer evolved. The outer integument differs from the inner one in its developmental pathway and in the genetic control governing tissue-layer formation[5,6], and the two integuments are thus clearly very different from each other.

Shi and colleagues describe extremely well-preserved fossils of extinct seed plants. They use these remarkable newly described fossils, as well as other similar-looking fossils reported earlier[2], to build a tree of relationships between plants. Their effort places all of these fossils on the plant family tree at a position close to that of flowering plants – they are very close relatives of modern angiosperms, and, as such, might provide clues to their origin. The fossils of these ancient relatives of flowering plants show remarkable diversity in the shape of their reproductive structures. Amazingly, these are not recently discovered fossil specimens; they were collected almost a century ago, deposited in museum collections and only recently unearthed for a second time (this time, from museum drawers by the authors), with their relevance for reconstructing the plant family tree now finally recognized.

These extinct plants had a cup-like structure, termed a cupule (Fig. 1), that surrounded the developing seed or seeds (each seed itself having just one integument, which typifies all gymnosperms, living and extinct). The role of these cupules is unknown, but they might have provided extra protection for the seed, or aided its dispersal.

Might the cupule be the precursor to the outer protective layer unique to flowering-plant seeds? There is another twist (pun intended) to solving the mystery of angiosperm seeds.

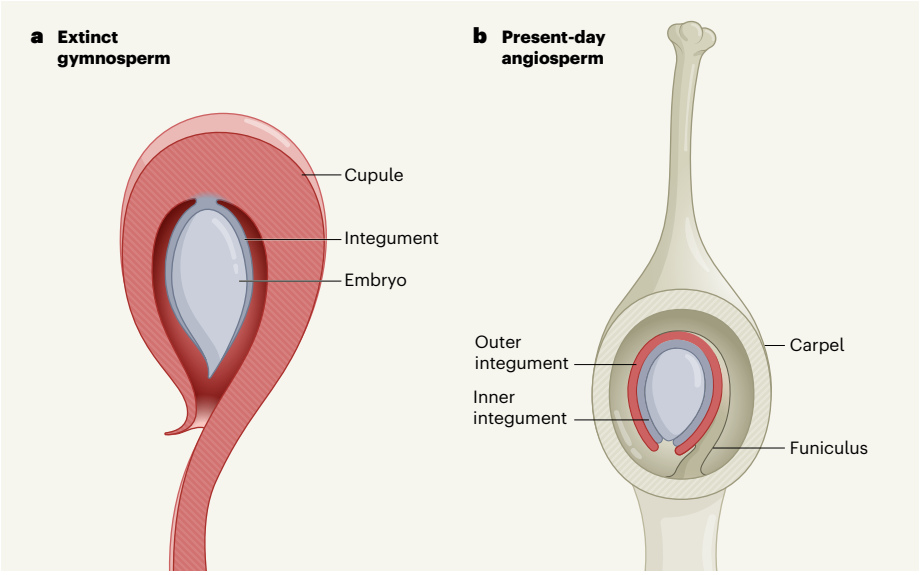

Figure 1 | Seed evolution. Shi *et al.*[1] present fossil evidence that sheds light on a long-standing mystery about the origin of the protective layer, termed the outer integument (or second integument), that surrounds the seeds of flowering plants (angiosperms). It is thought that flowering plants arose from now-extinct plants belonging to a group called the gymnosperms (living members of which include conifers). **a**, Gymnosperms have one integument that surrounds the embryo of a seed. A structure called the cupule, which might have provided protection or aided seed dispersal, formed the outer layer of ancient gymnosperm seeds. **b**, Flowering plants have inner and outer integuments. Shi and colleagues find that the cupule probably evolved to form the outer integument of flowering plants. Angiosperm seeds are connected to the carpel structure that surrounds them through a stalk called the funiculus. Shi and colleagues suggest that the funiculus evolved from the stalk of the gymnosperm cupule.

Flowering-plant seeds are also unusual in their overall structure — the top of the seed is bent back on the stalk that connects it to the plant body[5]. Imagine if, instead of standing upright with your head well away from your toes (analogous to the 'body plan' of a seed of a living gymnosperm), you were bent over, with your head next to your toes (echoing the layout of a flowering-plant seed). Crucially, in these newly described fossils, the cupules, with the seed(s) they surround, are also bent back on themselves in a fashion remarkably like the distinctive 'recurved' seeds of flowering plants. Eureka!

Shi *et al*. describe fossils that date to only approximately 126 million years ago, a time by which, by most estimates, angiosperms were already on the scene[3]. So what is the big deal? Similar cupule-bearing fossils are much older — including *Caytonia*, a fossil gymnosperm whose discovery first raised the possibility that similar extinct plants with cupules and seeds were close relatives, or even ancestors, of flowering plants[2,3]. They date to around 250 million years ago, long before most estimates of the time of origin of flowering plants[7–9]. Collectively, the fossils described by Shi and co-authors, together with the earlier-reported fossils with cupules, paint a clear picture showing that the second integument is derived from the cupule of an extinct gymnosperm. Mystery solved.

To be clear, the fossils described by Shi and colleagues do not correspond to the immediate ancestors of flowering plants; those fossils remain to be found. Nonetheless, they provide previously missing crucial information about the origin of angiosperms. But more fossils are badly needed to clarify angiosperm origin further.

Although Shi and colleagues' work seems to have solved the riddle of the outer integument of angiosperm seeds, other mysteries remain. These include the origin of the protective covering (the ovary) that collectively surrounds all of the seeds in flowers and that ultimately gives rise to fruit, another structure that transformed our planet and is essential to human survival. The origin of special pollen-bearing structures termed stamens in flowering plants also requires clarification. Another evolutionary enigma concerns the endosperm, which is unique to flowering plants.

"Amazingly, these are not recently discovered fossil specimens; they were collected almost a century ago."

There has long been a romantic view that the fossils required to resolve these and other questions must be discovered by palaeontologists working in the field with rock hammers in hand. But, as Shi and colleagues' paper demonstrates, perhaps other key pieces to the fossil puzzle don't need to be unearthed. Instead, they might be hiding in plain sight in palaeobotanical collections around the world, waiting for an intrepid scientist to simply open the right cabinet drawer.

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The author declares no competing interests.
This article was published online on 26 May 2021.