# Taiyuanostachya: An Abominable Angiosperm from the Early Permian of China

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# *Taiyuanostachya*: An Abominable Angiosperm from the Early Permian of China


## Abstract

Although angiosperms are can be clearly and strictly defined by their enclosed ovules, how old angiosperms are remains elusive. To solve this problem, the only reliable way is digging fossils. The currently widely accepted age for angiosperms is the Early Cretaceous, although this conclusion is facing increasing challenges pre-Cretaceous fossil evidence of angiosperms as well as molecular clocks. Here we report the outcome of our investigation on a Palaeozoic fossil plant, *Taiyuanostachya* gen. nov. Unlike previously thought, the fossil plant has both enclosed ovules and enclosed seeds. Since enclosed seeds are a feature characteristic of angiosperms, and enclosed ovules are idiosyncratic of angiosperms, the occurrence of both these features in *Taiyuanostachya* indicates that angiosperms, the single most diversified plant group on the Earth, may well have occurred in the Palaeozoic, and the origination of angiosperm appears to be much more complicated than assumed previously. Such a conclusion is astonishing for many but favors some molecular dating done decades ago.



**Key words**: angiosperm, Permian, Palaeozoic, evolution, China.

The age of angiosperms has been heatedly debated among botanists for a long time [1-37]. Although molecular clocks have suggested various earlier origins of angiosperms, ranging from the Carboniferous to the Jurassic[29,38,39], a conclusion in line with independent studies[6,10,15,21-24,40-44], their conclusions are largely ignored by palaeobotanists who prefer fossils to DNA sequences. Although Stebbins[45] stated that "the evolutionary line leading to the angiosperms entered a dark tunnel of ignorance at the end of the Paleozoic until the early Cretaceous", this statement was never proven true or corroborated by fossil evidence: Scott et al.[20] annihilated all pre-Cretaceous angiosperms, and thenceforth the status of study on origin of angiosperms remains unchanged[46] in spite of all progresses made in palaeobotany. The reason underlying such an academic stagnancy includes 1) a lack of well documented fossil evidence, which is the key to the problem[2], and 2), more importantly, a lack of consensus of criterion identifying angiosperms in the fossil world. Although there are recent reports of angiosperm trace in the Triassic and Jurassic [6,21-25,40,41], all of these reports were suspected by some palaeobotanists [46]. A merit of the paper[46] is that they clearly listed several features unique of angiosperms, which, if no controversy rose, could be used as criterion identifying a fossil angiosperm. Unfortunately, this possibility disappeared soon: the authors listed five exemplar fossil angiosperms that did not meet their own criterion in the same publication [46,47]. This refutation was stengthened by Friis et al.[48] who published another fossil angiosperm, *Hedyflora*, that did not honor this criterion[48,49]. To be conservative, here we adopted ovules enclosed before pollination as a criterion identifying fossil angiosperms, which has been raised and repeatedly applied previously [6,40,42,50-53] and is closely related to the core feature of angiosperms, angiospermy. Applying this criterion, we identified a new angiosperm, *Taiyuanostachya ovuilifera* gen. et sp. nov, from the Lower Shihhotse Formation of Shanxi, China. Both occurrence of enclosed ovules and enclosed seeds in *Taiyuanostachya* are suggestive of the occurrence of angiosperms in the Palaeozoic. Considering its Permian age, recognizing *Taiyuanostachya* as an angiosperm at least doubles the widely accepted age of angiosperms in the geological history, if *Archaefructus* is taken as the earliest record of angiosperms. Such a discovery will heavily influence the current understanding of angiosperm evolution and history.

*Taiyuanostachya* gen. nov

**Synonym**:

*Tingostachya tetralocularis* (Konno) Gao and Thomas 1987

**Diagnosis**: Fertile shoot consisting of a peduncle and a terminal reproductive organ. Leaves on peduncle ensiform, spirally arranged. Organ cylindrical, single or in twins. Lateral appendages vertically attached to the organ axis, whorled, with up-turning distals parallel to organ axis, with or without filamentous tips. Ovules/seeds spheroidal, attached to the organ axis, enclosed in lateral appendages. Central canal in lateral appendages connecting ovule/seed with exterior, filled with spongy materials, with an opening at the distal of the lateral appendages. Ovule orthotropous, unitegmic, with a micropyle. Seed with layered seed coat.

**Remarks**: The specimens studied here were previously described as *Tingostachya tetralocularis* (Konno) Gao and Thomas[54]. However, as Gao and Thomas admitted, they had "a rather different morphological interpretation to that proposed by Konno (1929)."[54] For example, their "sporophylls" were not in whorls of four, and their specimens have "certain undescribed features of sporophyll construction”. The assumed “adaxial surface” position of the spheroidal sporangia on the sporophyll pedicels cannot be ascertained, as it is within the lateral appendages (Figs. 1d, 2a-d, 3h, S2a-b, d, S3f, S4a-b, S5a,c). These suggest that the specimens Gao and Thomas studied have may not belong to *Tingiostachya tetralocularis* Konno (1929)

Although Gao and Thomas mentioned SEM observed “putative spores” in sporangia, they did not show any figure of such spores[54]. There is no trace of “tetralocular synangium” characteristic of *Tingostachya tetralocularis* Konno[54]. These made their claims of spores in *Tingostachya tetralocularis* (Konno) Gao and Thomas spurious. Such a lack of deepened understanding of *Taiyuanostachya* forced Gao and Thomas to admit that they even did not know the fossils they documented were a pteridophyte, a gymnosperm, or a progymnosperm. Our recognition of ovule with micropyle and seed with layered seed coat eliminated the existence of sporangia in *Taiyuanostachya*.

The presence of spongy materials in the central canal in lateral appendages of *Taiyuanostachya* is first time recognized in *Taiyuanostachya* gen. nov (Figs. 1e, 3i, S3f-g, S4a-b). However, in their documentation of *Tingiostachya tetralocularis* (Konno) Gao and Thomas, “a layer of light coloured sediment” has been seen “between two layers of compression material (Pl. 90, fig. 5; text-fig. 3C-E)[54]. Our SEM revealed more details of such materials and have convinced us that it may be related to the pollination of *Taiyuanostachya*, just as in basal angiosperms[55].

Considering the above differences from original diagnosis of *Tingostachya tetralocularis* Konno (Konno, 1929), our failure observing any trace of spores in the specimens, and our recognition of enclosed ovules/seeds and central canal filled with spongy materials in the specimens, we prefer to separate these specimens from *Tingostachya tetralocularis* (Konno) Gao and Thomas and establish a new genus *Taiyuanostachya* for the specimens documented here.

**Etymology:** *Taiyuan-* refers to the fossil locality, Taiyuan City, Shanxi, China; *-stachya* refers to the ear-like organ.

**Holotype:** *Taiyuanostachya ovuilifera* gen. et sp. nov

**Horizon**: the Lower Shihhotse Formation, Permian.

**Age:** the Early Permian (>272 Ma ago).

*Taiyuanostachya ovuilifera* gen. et sp. nov

(Figs. 1-4, S1-S5)

**Species diagnosis**: the same as that of the genus.

**Description**: The specimens are coalified compressions embedded in yellowish or greenish siltstones (Figs. 1a-d, S1a-c, S3a-d). The organ is cone-like structures paired or single on a peduncle (Figs. 1a-d, S1a-c). The peduncle is up to 29 mm long, and 2 mm wide (Figs. 1b-c). The organ is cylindrical in form, curved or straight in form, 3.3 to 4.3 cm long, 10 to 11 mm in diameter (Figs. 1a-d, 2a, S1a-c, S3a-d). Numerous lateral appendages are whorled, attached to the organ axis vertically, with up-turning distal parts that have filamentous tip (Figs. 1a-f, 2a, 3h, S1a-c, S2a-c, S3a-d,f, S4a-b, S5a,c). Lateral appendages are 4-5 mm long, 1.2-1.7 mm thick, approximately 8-10 per cycle (Figs. 1a-e, 2a, 3g-h, 4a, S1a-c, S2a-d). Lateral appendages in adjacent whorls alternate or opposite each other (Figs. 1d, 2a, 3h, 4a, S1a-c, S2c, S3a-d,f). Inside each lateral appendage, there is a central canal running into the distal (Figs. 1e-f, 3h-I, S4a-c, S3f-g, S4a-b, S5a, c) and an ovule directly attached to the axis (Fig. 1a-d, 2a-d, 3g-h, S5a,c). The central canal is filled with spongy materials (Figs. 1e-f, 3h-i, S3f-g, S4a-b, S5a,c), has an operculum in the distal part (Figs. 4a-c, S4a-b, S5a,c). Filamentous tips on the up-turning parts may range from 1 to 15 mm in length (Fig. 1d, f, 3h, S3f). Ovules are round-triangular in form, 1.5-1.6 mm long and 1.2-1.3 mm in diameter, with a distal micropyle and one layer of integument approximately 0.2 mm thick, attached to the axis (Figs. 3a-b, S2a-b, S3e-f, S4a-b, S5a-c). A seed is invisible to naked eyes in an intact lateral appendage but visible to naked eyes when the lateral appendage is broken basally (Figs. 1d, 2a-d, 3a-h, S2a,b,d, S3f, S4a-b), discoid in form, 1.2-1.4 mm long, 0.9-1.4 mm wide, 0.4 mm thick, with a sarcotesta 0.1 mm thick outside a sclerotesta 0.06- 0.14 mm thick (Figs. 2a-f, 3c-h). Cells of the sclerotesta are rectangular-shaped, arranged in files, while those of sarcotesta are more irregular and not arranged in well-defined files (Fig. 3e).

**Holotype**: GP0094.

**Further materials:** GP0093, GP0094-A, GP0095, B461.

**Remarks**: The seed described is *in situ* in the lateral appendage, suggestive of a fruit nature of the appendages. We prefer the word “lateral appendage” to “fruit” to be more neutral in our interpretation.

**Etymology:** *ovuilifera* refers to the ovules enclosed in the fossil.

**Locality**: 5 km north-east of East Hill Mine, Taiyuan, Shanxi province, northern China.

**Horizon and age**: the Lower Shihhotse Formation, Permian; the Early Permian (>272 Ma ago).

The core feature of angiosperms is “angiospermy”, which literally means enclosed seeds. However, as ODC (Offspring Development Conditioning) is almost a universal trend in sexually reproduced organisms [56], it is not surprising that some conifers enclose and thus protect their seeds after pollination [52]. So enclosed seeds are patent of angiosperms any more. Fortunately, enclosed ovules before pollination remains idiosyncratic of angiosperms. This is the reason Wang [42] proposed it as a criterion identifying fossil angiosperms. This is the criterion we adopt here and is the foundation for the following discussion.

Our so-called seed in Figs. 2a-f was previously interpreted as sporangium [57]. So it is necessary to clarify before further discussion. Although interpreted as sporangium, Gao and Thomas[54] failed to show any figure of *in situ* spore or pollen. Such an outcome implicitly rejects the sporangium interpretation. Our new observation indicate that there is a layered seed coat composed of sarcotesta and sclerotesta in the seed (Figs. 3c-f), a structure never expected for a sporangium. This is in line with the lack of spore/pollen in documentation of Gao and Thomas[54]. Although spore plants do have some structures like indusium protecting their sporangia, having sporangia enclosed as in *Taiyuanostachya* does do harm to dispersal of spores and thus is a disadvantage for the plant, this suggests that the seed (in our term) of *Taiyuanostachya* is unlikely to be a sporangium. The occurrence of shiny seed coat with sclerotesta of dense materials (Figs. 2a-f) eliminates the possibility of being sporangium. This conclusion is further strengthened by the discovery of micropyle and integument in the ovules of *Taiyuanostachya* (Figs. 3a-b), both structures unexpected for any sporangium. What is important is that these ovules are fully enclosed in the lateral appendages in *Taiyuanostachya*. Finally, the spongy materials filling the central canal (Figs. 1e-f, 3i, S3f-g, S4a-b) conjures to secretion secluding ovary in extant basal angiosperms [55]. Such observation suggests that the ovules in *Taiyuanostachya*, although not physically secluded (due to the presence of the canal), are isolated from the exterior space, and that the spongy materials may function like pollination drop or similar oozes in guiding the pollen tube to the micropyle for a successful pollination. All these converge to one conclusion that what seen in the lateral appendages of *Taiyuanostachya* are ovules and seeds.

As it is shown in Figs. 2a-f and 3c-f, seeds are clearly within the lateral appendages in *Taiyuanostachya.* This observation suggests that, at least, *Taiyuanostachya* has enclosed seeds, namely, "angiospermy". Ovules with characteristic features (micropyle and integument) are found enclosed in the lateral appendages in *Taiyuanostachya* (Figs. 3a-b), indicating the occurrence of "angio-ovuly", a feature strictly restricted to angiosperms, in *Taiyuanostachya*. The occurrence of "angiospermy" and "angio-ovuly" unequivocally pins down the angiospermous affinity of *Taiyuanostachya*.

It is noteworthy that the early age, organ morphology, organ organization, and associated fossils of *Taiyuanostachya* all fall out of the previous expectation of angiosperm evolutionary theories. Such a huge discrepancy between theories and fossil facts demand botanists to work hard to fill.

It is noteworthy that specimens of *Taiyuanostachya* (B461[58]; GP0093, GP0094, GP0095[54]) contemporary with *Primocycas chinensis* (B461[58]; GP0001, GP0027[54]), the earliest confirmed fossil record of Cycadales. All these plants belong the well-known Cathaysian Flora of the Lower Permian, which usually is characterized by the presences of *Alethopteris-Emplectopteris-Tingia-Cathaysiopteris* (Li and Yao, 1985). *Tingiostachya* and *Tingia* are frequently seen elements in the Cathaysian flora in the Early Permian[59]. Furthermore *Tingiostachya* and *Tingia* are widely spread in Asia. It appears that angiosperms co-evolved and flourished with the most ancient seed plants, Cycadales, throughout their histories, although, as Stebbins stated, angiosperms later "entered a dark tunnel of ignorance". Now is the time to bring this dark tunnel under light.

Although our study does not imply that all taxa related to *Tingiostachya* share exactly the same morphology with *Taiyuanostachya* gen. nov and thus are angiosperms, these taxa apparently deserve scrutinizing. As a commonly seen plant and an angiosperm in the Permian, *Taiyuanostachya* underscores this currently earliest record of angiosperms, its role in the Permian ecosystem, its far-reaching influence on plant systematics. The current lack of knowledge of the whole plant of *Taiyuanostachya* requires palaeobotanists to work hard to unveil the mystery surrounding itself.

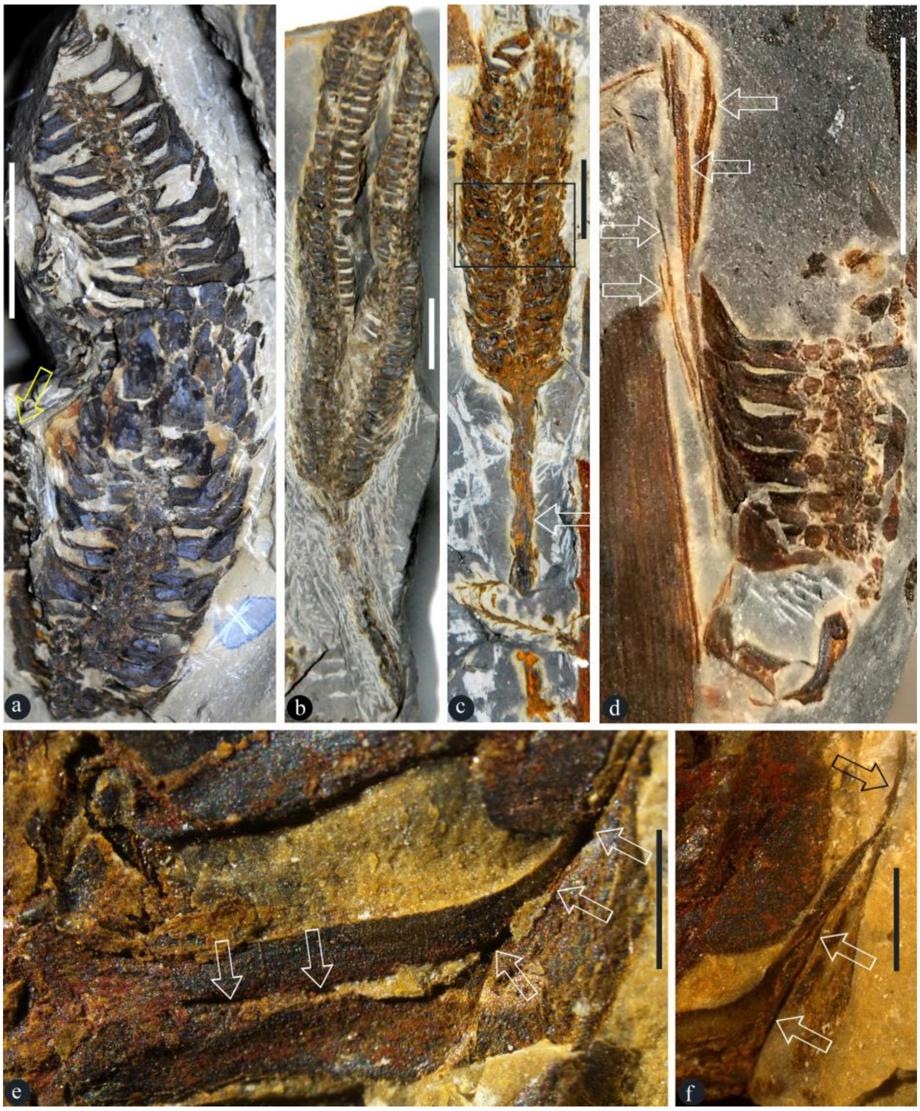


**Figure 1** ***Taiyuanostachya ovuilifera*** **gen. et sp. nov and the details of their lateral appendages. E-F, stereomicroscopy. A**. Holotype of *Taiyuanostachya* gen. nov, on one of the two facing slabs. GP0094. Note another partially preserved organ (arrow). Scale bar = 1 cm. **B**. Twin organ on a peduncle. GP0093. Scale bar = 1 cm. **C**. Whole organ with a long peduncle (arrow). GP0093. Scale bar = 1 cm. **D**. Partial organ. Note the filamentous tips (arrows) of lateral appendages. GP0095. Scale bar = 1 cm. **E**. Radial section of a lateral appendage showing canal (arrows) going through the appendage. GP0094. Scale bar = 1 mm. **F**. Detailed view of the distal of a lateral appendage, showing the canal (white arrows) and filamentous tip (black arrow). GP0094. Scale bar = 1 mm.

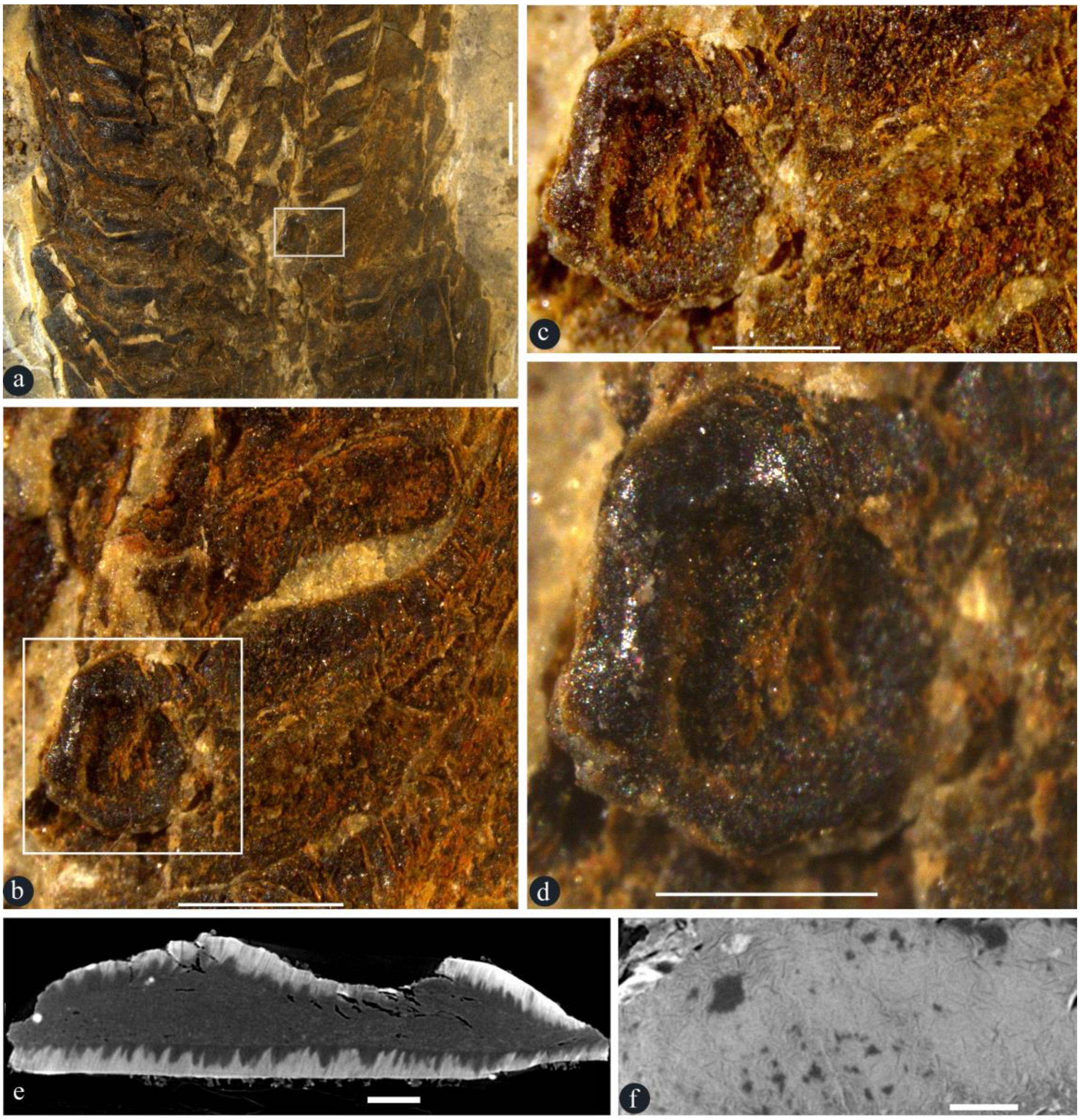


**Figure 2 Details of an *in situ* seed inside a lateral appendage. A-D, stereomicroscopy; E-F, micro-CT virtual sections.** GP0093. **A**. Partial view of the rectangle in Fig. 1c. Scale bar = 2 mm. **B**. Detailed view of the rectangle in Fig. 2a. Scale bar = 1 mm. **C**. Detailed view of the rectangle in Fig. 2b. Scale bar = 0.5 mm. **D**. Detailed view of the seed in Fig. 2c, showing the shiny seed coat. Scale bar = 0.5 mm. **E**. Virtual section of the seed in Fig. 2d, showing the seed coat surrounding the seed coat. Scale bar = 0.1 mm. **F**. Surface view of the seed coat, showing the sculpture. Scale bar = 0.1 mm.

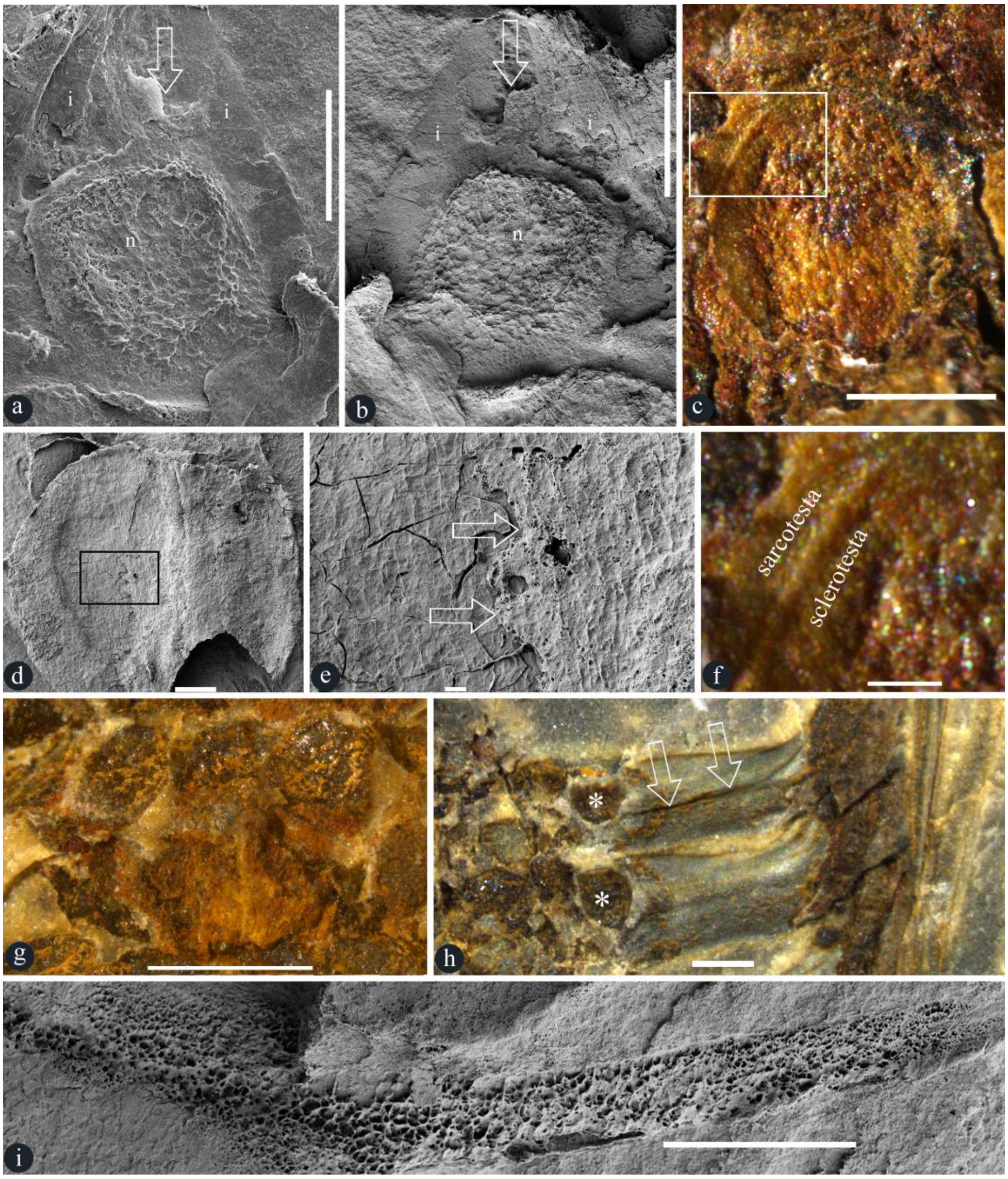


**Figure 3 Details of *in situ* ovules, seeds, and other in *Taiyuanostachya* gen. nov.** A-D, I are SEM, C, F-H are stereomicroscopy. A-F, I are of GP0094-A, G is of GP0094, H is of GP0095. **A**. An ovule with micropyle (arrow), nucellus (n), and integument (i). Scale bar = 0.5 mm. **B**. An ovule with micropyle (arrow), nucellus (n), and integument (i). Scale bar = 0.5 mm. **C**. A seed *in situ* in a lateral appendage. Scale bar = 0.5 mm. **D**. An *in situ* seed. Scale bar = 0.2 mm. **E**. Detailed view of the rectangle in Fig. 3d, showing sarcotesta (arrow, right) over the sclerotesta (left). Scale bar = 20 µm. **F**. Detailed view of the rectangle in Fig. 3c, showing sarcotesta (left) over the sclerotesta (right). Scale bar = 0.1 mm. **G.** Whorled arrangement of lateral appendage scars, suggestive of 8-10 lateral appendages per cycle. Scale bar = 1 mm. **H.** Two lateral appendages and their *in situ* ovules (asterisks). Note the central canal (arrows). Scale bar = 1 mm. **I.** Spongy filling in the canal in a lateral appendage. Refer to Fig. S4b. Scale bar = 1 mm.

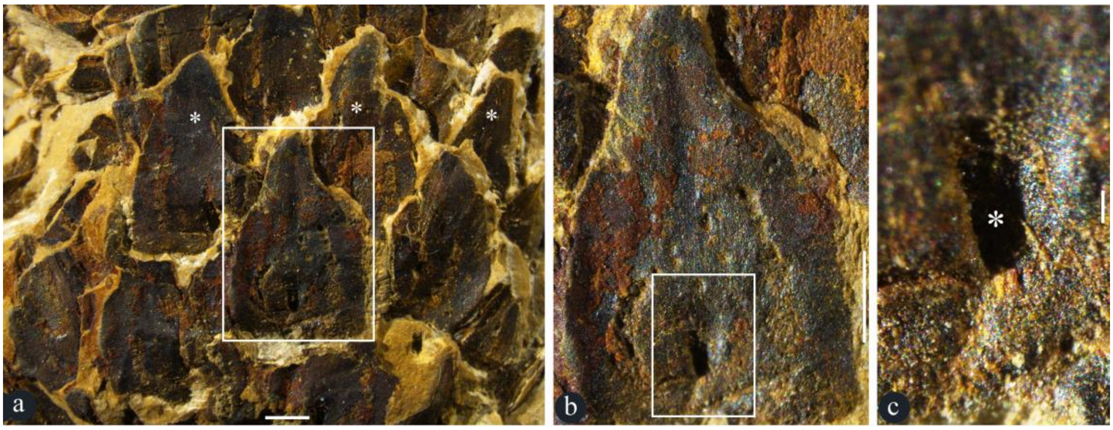


**Figure 4 Surface view of lateral appendages and Micro-CT of *Taiyuanostachya* gen. et sp. nov.** A-C are stereomicroscopy of GP0094. **A**. Alternate, whorled arrangement of lateral appendages (asterisks). Enlarged from Fig. 1a. Scale bar = 1 mm. **B**. A lateral appendage in the rectangle in Fig. 4a. Scale bar = 1 mm. **C**. Detailed view of rectangle in Fig. 4b, showing the operculum (asterisk) of the canal. Scale bar = 0.1 mm.

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