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Fossil and Living Cycads Say "No More Megasporophylls"

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Abstract

The origins of angiosperms and cycads are still mysterious. To understand the evolution of these groups as well as other gymnosperms it was impossible without mentioning a frequently used term “megasporophyll”. “Megasporophyll” is a concept that has been used widely in botany. This term is more or less related with the famous saying “Alles ist Blatt” by Goethe. This term became popular since Arber and Parkin hypothesized that the carpels in the Magnoliales were equivalent to and derived from former foliar parts bearing ovules along their margins (“megasporophyll”). Many botanists uncritically called the parts in all the reproductive organs of seed plants as “sporophylls”, no matter what they actually saw in the plants. However, the fact is that none of the reproductive parts (fossil or living), except those in the Cycadales, are foliar or leaf-like. The female parts in (fossil and extant) Ginkgoales, Coniferales, and Gnetales apparently have nothing to do with any foliar parts, as proven by previous studies. Among the living gymnosperms, Cycadales usually are taken as the most primitive and ancestral, therefore understanding the reproductive organs and their evolution in Cycadales will not only enhance our understanding of Cycadales, but also is hinged with our understanding of all seed plants in general. Interestingly, the female parts of Cycadales are the ones that demonstrate by far the greatest resemblance to leaves, at least in appearance. Thus whether the female parts of Cycadales are truly foliar is a key but rarely asked question hinged with the validity of the term “megasporophyll” and the systematics of seed plants. To verify the validity of this term and its implications, we examined the morphology of both fossil and extant cycads. Our fossil evidence includes the earliest unequivocal fossil of cycad reproductive organ, *Crossozamia chinensis* (Zhu and Du) Gao and Thomas, recovered from the Permian of China. Unlike seen in living cycads, the ovules in this fossil reproductive organ are apparently inserted on the adaxial rather than strictly the laterals of the female parts. Such an arrangement is not expected for a typical leaf, but rather demonstrates certain resemblance to the sporangia arrangement in *Archaeopteris*. Parallel to and agreeing with this, the ovules in living cycads, *Cycas taitungensis* Shen, Hill, Tsou and Chen, have their micropyles oriented to the adaxial rather than the laterals of the parts. Taking into consideration of previous experiment proving that the leaf-like appearance of *Cycas* “megasporophylls” is due to mechanical pressure and unexpected occurrence of amphicribral vascular bundles with secondary growth in the so-called “megasporophylls” of cycads, we conclude that the female parts of these Cycadales are actually branches bearing ovules. This conclusion rejects foliar nature of female parts in cycads and undermines the validity of the term “megasporophylls”, although the latter has been the most-widely accepted misnomer in botany. The by-product of eliminating this term is that the origins of Cycadales and angiosperms as well as homology of carpels become much easier than assumed before. Considering the long time the term “megasporophyll” inflicting botany and misleading botanists, the influence of eliminating this misnomer in botany cannot be exaggerated. It is not restricted to a single term and its usage, but permeates into all branches of botany, especially the systematics of Cycadales, Angiosperms, and other seed plants.

Keywords: Morphology; Megasporophyll; Cycads; evolution; Mechanical pressure

Introduction

Cycads are the oldest group among the extant seed plants [1]. Their long history dated back to the Permian and basalmost position among extant seed plants make cycads important and more insightful for seed plant evolution. Therefore cycads have been the focus of many botanical studies. “Megasporophyll” is a term frequently used to describe the female parts of gymnosperms, and carpels of angiosperms are frequently interpreted as metamorphosed megasporophylls [2,3]. The term “megasporophylls” per se implies that it is essentially a leaf in nature. However, this implication appears spurious in non-cycad gymnosperms (at least including Ginkgoales, Coniferales, Gnetales, Bennettitales, Caytoniales, etc.), the female parts of which are far from leaf-like in morphology [4-6]. “Megasporophyll” seems to find a foothold for its rationality in *Cycas*, the female parts of which appear leaf-like. Previously, doubt has been cast on the foliar nature of female parts in *Cycas* [7,8]. In their developmental experiment, Wang and Luo demonstrated that the female part of *Cycas sexseminifera*, when growing free of pressure from its adjacent peers, has its ovule shift to the adaxial rather than remain lateral in other naturally growing female parts in the same plant, implying that the leaf-like appearance of *Cycas* female parts is a consequence of mechanical pressure exerted by their neighbouring peers [8]. However, this conclusion is largely ignored probably due to inertia of thinking. To further enquire the nature of female parts in *Cycas*, we re-investigate the female parts of the oldest

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fossil cycad from the Permian of China and extant Cycad. Both fossil and extant cycads reject the foliar nature formerly assumed for cycad female parts.

Materials and Methods

The fossil specimens investigated here have been reported before [9,10]. These coalified compression specimens were collected from the Xiashihezi Formation (late Early Permian, >272 Ma) of Dongshan, Taiyuan, China in 1980s. Our re-investigation confirms the conclusion that these fossils currently represent the oldest unequivocal cycads and they are closely comparable to living *Cycas*. Furthermore formerly ignored important features of the fossils are revealed this time.

Cycas taitungensis Shen, Hill, Tsou and Chen is a cycad endemic to eastern region of Taiwan, China. Our materials were collected from an individual grown in the National Orchid Conservation Center of China.

The general morphology of the specimens was recorded with digital camera, and the details are photographed with stereomicroscopes equipped with digital cameras. All pictures were organized using a Photoshop 7.0 for publication.

Results and Discussion

Just like in extant *Cycas*, a fossil female part of *Crossozamia chinensis* [9,10] includes a terminal lamina and a pedicel that bears ovules/seeds on its sides (Figure 1a-1c). Different from the idealized “megasporophyll”, ovules/seeds on the same side are not arranged in two strict ranks (Figure 1b and 1e). Instead one of the funiculi of two adjacent ovules in the female part in Figure 1b overlaps the other, suggestive of different ovule orientations and that one is more oriented to the adaxial than the other. This implication from this specimen is confirmed by observation on more specimens. Several ovules/seeds of *Crossozamia chinensis* [9,10] are directly inserted on the adaxial surface of the female part. The ovule in Figure 1e is obviously located on the surface, not margins, of the pedicel, as indicated by the presence of sediment between the ovule funiculus and the pedicel. Furthermore, a more mature seed is apparently attached to the surface of a female part (Figure 1f and 1i). Parallel to these, an ovule in (Figures 1g and 1h) is apparently located on the surface rather than along the margin of the female part. These observations suggest that the formerly two dimensional foliar morphology assumed for fossil cycad female parts is an illusion resulted from over-simplification and careless observation. Instead the female parts of these fossil cycads are axial structure with three dimensional configurations.

The aforesaid conclusion on the nature of the female parts of fossil cycads is further strengthened by observations on extant cycads, either grown in natural or man-made condition. All ovules and seeds in the strobilus of *C. taitungensis* growing naturally are apparently consistently oriented to the adaxial of female parts (Figure 2a). This orientation is similar to that seen in the above fossil cycads. *Cycas rumphii* is another cycad frequently seen in south-eastern Asia, northern Australia, and eastern Africa. Although there is certain variation in ovule orientation in the female parts of naturally grown *C. rumphii*, at least some of the ovules are on the lateral of the female parts [11] as expected for foliar megasporophylls. To test whether such arrangement is due to mechanic pressure (as suggested by Wang and Luo, we perform similar manipulation on *C. rumphii*, namely, removing adjacent female parts to let the remaining female parts grow freely. As seen in Figure 1f and 1i all ovules of *Cycas rumphii* unexceptionally turn to the adaxial of the female parts (Figure 2b and 2c). Considering morphology of plant part is a function of its genetics and available space [12], we assume that plant parts growing in pressure-free environment, where genetics overwhelms, tend to display their “real” morphology. Observations on both living *Cycas* taxa concurrently suggest that the ovules in the precursor of cycads are most likely attached to the adaxial of female parts, just as seen in the above fossil cycads.

Our observations on both extant and living cycads reject the foliar nature previously assumed for cycad female parts, which are frequently termed as “megasporophylls” [1,3,9]. The term “megasporophyll” implies that female parts in seed plants are foliar in nature. Theoretically, a foliar organ (phyllome) should have bilateral symmetry (ad/abaxial polarity) [13]. Previous works have indicated that female parts in Ginkgoales, Coniferales, Gnetales, Bennettitales, and Caytoniales are not foliar or leaf-like [4,5,6,14]. Among Cycadales, female parts in Zamiaceae are not leaf-like, either [15]. All these make the commonly-used term “megasporophyll” spurious. The only female parts that demonstrate by far the greatest resemblance to leaves are those of *Cycas,* which is the last foothold for the rationality of “megasporophyll”. Now both fossil and extant cycads consistently point to the non-foliar nature of cycad female parts. Actually, incipient sign of invalidity of this term occurred long time ago. For example, concentric bundles (some even with secondary growth), abnormal ovule arrangement in cycads [15] and three dimensional vascular bundles branching in cycad “megasporophylls” [16] have cast doubt over the foliar nature of cycad female parts. Back to 1963, Meeuse cast doubt over the foliar nature of female parts in gymnosperms and suggested to replace “megasporophyll” with “megasporocladode” [7]. In short, all evidence converges to the same conclusion that the term “megasporophyll” is apparently a misnomer that should be discarded in botany.

The removal of the term “megasporophyll” paves the road for better understanding on origin and evolution of cycads and other seed plants. The assumed foliar nature of cycad female parts makes cycad ancestor mysterious, especially when the *Phasmatocycas*-based hypothesis is ruled out [17]. Searching for a precursor of the assumed foliar female parts in early land plants is now proven in vain, at least partially because all parts in early land plants are axes or axis-derived structures. However, this conundrum vaporizes when a female part of *Cycas* is interpreted as an axis or shoot. The fertile parts as that of *Archaeopteris* with sporangia borne on their adaxial [18,19] may give rise to *Cycas* female parts simply by shifting its adaxial sporangia to more lateral positions, owing to mechanical pressure or whatever other reasons. In this way, the origin of cycads seems to be in the reach of botanists. At the same time, female parts of all seed plants become homologous and comparable, making the evolutionary relationship among them easy to decipher. For example, the homology of angiosperm carpels has been a headache question for many, but this problem disappear when a “carpel” is separated into a placenta (ovule-bearing branch) and enclosing foliar part (carpel wall or ovarian wall). This interpretation has been proposed before [20,21] and is favored by recent studies on magnoliaceous carpels [22,23]. Apparently, the eradication of “megasporophyll” paves the road to more reasonable understanding of plant evolution and systematics.

Conclusion

Although widely-used in botany, “megasporophyll” is a misnomer in botany. This is suggested by both fossil and extant cycads. Eliminating this misleading term will help to decipher the mysteries about the origins of cycads and angiosperms.

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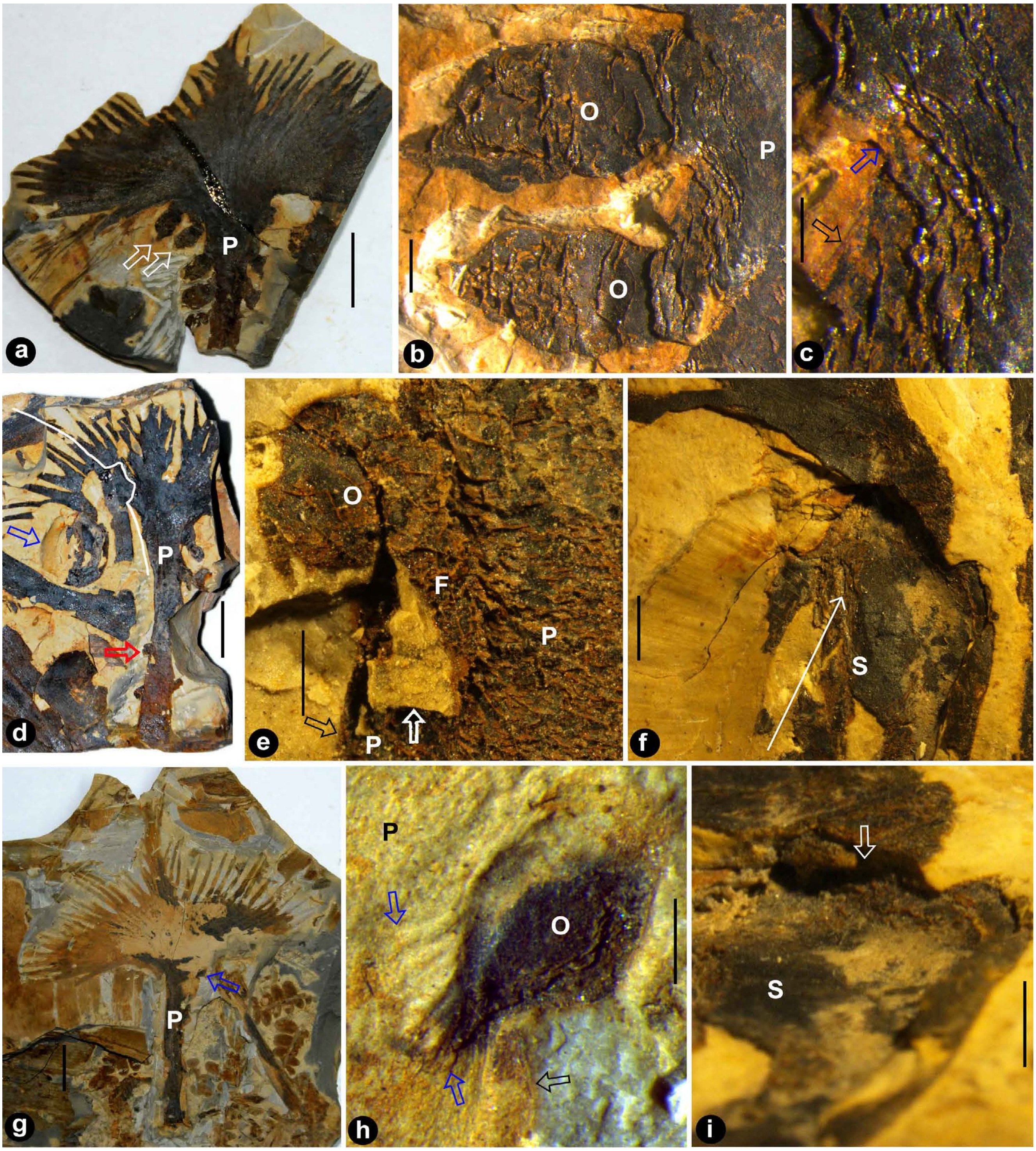

Figure 1: Female parts of a Permian fossil cycad, *Crossozamia chinensis* (Zhu and Du) Gao and Thomas, with attached ovules/seeds. **a**. A female part with a fan-shaped distal lamina and several ovules (arrows) attached to its pedicel (P). BMNH115131. Bar = 10 mm. **b**. Two ovules (O, arrowed in Figure 1a) physically connected to the same pedicel (P). Bar = 1 mm. **c**. Detailed view of two funiculi of ovules in Figure 1b. Note one of them (blue arrow) overlaps the other (black arrow). Bar = 0.5 mm. **d**. Two partially preserved female parts (separated by white line) with an attached ovule/seed. Note a seed (blue arrow) attached to a lamina segment and an ovule (red arrow) attached to the pedicel (P) of another female part. GP0001. Bar = 10 mm. **e**. Detailed view of red-arrowed ovule in Figure 1d. Note the ovule (O) is above the surface of the pedicel (P), a piece of sediment (white arrow) is between the funiculus (F) and pedicel margin (black arrow), suggestive of surface attachment of the ovule. Bar = 1 mm. **f**. Detailed view of the seed blue-arrowed in Figure 1d, connected to the lamina segment (upper black). Bar = 2 mm. **g**. A female part with a typical fan-shaped distal lamina, a pedicel (P), and an ovule (blue arrow). BMNH114993. Bar = 10 mm. **h**. Detailed view of the ovule arrowed in Figure 1g. Note the funiculus (between the blue arrows) of the ovule (O) is directly inserted on the surface at a position far from the lamina/pedicel margin (black arrow). Bar = 0.5 mm. **i**. The same seed (S) as in Figure 1f, showing its physical connection (arrow) to the lamina segment. Viewed following the direction of the arrow in Figure 1f, after warped certain degrees. Bar = 2 mm.

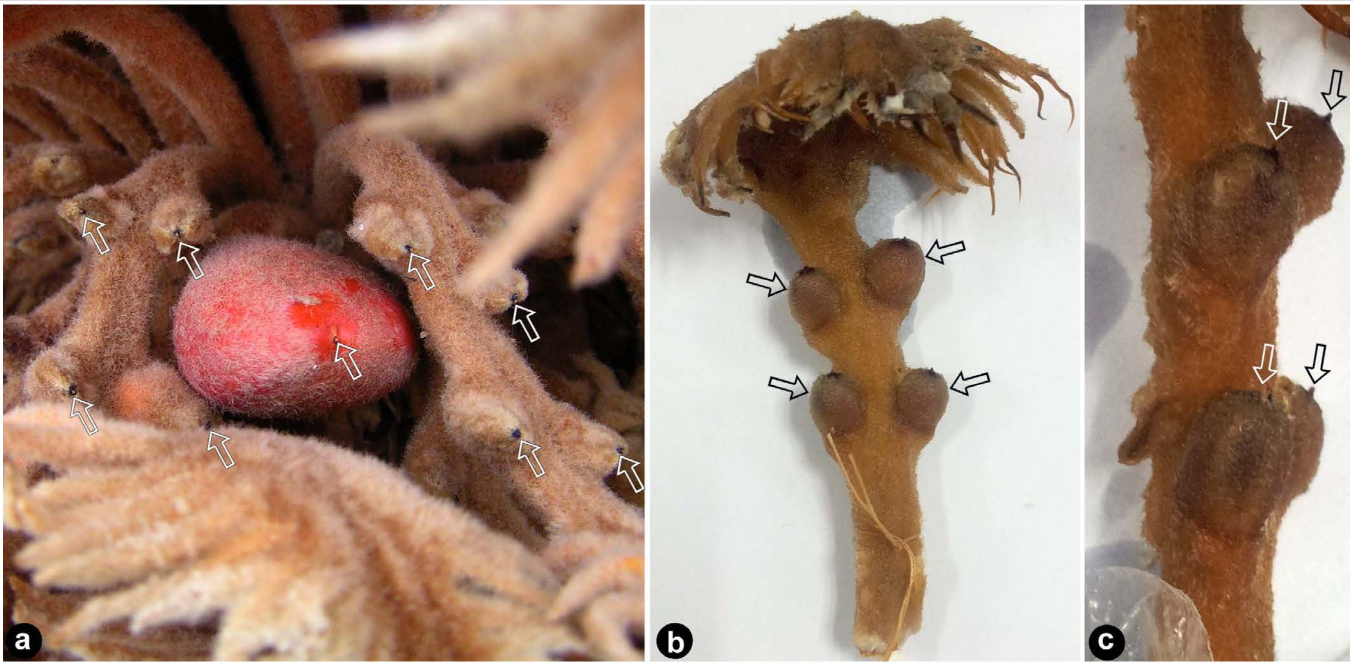

Figure 2: Female parts of living *Cycas* with attached ovules/seeds. **a.** Several female parts of *Cycas taitungensis* Shen, Hill, Tsou and Chen, with their ovule/seed tips (arrows) pointing to the adaxial. **b.** Adaxial surface view of a female part of *Cycas rumphii* Miq., which grows free of peer pressure, with four ovules pointing to the adaxial-lateral. **c.** Side view of the part in Figure 2b, showing the ovule tips (arrows) pointing to the adaxial (to the right).

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