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TRIGONOCARPUS LEEANUS, A NEW SPECIES FROM THE MIDDLE PENNSYLVANIAN OF SOUTHERN ILLINOIS¹

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ABSTRACT

A new species of *Trigonocarpus* Brongniart is described from the level of the Herrin (No. 6) Coal (Carbondale Formation, Kewanee Group) at Carterville, Illinois. The seed is three dimensionally preserved by authigenic cementation and exhibits a well preserved nucellar cast, integument and micropylar region. The specimen represents the largest pteridosperm compression-impression seed collected in North America and measures 10 cm from the apex of the micropyle to the chalazal end, and at least 5 cm in breadth. *Trigonocarpus leeanus* sp. n. is compared to the remaining forty-three taxa within the genus, and specifically with *Trigonocarpus grandis* Lesquereux, the one species with dimensions approaching it. An emended diagnosis, with designation of a lectotype, is presented for *Trigonocarpus grandis*. Correlation of the features displayed by *Trigonocarpus leeanus* sp. n. and the petrified taxa within *Pachytesta* Brongniart is attempted.

DESPITE the multitude of pteridosperm compression-impression megafossils recovered from North American Carboniferous sediments, reproductive organs attributable to seed ferns compose, on the average, less than one percent of Coal Swamp floras (Gastaldo, 1975). There are over 150 species of seeds, representing a number of families and orders, recognized in the strata of the Pennsylvanian. Approximately three-quarters of these species are preserved as compression-impressions, while the remaining are preserved as permineralizations. The nomenclatorial status of compression-impression seeds has been complicated by the fact that during preservation, diagnostic characteristics may be lost. This may result in the erection of numerous species based upon different preservational states of the same seed species. The number of recognized taxa, therefore, is undoubtedly inflated as a result of the variety of preservational conditions which are encountered. In addition to this problem of preservational diagenesis, the parentage of the majority of species is unknown, due to separation, perhaps at seed dispersal and prior to fossilization.

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Megafossil compression-impression seed (sensu Bierhorst, 1971, p. 396) genera and species have been primarily based upon the morphological appearance of the reproductive organ. Darrah (1969) recognizes four common types of seeds utilizing size and symmetry as delimiting characters. Although Seward (1917) and Arnold (1938) have discussed the problems inherent within classification schemes based solely upon symmetry, the characteristics displayed by most seed specimens are limited, and the only alternative is a recognized artificial system based upon form. In addition to the often-encountered seed forms, there are numerous, distinct, rare forms from which one might infer the existence of other gymnospermous families presently unrecognized (Darrah, 1969). The report is concerned with a specimen preserved by authigenic cementation collected from the overburden of the Herrin (No. 6) Coal at Carterville, Illinois. The Herrin (No. 6) Coal is placed within the Carbondale Formation of the Kewanee Group (Kosanke et al., 1960), and is Middle Pennsylvanian in age. Gastaldo (1975, 1977) reported twenty-six genera and fifty-two species from the locality, which is dominated by fern and seed fern foliage. One specimen of a seed, assignable to the Trigonocarpaceae, was recovered from the site, and is the largest pteridosperm compression-impression seed ever reported from North America.

DIAGNOSIS—*Trigonocarpus* leeanus sp. n. Gastaldo and Matten Fig. 1–2.

Ovoid-elliptical seed, 10 cm long from the apex of the micropyle to the chalazal end, and at least 5 cm in width. Nucellar cast elliptical, 7.5 cm long, 4.5 cm in breadth, and at least 1.7 cm in

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relief. The one visible primary ridge, standing 1.5 mm in relief, extends from the apex of the nucellar cast to the chalazal end; numerous secondary ridges averaging 6 per cm, extending the full length of the cast; numerous fine striations on the nucellar cast primarily oriented along the axis of the seed, but some occur at 90° to the axis; approximately 14 striations per mm; where striations coincide with secondary ridges, there are 6–8 striations per ridge. Attachment of seed unknown. Integument probably fleshy; extending 15 mm from the top of the nucellar cast to the preserved apex of the seed, and 18 mm from the top of the nucellar cast to the outer preserved edge. Integument tapers basally and appears to have been compressed; reticulately patterned; composed of raised areas of various dimensions separated by fine-line depressions. Micropyle extends at least 1.5 cm from the top of the nucellar cast; width undeterminable because of overlapping of integument.

Collection locality: Overburden of the Herrin (No. 6) Coal, S-13 Mine, Carterville, Illinois (Herrin 15' Quadrangle SE4-T9S-R1E).

Age: Middle Pennsylvanian, Carbondale Formation, Kewanee Group.

Holotype: Specimen 663.135a–c, and accompanying latex transfers. Southern Illinois University Paleobotanical Collection, Carbondale, Illinois 62901.

DESCRIPTION—The specimen (Fig. 1) collected from the Carterville locality is preserved in an ironstone concretion. Schopf (1975) terms this mode of preservation authigenic cementation. As a result of this mode of preservation, the alteration of the specimen appears to be minimal, primarily in the form of some flattening. The seed has retained much of its three dimensional form and measures 10 cm from the apex of the preserved micropylar region to the chalazal end, and at least 5 cm in breadth at its widest part. The seed displays a well preserved nucellar cast and integumentary region, but lacks any mode of attachment at the chalazal end. The term "nucellar cast" will be used in order to differentiate that portion of the specimen which occupies the topographic area of the nucellus. It is assumed that during fossilization, invading sediments not only filled the nucellus, but also the entire seed cavity inside the integument. Therefore, the "nucellar cast" is actually a cast of the inside of the integument, or the seed cavity. The morphological features which are displayed are of the inner integument, probably sclerotesta, rather than of the nucellus. Historically, though, the term "nucellar cast" has been used for this region of the seed, and this terminology will be followed throughout the remainder of the study. The specimen projects 17 mm above the base of the nodule, and if the seed were triangular in transverse section, as is the case with most species of *Pach-ytesta* (Taylor, 1965), the diameter of the seed would have probably been greater than 3.5 cm, but less than the 5.0 cm noted above.

The nucellar portion of the specimen appears ovoid, due to flattening, particularly in the chalazal region. One primary ridge is displayed, standing 1.5 mm in relief, and extending from the top of the nucellar cast to the chalazal end, dividing about $\frac{2}{3}$ of the way toward the base of the seed. It is believed that this division of the primary ridge is due to flattening of the specimen during diagenesis, and was not characteristic of the seed in life. Toward the summit of the nucellar cast, there appears to be additional tissue in relief which may have originally been integumentary, and possibly the remnants of a pollen chamber. Between the primary ridge and the edges of the specimen are numerous secondary ridges which extend the full length of the nucellar cast. These secondary ridges are less than 1 mm in width, and less than 0.5 mm in relief, and average about 6 per centimeter. In addition to these secondary ridges, the nucellar cast possesses very fine striations. Latex transfers (Chaloner and Gay, 1973; Watson and Alvin, 1976) were made of various parts of the nucellar cast and integument. A scanning electron micrograph of a latex transfer (Fig. 2) of the nucellar cast of the lower right quadrangle reveals these striations, as well as, the presence of the secondary ridges (at arrow). It must be noted that since the micrograph is of a transfer of the surface, the ridges appear as troughs and the troughs as ridges. These fine striations were scanned for any evidence of cellular arrangement in order to discern the origin of the pattern, but no cellular pattern was preserved. It was noted that the majority of the fine striations were oriented along the axis of the seed, although there are some which arc away from the axis and others which are perpendicular to it. The striations are approximately 35 μ m apart and may extend for quite some distance on the nucellar cast. Striations of identical nature were found, sporadically, on transfers of the integumentary region. These striations were also oriented as previously noted. It is, therefore, believed that these striations are an impression of the compressed integumentary layer, possibly sarcotestal, upon the specimen during preservation, and not a characteristic which would be useful as a diagnostic feature.

The integument of the seed is well preserved at the micropylar end, while in its course basally, it tapers, and appears to have been compressed laterally. The flange of flattened integumentary tissue extends 15 mm apically and 18 mm laterally, and was probably fleshy. Taylor (1965) reports that some species of *Pachytesta* possess

Species	Length	Width (in cm)
T. hexacostum Jackson	.7	.5
T. hookeri Dawson	.75	.5
T. minus Dawson	.3	.25
T. perpusillus Lesquereux	.258	.2555
T. perpusillus Brongniart	.9	.5
T. praetextus Bell	.675	.3–.4
T. pusilla Brongniart	.785	.45
T. sigillariae Dawson	.6	?

 TABLE 1. Species of Trigonocarpus Brongniart in North

 American Literature: less than 1 cm in length^a

^a Compiled from Bell, 1944; Dawson, 1861, 1866; Jackson, 1916; Lesquereux, 1884.

a two-parted integumentary layer composed of a sclerotesta and a distal sarcotesta. This twoparted integumentary feature is apparently preserved in T. leeanus. The sclerotestal layer is represented by the features of the seed cavity cast, herein termed nucellar cast, while the sarcotesta appears to be represented by the flattened integumentary tissue surrounding the nucellar cast. The reticulate pattern of the sarcotesta is composed of variously sized areas with delimiting fine-line depressions. Latex transfer studies reveal little about the actual morphology of the area, except for the presence of the fine striations as noted above. Possible interpretations of this reticulated integument may include: the pattern represents dried parenchytissue with broad islands matous of sclerenchymatous tissue; the reticulation is actually composed of fibers and the patches of tissue between were parenchymatous in nature; the pattern represents some sort of reticulate vascularization of the integument, but there is no evidence in the permineralized species to confirm this. The micropylar region appears to be preserved and extends at least 15 mm from the top of the nucellar cast. The actual width of the micropyle is not discernable because of the overlap of the integument.

DISCUSSION—Comparison with Trigonocarpus in North America—Trigonocarpus Brongniart (1828) is a form genus established for seed casts which are radially symmetrical, decorticated, and have their surface marked by three prominent ridges. Occasionally, the primary ridges may be accompanied by relatively smaller secondary ridges, and/or a lateral extension of the integumentary layer. The seeds are believed to

be attributable to the Medullosaceae. Brongniart (1874) instituted two other seed genera, Pachytesta and Tripterospermum, to accomodate similar three-angled forms. Oliver (1904) stated that the distinguishing characters between Trigonocarpus and Tripterospermum are unimportant, and Hoskins and Cross (1946) placed Tripterospermum into synonymy with Trigoncarpus. Pachytesta was initially instituted for large, structurally preserved seeds from the Stephanian of France, but the original diagnosis of the genus lacked illustrations. Figures of two species, Pachytesta incrassata and Pachytesta gigantea, were subsequently illustrated (Brongniart, 1881). Hoskins and Cross (1946) transferred to Pachytesta those seeds displaying sufficient internal anatomy previously described as Trigonocarpus, while retaining the latter genus for seeds preserved as compression-impressions. At the same time, Hoskins and Cross placed into synonymy with Trigonocarpus the genus Carpolithes Sternberg (1820), which is characterized by seeds appearing smooth, rounded or ovoid in structure, with no further definable characteristics. However, type specimens of Carpolithes were not reexamined to separate permineralized, anatomically preserved specimens from those displaying only external morphological features. For this reason, Carpolithes should be retained as a separate genus. It has been treated as such with respect to this study.

In order to compare our specimen with the forty-three species of Trigonocarpus reported in North America, we divided them into groups based upon size. Eight species (Table 1) are found to have lengths no greater than 1 cm, while twenty-five species (Table 2) possess lengths no greater than 4 cm. Ten species (Table 3) display an overall length greater than 4 cm, but less than 8 cm. The one Trigonocarpus species with dimensions approaching Trigonocarpus leeanus is Trigonocarpus grandis Lesquereux. This species was described and figured in the Coal Flora (Lesquereux, 1884, p. 821, pl. CXI, fig. 1-3) as a large, oblong-oval seed, rounded at both ends. Three specimens were figured showing smooth nucellar casts, the largest 7.5 cm long and 4 cm broad, possessing three primary ridges with three shorter and narrower intermediate ridges. The "pericarp" was described as thick, inflated, and truncate at the apex, even though only one specimen possessed a partial integument. The

Fig. 1, 2. Trigonocarpus leeanus sp. n. 1. Authigenically cemented specimen showing one primary ridge (pr) and numerous secondary ridges (sr) extending the entire length of the nucellar cast (n). Integument (i) shows reticulate pattern in distal portion of the seed and basal tapering and compression. Micropyle (m) extends from the apex of the nucellar cast at least 1.5 cm. $\times 1.9$. 2. Scanning electron micrograph of a latex transfer of the lower right quadrant of the nucellar cast showing fine striations, as well as a secondary rib (at arrow). See text for discussion of nucellar cast. $\times 72$.





three figured specimens (USNM 26018, 26019, 26020) were examined at the United States National Museum of Natural History and compared to the Carterville specimen. When one compares the illustrations of *T. grandis* in the Coal Flora to the actual specimens (Fig. 3-5 of the present paper), several inaccuracies are evident, necessitating their illustration and redescription here.

Specimen USNM 26018 is a sandstone cast of a trigonocarpalean seed from Stark County, Illinois, and measures 7.4 cm in length, 3.7 cm in width, and 2.4 cm in height (Fig. 3). Three primary ridges are evident. They extend the full length of the specimen and are connected to a circular projection at one end and to a circular depression at the other end. The primary ridge appears to be tripartite in morphology. There is a median ridge 1 mm in breadth flanked by two adjacent ridges, each 1.5 mm in breadth. This tripartite ridge appears to extend at least 3/4 the length of the nucellar cast in the figured view. Three secondary ridges are evident at one end only and do not extend the full length of the cast. One secondary ridge is found between every pair of primary ridges. There is no evidence of striations preserved on the nucellar cast. Specimen USNM 26019 is also a sandstone cast measuring 6.5 cm in length, 3.7 cm in width, and 2.6 cm in breadth (Fig. 4). Three primary ridges extend the entire length of the cast and appear tripartite, although these markings are faint. A faint impression of a single median secondary ridge occurs between each pair of primaries. The characteristics displayed by this specimen are poorly preserved. Specimen 26020 is not a cast, but an impression preserved in shale from Cannelton, Pa. (Fig. 5). An integument appears to be preserved but does not show any discernable features. The specimen measures 5.5 cm in length, and 3.3 cm in width. One primary ridge is exposed consisting of the same tripartite arrangement as noted above (Specimen 26018). The tripartite ridge exhibited by Trigonocarpus grandis may explain the division of the primary ridge in T. leeanus. Trigonocarpus leeanus may have had a similar arrangement in the lower third of the nucellar cast, and, as a result of flattening, the tripartite primary ridge was split apart. This tripartite primary ridge morphology, though, is not evident either immediately above the point of division, or in the upper part of the nucellar cast in the Carterville specimen. There is no evidence

 TABLE 2. Species of Trigonocarpus Brongniart in North

 American Literature: 1-4 cm in length^a

Species	Length	Width (in cm)
T. adamsii Lesquereux	1–2	1.5
T. ampullaeformis		
Lesquereux	2.7-3.5	1.5-2.2
T. avellanus Dawson	"size of a filbert"	
T. costatus Deevers	1-2	.7–1
T. dawsonianum White	'slender and	d narrower than
	T. k	ielenae''
T. excrescens Janssen	2–3	?
T. giffordii Lesquereux	2.5-3	1
T. helenae White	2.5	1
T. hexagonale Jackson	1.5	.8
T. hildrethii Lesquereux	3.5	1.75
T. intermedium Dawson	"larger than	T. olivaeformis"
T. kansaseanus Lesquereux	1.1-1.8	.7–.9
T. menzelianus		
Geoppert & Berger	2.5	1.5
T. multicarinatus		
Newberry	2.2	1.5
-		(incomplete)
T. multistriatus Lesquereux	2.5-3	2-2.5
T. oblongus Lindley & Hutton	2.5	1.9
T. olivaeformis		
Lindley & Hutton	2-3	1
T. ornatus Newberry	2.5	.9
T. ouachitensis Deevers	2	1
T. ovatum Jackson	1.2-1.3	.6–.7
T. perantiquus Dawson	2.5	1.3
T. racemosus Dawson	?	?
T. serratus Deevers	1.4	.7
T. starkianus Lesquereux	1.5-3	1–2
T. tricuspidatus Newberry	3.5	1.5

^a Compiled from Dawson, 1862, 1866, 1871; Deevers, 1937; Jackson, 1916; Janssen, 1940; Lesquereux, 1858, 1880, 1884; Newberry, 1853, 1873; White, 1900.

for a tripartite primary ridge on the counterpart of *T. leeanus*. As noted above, the tripartite primary ridge in *T. grandis* extends in relief for at least $\frac{3}{4}$ the length of specimen USNM 26018 and USNM 26020, and the full length of specimen USNM 26019. Although the largest specimen of *T. grandis*, USNM 26018, approaches the size of the nucellar cast of *T. leeanus*, it is believed that the two taxa are distinct. Due to the observation of new features concerning *T. grandis*, an emended diagnosis follows.

Emended diagnosis—Trigonocarpus grandis Lesquereux emend.

Ovoid-elliptical seeds measuring 5.5-7.4 cm in length, 3.3-3.7 cm in width, and 2.4-2.6 cm in

←

Fig. 3–5. Trigonocarpus grandis Lesquereux. **3.** USNM 26018 showing tripartite primary ridge extending in relief at least $\frac{3}{4}$ the length of the nucellar cast. The circular depression at which the three primary ridges converge is evident at the left hand side of the photograph. The dark band down the center of the figure is due to the presence of a band of tape on the type specimen. $\times 1.9$. **4.** USNM 26019 is a sandstone cast showing a tripartite primary ridge extending the full length of the nucellar cast. $\times 1.9$. **5.** USNM 26020 preserved in shale, showing a tripartite primary ridge extending almost the complete length of the nucellar cast. $\times 1.9$.

Species	Length	Width (in cm)
T. bertholletiformis Foster	5.4	2.7
T. dawesii Lindley & Hutton	3.5-5.5	1.7-2.7
T. grandis Lesquereux	5.5-7.4	3.3-3.7
T. juglans Lesquereux	4.5	3.5
T. magnus Newberry	5.5	4.5
T. noeggerathii Brongniart	2-5	2-2.5
T. saffordii Lesquereux	4.5	2.5
T. schultzianus		
Goepp. & Berg.	4-5	1.5-2.5
T. steecensis Berry	6.5	4.4
T. trilocularis Hildreth	5	3.8

 TABLE 3. Species of Trigonocarpus Brongniart in North American Literature: 4–8 cm in length^a

^a Compiled from Berry 1932; Hildreth, 1838; Lesquereux, 1866, 1880, 1884; Newberry 1873.

height. Three primary ridges extending the full length of the nucellar cast with a single, median secondary ridge, restricted to one end, occurring between each pair of primary ridges; primary ridge tripartite; median section 1 mm wide, flanked by two, 1.5 mm-wide sections; the primary ridges are connected to a circular depression at one end, and a circular projection at the other end. Integument poorly preserved; extending at least 6 mm apically from the top of the nucellar cast, and at least 3 mm laterally.

Lectotype: Trigonocarpus grandis Lesquereux, USNM 26018 (Lesquereux, 1884, pl. CXI, fig. 1), Lacoe Coll. 973a.

Lesquereux (1884) designated number 973 of the Lacoe collection as the type of *Trigonocarpus grandis* and illustrated the specimens (Pl. CXI, fig. 1–3). Lacoe's collection number 973 consists of three seeds (USNM 26018, 26019, 26020). Therefore, these three specimens are syntypes (International Code of Botanical Nomenclature, 1972—Art. 7, Par. 6). Thus, a lectotype must be selected from one of these three specimens (Art. 7, Par. 3). In our opinion, specimen USNM 26018 (Lacoe Coll. 973a) is most representative of this species.

Comparison of Trigonocarpus grandis with Trigonocarpus leeanus—Trigonocarpus grandis possesses three tripartite, primary ridges with three secondary ridges (one in each intercostal area). The three secondary ridges are found exclusively at one end of the seed. Trigonocarpus leeanus, however, apparently possesses a primary ridge composed of a single unit with numerous secondary ridges, extending the full length of the nucellar cast. In addition, T. leeanus exhibits a well preserved integument, while USNM 26020 displays a poorly preserved integument and cannot be directly compared. There is no evidence that the integument of T. grandis extended as great a distance apically and laterally as in *T. leeanus*. There is no indication on any specimen of *T. grandis* of the fine striations seen in *T. leeanus*, so that the average dimensions of these features cannot be compared.

Specimens assignable to other species of Trigonocarpus were examined at the United States National Museum of Natural History in order to discern if the fine striations observed in T. leeanus were preserved in other taxa. One species, Trigonocarpus ampullaeformis Lesquereux (1884), was found to possess similar striations on its nucellar region. Specimens USNM 26536 and USNM 26537 (Lacoe Coll. 975) are small trigonocarpalean seeds, measuring no more than 2.7 cm in length, elliptical-oblong in shape, and narrowed at the micropylar end into a tubular neck. Although the primary ridges are prominent, there is no evidence of secondary ridges. Specimen USNM 26536 displays the finely striated character better than specimen 26537, and approximately 18 striations are noted per millimeter. Therefore, the characteristic noted for T. leeanus is not restricted solely to it, and although it has never been mentioned in the literature, can be demonstrated in other species. The presence of these fine striations should be noted when preserved, but not used as a character for species delimitation, because they may represent the compressed integumentary region.

Comparison of Trigonocarpus leeanus with species of Pachytesta—Comparison between T. leeanus and those specimens which display internal preservation, and are therefore assignable to *Pachytesta*, has been attempted. The largest seed reported in the Carboniferous is *Pachytesta* incrassata Brongniart (1874) described from the Stephanian of France. The seed is reported to attain 10–11 cm in length (including the integument), 5-6 cm in diam, and is ellipsoidal in shape. Renault (1893, 1896) illustrates a specimen whose external morphology displays numerous alternating ridges and furrows along the axis of the integument. These furrows of the "testa" are 2–3 mm apart, in the widest portion of the seed, while the thickness of the integument is described as variable. The exterior of the seed is described as smooth with three prominent ridges. Taylor (1965) notes that the integumentary vascular system is composed of approximately 54 bundles located at the periphery of the sclerotesta. The sclerotesta is reported to be composed of two zones, of which the outer zone is composed of slightly elongated cells with intercellular spaces and pits, and bounded by an irregular zone of thick walled cells. It seems possible, therefore, that T. leeanus may exhibit these last two characteristics.

The alternating secondary ridges and grooves evident on the nucellar cast of *T. leeanus* may be a manifestation of the compressed integumentary vascularization or sclerenchyma banding in the outer part of the testa or of prominent nucellar vascularization. This may be a valid explanation for the presence of secondary ridges on some other species of *Trigonocarpus*.

The reticulated integumentary pattern of *T. leeanus*, composed of variously shaped "islands" separated by thin troughs, may be the manifestation of the outer zone of the testa composed of slightly elongated cells with intercellular spaces and pits (forming a lacunate system?). In that there are no internal anatomical features preserved in *T. leeanus*, these speculations can only be noted as possible explanations for the morphological characteristics observed.

Out of the twelve species of Pachytesta described by Taylor (1965), six are found within coal balls collected from the Herrin (No. 6) Coal. The one North American species which approaches the size of T. leeanus is Pachytesta gigantea Brongniart. The maximum length of the obovoid seed is reported to attain 9 cm, while the maximum diameter is 4.8 cm. The exterior of the seed is smooth, with three primary ridges, and equally spaced secondary ridges only at the apex. The preserved integument is composed of a sclerotesta of two zones, similar to the arrangement described for P. incrassata. There are, also, approximately 51 integumentary vascular bundles present. The characteristics observed on the specimen of T. leeanus may again be explained as the manifestation of the sclerotestal organization and the integumentary vascularization of P. gigantea. Two species of Pachytesta which exhibit numerous secondary ridges in the sclerotesta include P. composita Stewart (1958) and P. illinoiensis Arnold and Steidtman (1937). Both species attain a maximum length of only 4 cm.

It seems possible that the secondary ridge structure displayed on Trigonocarpus leeanus can be explained, then, in a number of ways. The secondary ridges may actually be the manifestation of the compressed integumentary vascularization and thereby align T. leeanus with a species which possesses a large number of integumentary vascular bundles. These ridges may possibly be a modification of the secondary ridge structure of the inner integument displayed by a seed similar to P. gigantea. The phenomenon of gigantism has been noted to occur in the Middle Pennsylvanian floras, particularly those of the Illinois Basin, and it may be possible that T. *leeanus* is a species related to *P. composita* or *P. illinoiensis*, and that the secondary ridges are compressed sclerenchyma banding of the sclerotesta. It may also be possible that the size of the seed, and the characteristics it displays, may be due to the presence of a developing embryo,

and hence, a change in morphology due to fertilization.

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