ON THE STRUCTURE AND RELATIONSHIPS OF A NEW PENNSYLVANIAN SPECIES OF THE SEED *PACHYTESTA*

by THOMAS N. TAYLOR *and* DONALD A. EGGERT

ABSTRACT. *Pachytesta berryvillensis* sp. nov., a small trigonocarpalean seed most closely resembling *P. pusilla*, is described and figured from petrifaction material of Upper Pennsylvanian age collected from southeastern Illinois.

TWO coal balls collected from the Mattoon Formation (of late Pennsylvanian age) near Berryville, Illinois have revealed 52 structurally preserved seeds of a new type. The seeds are ovoid, radially symmetrical, and measure 6·1–6·8 mm. long and 5·0–5·2 mm. in maximum diameter. Zonation of the integument is delimited into 3 principal layers; an outer parenchymatous sarcotesta containing sclerenchyma cells and numerous secretory canals, a middle 2-layered sclerotesta distinguished by the size and disposition of the individual fibres, and cuticular remains believed to represent remnants of an innermost endotesta. Nucellar attachment to the integument is confined to a small pad in the seed chalaza. Vascular tissue is present in the nucellus, but not observed in the integument.

SYSTEMATIC DESCRIPTION

Genus PACHYTESTA Brongniart 1874

Pachytesta berryvillensis sp. nov.

Plate 71, figs. 1–6; Plate 72, figs. 1–5; text-fig. 1

Diagnosis. Ovoid seeds 6·1–6·8 mm. long and 5·0–5·2 mm. in diameter with rounded base and short micropylar tube. Integument with three discernible layers; outer sarcotesta of loosely arranged, thin-walled cells and longitudinally directed secretory canals, bounded by isodiametric cells with thickened walls and dark contents. Middle sclerotesta consisting of an outer zone of fibre-like cells one cell deep and oriented at right-angles to seed axis, and inner zone of identical fibres showing longitudinal orientation, occasional fibres of inner zone radially disposed and projecting into seed cavity. Endotesta represented by cuticle. Integument differentiated into three primary ribs, well-developed in apex, recognizable as thin areas in the sclerotesta at mid-level and chalaza. Nucellus attached to integument only at base by small disc 1·0 mm. high and 1·2 mm. in diameter, apically differentiated into pollen chamber and nucellar beak. Nucellar vascular system of 28–35 flattened bundles that terminate at pollen chamber base; vascular configuration of integument unknown. Megaspore membranes ovoid and granulose.

Holotype (Plate 71, fig. 1). Slides and peels of Coal Ball 3687 A(5), Paleobotanical Collections, Department of Biological Sciences, University of Illinois at Chicago Circle.

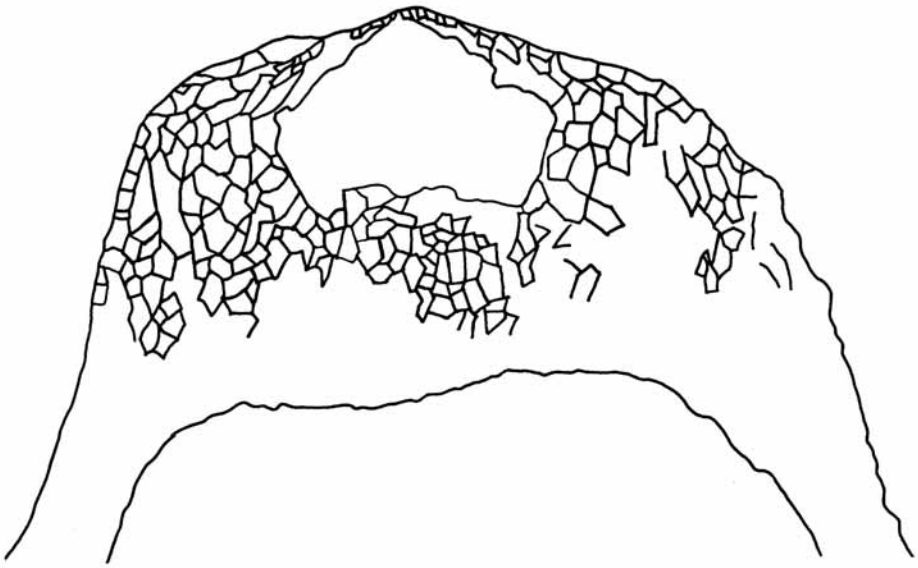
[Palaeontology, Vol. 12, Part 3, 1969, pp. 382–7, pls. 71–72.]

Paratypes. Slides and peels of Coal Ball 3687 B–D, and Coal Ball 735 in above collection.

Type locality. Berryville (Sec. 7, T 2 N, R 13 W), Sumner Quadrangle, Lawrence County, Illinois.

Stratigraphic position. Calhoun Coal, Mattoon Formation, McLeansboro Group.

Age. Late Pennsylvanian.



TEXT-FIG. 1. Median longitudinal section of immature pollen chamber showing fleshy nature of chamber walls and floor. (The illustration shows only the pollen chamber of the nucellus, no megaspore membrane is illustrated.)

Description.

Integument. The integument consists of three tissue systems. The outer layer, or sarcotesta, measures up to 1·6 mm. in thickness in the chalazal region (Pl. 71, fig. 1; Pl. 72, fig. 1), thins to several hundred microns near the mid-level and apex (Pl. 71, figs. 4, 5). It is constructed of thin-walled cells that show variability in both size and shape (Pl. 71, fig. 4; Pl. 72, fig. 1). Cells disposed toward the outer limits of the integument are larger and have more irregular shapes, while those cells more deeply positioned in the layer are smaller and have more uniform diameters. In the best-preserved specimens the sarcotesta is bounded by a variable number of layers of isodiametric cells with thickened walls and dark lumen contents (Pl. 71, fig. 4).

Numerous secretory canals up to several millimetres long further delimit the sarcotesta (Pl. 71, fig. 1; Pl. 72, fig. 5). These canals that lack septa parallel the long axis of the seed and are most abundant near the periphery of the tissue. The arrow in Pl. 72, fig. 6 shows the position of a 1–2 cell thick layer that is often noticeable between the inner limits of the sarcotesta and the outer limits of the sclerotesta.

Throughout the length of the seed a uniformly thickened sclerotesta constitutes the middle zone of the integument. Distally this layer is attenuated into a short micropylar tube 0·5 mm. long (Pl. 71, fig. 1); in the chalaza it extends 0·3 mm. into the seed cavity to form the nucellar disc (Pl. 71, fig. 1; Pl. 72, fig. 1).

The outer portion of the sclerotesta, approximately one-third of the total thickness of this layer, consists of thick-walled fibres averaging $76 \times 17\ \mu$ whose longitudinal axes are oriented perpendicular to the long axis of the seed (Pl. 71, fig. 2; Pl. 72, figs. 3, 6). The inner segment of the sclerotesta is formed of similar fibres, however, these cells show an orientation pattern that parallels the seed axis (Pl. 72, figs. 3, 6). Fibres of the inner limits of this layer have lobes that form a series of inwardly facing projections that sculpture the inner surface of the sclerotesta (Pl. 71, fig. 2; Pl. 72, figs. 3, 6). These projections from the fibres of the inner surface form a reticulum surrounding large lacunae which appear as conspicuous spaces in tangential section (Pl. 71, fig. 6).

A supposed inner flesh or endotesta, that constitutes the third component of the seed coat, is not preserved except for cuticular remains that apparently bounded this layer. This cuticle is seen in Plate 72, fig. 3 and fig. 6 (upper arrow) extending between the tips of the inwardly facing sclerotestal fibres. Near the base of the seed the cuticle of the endotesta becomes continuous with the outer cuticle of the nucellus. Orientation of the cuticular remains suggests that at some stage in the ontogeny of the seed a delicate endotesta occupied the lacunae formed in the inner surface of the sclerotesta. This tissue was either not preserved or became disorganized at some stage of the development of the megasporangium prior to that present in the specimens.

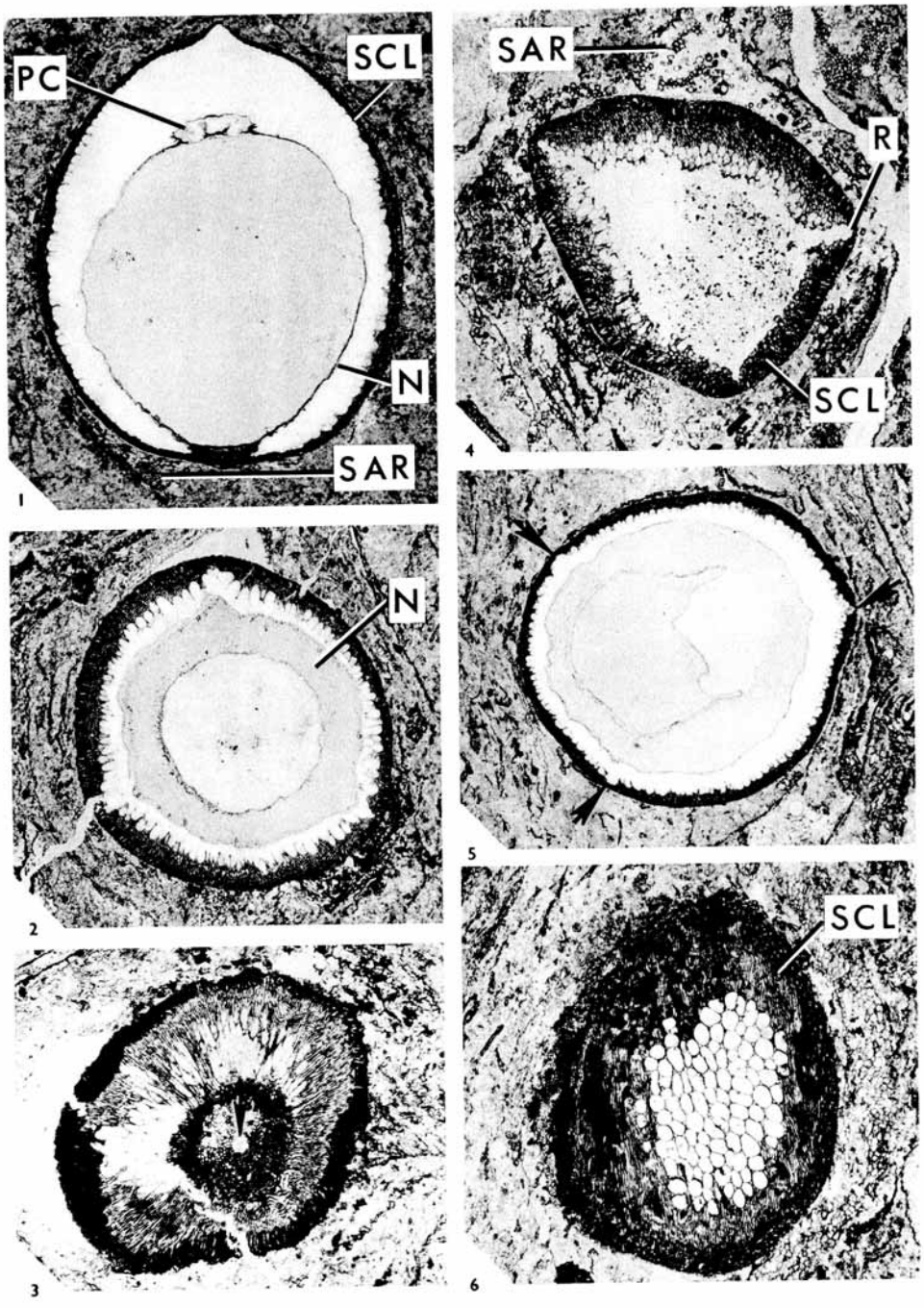
Three equidistantly spaced primary ribs extend radially for the length of the seed. They are prominent in the apex (Pl. 71, fig. 4), but are recognizable in mid-level and chalazal sections only as interruptions of the inner zone of the sclerotesta (Pl. 71, figs. 2, 5). Secondary ribs were not observed in any of the specimens.

Nucellus. The nucellus is continuous with the integument only at the chalaza where it is attached to a small disc-like extension of the sclerotesta that forms the nucellar disc (Pl. 71, fig. 1; Pl. 72, fig. 1). Early in development the apical portion of the nucellus forms a conical pollen chamber and nucellar beak that presumably engaged the lower orifice of the micropylar tube to ensure that pollen entered the chamber (text-fig. 1). In most of the specimens the nucellus is crushed and separated from the inner limits of the integument (Pl. 71, fig. 1). In some specimens a cutinized epidermis is all that remains of the nucellus.

In several seeds, however, the tissue of the nucellus is thick and shows little distortion. A median longitudinal section of the pollen chamber of one of these seeds is illustrated in text-fig. 1. It has a maximum diameter of 2·2 mm. and measures 1·2 mm. high. The

EXPLANATION OF PLATE 71

Figs. 1–6. *Pachytesta berryvillensis* sp. nov. (N = nucellus, PC = pollen chamber, R = rib, SAR = sarcotesta, SCL = sclerotesta). 1, Near median longitudinal section of seed; note presence of pollen grains in pollen chamber; C.B. 3687 A(5)bot No. 13, ×12. 2, Transverse section below mid-level; C.B. 3687 C(2)bot No. 4, ×16. 3, Transverse section of chalaza showing position of vascular bundle (arrow) and disposition of sclerotesta fibres; C.B. 3687 C(2)bot No. 8, ×22. 4, Transverse section of seed apex showing nature of ribs and integument zonation; C.B. 735 E(2)top No. 7, ×20. 5, Mid-level transverse section showing position of ribs (arrows); C.B. 735 C(2)bot No. 25, ×10. 6, Tangential section of integument showing lacunae between sclerotesta fibres; C.B. 735 F(2)top No. 5, ×20.



TAYLOR and EGGERT, Pennsylvanian seed *Pachytesta*

pollen chamber cavity is 0·7 mm. in diameter and 0·6 mm. high. The walls and pollen chamber floor are thick and constructed of exceptionally thin-walled cells. Epidermal cells of the distal end that will ultimately form the nucellar beak have only slightly thicker radial walls. In these specimens the disorganization and breakdown of cells at the distal end of the nucellus to form the pollen chamber had apparently only proceeded a short time prior to fossilization.

The megaspore membrane is thin and characterized by a granulose surface pattern.

Pollen. Approximately 40 pollen grains were observed in the pollen chambers of several seeds (Pl. 72, fig. 2). The largest number observed in a single chamber was 17. All of the grains are similar and consist of a psilate central body surrounded by a slightly elliptical bladder with reticulations on the inner surface (Pl. 72, fig. 2, 4). Diameter (greatest length of the bladder) varies from 72 to 81 μ. If compared with dispersed small spores the pollen grains present in the chamber of *Pachytesta berryvillensis* would be included in the genus *Florinites* as interpreted by Schopf, Wilson, and Bentall (1944). Pollen or pre-pollen grains have now been reported in the following species of *Pachytesta*: *P. incrassata* (Brongniart 1881), *P. gigantea* (Renault 1896, Taylor 1965), *P. vera* (Hoskins and Cross 1946, Taylor 1965), *P. hexangulata* (Stewart 1951), *P. illinoensis* (Stewart—personal communication), *P. pusilla* (Brongniart 1881), and *P. berryvillensis* reported here. Of these seeds *P. gigantea*, *P. hexangulata*, *P. illinoensis*, and probably *P. incrassata* all have large bilaterally symmetrical pre-pollen grains of the *Monoletes* type. Such grains are known to have been produced by some members of the Pteridospermales. *Pachytesta berryvillensis* and *P. vera* on the other hand contain pollen of the *Florinites* type that is known from a large number of pollen organs assignable to the Cordaitales. Whether the presence of these *Florinites* grains in seeds demonstrated as belonging to the Medullosan seed ferns is merely the result of contamination at the time of pollination, or reflects the occurrence of another group of Palaeozoic plants that have seed fern-like ovules and Cordaitalean-like pollen grains must await the discovery and report of additional seeds containing pollen grains and the determination of the biological affinities of *Florinites*.

Vascularization. A single vascular bundle penetrates the integument (Pl. 71, fig. 3; Pl. 72, fig. 1) and passes into the nucellus where it vascularizes that tissue. At a level of approximately 1·0 mm. above the point of attachment between nucellus and integument the nucellar vascular bundles form an almost continuous ring similar to the tracheal sheath that delimits seeds of the *Stephanospermum* type. At higher levels the vasculature of *P. berryvillensis* consists of a variable number (28–35) of closely spaced, but clearly distinct flattened bundles that continue to the region of the pollen chamber. Tracheids are variable in size and possess scalariform-helical secondary thickenings.

Although several scattered tracheids were observed in association with the sarcotesta, the general poor preservation of this tissue makes it impossible at this time to determine whether the integument of *P. berryvillensis* was vascularized, and if so, the number and disposition of the bundles.

DISCUSSION

The genus *Pachytesta* as currently interpreted includes radially symmetrical seeds having a rounded base and attenuated apex, a multiple-layered integument consisting of three principal zones, three primary ribs with secondary and tertiary ribs present or

absent, a nucellus free from the integument except at the base and apically forming a large pollen chamber, and vascular tissue in the form of distinct bundles in both nucellus and integument.

Of the 13 recognized species (Taylor 1965) size varies from ovoid seeds 7·0 mm. long and 4·0 mm. in diameter (*P. pusilla*) to obovoid forms 11·0 cm. long and up to 6·0 cm. in diameter (*P. incrassata*). Variability of the three principal tissues of the integument (sarcotesta, sclerotesta, endotesta) ranges from those examples where little differentiation is present in any of the zones (e.g. *P. stewartii*) to those forms where the histology is extremely complex (e.g. six recognizable zones of the sarcotesta in *P. saharasperma*). The arrangement of the individual fibre-like cells that make up the sclerotesta are in three general patterns that have been described by the terms tangential, radial, and intermediate. These three types of sclerotesta are exemplified by *P. illinoensis*, *P. hexangulata*, and *P. hoskinsii* respectively.

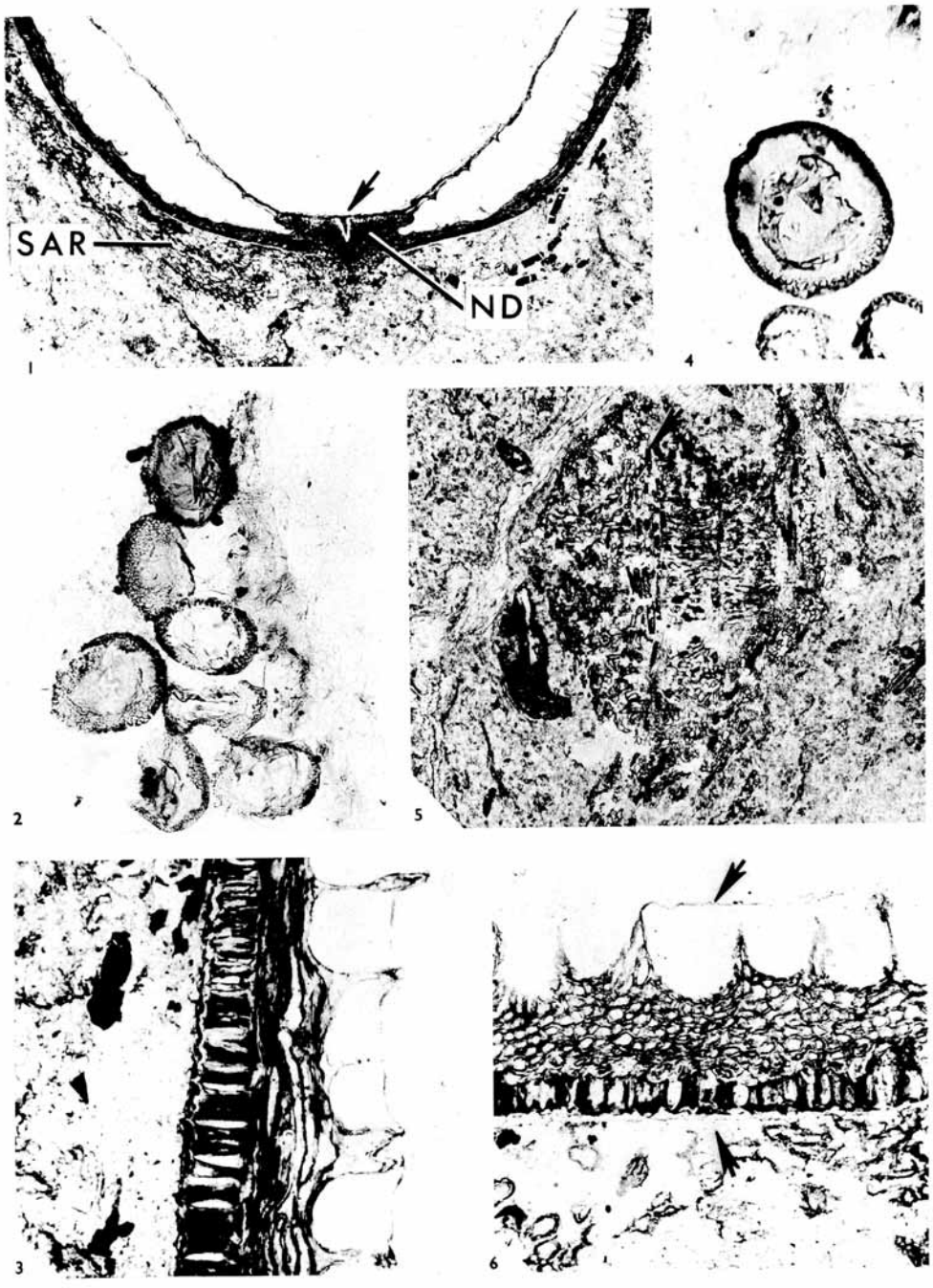
Radial extensions of the sclerotesta that form the primary ribs may be prominent with parenchymatous trabeculae as in *P. vera*, or may be absent and marked only by indentations or thin areas in the corresponding position within the sclerotesta (e.g. *P. gigantea*). Secondary and tertiary ribs may number as many as 42 in *P. illinoensis* or be totally absent as demonstrated by *P. stewartii*. Vascularization of the integument may vary from 6 bundles in *P. shorensis* to 54 in *P. incrassata*. In two previously described species (*P. hoskinsii* and *P. pusilla*) the pattern and number of integumentary vascular bundles is unknown. The integumentary vascular pattern varies from 8 bundles in *P. olivaeformis* to more than 40 in specimens of *P. gigantea*. Nothing is known about the nucellar vascular system of *P. noei*, and *P. incrassata*, while in *P. pusilla* only the presence of nucellar tracheids has been reported.

When compared with other species of *Pachytesta*, *P. berryvillensis* appears most similar to *P. pusilla* known only from the Late Pennsylvanian equivalent of France. Size range for the few specimens reported (Brongniart 1874, Oliver 1904) includes seeds 6·5–8·5 mm. long and 4·0–5·0 mm. in maximum diameter with the distal end attenuated into a short micropylar tube. Thin-walled, isodiametric parenchyma cells characterize the very incompletely preserved portion of the sarcotesta. The sclerotesta is similar to that of *P. berryvillensis*, in that an outer palisade-like layer, and an inner layer of longitudinally oriented fibres are present. In *P. pusilla* radially disposed fibres are absent from the inner surface of the sclerotesta. The presence of an endotesta is known only from cuticular remains in both species. Vascularization of the nucellus is

---

EXPLANATION OF PLATE 72

Figs. 1–6. *Pachytesta berryvillensis* sp. nov. (ND = nucellar disc, SAR = sarcotesta). 1, Median longitudinal section of seed chalaza showing position of vascular bundle (arrow) and extent of sarcotesta; note secretory canals at right of photograph; C.B. 3687 A(5)bot No. 17, ×21. 2, Several *Florinites* pollen grains within chamber; C.B. 735 C(2)bot No. 70, ×250. 3, Longitudinal section of sclerotesta showing orientation of cells and inward projecting fibres of inner layer; C.B. 3687 A bot No. 12, ×120. 4, *Florinites* pollen grain observed on peel preparation; C.B. 735 E(2) top No. 3, ×375. 5, Tangential section of sarcotesta showing longitudinally directed secretory canals; C.B. 3687 B(1) top No. 27, ×16. 6, Transverse section of sclerotesta showing disposition of cells and inwardly projecting fibres; upper arrow indicates position of endotesta cuticle and lower arrow position of thin-walled layer between sarcotesta and sclerotesta; C.B. 735 H(2)bot No. 16, ×120.



TAYLOR and EGGERT, Pennsylvanian seed *Pachytesta*

reported in *P. pusilla*, however, no bundle number is given and nothing is known regarding a vascular system in the integument.

The unique occurrence of radially disposed fibres making up the inner layer of the sclerotesta of *P. berryvillensis* extends an already broad range of anatomical variability of the integument of seeds assignable to the genus *Pachytesta*. To our knowledge the only other seed that shows integument ornamentation of the inner surface is *Albertlongia incostata* (Taylor 1967) from the Middle Pennsylvanian of Illinois. Specimens of this taxon are radially symmetrical and measure 2·0 cm. long and 1·4 cm. in diameter. The apex is rounded; the base extended into a pedicel 2·2 mm. long. Features in common with the genus *Pachytesta* include a heterogeneous integument of three principal tissues, a double vascular system, and a nucellus that is attached to the integument only at the base. In *Albertlongia* the inner surface of the sclerotesta appears as an uneven series of broad ridges and furrows that extend from apex to chalaza, whereas the individual ornamentations of *P. berryvillensis* are the result of relatively few inwardly projecting fibres. The consistent absence of primary ribs of the integument either in the form of prominent radial extensions, or in the presence of indentations or thin areas in the sclerotesta of *Albertlongia*, currently serves to distinguish the genera *Pachytesta* and *Albertlongia*.

Our ability to interpret the significance of internal ornamentation patterns in the integument of Palaeozoic seeds is extremely limited in that at present we can not properly distinguish between those features which are consistent throughout ontogeny of a given species versus those that changed during the course of development. The ability to distinguish phylogenetic features from ontogenetic stages must await the discovery of additional seeds that will adequately document the course of Palaeozoic ovule development.

Acknowledgement. This research was supported by National Science Foundation Grants GB–6834 and GB–4126.

REFERENCES

BRONGNIART, A. 1874. Étude sur les graines fossiles trouvées à l'état silicifié dans le terrain houiller de Saint-Étienne. Deuxième partie. *C. r. Acad. Sci.* (*Paris*), **79,** 427–35.

—— 1881. *Recherches sur les graines fossiles silicifiées*. Paris.

HOSKINS, J. H. and CROSS, A. T. 1946. Studies in the Trigonocarpales. Pt. 1. *Pachytesta vera*, a new species from the Desmoinesian Series of Iowa. *Amer. Midl. Nat.* **36,** 207–50.

OLIVER, F. W. 1904. Notes on *Trigonocarpus* Brong. and *Polylophospermum* Brong., two genera of Palaeozoic seeds. *New. Phytol.* **3,** 96–104.

RENAULT, B. 1896. Bassin houiller et permien d'Autun et d'Épinac. Fasc. 4. Flore fossile. Deuxième partie (Text) 1–578, *Études gîtes minér. France*.

SCHOPF, J. M., WILSON, L. R., and BENTALL, R. 1944. An annotated synopsis of Paleozoic fossil spores and the definition of generic groups. *Rep. Inst. Ill. St. Geol. Surv.* **81,** 1–73.

STEWART, W. N. 1951. A new *Pachytesta* from the Berryville locality of southeastern Illinois. *Amer. Midl. Nat.* **46,** 717–42.

TAYLOR, T. N. 1965. Paleozoic seed studies: a monograph of the American species of *Pachytesta*. *Palaeontographica*, **B117,** 1–46.

—— 1967. Paleozoic seed studies: on the structure of *Conostoma leptospermum* n. sp., and *Albertlongia incostata* n. gen. and sp. Ibid. **B121,** 23–9.

THOMAS N. TAYLOR
DONALD A. EGGERT
Department of Biological Sciences
University of Illinois at Chicago Circle
Chicago, Illinois

Typescript received 17 September 1968