Ultrastructural analysis of selected Cretaceous megaspores from Argentina

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ABSTRACT–Detailed ultrastructural analysis of an assemblage of Lower Cretaceous megaspores from the Baqueró Formation of Argentina allows a complete description of two new taxa as well as additional information on the structure of several previously described types. *Erlansonisporites sparassis* displays a complex wall stratification, a separable surface reticulum, and attached microspores. *Horstisporites iridodea* sp. nov. possesses an elaborately patterned wall like that seen in several extant species of the modern lycopod genus *Selaginella*. On the basis of developmental information from modern heterosporous lycopod megaspores, the mesospore bearing *Bacutriletes triangulatus* sp. nov. is recognised as an aborted product of a meiotic tetrad. Also reported from this locality are *Hughesisporites patagonicus*, *Bacutriletes* sp. A, and an additional loosely defined megaspore type with characteristic clavae. Transmission electron microscopy provides the opportunity to infer previously unattainable biological information from dispersed spores. Such studies provide new insights as a foundation for the further elucidation of the developmental and evolutionary significance of wall construction in heterosporous pteridophytes.

INTRODUCTION

Since the first report of Cretaceous megaspores from Argentina (Archangelsky, 1963), relatively few studies have appeared (Archangelsky, 1965; Gamerro, 1975a,b; 1977; Baldoni & Taylor, 1985), and only the most recent has utilised the increased resolution available through transmission electron microscopy. Megaspore assemblages are significant not only for their value in biostratigraphy, but also because, in many instances, they represent the only surviving record of a diverse vegetational component from a particular point in geological time.

The intent of this paper is to provide new information about several Cretaceous megaspores utilising both scanning and transmission electron microscopy. The utilisation of increased resolution offers the opportunity to describe new taxa more completely, as well as to augment the information available on previously described taxa. The megaspores from these sediments are extremely well preserved, and offer insight into several biologically significant areas beyond a taxonomic record of pteridophyte diversity.

MATERIALS AND METHODS

A number of well preserved megaspores were recovered by hydrofluoric acid maceration from light brown volcaniclastic sediments from the Tico Amphitheater, Santa Cruz Province, Argentina (Fig. 1). Stratigraphically, the fossils come from the Baqueró Formation which is considered to be Early Cretaceous (Early Aptian) (Archangelsky, 1963) at this locality.

The microfossils occur near the base of the formation, in the lowermost of several fossiliferous lenses.

Preparation of samples for scanning electron microscopy involved attachment of the specimens directly to standard stubs with either double-sided tape or colloidal silver paint. Specimens were viewed and photographed with an Hitachi HS-500 operating at 25 KV. Transmission electron microscopy involved dehydration of acetolysed specimens in a graded ethanol series (70%, 85%, 95%, 100%, 20 minutes between changes), transfer to 100% acetone, and gradual infiltration with Spurr low viscosity embedding medium with decreasing ratios of acetone to Spurr resin (3:1, 1:1, 1:3, 2 changes in fresh resin, at least eight hours between changes). The resin infiltrated specimens were then placed in aluminium pans or between plastic coated glass slides, and polymerised in a 70°C oven overnight. Megaspores were cut from the plastic wafers, glued in the desired orientation to flat blocks of Spurr, and sections cut with a diamond knife. Sections were collected on 1 × 2 mm copper slot grids and dried onto formvar support film. Ultra-thin sections were stained with varying combinations of potassium permanganate (1.5% in buffered aqueous solutions; pH 6.5), uranyl acetate (1% aqueous solution) and lead citrate (Venable & Coggeshall, 1965). (A three number sequence denoting the stain schedule employed will be indicated in the figure caption of each photomicrograph. These characters will be separated by hyphens and will signify the duration of staining, in minutes, of

each of the stains in the order in which they appear above).

The system of form genera established by Potonié (1956) for dispersed palynomorphs has been adopted here. Although the system is artificial, it does provide a consistency and order that we believe is preferable to speculation regarding taxonomic identity. The lack of a suitable data base of developmental information on extant megaspores obviates the use of non-committal terminology. The term sclerine has been proposed (Erdtman, 1952) for this reason, but it has also been consistently used in connection with homosporous fern spores. Adopting this term for probable lycopod megaspores could be construed as implying some type of homology when none is intended. It seems equally undesirable to erect new non-committal terminology, therefore ultrastructural descriptions are in the most general terms possible. Of palynological terminology, only the term mesospore is used because the nature of this structure is discussed relative to its developmental significance.

SYSTEMATIC DESCRIPTIONS
Turma Triletes (Reinsch) Dettmann, 1963
Subturma Azonotriletes (Luber) Dettmann, 1963
Infraturma Muronati Potonié & Kremp, 1954
Genus *Erlansonisporites* Potonié, 1956
Type species *Erlansonisporites erlansonii* (Miner) Potonié, 1956
Erlansonisporites sparassis (Murray, 1939) Potonié, 1956
(Pl. 1, figs. 1–5; Pl. 2, figs. 1–2)

Description. The specimens from Argentina (approx. 30) are radial, trilete, and range in size from 380–510 μm in diameter (Pl. 1, fig. 1). The laesurae are from 3/4–1 times the spore radius in length. Ornamentation consists of a dense reticulum with muri projecting up to 30 μm above the spore surface. The laesurae extend out approx. 110 μm. The convoluted nature of these laminar muri tends to obscure the size and shape of the
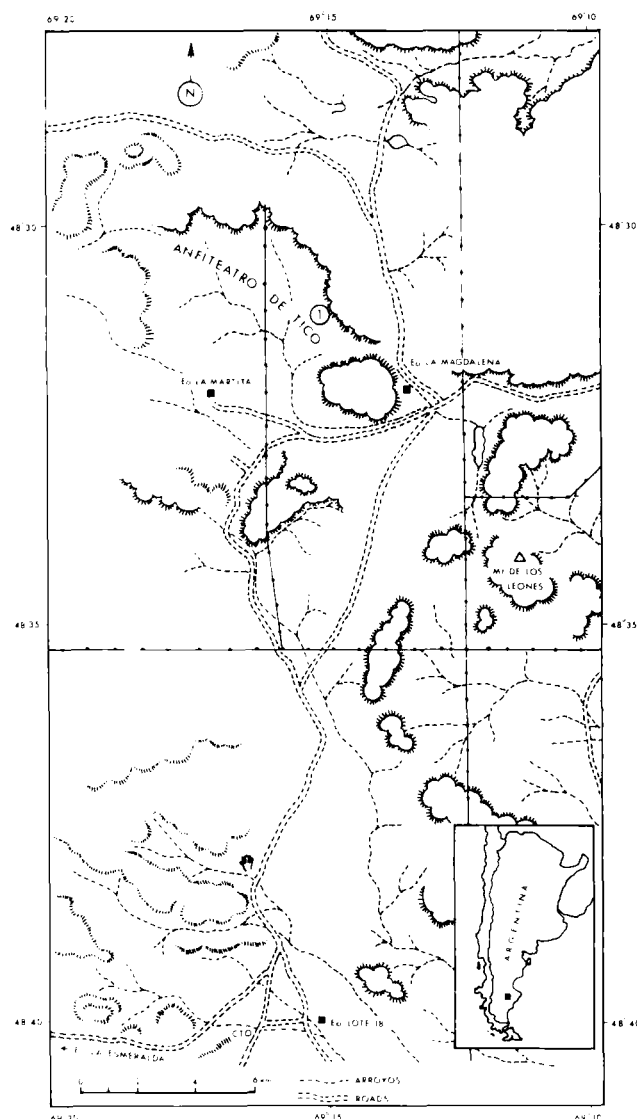

Fig. 1. Locality map of fossiliferous lens in the Tico Amphitheater (Anfiteatro de Tico) which yielded the described megaspores (circled number 1). Ea = estancia or ranch.

Explanation of Plate 1

Figs. 1–7. *Erlansonisporites sparassis* and associated microspores.

Fig. 1. Proximal view showing intact reticulum and raised trilete suture. Note attached microspore at arrow (×250).

Fig. 2. Proximal view of specimen from which the membranous reticulum has been removed. The trilete suture is still discernible (×200).

Fig. 3. Cross-section of sporoderm in non-sutural region. Arrow denotes region where reticulum is separated from the remainder of the sporoderm (0–15–7) (×1060).

Fig. 4. Cross-section of sporoderm in sutural region. Note attached microspore at arrow (0–15–7) (×1650).

Fig. 5. Microspore attached to surface of megaspore (×6000).

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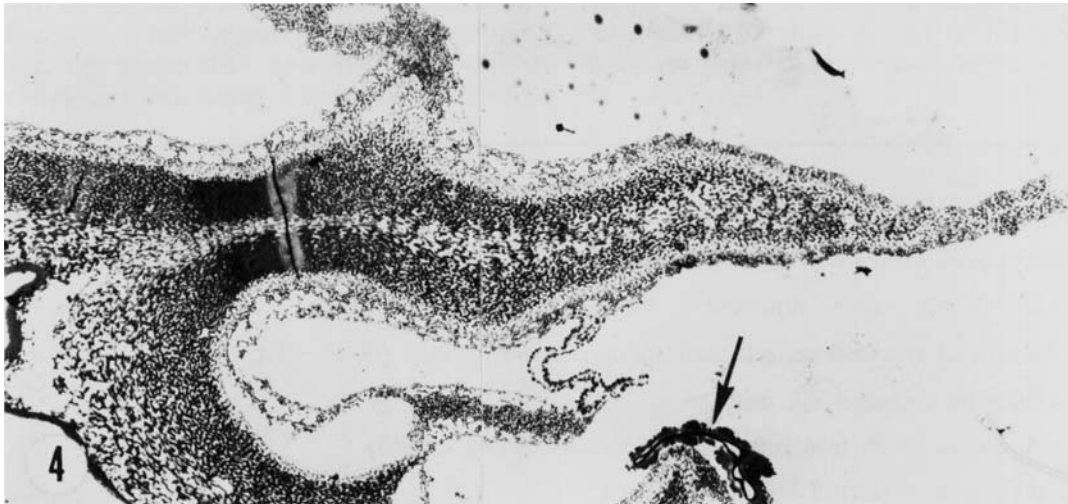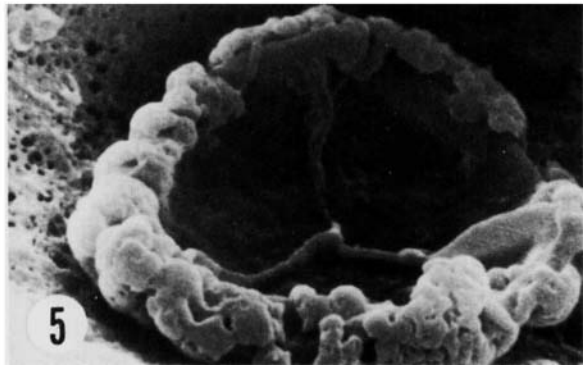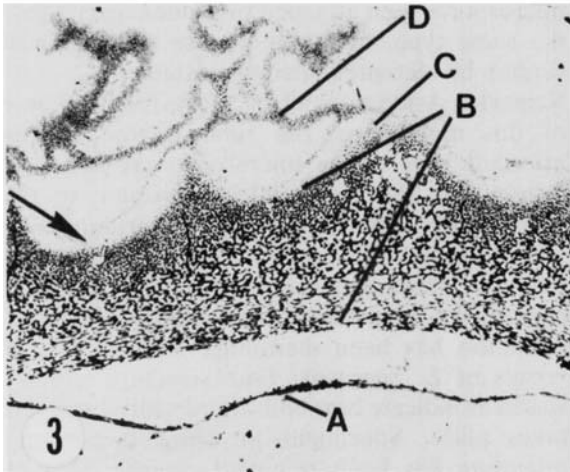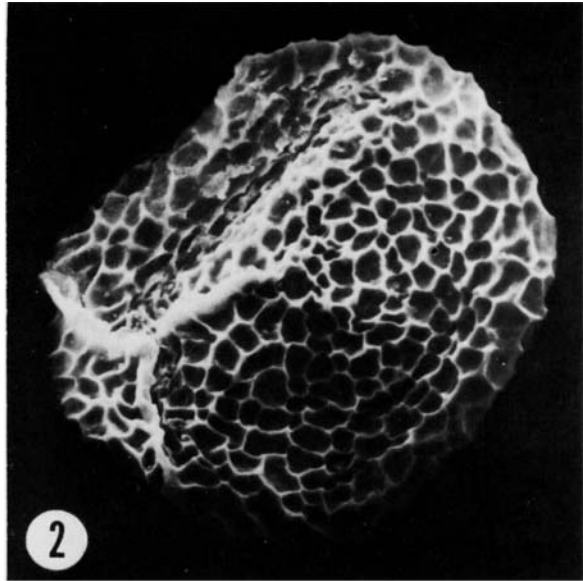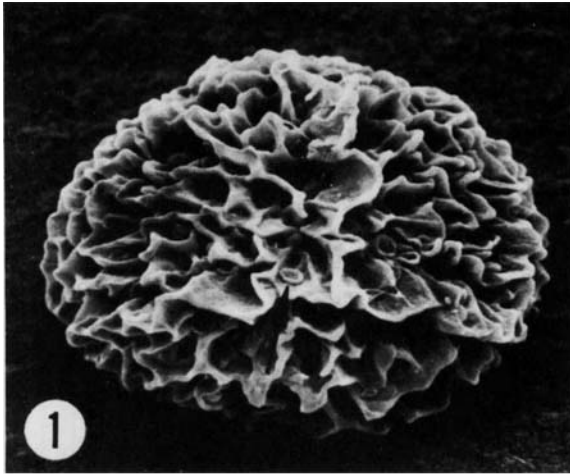
lumina they enclose except in specimens where all or part of the muri have been removed (Pl. 1, fig. 2). Lumina are irregularly shaped and range in size from 8–35 μm in their maximum dimension.

At the ultrastructural level, the sporoderm consists of several discrete zones (Pl. 1, fig. 3). The innermost layer (A) is 300–600 nm in thickness except beneath the suture where it thickens to approx. 1.2 μm. In places, this layer appears lamellated. Layer B is the thickest portion of the wall and shows a gradational change of structure in the direction of the spore surface (Pl. 1, fig. 3). When in contact with the innermost layer of the sporoderm, the sporopollenin units appear disjunct, compressed, and tend to be elongated parallel to the spore surface. In the centre of this zone, the units become less compressed and more interconnected, enclosing large lacunae. In the outer portion of the layer, the wall material becomes more compact. Bases of the muri have their origin in the outermost portions of this layer, and appear as peaks projecting into the mural elements. The innermost portions of this layer and the first sporoderm layer commonly separate from the remainder of the spore wall (Pl. 1, fig. 3).

Layer C of the sporoderm is thin (1.0 μmm), lightly staining, and diffuse. The wide spacing and fragile nature of the components render this portion of the wall less structurally competent. The separation of the muri takes place along this zone of weakness.

The outermost layer of the spore wall (D) includes the muri. It is constructed of spongy material (Pl. 1, fig. 3), and appears similar to the layer which forms the bases of the muri. The suture in *E. sparassis* is formed by the outward projection of all but the innermost sporoderm layer (Pl. 1, fig. 4). Material of the three main sporoderm layers extends out to nearly the tip of the sutural groove.

Microspores attached to this type of megaspore are approximately 10–15 μm in diameter, and generally compressed (Pl. 1, fig. 5; Pl. 2, fig. 1). Laesurae extend for nearly the entire spore radius and are slightly elevated (to 1.2 μm). The interradial area (Pl. 1, fig. 5) is often smooth, with the equatorial and distal surfaces possessing a verrucate ornament with elements up to 1.4 μm in height (Pl. 2, fig. 1). Ultra-thin sections indicate that a thin layer of the sporoderm surrounds the entire spore and forms the suture. This zone is thinnest on the proximal surface (approx. 140 nm thick), and increases to about 400 nm toward the distal surface (Pl. 2, fig. 2). An additional layer covers the equatorial and distal surfaces and forms the verrucae. The two layers stain with different intensities, but little structure can be detected within the layers. All of the microspores seen attached to similar specimens were of the same type, but their precise taxonomic affinities cannot be definitely demonstrated.

Remarks. Aside from a basic ultrastructural description of this megaspore, the finer degree of resolution afforded by electron microscopy provides additional insight into the structural organisation of the spore wall. Singh (1964) expresses uncertainty as to the identification of this taxon in his samples, because the oxidative treatment used to induce translucency disrupted the membranous lamellae. This same phenomenon has been mentioned by Harris (1961) for spores of *E. sparassis*. Fine structural studies of *E. sparassis* indicate how and where sporoderm separation takes place. Specimens in which a portion of the reticulum has been removed, suggest that alternate preservational conditions of this spore type can appear quite different, and might even be assigned to different dispersed spore taxa. Other megaspores assignable to species within this genus possess quite a different

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Explanation of Plate 2

Figs. 1–2. Microspores associated with *Erlansonisporites sparassis*.

Fig. 1 Distal view of microspore attached to megaspore surface (×6000).

Fig. 2. Cross-section of microspore attached to megaspore surface (0–15–7) (×2650).

Figs. 3–8 *Horstisporites iridodea* sp. nov.

Fig. 3. Proximal surface with fine reticulum and raised trilete (×60).

Fig. 4. Distal surface in reflected light (×45).

Fig. 5. Surface of innermost wall region showing randomly oriented strands of sporopollenin (×4000).

Fig. 6. Distal surface of specimen in Fig. 4 with SEM (×60).

Fig. 7. Section of wall showing patchwork pattern (10–10–2) (×3000).

Fig. 8. Cross-section of innermost wall layer showing randomly orientated strands of wall material in various planes of section (0–15–7) (×15,000).
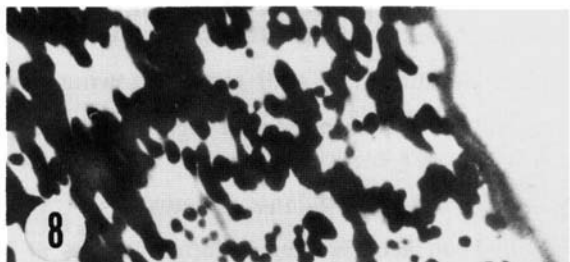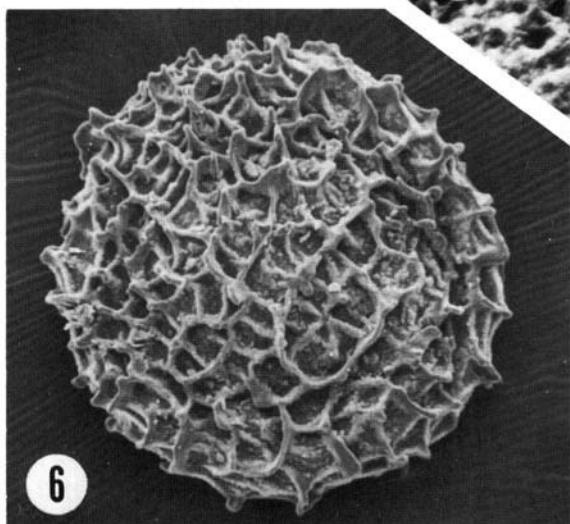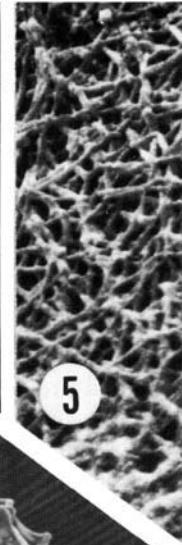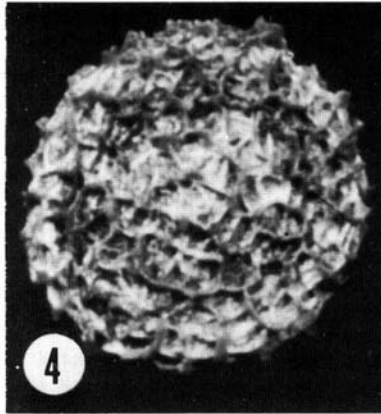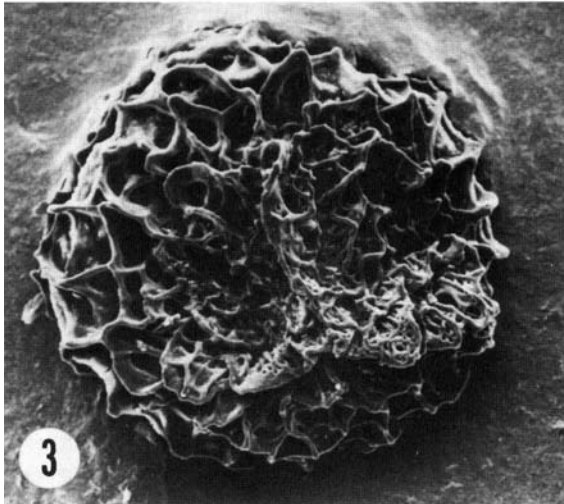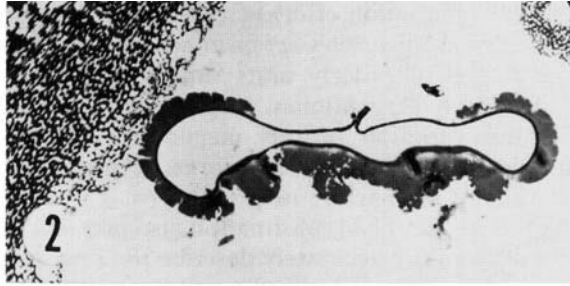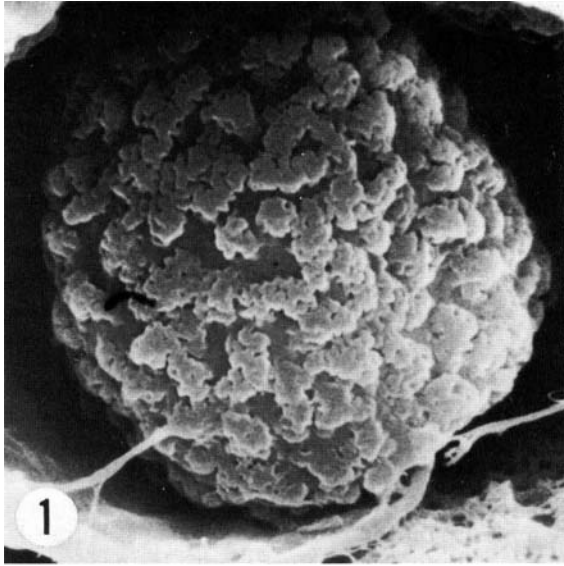
ultrastructural organisation. Bergad (1978) described specimens of *Erlansonisporites spinosus* which possess a wall constructed of orderly units similar to those described from an Argentinian megaspore named herein. Natural variation of this magnitude is not surprising since it occurs in megaspores of modern *Selaginella* (Taylor & Taylor, in press).

Combined SEM and TEM information also provides the opportunity to more accurately describe the microspore type which is assocated with these megaspores. It is interesting to note that the removal of the distal reticulum from this megaspore would also effect removal of the accompanying microspores. Speculation on the possible significance of this phenomenon would be premature until further information is available on reproductive strategies in extant heterosporous pteridophytes.

With regard to comparison with living taxa, the inner two sporoderm layers of *E. sparassis* bear some similarity to those described by Tryon & Lugardon (1978) in the megaspore from *S. martensii*. This similarity extends primarily to the presence of a dense inner layer (a feature which may prove to be universal among viable megaspores, both fossil and living), and to the degrees of compression of the various wall regions. As more megaspores, both fossil and living, are described at the fine structural level, these features which appear to be widespread, most likely will be demonstrated to reflect a consistent and successful developmental pattern.

Turma Triletes (Reinsch) Dettman, 1963
Subturma Azonotriletes (Luber) Dettman, 1963
Infraturma Muronati Potonié & Kremp, 1954
Genus *Horstisporites* Potonié 1956
Type species *Horstisporites (Triletes) reticuliferus* (Dijkstra) Potonié, 1956
Horstisporites iridodea Taylor & Taylor sp. nov.
(Pl. 2, figs. 3–8; Pl. 3, figs. 1–3)

Derivation of name. From the Greek, *irido*- meaning rainbow and -*odea* for resembling. The resemblance to a rainbow refers to the opalescent glitter of the sporoderm in reflected light.

Diagnosis. Megaspores, radial, trilete, circular; thick sporoderm with a coarse perfect reticulum on the distal and equatorial regions, reticulum covered by anastomosing network of variably sized strands of wall material on the proximal surface; laesurae 1/2–2/3 the spore radius, curvaturae may be present; sporoderm opalescent in reflected light.

Holotype. Pl. 2, figs. 4, 6. Acquisition number 17,494 in the Paleobotanical Collections, The Ohio State University.

Locality and horizon. Tico Amphitheater, Santa Cruz Province, Argentina. Near base of the Baqueró Formation, Early Aptian.

Description. Megaspores of this type (approx. 25 specimens) range in size from 1150–1350 μm in diameter (Pl. 2, fig. 3). Equatorial and distal ornamentation is composed of a coarse perfect reticulum (i.e. all lumina are completely enclosed by muri) with muri up to 50 μm in height, and distinct polygonal lumina ranging from 51–136 μm in diameter (average diameter = 85 μm; Pl. 2, figs. 4, 6). In the proximal region of the spore (Pl. 2, fig. 3), the reticulum is overlain by an

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Explanation of Plate 3

Figs. 1–3. *Horstisporites iridodea* sp. nov.

Fig. 1. Section through sporoderm in sutural region. Elements of the proximal reticulum appear disjunct due to attachment in other planes of section (10–10–2) ($\times$ 700).

Fig. 2. Surface of outermost wall region showing loose spongy organisation ($\times$ 15,000).

Fig. 3. Cross-section of outermost wall region. Note the gradation to patchwork organisation toward the lower right (10–10–2) ($\times$ 7000).

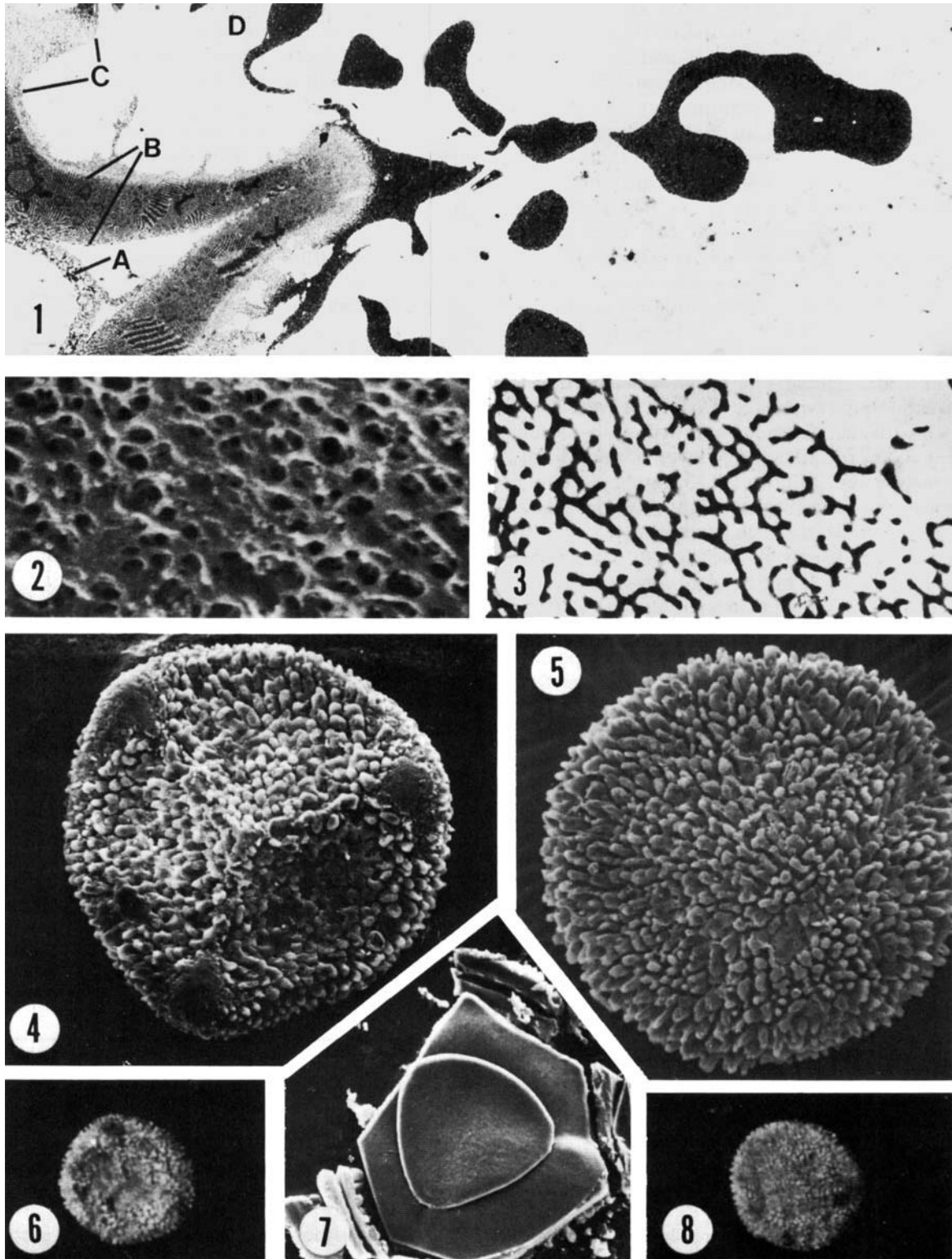Figs. 4–8. *Bacutriletes triangulatus* sp. nov.

Fig. 4. Proximal surface showing bulbous regions at laesurae tips ($\times$ 175).

Fig. 5. Distal surface showing dense ornamentation ($\times$ 175).

Fig. 6. Proximal surface in reflected light (($\times$ 45).

Fig. 7. Spore dissected to reveal smooth internal body (mesospore) ($\times$ 150).

Fig. 8. Distal surface in reflected light ($\times$ 45).

anastomosing network of variably sized strands of wall material which reach their maximum thickness and development over the trilete suture and project to a height of 120 μm. Laesurae extend from 1/2–2/3 the spore radius. Curvaturae may be present. In reflected light, the sporoderm displays an opalescence of various colours which is a result of the sporoderm organisation.

At the fine structural level, the sporoderm consists of four recognisable layers (Pl. 3, fig. 1). The innermost (A) is formed of rather loosely organised linear filaments which appear to lack any consistent orientation (Pl. 2, figs. 5, 8). This layer grades outward into a region (B) which displays a highly ordered patchwork pattern in section view (Pl. 2, fig. 7; Pl. 3, fig. 1). This pattern is produced by the repetition of a basic plate-like unit, the structure of which was determined by serial sectioning (Taylor & Taylor, in press).

The patchwork region grades outward into a loosely organised, uncompressed, spongy layer (C) and forms the basal portions of the muri (Pl. 3, figs. 2, 3) which appear translucent in transmitted light. The tips of the muri and the elements of the anastomosing network on the proximal surface form the fourth sporoderm stratum (D), are spongy but densely constructed, and appear nearly electron opaque in transverse view (Pl. 3, fig. 1).

Comparison. No other species of *Horstisporites* possesses any sort of proximal elaboration of the surface reticulum, or has a reticulum as coarse. Several extant species of *Selaginella*, as well as four dispersed fossil megaspores possess a very similar internal wall organisation (Taylor & Taylor, in press). *Erlansonisporites spinosus* (Bergad, 1978) bears the diaphanous muri characteristic of that genus, but is considerably smaller than *H. iridodea*, and lacks a proximal reticulum. Both species possess a wall stratification pattern that is similar in organisation and thickness. *Thylakosporites retiarius* (Hughes) Potonié, 1956 also possesses a wall structure like that in *H. iridodea* including a coarse surface reticulum. The reticulum, however, is readily detached, and not present at all in the interradial areas.

Bergad (1978) also described *Ricinospora cryptoreticulata*, a Cretaceous megaspore type from North Dakota, which possesses this unusual ultrastructural sporoderm pattern, as well as a coarse separable reticulum. We have seen no evidence of a separable reticulum in *H. iridodea*. Finally, *Horstisporites opalinus* Huckriede, 1986 is considerably smaller than *H. iridodea* and possesses a much finer and more weakly developed reticulum with no proximal elaboration.

Turma Barbates Madler, 1954
Genus *Hughesisporites* Potonié, 1956
Type species *Hughesisporites (Triletes) galericulatus* (Dijkstra)
Potonié, 1956
Hughesisporites patagonicus Archangelsky, 1963
(Pl. 6, Figs. 3–5)

Description. The specimens assignable to this taxon (approx. 30) are radial, circular to subtriangular, trilete, and 500 μm in longest equatorial diameter. The laesurae are 7/8–1 times the spore radius, strongly elevated (to 70 μm), and taper abruptly to the proximal spore surface near the equator (Pl. 6, fig. 3). Surface ornamentation consists of coarse verrucae which are low to absent on the distal surface, and more prominent and consistently present on the proximal surface.

The sporoderm consists of at least four distinct regions (A–D; Pl. 6, fig. 4). The interior of the spore is lined with a thin dense layer (A) 1–4 μm in thickness which appears finely lamellated or has a vesiculate appearance at high magnification. A separation may occur between this layer and the remainder of the spore wall. The remainder of the sporoderm is spongy. Units of the second zone (B) are densely packed, and in places show a somewhat lamellated construction. The second layer grades rather abruptly into a third zone (C) which is much more diffuse. Lacunae are present in this region and may have resulted from expansion or local removal of wall material. Near the surface of the spore, the wall units become finer and more densely

Explanation of Plate 4

Figs. 1–3. *Bacutriletes triangulatus* sp. nov.

Fig. 1. Detailed cross-section of mesospore (M) and main sporoderm. Note deformation in ornamental element (10–10–2) (×3000).
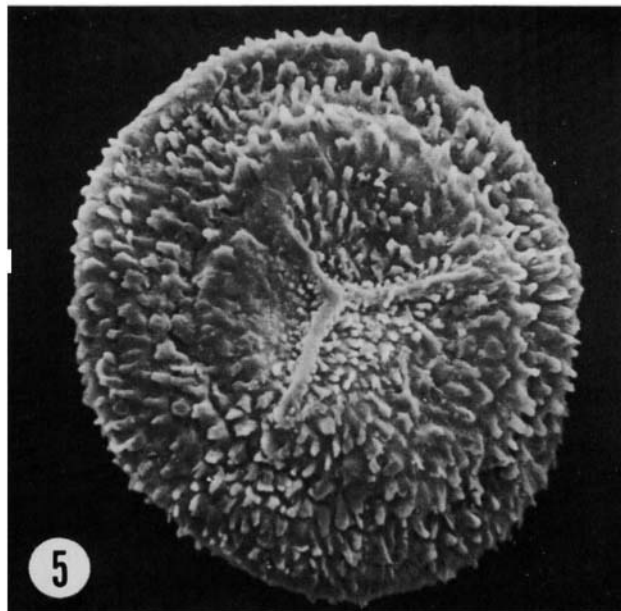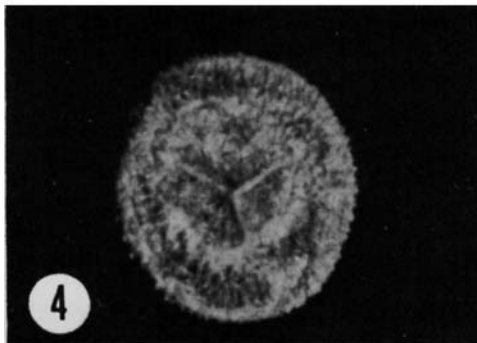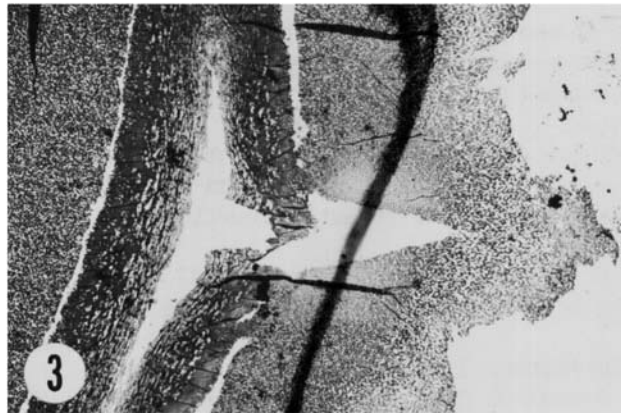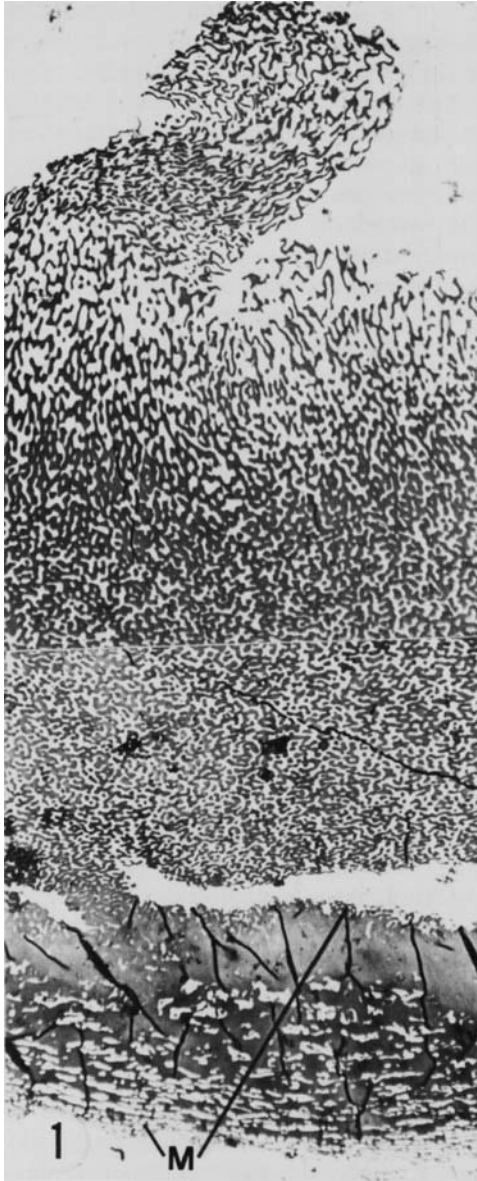
Fig. 2. Cross-section of entire spore showing relationships between mesospore and sporoderm (10–10–2) (×250).

Fig. 3. Detailed cross-section of sutural region (10–10–2) (×700).

Figs. 4–5. *Bacutriletes* sp. A.

Fig. 4. Proximal surface in reflected light (×45).

Fig. 5. Surface of specimen in fig. 4 (×100).

packed (D). This trend continues to the surface where the units form a dense surface coating. Layer A is present at the base of the suture (Pl. 6, Fig. 5), but B is cut by the suture. The elevated laesurae are formed by a protrusion of layers C and D.

Turma Triletes (Reinsch) Dettmann, 1963
Subturma Azonotriletes (Luber) Dettmann, 1963
Infraturma Apiculati (Bennie & Kidston) Potonié, 1956
Genus *Bacutriletes* (van der Hammen) Potonié, 1956
Type species *Bacutriletes (Selaginellites) greenlandicus* (Miner)
Potonié, 1956
Bacutriletes triangulatus sp. nov.
(Pl. 3, figs. 4–8; Pl. 4, figs. 1–3)

Derivation of name. Refers to the consistently sub-triangular shape which is unique within the genus.
Diagnosis. Megaspore, radial, trilete, subtriangular; ornamentation of densely packed baculae or clavae which may fuse on their edges, often reduced in interradial regions; laesurae follow long axes of the spore to 2/3 of diameter and contact expanded knoblike areas at the corners.
Holotype. Pl. 3, fig. 5. Acquisition number 17,495 in the Paleobotanical Collections, The Ohio State University.
Locality and horizon. Tico Amphitheater, Santa Cruz Province, Argentina. Near the base of the Boguero Formation, Early Aptian.
Description. This megaspore type is radial, trilete, subtriangular, and ranges from 510–640 μm in maximum diameter (6 specimens), with an average diameter of 540 μm. Laesurae follow the long axes of the spore and extend 2/3 of the distance to the spore margin where they contact expanded knoblike regions which mark the corners of the triangular shape (Pl. 3, figs. 4, 6). Proximal and distal (Pl. 3, figs. 5, 8) surfaces are

ornamented with densely packed ornamental elements consisting of baculae or clavae which may fuse on their edges to form more complex ridgelike elements. These elements range from 17–25 μm in height on all surfaces, except the swollen tips of the laesurae where they may be absent (Pl. 3, fig. 4), and the interradial regions where they are often reduced.

The sporoderm is divided into two distinct regions. An outer spore wall comprises the thickest portion of the sporoderm and may enclose an inner body which is similarly shaped, smooth, and about 1/2 as large in maximum diameter (mesospore; Pl. 3, fig. 7; Pl. 4, fig. 2). In transverse view the mesospore wall is about 10–15 μm in thickness, and consists of darkly stained wall material which appears to enclose a series of variably sized and irregularly shaped vesicles (Pl. 4, fig. 1). Closest to the spore lumen the vesicles are compressed, and the wall material between adjacent vesicles thins. In the region of the mesospore surface additional wall material is present and encloses fewer and slightly less compressed vesicles. The outermost portion of the wall has a spongy appearance like that seen in the outer wall, but is free from it except near the sutural groove (Pl. 4, fig. 2).

The outer spore wall possesses a spongy organisation in which several zones can be recognised (Pl. 4, fig. 1). Closest to the mesospore, the wall units are densely packed and compressed. In the region of the spore surface, the outer wall units gradually become less compressed. At a level 4–5 μm from the surface, the wall units become densely packed and are elongated perpendicular to the surface (Pl. 4, fig. 1). The units remain orientated in this manner, but become more loosely organised just beneath the spore surface and into the ornamental elements. The laesurae of this megaspore consist of thickened and elevated regions of the outer spore wall over a well developed sutural groove (Pl. 4, figs. 2, 3) which traverse all wall layers.
Remarks. Since the mesospore in extant *Selaginella*

Explanation of Plate 5

Figs. 1–3. *Bacutriletes* sp. A.

Fig. 1. Distal surface showing reduced ornamentation (×100).

Fig. 2. Cross-section of sporoderm in non-sutural region. Note separation of basal layer from main sporoderm (arrow) (0–15–7) (×1650).
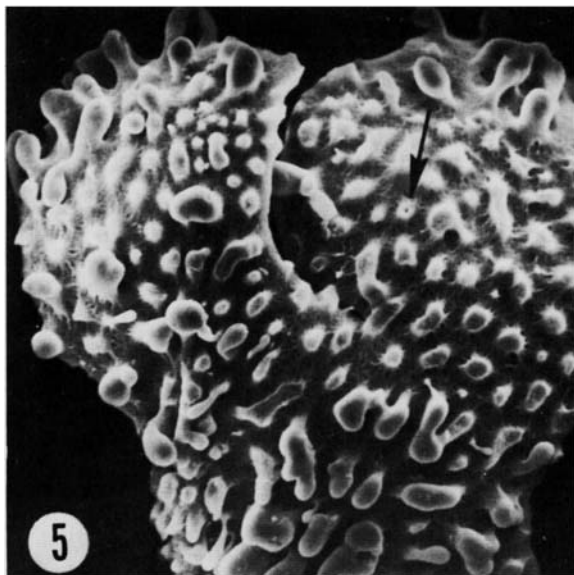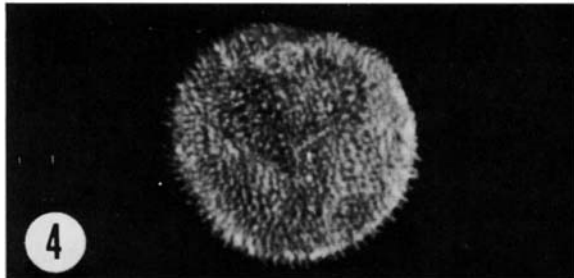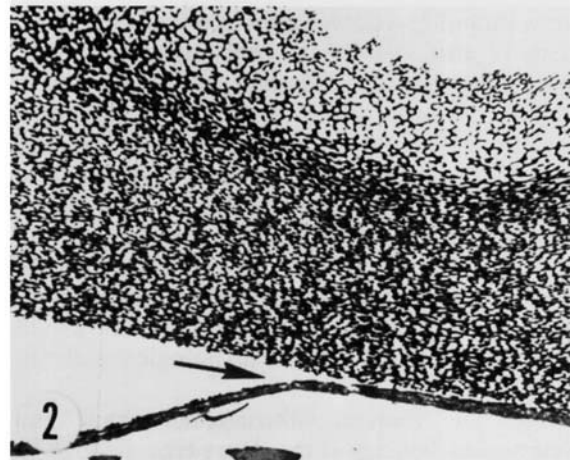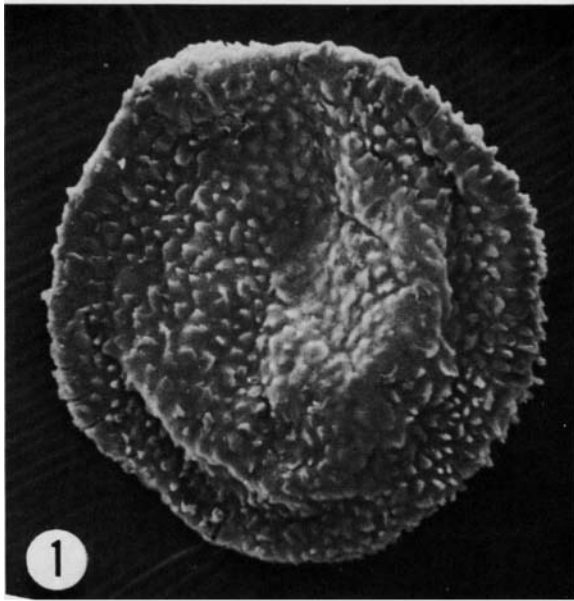
Fig. 3. Section of sporoderm showing basal layer with lamellae (0–15–7) (×40,000).

Figs. 4–6. *Bacutriletes* sp. indet.

Fig. 4. Proximal surface in reflected light (×45).

Fig. 5. Fragment of megaspore with a variety of ornamental elements. Note site where element has been removed (arrow) (×250).

Fig. 6. Detail of clavate ornamental element (×3000).

megaspores probably represents the remains of aborted cytopolasm (Pettitt, 1966), it seems unwise to base taxonomic categories on presence or absence of a mesospore in fossil specimens. Rather, taxa should, if at all possible, be based on more consistent external features as in the case of *B. triangulatus*. Using modern analogues for comparison (Pettitt, 1966; Taylor, 1987) it is probable that this megaspore was aborted prior to dispersal from the sporangium. Its presence in the dispersed state further underscores the necessity of considering developmental information in the establishment of taxa, and analysis of palynological assemblages.

Comparison. The marked subtriangular shape and bulbous corner thickenings of this spore type distinguish it clearly from all other species of *Bacutriletes*.

Turma Triletes (Reinsch) Dettmann, 1963
Subturma Azonotriletes (Luber) Dettman, 1963
Infraturma Apiculati (Bennie & Kidston) Potonié, 1956
Genus *Bacutriletes* (van der Hammen) Potonié, 1956

Type species *Bacutriletes (Selaginellites) greenlandicus* (Miner)
Potonié, 1956
Bacutriletes sp. A
(Pl. 4, figs, 4, 5; Pl. 5, figs. 1–4)

Description. This megaspore type (approx. 10 specimens) is circular, trilete, and ranges in diameter from 680–850 μm (average 730 μm; Pl. 4, figs. 4, 5). Ornamentation consists of a variety of appendage morphologies, the most common of which are distal elements (Pl. 5, fig. 1) in the form of reduced coni or verrucae. On the proximal half of the spore (Pl. 4, fig. 5) are baculae, generally with expanded (i.e. clavae), or pointed tips (i.e. spinae). All elements range from 6–30 μm in length. Ornamentation is usually reduced in the interradial areas (Pl. 4, fig. 5). Laesurae are elevated or may be set in a shallow depression and extend from 1/2–7/8 of the spore radius. Projecting from the sides of the laesurae into the groove are short spinae. Contact faces are defined by the change in ornamentation from the interradial areas to the remainder of the spore body.

The wall is 20–30 μm thick with as many as four distinguishable regions (Pl. 5, fig. 2). An innermost basal layer is present, 1.0–1.5 μm thick, and composed of tightly packed spongy material (Pl. 5, fig. 3). This layer easily separates from the remainder of the spore wall (Pl. 5, fig. 2). Toward the outer surface, the spongy material becomes gradually more delicate, and then coarser following the contour of, and at a level approx. 10 μm beneath, the spore surface. This is superceded by a much looser and more delicate zone which extends to the spore surface. Surface appendages appear compressed, probably due to preservational effects.

Remarks. These Argentinian megaspores compare favourably with *Bacutriletes dijkstrae* with regard to overall size and the lack of distal ornamentation. However, the elements that form the ornamentation of the Argentinian specimens (6–30 μm) do not fall within the given size range for the closest comparable species, *B. dijkstrae* (30–60 μm). Until the increased resolution afforded by the SEM is utilised to examine the finer ornamental components of *B. dijkstrae*, it seems unwise to erect a new taxon based on subtle differences of this type. This is especially true in light of the fact that another slightly different Argentinian megaspore possesses very similar ultrastructural features, suggesting the presence of a single, variable taxon.

Bacutriletes sp. indet.

There are a number of megaspores at this locality (approx. 20 specimens) which are ornamented with clavae, baculae, and verrucae in various combinations. Many of these megaspores vary greatly in size, sutural characteristics, and extent and density of ornamentation. However, all share the same ornamental elements in slightly different combinations. An added problem is the fact that these elements of the ornament are delicate and subject to removal. Extent and density of

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Explanation of Plate 6

Figs. 1–2. *Bacutriletes* sp.

Fig. 1. Cross-section of sporoderm in sutural region. Sutural groove at arrow (0–15–7) (× 660).

Fig. 2. Cross-section of sporoderm in non-sutural region showing an intact clavate element and site where an element has been removed (arrow) (0–15–7) (× 840).

Figs. 3–5. *Hughesisporites patagonicus*.

Fig. 3. Proximal surface showing elevated laesurae (× 100).

Fig. 4. Cross-section of sporoderm in non-sutural region (10–10–2) (× 700).

Fig. 5. Cross-section of sporoderm in sutural region (0–15–7) (× 1660).
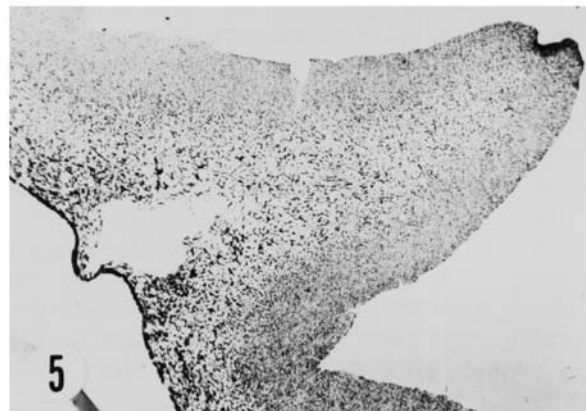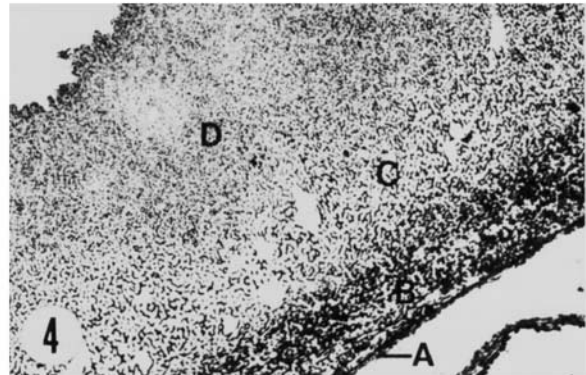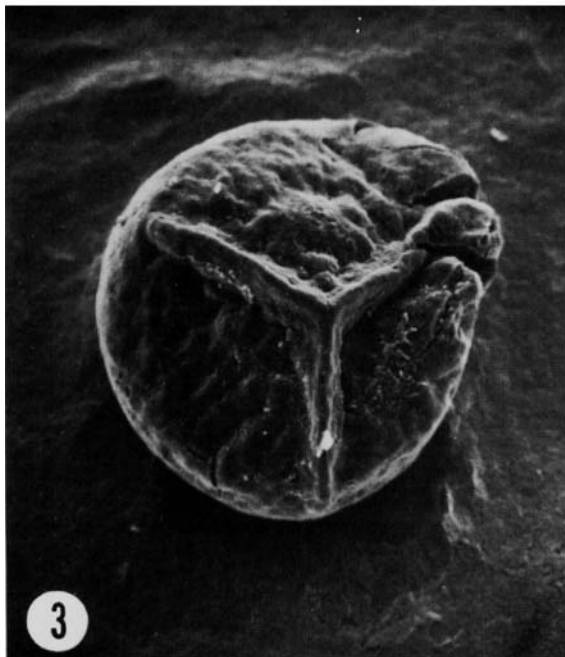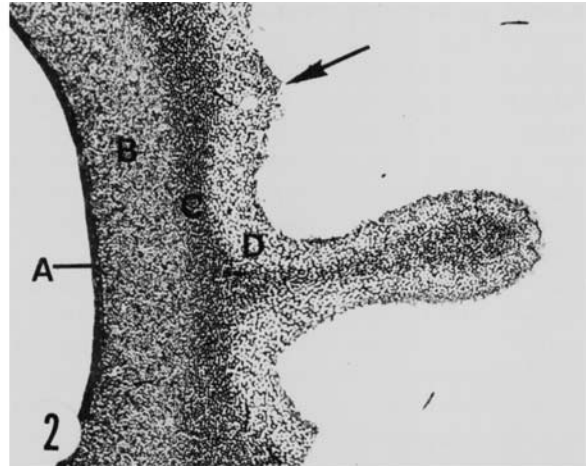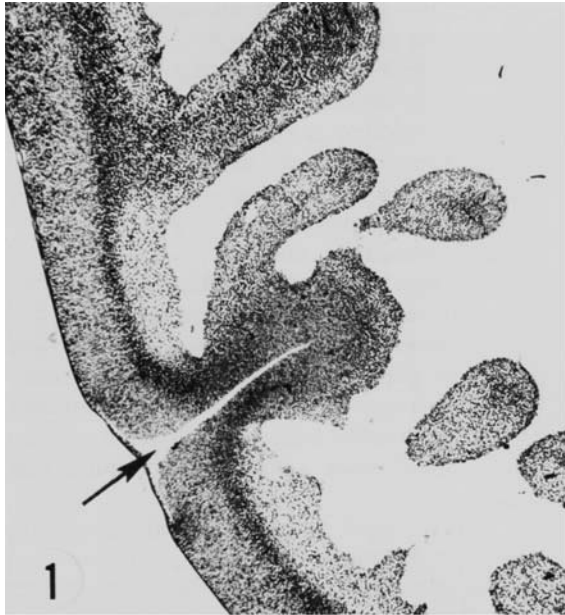
ornamentation are thus unreliable characters. This leaves size, shape, sutural characteristics, together with ultrastructure as potential delimiting factors. All of these characters are variable. In short, a wide variety of megaspores possess similar ornamental elements, but the present sample size provides insufficient resolution to delimit any coherent groups. In spite of this, the general characteristics of the megaspores and their ornamentation will be briefly outlined.

Description. These megaspores are radial, circular-subcircular, trilete, and range from 500–800 μm in diameter (Pl. 5, fig. 4). They are ornamented with variable appendages including clavae (Pl. 5, fig. 5), which may bifurcate, baculae, verrucae, or more complex units formed from basal fusion of the above three (Pl. 5, fig. 6). Appendages range from 17–34 μm in length. The trilete sutures are elevated and un-ornamented, or covered with appendages. Laesurae range from 1/2–1 times the spore radius. Extent and density of ornamentation is variable.

When the sporoderm wall is examined, there may be up to four distinguishable wall regions, differing in the degree of compression of the spongy material (Pl. 6, figs 1, 2). The innermost layer is a dense basal layer 0.5–1.5 μm in thickness (A), which grades abruptly into a less dense zone (B) 9–13 μm thick. A zone of intermediate density (C) is situated in the interior of the wall and extends upward to form a core within the ornamental elements (Pl. 6, fig. 2). The material which forms the outermost spore layer (D) is the least dense of all the wall regions. A proliferation of wall material, which may include ornamental elements, occurs over the suture (Pl. 6, fig. 1).

Remarks. The only other megaspores which possess appendages similar to those of the Argentinian specimens are *Bacutriletes cutchensis* (Singh, Srivastava & Roy, 1963), *B. dijkstrae* (Singh, Srivastava & Roy, 1963), *B. clavatus* Marcinkiewicz and *B. hamatus* Marcinkiewicz. In the case of the former two, the appendages are 30–60 μm in length, considerably longer than those of the Argentinian material. This discrepancy precludes the assignment of these specimens to either of these taxa since appendage morphology is a key criterion of taxon definition within *Bacutriletes*. In the case of *B. clavatus*, the available illustrations show shorter and broader appendages, and in *B. hamatus*, the appendages are narrow but too long (to 90 μm) and hooked.

DISCUSSION

The spongy organisation present in these and most megaspores is remarkably persistent, ranging from Devonian to present. The imprecise term, spongy, undoubtedly reflects our inability to adequately distinguish and define the subtle differences which exist both throughout geological history, and between contem-poraneous taxa. From an evolutionary perspective, it has been suggested (Taylor & Zavada, 1986) that a spongy wall organisation like that present in Medullosan pteridosperm pollen may be selectively advantageous. Pollen grains which possess this organisation (e.g. *Monoletes*) have the ability to increase in size (to 500 μm) and maximise mechanical strength without the concomitant increase in wall thickness and weight which would be necessary with comparable size increase in a solid wall. In addition, the spongy organisation allows the flexibility within the wall necessary to accommodate large increases in cytoplasmic volume. This is particularly relevant in the case of lycopod megaspores which may attain sizes in excess of 4000 μm. This volumetric flexibility may help explain the ubiquitous basal layer present in most viable lycopod megaspores.

Several types of gymnospermous remains have been described from this locality, but this is obviously an incomplete picture of the flora. As with many other localities, a greater diversity of pteridophytes is revealed by the dispersed spore record which represents the only information available on these inconspicuous floral elements. While the paucity of megafossil remains prevents us from gathering morphological information on the parent plants, it does not preclude us from acquiring some type of biological information.

If we can characterise the various wall construction patterns and correlate them with modern analogues, they can be analysed developmentally. We can then begin to address questions regarding the developmental significance of various wall layers, the consistent coincidence of certain strata, the taxonomic distribution of different construction types, and the changes of megaspore wall structure through time. These aims can be most actively pursued by a combined approach from three directions; 1) developmental studies of extant heterosporous plants, 2) developmental studies of *in situ* spores from fossil plants, and 3) investigation of dispersed megaspore assemblages. This contribution represents a significant portion of the latter of these approaches, and the remaining two are in progress.

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