REVIEW
OF
PALAEOBOTANY
AND
PALYNOLOGY

Early seed plants in the Southern Hemisphere: I. Associated ovulate and microsporangiate organs from the Carboniferous of Peru

Diane M. Erwin[a], Hermann W. Pfefferkorn[a] and Vera Alleman[b]

[a]*Department of Geology, University of Pennsylvania, Philadelphia, PA 19104-6316, USA*
[b]*Facultad de Ciencias Biologicas, Universidad Ricardo Palma, Lima, Peru*

ELSEVIER

Early seed plants in the Southern Hemisphere: I. Associated ovulate and microsporangiate organs from the Carboniferous of Peru

Diane M. Erwin[a], Hermann W. Pfefferkorn[a] and Vera Alleman[b]

[a]*Department of Geology, University of Pennsylvania, Philadelphia, PA 19104-6316, USA*
[b]*Facultad de Ciencias Biologicas, Universidad Ricardo Palma, Lima, Peru*

(Received March 16, 1993; revised and accepted August 25, 1993)

ABSTRACT

Erwin, D.M., Pfefferkorn, H.W. and Alleman, V., 1994. Early seed plants in the Southern Hemisphere: I. Associated ovulate and microsporangiate organs from the Carboniferous of Peru. Rev. Palaeobot. Palynol., 80: 19–38.

A new type of pteridosperm ovulate fructification has been recovered from Carboniferous sediments on the Paracas peninsula of Peru, South America. Co-occurring in a monospecific assemblage with the ovulate fructification are fragments of microsporangiate branch systems that display a progymnosperm-like grade of organization. The ovulate branch system together with hundreds of dispersed seeds are described and named *Oclloa cesariana* gen. et sp. nov. *Oclloa* ovules are acupulate, up to 11.0 mm long, 4.0 mm wide, and borne singly on the slender forked ultimate branchlets of primary laterals that are alternately arranged along a central axis. The integumentary lobes are fused laterally and to the nucellus in the basal one-half to two-thirds of the seed. At levels just below the pollen chamber, the integument separates distally into a whorl of 5–9 free, tentacle-like lobes. Minute projections line the margins and possibly inner surfaces of the free apical lobes. Internally, megasporangia display a pollen chamber, short lagenostome, and remnants of the central column; all features indicative of hydrasperman reproduction. Morphologically, *Oclloa* closely resembles the genus *Physostoma*, but our observations of the acupulate nature and other structural features distinguish it from this taxon. *Oclloa* is the first well documented acupulate lagenostomalean seed found outside of tropical Euramerica. Moreover, it provides the first positive evidence that not all ovules modified for hydrasperman reproduction were produced by cupulate branch systems. Found exclusively associated with *Oclloa* are microsporangiate branch systems that bear groups of 2–4 unfused, banana-shaped sporangia that are similar to *Zimmermannitheca*. However, based on differences in shape and number of sporangia per cluster, cluster symmetry, and branch system morphology, the specimens are assigned to the new taxon *Obandotheca laminensis* gen. et sp. nov.

Introduction

Our present knowledge of Late Devonian/Early Carboniferous pteridosperms rests almost exclusively on megafossils collected from localities in North America and Europe. Within the last three decades intense study has been devoted to early seed plant remains primarily from the USA (e.g. Rothwell and Erwin, 1987; Rothwell et al., 1989; Matten, 1992a; Rothwell and Serbet, 1992; Serbet and Rothwell, 1992), Belgium (Fairon-Demaret and Scheckler, 1986, 1987), Scotland (e.g. Long, 1960a–c, 1961a,b, 1963, 1969, 1979; Scott and Meyer-Berthaud, 1985; Scott et al., 1985; Meyer-Berthaud, 1986; Meyer-Berthaud and Galtier, 1986; Scott and Galtier, 1988; Rothwell and Wight, 1989; Bateman and Rothwell, 1990; Scott, 1990), Ireland (e.g. Matten et al., 1980a,b, 1984; May and Matten, 1983; Matten, 1992b), and France (e.g. Meyer-Berthaud, 1984; Galtier and Rowe, 1989, 1991; Rowe and Galtier, 1990). Although these localities may differ in taxonomic composition and depositional setting, they all preserve early seed ferns that once flourished in Euramerica, a region characterized by a warm, humid tropical climate during the Carboniferous. In sharp con-

trast very little is known about the seed plants that inhabited the northern and southern temperate climatic zones of the late Paleozoic (Ziegler, 1990).

In this paper we characterize and name the reproductive organs of a pteridosperm from a southern warm temperate region as preserved in the early Late Carboniferous of Peru. The ovulate remains described here as *Oclloa cesariana* gen. et sp. nov. include a fructification bearing acupulate lagenostomalean-type preovules and over 100 dispersed seeds that display a nucellus modified for hydrasperman reproduction. *Oclloa* represents the first well documented occurrence of acupulate lagenostomalean seeds outside tropical Euramerica. Co-occurring with *Oclloa* is the microsporangiate fructification *Obandotheca laminensis* gen. et sp. nov. *Obandotheca* displays terminal clusters of nonsynangiate microsporangia and, therefore, morphologically is more like a progymnosperm than a pteridosperm. Although these taxa occur as isolated organs, they are found together with only one type of pteridosperm stem, frond, and *Sphenopteris*-type foliage as a monotypic assemblage preserved in a single stratigraphic horizon. This association strongly suggests that the assemblage represents a single biological species. In this paper, we describe *Oclloa* and *Obandotheca* and discuss the affinities of these organs and their implications for the classification and phylogenetic relationships of the taxon they represent. The whole plant reconstruction and paleoecology of *Oclloa* will be presented elsewhere.

Geologic setting, age, and depositional interpretation

The Carboniferous of the Paracas peninsula occurs in the southern coastal region of Peru as a small isolated area. The peninsula is part of the Cordillera de Costa (Fig. 1) which is underlain by the Arequipa Massif, a terrain that collided with the South American continent in the early Paleozoic, and undoubtedly was part of the continent by Devonian time (Issacson and Sablock, 1990). Fossils described in this paper come from an outcrop on the Paracas peninsula referred to here as the "La Mina" section (Fig. 1). The section

is an 170 m thick sequence of interlayered sandstones, siltstones, shales, and coal (Fig. 2). These strata have been included by earlier authors in the Ambó Group, a lithostratigraphic unit of Mississippian age that was created for beds several hundred kilometers away in the Andes.

With respect to a biostratigraphic and chronostratigraphic age assignment, the beds at Paracas have posed many problems. Plant megafossils are the only datable material currently available. Early in the century the beds were dated as Late Carboniferous, but after 1930 they were considered to be Early Carboniferous (see Alleman, 1985, for overview). Archangelsky et al. (1981) have suggested a Middle Carboniferous age (i.e. in the Russian sense) which would be equivalent to early Late Carboniferous by other standards. The age determination problem stems from the fact that the La Mina section was deposited in a warm temperate climatic region which was not recognized until recently (Alleman and Pfefferkorn, 1988; Pfefferkorn and Alleman, 1989) and for which no stratotype or data exist from elsewhere. As such, all previous age assignments were based on comparisons of Paracas fossil taxa with those from either Euramerica (tropical) or Gondwana (cool temperate belts).

Presently, we have identified four genera in the Paracas flora with known stratigraphic ranges in other climatic belts. *Tomiodendron* occurs in the Angara floral realm from the Tournaisian through the Namurian. "*Triphyllopteris*" occurs in the Euramerican floral realm from late Tournaisian through early and middle Visean, while *Fryopsis* is known in the Euramerican floral realm from middle Tournaisian time into basal Namurian (Wagner, 1979). The first occurrences of *Nothorhacopteris* have been found in the Gondwana floral realm in the latest Visean in Australia (Roberts et al., 1991) or in the latest Namurian in Argentina (Wagner, 1979). There is no stratigraphic interval where all four ranges overlap. If we minimize the extension of ranges of the four taxa and give greater value to first occurrences rather than last occurrences, the age of the La Mina section is most likely early Late Carboniferous (i.e. Namurian).
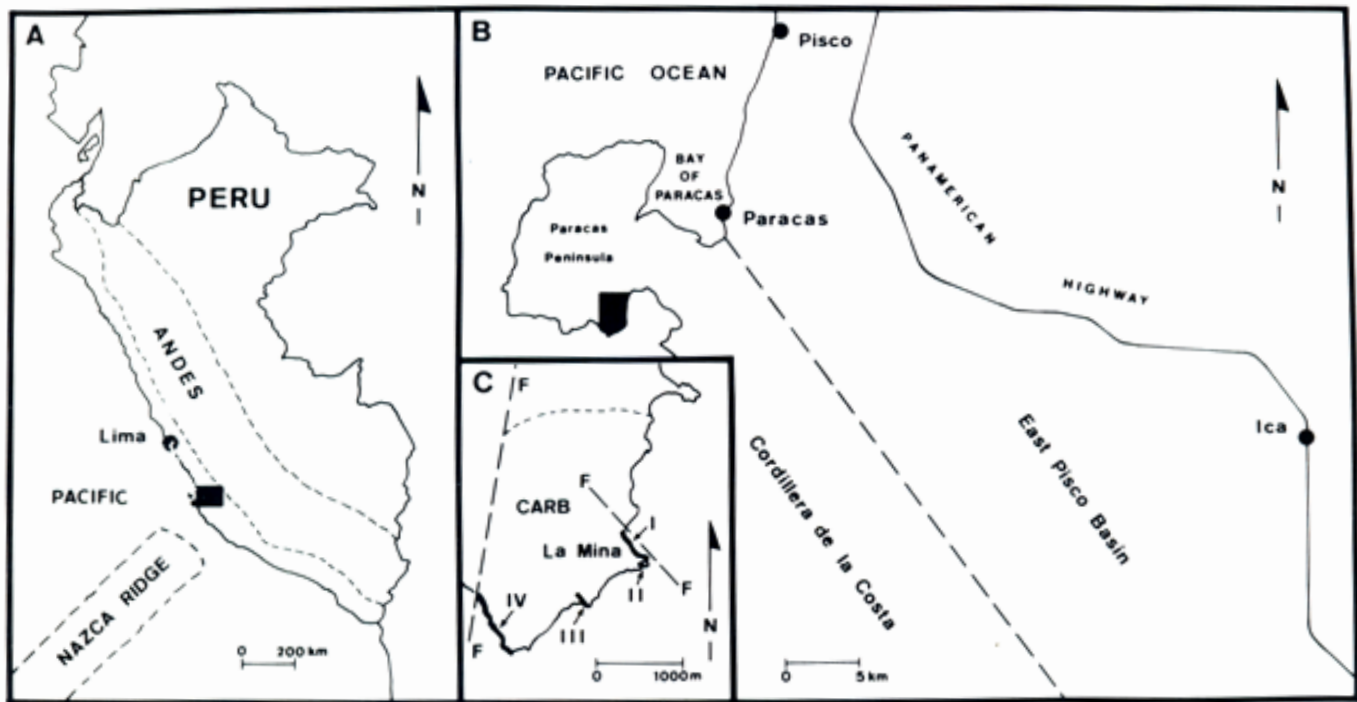
Fig. 1. Locality maps. (A) Position of Paracas peninsula (black) on coast of Peru. (B) Study area (black) on the Paracas peninsula. (C) Location of La Mina section at I. Other Carboniferous outcrops at II, III, and IV; F=fault.
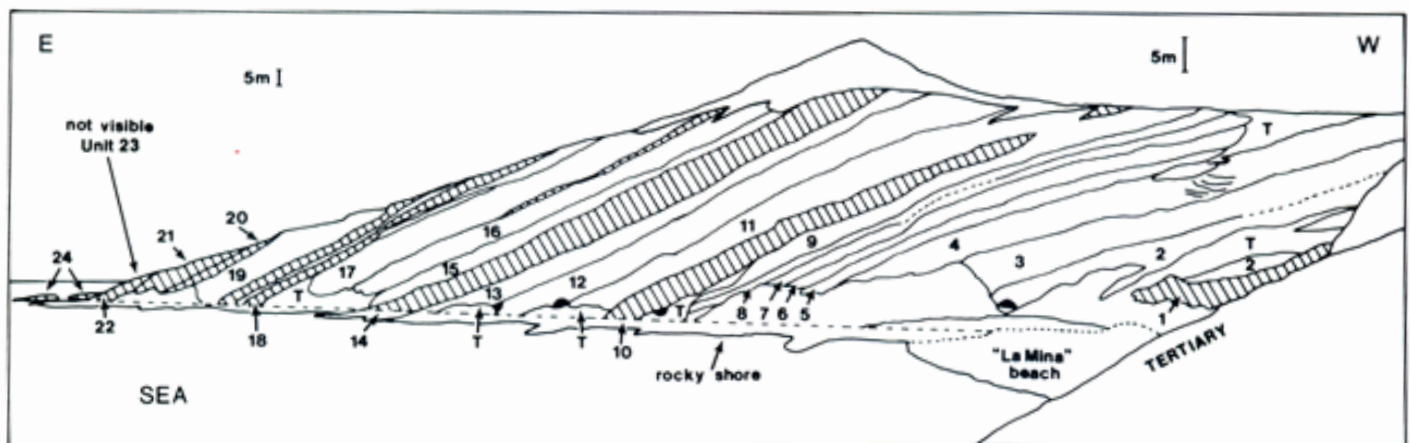

Fig. 2. View of La Mina section. The numbered beds represent the stratigraphic units distinguished for collection purposes. Hatched beds consist of sandstones, while other units contain beds of shale, siltstone, thinner sandstones, and coal. Four mine openings marked in black. T=talus.

Sedimentological studies (Nuñez del Prado, 1991a,b) indicate that the lower beds of the La Mina section (Units 1–14; Fig. 2) are fluvial deposits. Channels, levees, and diverse flood plain environments characterize these beds. Units 15–19 were deposited in a coastal plain where tides in the freshwater environment controlled flooding and other fluvial processes. Units 20–22 represent a beach barrier bar complex that protected a coastal plain. Coastal plain facies return in Unit

23, while Unit 24 is probably another beach complex.

The fossiliferous beds of Unit 19 are divided into 8 subunits. Specimens of *Oclloa* and *Obandotheca* occur together with pteridospermous vegetative organs as a monospecific assemblage in subunit 19.8. This assemblage represents what appears to be the remnants of a pteridosperm monoculture that was levelled by floodwaters that inundated the coastal plain environment. This

interpretation is based on the combination of observed primary sedimentary structure and taphonomy of the plant fossils.

Materials and methods

Material of *Oclloa* includes an ovulate branch system, over 100 detached seeds, and several isolated megasporangia. Specimens of *Obandotheca* include two larger fertile branch systems, several smaller fragments of sporangia-bearing axes, and isolated sporangia. Both reproductive organs co-occur exclusively with one type of stem and leaf. Together these plant remains form a monospecific assemblage which extends throughout the upper part of Unit 19 (subunit 19.8; Fig. 2).

The specimens are preserved either as adpressions or as a combination coalified compression/cast. Seeds preserved as compression/casts show a three-dimensional cast of the nucellus surrounded by coalified remains of the integument. Casts of the microsporangia occur either exposed on the rock surface fractured in various planes of section or are completely buried in the matrix. In the latter case they are represented by the thin coaly outline of the sporangium wall.

Specimens were prepared for study and photography by dégagement. Widths of seeds and sporangia were taken at mid-level. Seed lengths were measured from the tip of the longest integumentary lobe to the base of the seed. Seed and sporangia morphology was further elucidated by coating selected specimens with Eukitt mounting medium and then sectioning them into 2 mm wafers using a Raytech diamond-blade thin-sectioning saw. Wafers were then affixed to microscope slides with Duro epoxy and progressively sectioned by polishing with carborundum powder on a glass plate at approximately 0.25 mm increments. Morphological interpretations and final reconstruction of the fertile material was done by making tracing paper overlays of camera lucida drawings of sectioned specimens, in conjunction with their "part" and "counterpart" surface equivalents. Before photographing, some specimens were covered with Eukitt mounting medium to enhance contrast, while others were immersed in water.

In this paper, "ovules" refer to attached specimens while the isolated specimens are referred to as "seeds" (Rothwell and Scheckler, 1988). Because the proximal portions of the fertile branch systems are missing, their original position on the frond is not clear. Therefore, the terms "first-order, second-order, etc., " are used to describe the axes of the fertile systems.

All specimens (RPT numbers) are the property of and will be deposited in the Natural History Museum of the Universidad Ricardo Palma in Lima, Peru. They are on temporary loan to the Department of Geology, University of Pennsylvania, Philadelphia, PA, USA.

Systematic description

Class PTERIDOSPERMOPSIDA

OCLLOA Erwin, Pfefferkorn et Alleman, *gen. nov.*

Type: O. cesariana Erwin, Pfefferkorn et Alleman, *sp. nov.*

Diagnosis: Preovules adpressions, acupulate, borne singly on slender, forked terminal axes of second-order laterals arranged alternately along the first-order axis. Branch systems nonplanate; axes with longitudinal striations. Seeds elongate, truncate to slightly rounded at the base. Integument of 5–9 (10) lobes, fused only in basal one-half to two-thirds of seed; lobes extending distally as separate lanceolate arms, gradually incurved toward nucellar apex; free lobe margins and inner surface (?) lined with narrow, irregular to club-shaped projections. Nucellus fused to integument only in the lower half to two-thirds of the nucellus; free apical region modified into dome-shaped pollen chamber and terminal lagenostome. Lagenostome very short, tubular, with slightly flared orifice.

Oclloa cesariana Erwin, Pfefferkorn et Alleman, *sp. nov.*

Diagnosis: Characters the same as for the genus. First-order axis five times forked, 6 cm long and 2 mm wide basally, becoming progressively shorter and narrower between successive forks, intervals

between forks, 2.0, 1.5, 1.0, and 0.7 cm. Distally, second-order axes become shorter, narrower, and less branched, bearing alternately arranged third-order axes. Most complete fertile second-order axis two times forked, 4.5 cm long and 2 mm wide basally, narrowing to 0.6–0.8 mm before terminating in a single ovule. Attached ovule 9.0 mm long, dispersed seeds typically up to 11.0 mm long and 2.5–4.0 mm wide. Integument with smooth outer surface, lobe margins and inner surface (?) with minute projections ca. 0.3 mm long; lobes from level of separation 4.0–5.5 mm long and 0.4–0.8 mm wide tapering to blunt tip, triangular (?) in cross section. Nucellus 5.0–6.0 mm long and 2.0–2.3 mm wide.

Holotype: Compressed branch system with attached ovule, Universidad Ricardo Palma Natural History Museum specimen No. RPT-90-51B (Plate I, 1, 2; Plate II, 1), compressed fertile branch system; RPT-90-51A (counterpart).

Paratypes: partial cast of seed, RPT-90-36 (Plate I, 3); compressed megasporangium, RPT-90-39B (Plate I, 4); compressed seed, RPT-90-51B (S1) (Plate I, 5, 8); compression/cast of seed, RPT-90-42B (Plate I, 6); compressed seed, RPT-90-43A (Plate I, 7); compression/cast of seed, RPT-91-309A (Plate I, 11); compression/cast of seed, RPT-91-24A (Plate II, 2); compressed seed, RPT-91-70E$_5$ (Plate II, 3). Specimens not figured: compressed seeds, RPT-90-43B, RPT-90-47, RPT-90-53, RPT-91-24B, RPT-91-26, RPT-91-39A, B, RPT-91-258, RPT-91-269A, B, RPT-91-275A, B; RPT-91-313A; megasporangia, RPT-90-39A, RPT-91-41A.

Etymology: Genus named for Mama Ocllo, who according to Inca tradition was the first woman created on Earth by the Sun god Inti. The species is named for Dr. Silvia N. Césari in recognition of her contributions to our knowledge of Carboniferous floras in South America.

Type locality: Subunit 19.8 of the La Mina section on the Paracas Peninsula, 11 km SSW from Paracas, Peru. UTM, Zone 18, 3-57-800E, 84-61-200N.

Age: Earliest Late Carboniferous

OBANDOTHECA Erwin, Pfefferkorn et Alleman, *gen. nov.*

Type: *O. laminensis* Erwin, Pfefferkorn et Alleman, *sp. nov.*

Diagnosis: Fertile branch systems slightly three-dimensional consisting of a first-order axis bearing alternately arranged second-order axes. Second-order axes attached to first-order axis at angles between 50–70°; bearing pinnately arranged fertile third-order axes at right angles to second-order axis. Third-order axes pinnately branched, bearing small groups of unfused, loosely arranged sporangia on cruciately forked ultimate divisions. Axes lacking sterile foliage.

Obandotheca laminensis Erwin, Pfefferkorn et Alleman, *sp. nov.*

Diagnosis: Characters the same as for the genus. First-order axis 2.7 cm long and 1.5 mm wide. Sporangia 2.5–3.5 mm long and 1.0–1.3 mm wide, elongate, tapering to a short blunt tip ca. 0.5 mm long, one to two pairs per ultimate division.

Holotype: Compressed microsporangiate branch system, Universidad Ricardo Palma Natural History Museum specimen No. RPT-91-27B (Plate I, 9); compressed fertile lateral, RPT-91-27A (counterpart).

Paratypes: RPT-91-309A, B (Plate I, 10). Specimens not figured: compressed fragments of fertile branch systems and sporangia, RPT-91-21, RPT-91-309A, C.

Etymology: Genus named for biologist Carlos Obando Llajaruna, Director of the Preserva Natural de Paracas, in recognition of his continued support for scientific studies at Paracas. Specific epithet named for the La Mina locality.

Type locality: Unit 19.8 of the La Mina section on the Paracas Peninsula, 11 km SSW from Paracas, Peru. UTM, Zone 18, 3-57-800E, 84-61-200N.
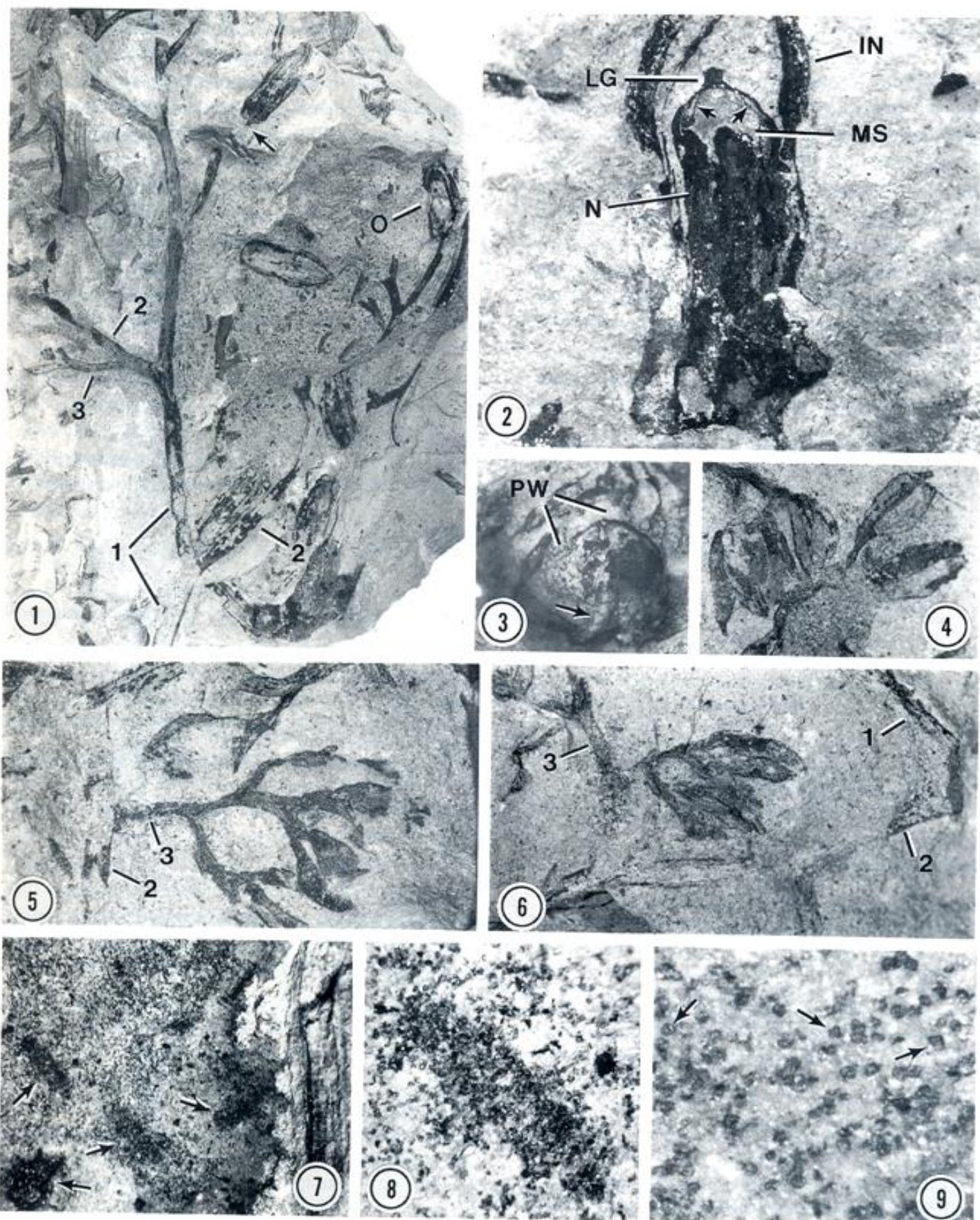
Age: Earliest Late Carboniferous

PLATE I
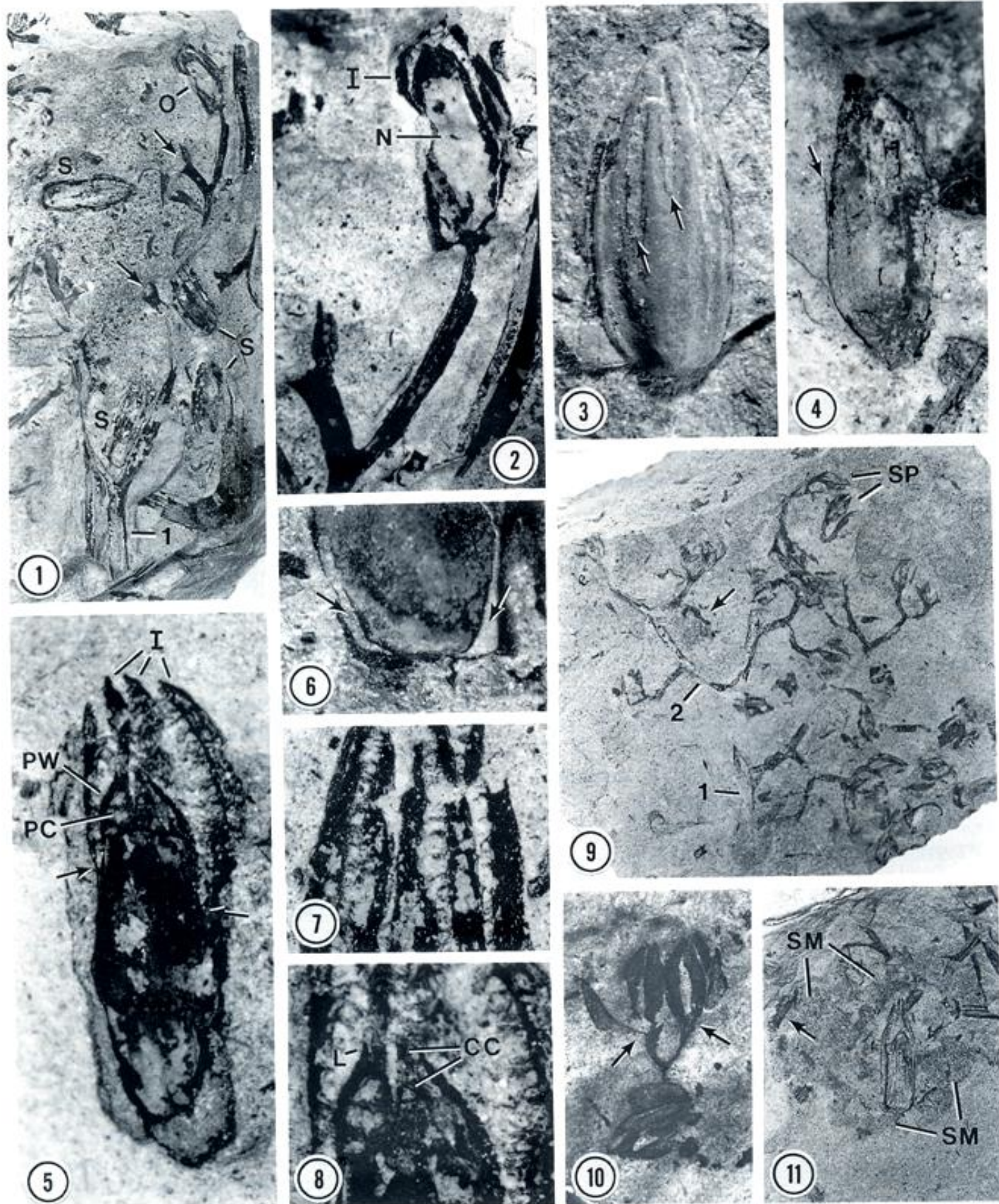
(for description see p. 26)

PLATE II

Description

Ovulate branch systems

To date, sampling of subunit 19.8 has shown that detached seeds are more common in this bed than the modified branch systems that bore them. The holotype consists of a first-order axis 6 cm long that bears alternately arranged second-order laterals (Plate II, 1). The first-order axis is 2 mm wide at the base and narrows distally to 1 mm before ending blindly on the rock surface (Plate II, 1). It forks five times to yield alternately arranged second-order axes at regular intervals of

2.0, 1.5, 1.0, and 0.7 cm, respectively (Plate II, 1). Each branching of the first-order axis appears to be nearly isotomous so that at least initially the widths of the first- and second-order axes are equal.

All second-order axes except for the basal one are missing distal portions of their lateral and terminal axes (Plate II, 1). The basalmost second-order axis forks twice and is 4.5 cm long and 2.0 mm wide at the base, but narrows distally to 0.6–0.8 mm where it terminates in a single ovule (Plate I, 1, 2). Length to the first fork is 2.0 cm, then decreases to 1.5 cm between the first and second forks, and decreases distally to 0.8 cm between the second fork and the base of the ovule.

PLATE I (see p. 24)

Oclloa cesariana gen. et sp. nov. and associated microsporangiate remains, *Obandotheca laminensis* gen. et sp. nov.

1. Basalmost second-order axis showing attachment of one terminal ovule (*O*), and four detached seeds (*S*). RPT-90-51B. × 1.5.
2. Distalmost fork of second-order axis showing ovule and longitudinal view of nucellus (*N*) surrounded by remnants of the integument (*I*). RPT-90-51A. × 4.
3. Seed cast showing integumentary lobes fused at different levels (arrows). RPT-90-36. × 5.
4. Cast of nucellus showing faint longitudinal striations on surface and possible remnants of the integument (arrow). RPT-90-39B. × 10.
5. Seed split longitudinally showing five integumentary lobes (*I*), pollen chamber (*PC*), pollen chamber wall (*PW*), fusion of integument to nucellus at levels just below pollen chamber (arrows), and lobed appearance of the integument at the base of the seed. RPT-90-51B. × 10.
6. Seed cast showing integument separated from the base of the nucellus (arrows). RPT-90-42B. × 10.
7. Seed apex showing eight integumentary lobes and projections on lobe margins. RPT-90-43B. × 10.
8. Apex of seed in 5 showing lagenostome (*L*) and remnants of central column (*CC*). RPT-90-51B. × 15.
9. Fertile portion of *Obandotheca* showing first-order axis (*I*), alternately arranged second- and third-order axes, and terminal linear sporangia (*SP*). Arrow indicates position of fertile ultimate branchlets in Plate II, 6. RPT-91-27B. × 2.
10. Fertile ultimate branchlet showing basal fork with two groups of four unfused terminal sporangia attached to each division (arrows). RPT-91-309A. × 5.
11. Seed surrounded by masses of small, circular to subtriangular-shaped spores (dark stains at *SM*). RPT-91-309A. × 1.8.

PLATE II (see p. 25)

Oclloa cesariana gen. et sp. nov. and *Obandotheca laminensis* gen. et sp. nov.

1. Ovulate branch system showing first-order axis (*I*), alternate arrangement of second-order axes (*2*) with third-order axes (*3*), and basal fertile first-order axis with terminal ovule. Stalk indicated by arrow. RPT-91-51B. × 1.
2. Longitudinal view of a seed split at the level of the nucellus (*N*) showing the distal outline of the megaspore (*MS*) at arrows and the apical knob-like lagenostome atop the pollen chamber. RPT-91-70E$_5$. × 10.
3. Top view of compression/cast of seed showing dome-shaped pollen chamber outlined by the pollen chamber wall (*PW*) surrounded by integumentary lobes. Note ridge representing sediment-filled integumentary lobe (arrow). RPT-91-24A. × 10.
4. Terminal clusters of longitudinally compressed microsporangia showing banana-shaped outline and tip morphology. RPT-91-24A. × 5.
5. Fertile third-order lateral (*3*) attached to the basalmost second-order axis (at *2*) on the counterpart of specimen in Plate I, 9. Note unfused pairs of sporangia and right angle attachment of third-order axis. RPT-91-24B. × 5.
6. More distal third-order lateral (at *3*) to that in 5 showing twice forked ultimate branchlet bearing pairs of sporangia. RPT-91-24A. × 5.
7. Close-up of Plate I, 11, showing seed with associated spores and possible remains of sporangia (arrows). RPT-91-309A. × 6.2.
8. Detail of elliptical-shaped mass of spores. RPT-91-309A. × 20.
9. Close-up of central area of rock surface illustrated in 7 showing dispersed spores. Note subtriangular shape of spores (arrows). RPT-91-309A. × 50.

Two third-order laterals diverge from one side of the second-order axis and lie in the same plane as the specimen (Plate I, 1). Their length/width dimensions are 3.5×1.2 mm and 3.0×1.0 mm, respectively. Although the two third-order axes are incomplete distally, each appears to have forked again yielding two narrower fourth-order axes (Plate I, 1, 2). Based on their widths (0.6–0.7 mm), it is possible that one or both fourth-order axes also bore an ovule.

In life, the ovule-bearing branch systems appear to have been somewhat three-dimensional rather than truly planate. This interpretation is based on the orientation of the second- and third-order axes relative to the plane of the specimen. The first (proximal), second, and fourth second-order axes are parallel to the bedding plane. However, the third extends into the matrix below this plane, while the base of the fifth overlaps with the first-order axis suggesting that it projected above the plane before being compressed.

Ovules/seeds

Seeds of *Oclloa* are 9.0–11.0 mm long and 2.5–4.0 mm wide. They show a variable range in overall form as seen compressed on the rock surface. In some seeds the base is truncate (Plate I, 2, 6, 11; Plate II, 2), while in others it is slightly more concave and rounded (Plate I, 1, 3) or is compressed in such a way that it appears lobed (Plate I, 5). Seeds either gradually widen from the base to midlevel then narrow toward the apex (Plate I, 3), or maintain nearly the same width throughout the lower half of the seed then reach their maximum expansion at or slightly above the level of the pollen chamber (Plate I, 1, 5, 11). Many of the dispersed seeds show vestiges of a short stalk, 0.5–0.7 mm long × 0.5–0.7 mm wide (Plate II, 1-arrow, 2). In addition to the larger specimens, three smaller seeds were found with dimensions of 4.0×2.0 mm, 5.0×2.0 mm, and 5.0×3.5 mm. Except for their diminutive size, these specimens correspond in all other features to the larger seeds and therefore probably represent an immature stage.

Lobes of the integument are fused laterally in the chalazal half to two-thirds of the seed but separate distally into a whorl of finger-like extensions that surround the apex of the nucellus (Plate I, 3; Fig. 3a–c). However, fusion between the integument and nucellus is somewhat difficult to judge due to differences in preservation. In some specimens, fusion occurs from the chalaza to levels just below the pollen chamber (Plate I, 5), while in others there is apparently little or no fusion at all (Plate I, 2, 6). The latter condition is best illustrated by the seed shown in Plate I, 6. The integument in the basal region of this ovule is separated from the nucellus by sediment-filled gaps (arrows). A similar infilling of sediment is evident in specimens where the nucellus is preserved as a cast surrounded by the compressed coalified remains of its integument (e.g. Plate I, 6). The nucellar casts "pop out" easily and occasionally when removed reveal a thin layer of sediment underneath. One
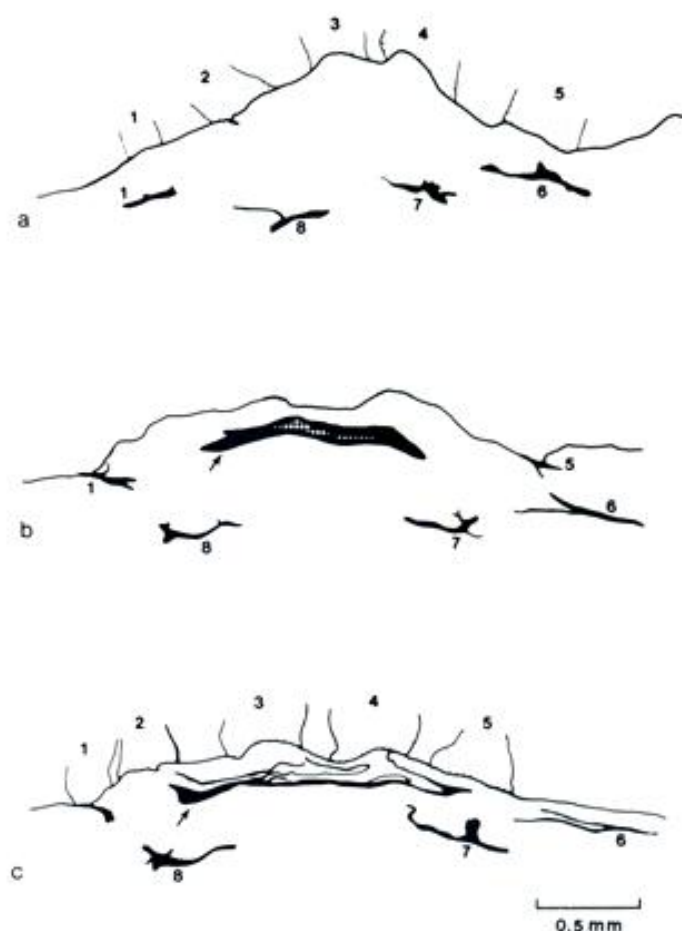

Fig. 3. Camera lucida drawings of slightly oblique cross-sections of a seed apex at levels of (a) 2, (b) 3, and (c) 4 mm from the apex. Integumentary lobes embedded in matrix shown in black; those on wafer surface stippled. Arrows = nucellus, cross hatched = pollen chamber. RPT-91-27C.

possible explanation for the occurrence of sediment in this area is that the integument and nucellus were never fused. Lack of fusion would create a space between the two where sediment could accumulate. The presence of isolated megasporangia and, to a lesser degree, empty integuments may provide further evidence for this interpretation. Megasporangia do occur dispersed in the matrix (Plate I, 4); however, these are very rare among the more than 500 rock samples examined. These rocks contain over 100 seeds, but less than half-a-dozen isolated megasporangia. Recognizing integuments as being truly empty is more difficult. What may appear to be an empty integument on one rock surface may in fact be a seed that has been split in half, with one half showing an apparent empty integument, while the other half contains the nucellus.

The other interpretation is that the two were fused initially but became separated either by physical means or the tissues in this area were not preserved. Studies of anatomically preserved lagenostomalean seeds show that inner cells of the integument and nucellus are relatively thin-walled (Rothwell and Wight, 1989) and even in the permineralized state are poorly preserved (Oliver, 1909; Leisman, 1964). Most seeds of *Oclloa* that possess both an integument and nucellus show evidence of fusion (Plate I, 5; Plate II, 2). Fusion between the two occurs from the chalaza distally for one-half to two-thirds the length of the nucellus (Plate I, 5; Plate II, 2) and never extends above the level of the pollen chamber floor. At these levels the integument separates into 5–9 free, apical lobes which gradually curve inward over the apex of the nucellus (Plate I, 5, 7, 8; Fig. 4a). The lobes are 4.0–5.5 mm long and 0.4–0.8 mm wide at the base tapering to a blunt tip (Plate I, 1, 5). As seen in the exposed apex of a seed buried in the matrix, the nucellus is dome-shaped and surrounded by the partial cast and coalified remains of its integument (Plate II, 3). Casts of two lobes are marked by narrow ridges running lengthwise along the outer surface of the seed (Plate II, 3-arrow). Their external shape and outline in cross section suggest that the lobes were possibly triangular at levels above their separation from the nucellus. In some specimens, narrow irregularly-shaped projections,

ca. 0.3 mm long, line the margins (Plate I, 5–7; Fig. 4a) and possibly the inner surface of the lobes, but were not observed on the outer surface of the integument. These structures may be remnants of glands, trichomes, or possibly tooth-like structures (Plate I, 7). Near the base of some lobes, the processes between adjacent lobes entertwine forming a loose meshwork.

Megasporangia are oblong (Plate I, 2, 4, 5) and three times longer than broad. They range in size from 5.0 to 6.0 mm long and 2.0 to 2.3 mm wide. Most are surrounded by an integument, but occasionally small, ovoid casts occur dispersed in the matrix (Plate I, 4). Size of the dispersed structures suggest that they most likely represent casts of megasporangia rather than megaspores. Moreover, the surface of some show faint longitudinal striations or ribs (Plate I, 4) which may represent pressure marks left behind by the adpressed lobes of the integument.

The nucellar apex of *Oclloa* displays a short lagenostome, dome-shaped pollen chamber, and central column; all modifications attributed to preovules with hydrasperman reproductive biology (Rothwell, 1985, 1986; Rothwell and Scheckler, 1988). In one specimen the pollen chamber was filled with sediment and its position marked by two small bulges enclosed by coalified remnants of the pollen chamber wall (Plate I, 5, 8). Located between the two bulges is a separate coalified protrusion that extends distally to a level slightly above the lagenostome (Plate I, 8, *CC*). The form and position of this structure suggests that it may represent the central column. In another specimen the pollen chamber is represented by narrow sediment-filled areas internal to the pollen chamber wall (Plate II, 2). Atop the pollen chamber is a short protuberance, 0.2–0.3 mm long and 0.2–0.3 mm wide (Plate II, 2). This structure most likely represents both lagenostome and central column based on the position of the megaspore membrane. As seen in Plate II, 2, the megaspore (*MS*) nearly fills the entire pollen chamber (arrows indicate possible megaspore wall or upperlimit of megagametophyte), while its distalmost end is flush with the ceiling of the pollen chamber. Such an orientation suggests that the seed was in a post-pollination stage where growth of the megagameto-
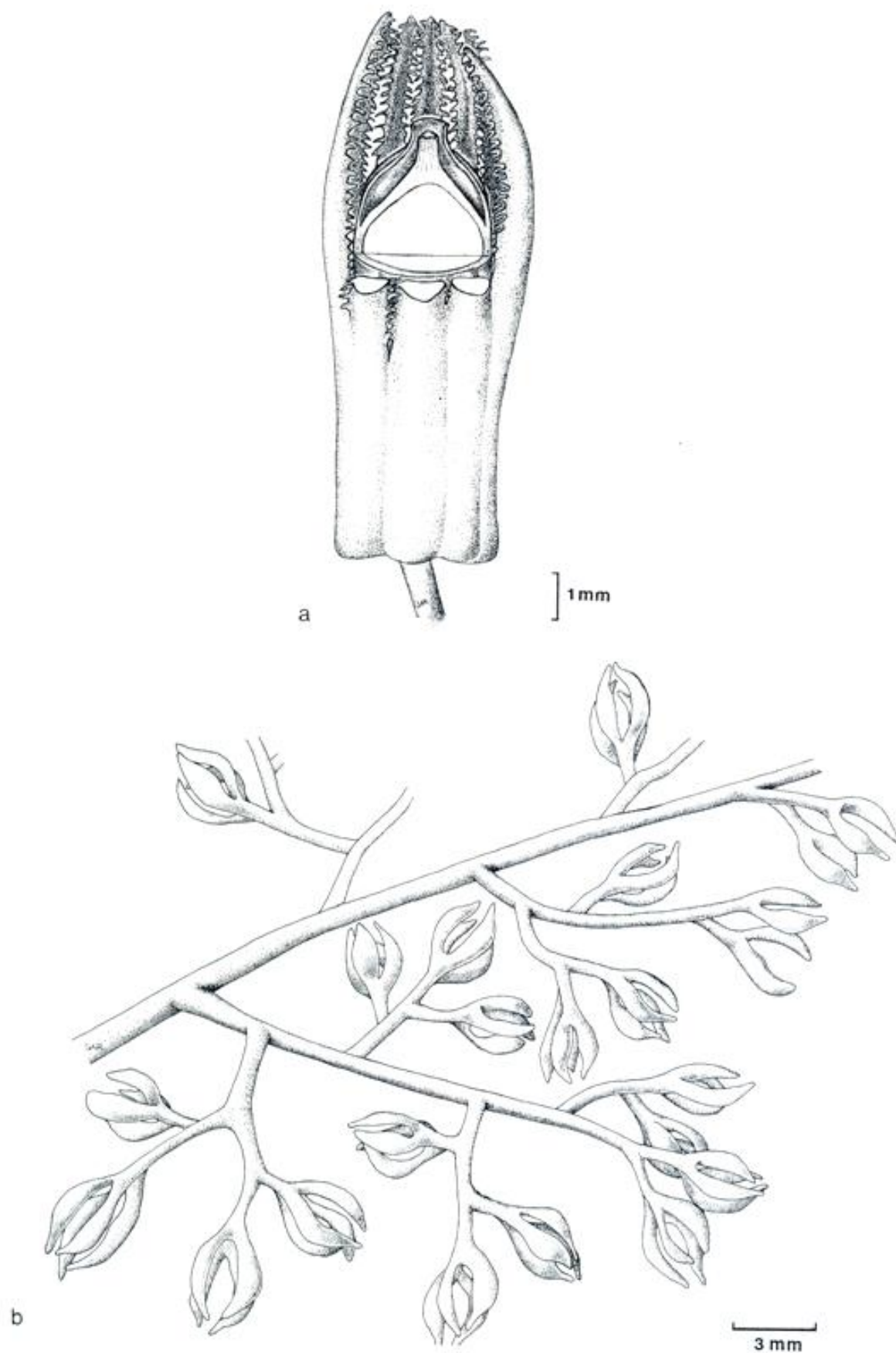
Fig. 4. *Oclloa cesariana* gen. et sp. nov. (a) Reconstruction of seed showing internal view of nucellar apex. (b) *Obandotheca laminensis* gen. et sp. nov. Reconstruction of microsporangiate branch system.

phyte had already pushed the central column into the lagenostome (Rothwell and Scheckler, 1988).

Microsporangiate branch systems

Closely associated with the ovulate and vegetative organs are remnants of microsporangiate branch systems. The holotype is a fragment consisting of a first-order axis 2.7 cm long and 1.5 mm wide at the base (Plate I, 9). This axis bears smooth alternately-arranged second-order laterals that appear flexuous as they follow the irregular contour of the rock surface (Plate I, 9). The basalmost second-order axis is the longest and most branched, while each more distal second-order axis becomes progressively shorter, narrower at the base, and less branched (Plate I, 9). Similarly, each second-order lateral bears alternately arranged third-order axes that become more coalesced distally (Plate I, 9; Fig. 4b).

The specimen illustrated in Plate I, 9, shows three of five second-order laterals pinnately arranged along the first-order axis. They diverge from the first-order axis at angles of 50° or more and are oriented more or less in the same plane. The length between second-order axes decreases from 7.0 mm between the first (basal) and second second-order laterals to 5.0, 4.5, and 4.0 mm, respectively, as one moves distally. Width of the proximal second-order axis at the base is ca. 1.3 mm, the four more distal laterals measure 1.0, 0.8, 0.6, and 0.5 mm, respectively. The basalmost second-order axis is 2.5 cm long and shows a terminal bifurcation with two of four third-order axes visible (Plate I, 9). Many of the third-order axes are attached at a 90° angle (Plate I, 9).

Microsporangia

Microsporangia are borne in groups of 2–4 at the ends of the ultimate divisions of the second- and third-order axes (Plate I, 9, 10; Plate II, 5, 6; Fig. 4b). The sporangia-bearing axes are about 0.5 mm wide. In some groups of four, the ultimate axis forks once then each division immediately forks again in a plane at right angles to the first division (i.e. cruciately) with each second division axis bearing a sporangium. These divisions may

occur at the same levels and very close together thus giving the two pairs of sporangia the appearance of being joined at the base (Plate I, 10) and a radial arrangement, while in others the two divisions are more widely spaced.

The sporangia are 2.5–3.5 mm long and up to 1.0 mm wide. In general they have a banana-shaped outline as seen compressed on the rock surface, but specimens do show minor variations in this shape. Some are widest in the middle whereas in others the maximum diameter occurs at levels either above or below the midregion. Each sporangium apex forms a short rounded tip ca. 0.5–0.6 mm long (Plate II, 4). Although in-situ spores have yet to be recovered, thousands of spores, 40–60 μm wide, form a dense covering on the rock surface surrounding a seed (Plate I, 11; Plate II, 7, 9). Also occuring with the spores is an *Obandotheca* sporangium (Plate I, 11-arrow) and several elliptically-shaped localized concentrations of spores that may represent the former contents of *Obandotheca* sporangia (Plate II, 7, 8). However, due to the high rank of coalification, the spores are not well preserved showing only their size and shape as seen compressed on the surface of the rock . They are circular to subtriangular (Plate II, 9-arrows). Neither reflected light nor scanning electron microscopy has yielded conclusive evidence of a trilete mark or other distinctive surface features.

Discussion

Comparison of Oclloa *to late Paleozoic ovules*

Using a number of different characters, *Oclloa* is compared first to compressed seeds that possess an integument with an apical whorl of unfused, tentacle-like lobes followed by comparison to similar permineralized forms. Although *Oclloa* is acupulate, the state of this character in the other seeds is putative because attachment is not yet known.

Compressions

Numerous compressed seeds and portions of ovulate branch systems have been reported from the Early Carboniferous of Euramerica (e.g. Kidston, 1916; Seward, 1917; Arnold, 1939, 1948a;

Gensel and Skog, 1977). *Lagenospermum* Nathorst (1914) is a taxon that was established for compressed cupulate seeds corresponding in morphology to the permineralized genus *Lagenostoma* Williamson (1877). However, since circumscription of *Lagenospermum* many ovoid structures have been assigned to this genus (Gensel and Skog, 1977, and references cited therein), most of which are probably not congeneric with *Lagenostoma*, especially in light of the diversity now known among Late Devonian/Early Carboniferous permineralized seeds (e.g. Long, 1961a; Matten et al., 1984; Scott et al., 1984, 1985, 1986; Rothwell, 1986; Scott and Galtier, 1988; Galtier and Rowe, 1989; Rothwell and Wight, 1989; Bateman and Rothwell, 1990; Rowe and Galtier, 1990; Scott, 1990).

For example, in *L. imparirameum* Arnold from the Lower Carboniferous of North America, the outer lobed structure has been interpreted as a cupule (Arnold, 1939; Gensel and Skog, 1977), although the elliptical body within this structure has not been shown conclusively to be an integumented megasporangium (Gensel and Skog, 1977). However, if this structure were an integument, *L. imparirameum* still differs from *Oclloa* in having 6 lobes that are unfused laterally and are entirely free from the nucellus. Among species of *Lagenospermum*, *L. sinclairi* Arber from the Westphalian of Scotland, is most similar in size and morphology to *Oclloa*. However, in this species, the "cupules" and "seeds" are comparable to the integument and nucellus, respectively, in *Oclloa*.

Pterispermostrobus bifurcatus Stopes (1914) from Westphalian deposits of eastern Canada is another fertile branch system that superficially resembles *Oclloa*. However, like *Lagenospermum* the taxon is problematical and the fertile units have been interpreted to be cupulate.

Compressions of putative acupulate ovulate remains are also known from Lower Carboniferous localities in Argentina. One is a single seed-like structure in possible connection with foliage assigned to *Diplothmema bodenbenderi* (Kurtz) Césari (Fauque et al., 1989). This specimen was compared to *Genomosperma kidstonii* Long, but important details of its morphology and attach-

ment are not clearly visible. The specimen is 7 mm long and described as having at least four lobes. However, unlike *Oclloa*, its pear-shaped central body is surrounded by very narrow lobes with a whisp-like aspect and it has an integument that is free from the nucellus.

Long (1961b) illustrated and briefly described compressions of small seeds terminating slender bifurcating axes from the Lower Carboniferous Foulden flora of Scotland. Long's specimen (1961b, plate IV, fig. 36) shows three elliptical bodies borne on the slender terminal branchlets of a twice forked, overtopped branch system composed of *Tristichia ovensii*-type axes. He noted that "the middle seed" had a possible cupule-like covering but because the specimen was so poorly preserved there was no real evidence to support this interpretation. In a re-investigation of the Foulden flora, Scott and Meyer-Berthaud (1985) collected additional samples of these small unnamed seeds which they interpret to be acupulate. However, the material shows no distinct morphological features of the integument or nucellus. Therefore, the only comparison that can be noted at this time is that *Oclloa* differs in being nearly three times larger than the Foulden seeds.

Permineralizations

Among Early Carboniferous permineralized seeds, the two genera *Genomosperma* Long and *Physostoma* Williamson compare most favorably to *Oclloa* with respect to integument and nucellus morphology. Table I summarizes selected characteristics for the known species of these two genera and *Oclloa*.

Oclloa is most similar to *Genomosperma* in size, falling well within the range of *G. kidstonii* (Table I). *Genomosperma latens* is smaller, but this species has a slightly larger nucellus. Also, *Oclloa* is most similar to *G. kidstonii* in lobe number (Table I). Both species differ from *Oclloa* in lacking fusion between the integument and nucellus, and in the amount of lateral fusion between lobes. Lobes of *G. kidstonii* are entirely free, while those of *G. latens* are fused at the base, but only for a very short distant (< 1.0 mm). Also present in *Genomosperma* is a pad of tracheids at the base of the nucellus, a feature not observable in *Oclloa*.

TABLE I

Comparison of *Oclloa cesariana* to permineralized Carboniferous lagenostomalean seeds with free, apical, tentacle-like integumentary lobes and possible noncupulate attachment

Taxon and reference	Age[a] and locality	Lobe No.[b]	Lobe to lobe fusion	Integument to nucellus fusion	Integument modifications	Seed size $L \times W$ (mm)	Nucellus size $L \times W$ (mm)
Genomosperma latens Long, 1960a	EC (Tour./Vis.) Scotland	7–8 (8)	Basal one-third (ca. 0.9 mm)	None	None	6.9–8.4 × 4.5	6.7–8.0 × 2.5–2.75
G. kidstonii Long, 1960a	EC (Tour./Vis.) Scotland	6–11 (8)	Fused at base (ca. 0.4 mm)	None	None	10.0–15.0 × 3.0	5.0–6.5 × 0.7–2.5
Physostoma calcaratum Leisman, 1964	LC (Westp. C/D) Kansas	6–10 (8)	Basal one-half of seed	Basal two-thirds of nucellus/symm.	Lobe bases with spur-like extensions/ epidermis with secretory cells	3.5 × 1.75	2.5–3.0 × 1.5
P. elegans Oliver, 1909	LC (Westp. A) England	9–12 (10)	Basal two-thirds of seed	Basal two-thirds of nucellus/symm.	Outer lobe surface with clavate trichomes	5.5–6.0 × 2.25	4.0(+) × 2.0
P. stellatum Holden, 1954	LC (Westp. A) England	6–7 (6)	Basal two-thirds of seed(?)	Basal two-thirds of nucellus/ symm.(?)	Lobes form sharp longitudinal ridges	2.75 × 1.25	?
Oclloa cesariana gen. et sp. nov.	LC (earliest) Peru	5–9 (8)	Basal one-half to two-thirds of seed	Basal half to two-thirds of nucellus/asymm.	Lobe margins/inner surfaces? with projections	9.0–11.0 × 2.5–4.0	5.0–6.0 × 2.0–2.3

[a]*EC* = Early Carboniferous; *LC* = Late Carboniferous; *Tour.* = Tournaisian; *Vis.* = Visean; *Westp.* = Westphalian.
[b]Most common number shown in parentheses.

Physostoma includes four species: *P. elegans* Oliver ex Williamson, *P. stellatum* Holden, *P. calcaratum* Leisman, and *P. winchellii* Arnold. Arnold (1948b) proposed the last species, *P. winchellii*, for macerated seed cuticles from the early Pennsylvanian of Michigan. These cuticles have a large apical bulge or "cap" which Arnold interpreted as the free portion of the nucellus. A similar "bulge" is present in *P. elegans*. This feature was used by Arnold as the basis for assigning the Michigan cuticles to *Physostoma*. However, the enclosing structures or mode of attachment of the cuticles still remains unknown.

Of the three remaining species, *Oclloa* is like *P. elegans* in size, yet it is still substantially larger than this species, and nearly three times larger than *P. stellatum* and *P. calcaratum*. *Physostoma elegans* and *P. calcaratum* show overlap in number of integumentary lobes. *Physostoma calcaratum* has 6–10, nearly the same as *Oclloa*, while *P. elegans* has typically 9–12. Distinct features characterize the integument of each taxon. In *P. calcaratum* each lobe forms a narrow spur-like projection at the base, while the lobes of *P. stellatum* form sharp longitudinal ridges that run the full length of the seed. *Physostoma elegans* and *Oclloa* have an integument with trichomes; however, in *P. elegans* trichomes cover the entire outer surface, whereas in *Oclloa* they are restricted to the margins and possibly inner surfaces of the free apical lobes. In *Physostoma*, the upper limit of fusion between individual lobes and between the integument and nucellus appears to be symmetrical, or in other words, the lobes separate at the same level (e.g. Leisman, 1964). However, fusion in *Oclloa* is asymmetrical or uneven and the lobes separate at different levels (e.g. Plate I, 3, 5). While the degree of variation of these two characters

among the specimens of species of *Physostoma* is not clear, and oblique sections may obscure interpretation in permineralized seeds, fusion asymmetry is a consistent feature among specimens of *Oclloa*.

Physostoma is based on anatomical descriptions of isolated seeds formally described by Oliver (1909) and later emended by Holden (1954). Seeds of *Physostoma* are radial and ribbed. The integument consists of an apical whorl of separate, tentacle-like segments that are fused both laterally and to the nucellus from the chalaza to the level of the pollen chamber. Each segment is composed of thin-walled cells and has a single vascular strand. The pollen chamber is bell-shaped due to an apparent mound-shaped invagination of the pollen chamber floor which extends for some distance into the pollen chamber. This is most pronounced in the specimens of *P. elegans* figured by Oliver (1909, plate 5, fig. 4) and Seward (1917, p. 311, fig. 493C). In *P. calcaratum* a similar situation occurs where the megaspore, which is closely appressed to the nucellus, has an apical bulge that protrudes into the pollen chamber (Leisman, 1964). Although similarities between *Oclloa* and *Physostoma* include a lobed integument fused laterally and to the nucellus and have a similar form of the upper part of the pollen chamber and lagenostome, *Oclloa* differs in size and mode of preservation. Also, *Oclloa* is known only from compressions and is acupulate, whereas in *Physostoma* seeds are permineralized and the mode of attachment is not yet known. Moreover, megaspores of *Oclloa* have yet to be recovered so whether they had an apical bulge or not has to be determined. Although *Oclloa* shares many morphological features with *Physostoma*, until more is known about the vegetative organs of both plants a separate name is proposed for the Paracas ovulate remains.

Comparison of Obandotheca *to pteridosperm microsporangiate organs*

Comparison of *Obandotheca* to lyginopterid microsporangiate or prepollen organs that are similar, e.g. *Telangium* (Benson, 1904; Jennings, 1976; Long, 1979) and *Telangiopsis* (Eggert and

Taylor, 1971), shows that *Obandotheca* differs from these in having nonsynangiate sporangia. Therefore, based on this latter feature, *Obandotheca* is most comparable to the upper Mississippian taxon *Zimmermannitheca* Remy and Remy (1959) described from Europe.

Zimmermannitheca is based on material representing only the detached portions of ultimate fertile branchlets, whereas the Peruvian material is more complete and hence more is known about the organization of the fructification. Because the generic concept of *Zimmermannitheca* is a very broad one, the Peruvian specimens could be assigned to the genus as a new species; however, based on differences in sporangia and fructification morphology presented below we have elected to circumscribe a new taxon for the South American material and propose the name *Obandotheca laminensis* gen. et sp. nov. for this taxon.

Sporangia of *Zimmermannitheca* are up to 5 mm long and 0.8 mm wide, show distinct longitudinal striations, with the distal end of the sporangium modified into a relatively long acuminate tip. They are borne mostly in tight radial clusters of 2–7 at the ends of very slender dichotomized axes, 0.25 mm wide (Remy and Remy, 1959), and form a basal cup-like structure from which the sporangia flare outward. Spores of *Zimmermannitheca* are relatively large, ranging from 90 to 100 μm in diameter.

Sporangia of *Obandotheca* on the other hand, are shorter and slightly wider measuring up to 3.5 mm in length and 1.0–1.3 mm in width. The sporangia lack a striated surface and the apex ends in a short blunt tip. *Obandotheca* sporangia are borne in pairs on the ultimate axes of alternately arranged third-order laterals that are attached at right angles to second-order axes. The second-order laterals in turn are alternately arranged along a larger first-order axis. The ultimate axes are ca. 0.5 mm wide and appear to fork in a cruciate fashion yielding up to two pairs or four sporangia (Plate II, 5, 6; Fig. 4b). Unlike *Zimmermannitheca*, those groups containing four sporangia have a looser arrangement with the sporangia curving inward toward the center of the group rather than flaring outward away from the center. Although microspores or pollen have not been found inside

a sporangium, a seed was found surrounded by a mass of small spores, 40–60 µm wide (Plate I, 11). Also, in close proximity to this seed are the remnants of several *Obandotheca* microsporangia (Plate I, 11-arrow).

Classification and phylogenetic implications

The importance of both ovule and cupule morphology in making accurate taxonomic identifications among cupulate gymnosperms has been demonstrated by Rothwell and Scheckler (1988) and Rothwell and Wight (1989). However, because *Oclloa* is acupulate this limits the number and type of characters that can be used to distinguish this taxon from other acupulate taxa with a similar morphology. As such, this stresses the important role that both the vegetative and reproductive organs will play in the taxonomic identification and classification of this plant. Seven groups of Paleozoic (i.e. Late Devonian and Carboniferous) seed ferns are presently recognized: the Elkinsiaceae, Stenokoleaceae, Buteoxylonaceae, Calamopityaceae, Lyginopteridaceae, Medullosaceae, and Callistophytaceae. Of these *Oclloa* shares certain aspects of seed morphology with the Elkinsiaceae, Medullosaceae, and Lyginopteridaceae. Ovules have yet to be found in organic connection in either the Buteoxylonaceae or the Calamopityaceae (Galtier, 1988). Although the seed *Lyrasperma* Long is often found associated with calamopityacean vegetative organs (Long, 1960c; Retallack and Dilcher, 1988), recent discovery of *Coumiasperma remyi* associated with calamopityacean vegetative remains suggests a greater diversity in seed morphology within the Calamopityaceae (Galtier and Rowe, 1989, 1991).

Unlike *Oclloa*, ovulate fructifications of the Elkinsiaceae are cupulate and borne on cruciately forked branching systems (Rothwell et al., 1989; Serbet and Rothwell, 1992). The Medullosaceae resemble *Oclloa* in being acupulate but differ from *Oclloa* in having ovules with a well-defined micropyle, simple pollen chamber, an integument free from the nucellus, and ovules borne in the place of pinnules on otherwise vegetative fronds. The ubiquity of this latter feature among the Medullosaceae, however, has been questioned by

the recent discovery of *Stephanospermun konopeonus* (Langford) (Drinnan et al., 1990).

Oclloa resembles most closely the Lyginopteridaceae. Common features between the two taxa include an integument fused to the nucellus and a hydrasperman pollen chamber. The primary difference between them is the lack of a cupule in *Oclloa*. As is currently recognized, the concept of Lyginopteridaceae is a highly artificial one that is based largely on anatomical characters of isolated stems, petioles, ovules, and pollen organs primarily from Pennsylvanian-aged deposits in North America and Europe (Taylor and Millay, 1981; Taylor and Stubblefield, 1986; Serbet and Rothwell, 1992). Those lyginopterid-like organs which are Mississippian in age remain poorly known and are often only tentatively assigned to this group (Galtier, 1988). Therefore we consider assigning *Oclloa* to the Lyginopteridaceae based only on fructification and seed characters premature at this time since it still is not clear where on the fronds the fertile branch systems were borne. Among the specimens examined so far, there is no indication that fertile branches were borne in an axillary position on any of the frond segments as in some pteridosperms (Rowe, 1988; Matten, 1992b). Also, considering the age of *Oclloa*, the vegetative similarities between the Lyginopteridaceae and Calamopityaceae, and our poor understanding of the reproductive organs of the Calamopityaceae, we cannot totally rule out possible affinities of *Oclloa* with this latter group. Therefore, based on currently available evidence we consider that *Oclloa* at the present time is best assigned to the class Pteridospermopsida.

The earliest known gymnospermous seeds are small (up to 7 mm long), borne on cruciately-forked cupulate systems, and modified for hydrasperman reproduction (Rothwell, 1986; Rothwell and Scheckler, 1988). Similarities between *Oclloa* and the earliest seeds include hydrasperman reproduction, comparable shape and number of integumentary lobes, and a similar amount of fusion between the integumentary lobes and between the integument and nucellus. Seeds of *Oclloa* differ in being larger (9–11 mm long), stratigraphically younger, acupulate, and borne

singly at the terminal ends of pinnate laterals attached to a more or less planate branch system. Likewise, among Early Carboniferous lagenostomalean seeds for which attachment is known most are cupulate and relatively small. Therefore, the fertile systems of *Oclloa* which have megasporangia that are acupulate, borne terminally, and are surrounded by a telomic integument suggests that plants bearing this type of seed could have originated within different evolutionary lineages.

One possibility based on the younger age of *Oclloa*, suggests that at least one lineage evolved from cupulate ancestors via reduction or loss of the cupule accompanied by an increase in seed size. Loss of the cupule may have evolved in response to selection pressures related to an increased efficiency in pollen capture. Niklas (1983) has shown in simulated wind pollination experiments on Carboniferous ovules that the presence of a cupule did significantly reduce the potential for pollination. In *Eurystoma angulare* Long for example, once the cupule was removed this ovule morphology became the most efficient for wind pollination. Moreover, Niklas demonstrated that by removing the hairs from the integument of *Physostoma elegans*, the morphology most like that of *Oclloa*, the efficiency was only slightly less than that of the acupulate *E. angulare*.

The other alternative is that *Oclloa* originated from a different evolutionary lineage, one in which a more "primitive" seed morphotype was retained. Such a lineage may have diverged early on, perhaps during the Frasnian, the time proposed for the origin of gymnospermy (Rothwell and Scheckler, 1988), from a plexus of aneurophytalean/gymnospermous plants characterized by single terminal megasporangia modified for hydrasperman reproduction that were surrounded by an apical whorl of unfused preintegumentary lobes. As such, this suggests that the hypothetical ancestral stock of *Oclloa* could have had a morphology like that found in *Genomosperma kidstonii* or *G. latens*. From such an archetype *Oclloa* could have been derived by acropetal fusion of the lobes and fusion between the integument and nucellus.

Conclusions

Oclloa represents the first positive evidence that ovules modified for hydrasperman reproduction

are not all cupulate and therefore the presence of a hydrasperman pollen chamber is not correlated with presence of a cupule. Lack of a cupule in the stratigraphically younger *Oclloa* suggests that at least one lineage evolved in which naked ovules were selected for, perhaps in response to changing environmental conditions related to pollination by wind and/or other ecological factors related to seed dispersal. Detached seeds of *Oclloa* do show a short stalk about 1.0 mm long suggesting that they did abscise as a unit. Moreover, these naked ovules could have originated from either cupulate ancestors through loss of the cupule or alternatively through modifications involving the progressive acropetal fusion of preintegumentary lobes in early gymnospermous plants with less specialized hydrasperman preovules.

As study of Paleozoic gymnosperms continues it becomes more evident from the diversity of isolated reproductive and vegetative organs that the importance of these fossils in resolving questions of gymnosperm origins, phylogeny, and classification rests in our ability to accurately reassemble them into the whole plants they once were. Since establishment of the Pteridospermae by Oliver and Scott (1904), only a few early gymnosperms with lagenostomalean-type preovules have been reconstructed as whole plant taxa, *Lyginopteris hoeninghausii*, *Elkinsia polymorpha* (Rothwell and Serbet, 1992; Serbet and Rothwell, 1992), and *Laceya hibernica* (Matten, 1992b). With future work, the Paracas ovulate remains together with their associated microsporangiate and vegetative organs afford a similar opportunity to add to our knowledge of early pteridosperms as whole organisms. Incorporating this type of data into our present systematic framework will allow us to test more rigourously hypotheses regarding the origin, evolution, and systematics of this historically important plant group.

References

Alleman, V., 1985. Paleontologia de los carbones paleozoicos Peruanos. 1° Symp. Nac. Carbon., Lima, pp. 5/1–5/12.

Alleman, V. and Pfefferkorn, H.W., 1988. Licopodos de Paracas: Significacion geologica y paleo-climatologica. Bol. Soc. Geol. Perú, 78: 131–136.

Arber, E.A.N., 1905. On some new species of *Lagenostoma*, a type of pteridospermous seed from the Coal Measures. Proc. R. Soc. London B, 76: 245–259.

Archangelsky, S., Azcuy, C.L. and Wagner, R.H., 1981. Three dwarf lycophytes from the Carboniferous of Argentina. Scr. Geol., 64: 1–35.

Arnold, C.A., 1939. *Lagenospermum imparirameum* sp. nov., a seed-bearing fructification from the Mississippian of Pennsylvania and Virginia. Bull. Torrey Bot. Club, 66: 297–303.

Arnold, C.A., 1948a. Paleozoic seeds II. Bot. Rev., 14: 450–472.

Arnold, C.A., 1948b. Some cutinized seed membranes from the coal-bearing rocks of Michigan. Bull. Torrey Bot. Club, 75: 131–146.

Bateman, R.M. and Rothwell, G.W., 1990. A reappraisal of the Dinantian floras at Oxroad Bay, East Lothian, Scotland. 1. Floristics and the development of whole-plant concepts. Trans. R. Soc. Edinburgh Earth Sci., 81: 127–159.

Benson, M., 1904. *Telangium scotti*, a new species of Telangium (*Calymmatotheca*) showing structure. Ann. Bot., 18: 161–176.

Drinnan, A.N., Schramke, J.M. and Crane, P.R., 1990. *Stephanospermum konopeonus* (Langford) comb. nov.: a medullosan ovule from the Middle Pennsylvanian Mazon Creek flora of northeastern Illinois, U.S.A. Bot. Gaz., 151: 385–401.

Eggert, D.A. and Taylor, T.N., 1971. *Telangiopsis* gen. et sp. nov., an Upper Mississippian pollen organ from Arkansas. Bot. Gaz., 132: 30–37.

Fairon-Demaret, M. and Scheckler, S.E., 1986. A propos de *Moresnetia*. L'évolution des gymnosperms, approche biologique et paléobiologique. Coll. Fondation Louis Emberger-Charles Sauvage, Univ. Sci. Techn. Languedoc, Montpellier. Resumés des communications, p. 19.

Fairon-Demaret, M. and Scheckler, S.E., 1987. Typification and redescription of *Moresnetia zalesskyi* Stockmans, 1948,

an early seed plant from the Upper Famennian of Belgium. Bull. Inst. R. Sci. Nat. Belg., 57: 183–189.

Fauque, L., Limarino, C., Césari, S. and Sabattini, N., 1989. El Carbonifero Inferior fosilifero del area del Rio La Troya, sudoeste de la provincia de La Rioja. Ameghiniana, 26: 55–62.

Galtier, J., 1988. Morphology and phylogenetic relationships of early pteridosperms. In: C.B. Beck (Editor), Origin and Evolution of Gymnosperms. Columbia Univ. Press, New York, NY, pp. 135–176.

Galtier, J. and Rowe, N.P., 1989. A primitive seed-like structure and its implications for early gymnosperm evolution. Nature, 340: 225–227.

Galtier, J. and Rowe, N.P., 1991. A new permineralized seed-like structure from the basalmost Carboniferous of France. Neues Jahrb. Geol. Paläontol. Abh., 183: 103–120.

Gensel, P.G. and Skog, J.E., 1977. Two early Mississippian seeds from the Price Formation of southwestern Virginia. Brittonia, 29: 332–351.

Holden, H.S., 1954. The morphology of a new species of pteridosperm seed from the Yorkshire Coal Measures. Ann. Bot., 18: 407–416.

Issacson, P.E. and Sablock, P.E., 1990. Devonian paleogeography and paleobiogeography of the central Andes. In: W.S. McKerrow and C.R. Scotese (Editors), Paleozoic Paleogeography and Biogeography. Geol. Soc. London Mem., 12: 431–435.

Jennings, J.R., 1976. The morphology and relationships of *Rhodea, Telangium, Telangiopsis*, and *Heterangium*. Am. J. Bot., 63: 1119–1133.

Kidston, R., 1916. XXII.—Contributions to our knowledge of British Paleozoic Plants. Part I. Plants from the Scottish Coal Measures. Trans. R. Soc. Edinburgh, 51: 709–720.

Leisman, G.A., 1964. *Physostoma calcaratum* sp. nov., a tentacled seed from the Middle Pennsylvanian of Kansas. Am. J. Bot., 51: 1069–1075.

Long, A.G., 1960a. On the structure of *Calymmatotheca kidstoni* Calder (emended) and *Genomosperma latens* gen. et sp. nov., from the Calciferous Sandstone Series of Berwickshire. Trans. R. Soc. Edinburgh, 64: 29–44.

Long, A.G., 1960b. On the structure of *Stamnostoma huttonense* gen. et spec. nov.—a pteridosperm seed and cupule from the Calciferous Sandstone Series of Berwickshire. Trans. R. Soc. Edinburgh, 64: 201–215.

Long, A.G., 1960c. On the structure of *Samaropsis scotica* Calder (emended) and *Eurystoma angulare* gen. et sp.nov., petrified seeds from the Calciferous Sandstone Series of Berwickshire. Trans. R. Soc. Edinburgh, 64: 261–280.

Long, A.G., 1961a. Some pteridosperm seeds from the Calciferous Sandstone Series of Berwickshire. Trans. R. Soc. Edinburgh, 64: 401–419.

Long, A.G., 1961b. *Tristichia ovensi* gen. et sp. nov. a prostelic Lower Carboniferous pteridosperm from Berwickshire and East Lothian, with an account of some associated seeds and cupules. Trans. R. Soc. Edinburgh, 64: 477–489.

Long, A.G., 1963. Some specimens of *Lyginorachis papilio* Kidston associated with stems of *Pitys*. Trans. R. Soc. Edinburgh, 65: 211–224.

Long, A.G., 1969. *Eurystoma trigona* sp. nov., a pteridosperm

ovule borne on a frond of *Alcicornopteris* Kidston. Trans. R. Soc. Edinburgh, 68: 171–182.

Long, A.G., 1979. Observations on the Lower Carboniferous genus *Pitus* Witham. Trans. R. Soc. Edinburgh, 70: 111–127.

Matten, L.C., 1992a. Studies on Devonian plants from New York State: *Stenokoleos holmesii* n. sp. from the Cairo Flora (Givetian) with an alternative model for lyginopterid seed fern evolution. Cour. Forsch.-Inst. Senckenberg, 147: 75–85.

Matten, L.C., 1992b. Reconstruction of *Laceya* an upper Devonian seed plant. Organ. Int. Paleobot., IV Conf., Paris, Abstr., p. 105.

Matten, L.C., Lacey, W.S. and Lucas, R.C., 1980a. Studies on the cupulate seed genus *Hydrasperma* Long from Berwickshire and East Lothianin Scotland and County Kerry in Ireland. Bot. J. Linn. Soc., 81: 249–273.

Matten, L.C., Lacey, W.S., May, B.I. and Lucas, R.C., 1980b. A megafossil flora from the uppermost Devonian near Ballyheigue, Co. Kerry, Ireland. Rev. Palaeobot. Palynol., 29: 241–251.

Matten, L.C., Tanner, W.R. and Lacey, W.S., 1984. Additions to the silicified Upper Devonian/Lower Carboniferous flora from Ballyheigue, Ireland. Rev. Palaeobot. Palynol., 43: 303–320.

May, B.I. and Matten, L.C., 1983. A probable pteridosperm from the uppermost Devonian near Ballyheigue, Co. Kerry, Ireland. Bot. J. Linn. Soc., 86: 103–123.

Meyer-Berthaud, B., 1984. *Stenomyelon* from the Upper Tournaisian of the Montagne Noire (France). Can. J. Bot., 62: 2297–2307.

Meyer-Berthaud, B., 1986. *Melissiotheca*: A new pteridosperm pollen organ from the Lower Carboniferous of Scotland. Bot. J. Linn. Soc., 93: 277–290.

Meyer-Berthaud, B. and Galtier, J., 1986. Studies on a Lower Carboniferous flora from Kingswood near Pettycur, Scotland. 2. *Phacelotheca*, a new synangiate fructification of pteridospermous affinities. Rev. Palaeobot. Palynol., 48: 181–198.

Millay, M.A. and Taylor, T.N., 1979. Paleozoic seed fern pollen organs. Bot. Rev., 45: 301–375.

Nathorst, A.G., 1914. Zur fossilen Flora der Polarländer. Teil I. Nachträge zur paläozoischen Flora Spitzbergens. Norstedt and Söner, Stockholm, 110 pp.

Niklas, K.J., 1983. The influence of Paleozoic ovule and cupule morphologies on wind pollination. Evolution, 37: 968–986.

Nuñez del Prado, H., 1991a. Análisis sedimentológico preliminar y paleoambiente de sedimentación de la serie carbonifera de Paracas (Ica-Perú). VII Congr. Peruano Geol., Lima, pp. 45–48 (Extended abstr.).

Nuñez del Prado, H., 1991b. Preliminary sedimentological analysis and depositional system of the Carboniferous at Paracas Peninsula, Peru. XII Int. Congr. Carboniferous and Permian Geology and Stratigraphy, Buenos Aires, pp. 63–64 (Abstr.).

Oliver, F.W., 1909. On *Physostoma elegans* Williamson, an archaic type of seed from the Paleozoic rocks. Ann. Bot., 23: 73–119.

Oliver, F.W. and Scott, D.H., 1904. On the structure of the Paleozoic seed *Lagenostoma lomaxi*, with a statement of the evidence upon which it is referred to *Lyginodendron*. Philos. Trans. R. Soc. London., 197B: 193–247.

Pfefferkorn, H.W. and Alleman, V., 1989. New climatic belt in Carboniferous of the southern hemisphere. 28th Int. Geol. Congr., Washington, DC, Abstr. 2-602 (Abstr.).

Remy, R. and Remy, W., 1959. *Zimmermannitheca cupulaeformis* n. gen. n. sp. Monatsber. Dtsch. Akad. Wiss. Berlin, 1: 767–776.

Retallack, G.J. and Dilcher, D.L., 1988. Reconstructions of selected seed ferns. Ann. Mo. Bot. Gard., 75: 1010–1057.

Roberts, J., Claoué-Long, J.C. and Jones, P.J., 1991. Calibration of the Carboniferous and early Permian of the Southern New England Orogen by shrimp ion microprobe zircon analyses. Newslett. Carboniferous Stratigr., 9: 15–16.

Rothwell, G.W., 1985. The role of comparative morphology and anatomy in interpreting the systematics of fossil gymnosperms. Bot. Rev., 51: 319–327.

Rothwell, G.W., 1986. Classifying the earliest gymnosperms. In: R.A. Spicer and B.A. Thomas (Editors), Systematic and Taxonomic Approaches Palaeobotany. Systematics Assoc. Spec. Vol., 31. Clarendon, Oxford, pp. 135–161.

Rothwell, G.W. and Erwin, D.M., 1987. Origin of seed plants: an aneurophyte/seed-fern link elaborated. Am. J. Bot., 74: 970–973.

Rothwell, G.W. and Scheckler, S.E., 1988. Biology of ancestral gymnosperms. In: C.B. Beck (Editor), Origin and Evolution of Gymnosperms. Columbia Univ. Press, New York, NY, pp. 85–134.

Rothwell, G.W. and Serbet, R., 1992. Pollination biology of *Elkinsia polymorpha*, implications for the origin of gymnosperms. Cour. Forsch.-Inst. Senckenberg, 147: 225–231.

Rothwell, G.W. and Wight, D.C., 1989. *Pullaritheca longii* gen. et sp. nov. and *Kerryia mattenii* gen. et sp. nov., Lower Carboniferous cupules with ovules of the *Hydrasperma tenuis*-type. Rev. Palaeobot. Palynol., 60: 295–309.

Rothwell, G.W., Scheckler, S.E. and Gillespie, W.H., 1989. *Elkinsia* gen. nov., a Late Devonian gymnosperm with cupulate ovules. Bot. Gaz., 150: 170–189.

Rowe, N.P., 1988. New observations on the Lower Carboniferous pteridosperm *Diplopteridium* Walton and an associated synangiate organ. Bot. J. Linn. Soc., 97: 125–158.

Rowe, N.P. and Galtier, J., 1990. A Lower Carboniferous plant assemblage from La Serre (Montagne Noire, France). Part II. Gymnosperms. Rev. Palaeobot. Palynol., 63: 91–115.

Scott, A.C., 1990. Preservation, evolution, and extinction of plants in Lower Carboniferous volcanic sequences in Scotland. In: G.M Lockley and A. Rice (Editors), Volcanism and Fossil Biotas. Geol. Soc. Am. Spec. Pap., 244: 25–38.

Scott, A.C. and Galtier, J., 1988. A new Lower Carboniferous flora from East Lothian, Scotland. Proc. Geol. Assoc., 99: 141–151.

Scott, A.C. and Meyer-Berthaud, B., 1985. Plants from the Dinantian of Foulden, Berwickshire, Scotland. Trans. R. Soc. Edinburgh Earth Sci., 76: 13–20.

Scott, A.C., Galtier, J. and Clayton, G., 1984. The distribution of Lower Carboniferous anatomically preserved floras in Western Europe. Trans. R. Soc. Edinburgh Earth Sci., 75: 311–340.

Scott, A.C., Galtier, J. and Clayton, G., 1985. A new late Tournaisian (Lower Carboniferous) flora from Kilpatrick Hills, Scotland. Rev. Palaeobot. Palynol., 44: 81–99.

Scott, A.C., Meyer-Berthaud, B. and Galtier, J., 1986. Studies on a new Lower Carboniferous flora from Kingswood, near Pettycur, Scotland. I. Preliminary report. Rev. Palaeobot. Palynol., 48: 161–180.

Serbet, R. and Rothwell, G.W., 1992. Characterizing the most primitive seed plants. I. A reconstruction of *Elkinsia polymorpha*. Int. J. Plant Sci., 153: 602–621.

Seward, A.C., 1917. Fossil Plants. Vol. III. Pteridospermeae, Cycadofilices, Cordaitales, Cycadophyta. Cambridge Univ. Press, Cambridge, 655 pp.

Stopes, M.C., 1914. The "Fern Ledges" Carboniferous flora of St. John, New Brunswick. Can. Dep. Min. Mem., 41, 168 pp.

Taylor, T.N. and Millay, M.A., 1981. Morphologic variability of Pennsylvania lyginopteid seed ferns. Rev. Palaeobot. Palynol., 32: 27–62.

Taylor, T.N. and Stubblefield, S.P., 1986. The role of repro-
ductive organs in the classification of fossil plants. In: R.A. Spicer and B.A. Thomas (Editors), Systematic and Taxonomic Approaches Palaeobotany. Systematics Assoc. Spec. Vol., 31. Clarendon, Oxford, pp. 135–161.

Wagner, R.H., 1979. Megafloral zones of the Carboniferous. In: P.K. Sutherland and W.L. Manger (Editors), Biostratigraphy. XII. Int. Carboniferous Congr., 2, pp. 109–134.

Williamson, W.C., 1877. On the organization of the fossil plants of the Coal Measures—Part VIII. Ferns (continued) and gymnospermous stems and seeds. Philos. Trans. R. Soc. London, 167: 213–270.

Ziegler, A.M., 1990. Phytogeographic patterns and continental configurations during the Permian period. In: W.S. McKerrow and C.R. Scotese (Editors), Paleozoic Paleogeography and Biogeography. Geol. Soc. London. Mem., 12: 363–379.