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PERMINERALIZED SEED PLANTS FROM THE LATE PERMIAN OF SOUTHERN CHINA: A NEW SPECIES OF *CARDIOCARPUS*

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A new species of permineralized ovule is reported from a previously undocumented diverse fossil plant assemblage preserved in volcaniclastic tuff from the Late Permian Xuanwei Formation at the Huopu coal mine in Guizhou Province, China. The ovule is large and platyspermic, with 180° rotational symmetry. It has a pronounced commissure that distally divides the integument into two valves. The integument comprises a two-part sarcotesta, a sclerotesta also divided into two parts, and an endotesta that is unusually thick in the central part of the ovule and at the apex. Fusion of the nucellus to the integument occurs only at the chalaza, and the nucellar apex is small, consisting of a proximal pollen chamber and a distally extending tubular projection. A single vascular bundle enters the base of the ovule and divides in the major plane at the boundary of the inner and outer sarcotesta to form two integumentary bundles, one to each side of the ovule, with the nucellar bundle continuing to the base of the nucellus, where it forms a small vascular cup. The gross morphology and the pattern of vascularization of the ovule fit the circumscription of the morphogenus *Cardiocarpus* Brongniart, to which the ovule is here assigned, but are distinct from previously recognized morphospecies leading to the erection of *Cardiocarpus huopuensis* sp. nov. In *C. huopuensis* sp. nov., tissues of the outer sarcotesta are rarely preserved and where present occur external to a zone of poorly preserved cells that suggests exfoliation of the outer sarcotesta through ontogeny. Although the identity and, hence, affinity of the parent plant for *C. huopuensis* sp. nov. are unknown, previous evidence shows ovules of this kind to be produced by either a coniferophyte or a seed fern (pteridosperm).

Keywords: ovule, cardiocarpalean, *Cardiocarpus*, coniferophyte, pteridosperm, tuff.

Introduction

Seed plants are an important component in many Late Paleozoic fossil plant assemblages and in general show increasing complexity and diversity through this time corresponding to their early radiation and diversification (Stewart and Rothwell 1993; Taylor and Taylor 1993). Much of our existing knowledge of Paleozoic seed plants comes from their isolated seeds and ovules; few seed plants of this age have been reconstructed as whole-plant species (e.g., Retallack and Dilcher 1988; Rothwell and Serbet 1994; Hilton and Bateman 2006). Of the available evidence on Paleozoic ovules and seeds, the highest-quality observations come from a relatively small number of sources worldwide in which anatomically preserved specimens occur. Foremost in these are the Upper Carboniferous coal ball assemblages from Europe and North America (Phillips 1980; Stewart and Rothwell 1993; Taylor and Taylor 1993; Galtier 1997) and their broadly comparable assemblages preserved in chert from the latest Carboniferous to the basalmost Permian of France (Brongniart 1874, 1881; Combourieu and Galtier 1985; Doubinger et al. 1995). Collectively, these assemblages are instrumental in shaping our understanding of the Late Paleozoic wetland plant communities that spanned vast tracts of lowland Euramerica during the Upper Carboniferous before their demise during the earliest Permian (Phillips 1980; Phillips et al. 1985; DiMichele and Hook 1992; Cleal and Thomas 1999; DiMichele et al. 2001, 2002). In comparison, Permian-aged floras are poorly known but include important accounts of anatomically preserved seed plants from Antarctica (e.g., Taylor and Taylor 1987, 1992; Klavins et al. 2001; McManus et al. 2002), Australia (e.g., Nishida et al. 2003), and China (e.g., Tian et al. 1996; Wang 1998; Hilton et al. 2001*a*, 2001*b*, 2004; Wang et al. 2003*a*, 2003*b*).

In China, anatomically preserved fossil assemblages are relatively common in the Permian where they range from the Lower Permian Taiyuan Formation in northern China to the latest Permian Wangjiazhai Formation in southern China (Tian et al. 1996). The best known of these assemblages is the Taiyuan Formation in which anatomically preserved fossil plants occur in both coal balls (Tian et al. 1996; Hilton et al. 2002; Wang et al. 2003*a*, 2003*b*) and volcaniclastic tuffs (Hilton et al. 2001*a*, 2001*b*). The flora of the Taiyuan Formation shows the presence of taxa previously considered characteristic of Euramerican-style wetland plant communities persisting into the Permian of Cathaysia and demonstrate that the demise in coal-forming plant communities in North

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America and Europe toward the end of the Carboniferous represents a regional loss of plant taxa rather than a global extinction event (Hilton et al. 2002; Hilton and Cleal 2003). Comparable studies on the Upper Permian floras of China are, however, in their infancy, and only a handful of sites containing permineralized specimens have been studied in detail. Although the taxonomically diverse coal ball assemblage from the Wangjiazhai Formation in Guizhou Province remains the most promising Upper Permian paleobotanical locality in China, only general accounts of its floristic composition are currently available (Tian and Zhang 1980; Tian et al. 1996), and detailed taxonomic investigations are now required. Information from other sites in which anatomically preserved plants are known is also restricted; individual localities either contain a limited diversity of taxa and lack seed plants (for recent summary, see Wang et al. 2003*c*) or are diverse and include seed plants but are fragmentary, preventing the reconstruction of entire plant organs or whole-plant species (e.g., Hilton et al. 2004). Notwithstanding, the Upper Permian anatomically preserved plant assemblages from southern China are important because they record the further persistence of key elements of the wetland plant communities recognized from the Lower Permian of China and the Upper Carboniferous to the basalmost Permian of Europe and North America (Tian and Zhang 1980; Hilton et al. 2004). Despite being incompletely known, the Upper Permian floras of southern China represent the youngest of the Late Paleozoic coal swamp plant communities and are therefore of considerable evolutionary importance.

In this article we report the first species to be described from a recently discovered diverse plant fossil assemblage preserved in volcaniclastic tuff from the Upper Permian Xuanwei Formation at the Huopu coal mine in Guizhou Province. This assemblage has not undergone the high levels of taphonomic disarticulation and fragmentation observed in other contemporaneous tuff assemblages from the Xuanwei Formation (Hilton et al. 2004) and therefore provides a new assemblage from which to accurately characterize the Upper Permian plant communities from southern China.

Locality Information and Stratigraphy

Specimens were collected from tuffaceous sediments found in mine spoil at the Huopu coal mine in Panxian County, Guizhou Province, China (fig. 1). This mine extracts coal from the Xuanwei Formation, a series of continental sediments, paralic coal swamp deposits, and interbedded tuff horizons (Yao et al. 1980; Zhao et al. 1980; Shao et al. 1998). The Xuanwei Formation crops out in Xuanwei and Fuyuan counties in eastern Yunnan Province and Panxian County in western Guizhou Province.

Lithologically, the tuff is pale green in color, weathering to a yellow-gray. It comprises predominantly feldspars, abundant bright-green-colored authigenic clay minerals, and occasional lithic fragments and is bound by early-stage diagenetic carbonate cement. Within the tuff delicate plant tissues are frequently preserved, showing that permineralization occurred rapidly after deposition and without time for tissues to degrade before mineralization. Plant fossils typically range from 3 to 80 mm long in axis length and include wetland (lycopsids, sphenopsids, ferns, gigantopterid seed plants) as well as drier habitat plants (seed ferns, coniferophytes). Additional work on this assemblage is currently in progress. Although the assemblage includes specimens that have been broken by taphonomic processes, many complete specimens (such as the larger of the ovules described here) also occur, from which recognition and characterization of plant morphospecies are possible. The geological characters of the tuffaceous sediments, as well as reports on individual taxa from this assemblage, will be the focus of subsequent articles. The Xuanwei Formation is considered to be from Wuchiapingian to Changhsingian stages of the Upper Permian, with this determination coming from regional-scale correlation and fossil plant biostratigraphy (Zhao et al. 1980; Shen 1995; Shao et al. 1998; Glasspool et al. 2004).

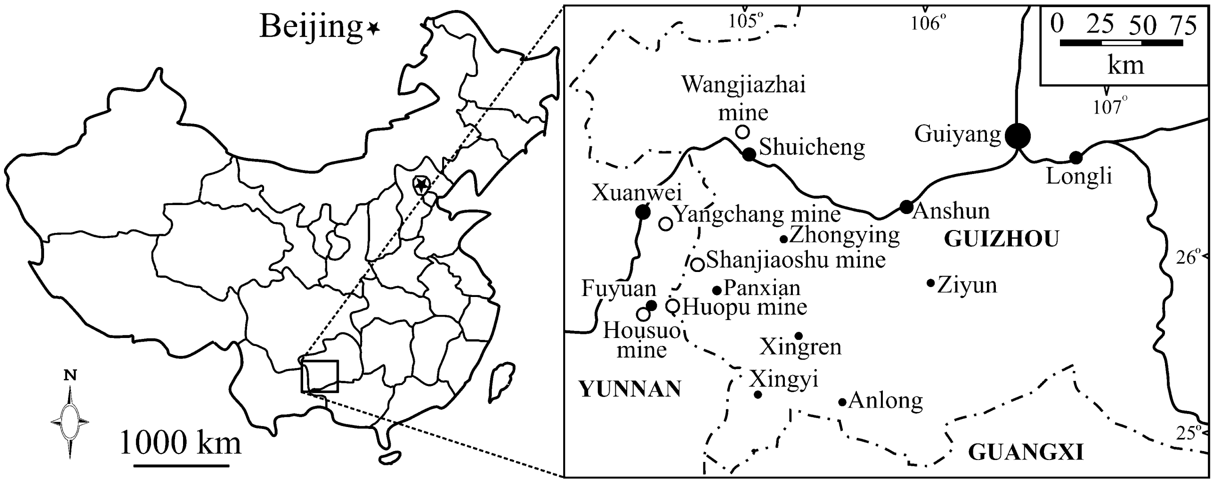

Fig. 1 Outline map of China showing provincial boundaries, with study area in Yunnan and Guizhou Provinces shown in enlarged boxed area. Major towns are shown by filled circles, coal mines by open circles, provincial boundaries by dashed lines, and major roads by solid lines.

Material and Methods

Five blocks of volcanic tuff were collected from mine spoil at the Huopu mine between 1998 and 2001 and were numbered GPP2-0001 to GPP2-0005. Each block contained abundant and well-preserved fossil plants, although the majority of the larger specimens, including the ovules described here, were contained in a single block (GPP2-0003). Tuff blocks were cut with 1-mm-thick rock saws to reveal fossil plants, and then suitable surfaces were prepared using the acetate peel technique (Galtier and Phillips 1999). HCl was used to etch the carbonate matrix, typically for 20–35 s per surface. Specimens were mounted on slides using Eukitt. Low-power observations were made using a Zeiss Stemi SVII photomicroscope, and high-power observations were made using a Zeiss Axioskope. In both cases, digital images were taken using a Q-Imaging Micropublisher 5.0 digital camera, with images adjusted in Adobe Photoshop (ver. 7), and plates were constructed using CorelDRAW (ver. 12). Specimens illustrated in this article represent individual peels selected from serial peels made in the same planes.

Two examples of this species have been recognized and are detailed here: specimens A and B. Specimen A, which is designated as the holotype, is revealed in longitudinal section in the minor plane. The two adjacent surfaces to the initial saw cut that revealed the ovule are numbered GPP2-0003F and GPP2-0003 E/Bot, respectively. One half of specimen A (corresponding to peeled surface GPP2-0003F) was then cut at midlevel to reveal one half of the ovule in transverse section, with these peels numbered GPP2-0003 M/Top and GPP2-0003 M/Bot, respectively, for the different cut surfaces. The lower part of the ovule was cut again, this time in the major plane, and the surface was numbered as GPP2-0003 K-2/Top. Specimen B, which is designated as the paratype, has only its apical part preserved and is revealed in transverse section (fig. 2*d*; fig. 4*f*; fig. 5*a*, 5*b*). It is represented by peels GPP2-0003-I-1 to GPP2-0003-I-9.

Description

General Features

Ovules are platyspermic and have 180° rotational symmetry (Rothwell 1986; Hilton et al. 2003). They are elliptical in transverse section (fig. 2*d*) and ovate in longitudinal section through the minor plane (fig. 2*a*–2*c*). Dimensions of specimen A approach 15 mm long, 12–15 mm in the major plane, and 7–8 mm in the minor plane, while specimen B is approximately 10 mm in the major plane and 5–6 mm in the minor plane. In longitudinal section, the chalaza is rounded and has no evidence of a pedicle or a stalk (fig. 2*a*, 2*b*). An integumentary commissure is present in the major plane, where it extends for between 30% and 50% of the integument length (fig. 2*a*, 2*c*, 2*d*) and divides the distal part of the integument into two equal valves.

Integument

The integument is of irregular thickness; it is thicker near the chalaza, where it approaches 2 mm (fig. 2*b*, 2*e*), and thins toward the apex (fig. 2*c*). However, in specimen A (fig. 2*a*), the central region of the integument is unusually thick and bulges into the seed cavity; this feature is not observed in specimen B because it preserves only the apical portion of the ovule (fig. 2*d*). The outermost layer of the integument is the sarcotesta; no epidermis has been observed. The sarcotesta is generally 500 μm thick and consists of two parts. The outer sarcotesta is preserved only in a few places and comprises radially aligned columnar cells (fig. 3*a*, 3*b*). It is 300–380 μm thick and comprises radially elongated cells with a diameter of 20–40 μm. The outer sarcotesta occurs immediately external to a zone of poorly preserved cells but, where observed, runs adjacent and parallel to the remaining inner parts of the sarcotesta (fig. 3*a*, 3*b*). The inner sarcotesta is 150–200 μm thick and consists of nearly isodiametric cells (fig. 3*c*, 3*d*), and in this layer, cell size typically decreases inward (fig. 3*d*, 3*f*). The inner boundary of the sarcotesta is gradational; sarcotestal cells integrade with the sclerotesta, so an abrupt boundary is not observed (fig. 3*c*–3*f*).

The sclerotesta comprises two parts, an outer zone of larger cells and an inner zone of smaller cells. The outer zone is 1.5–2 mm thick and thins toward the apical part (fig. 2*a*, 2*c*). It comprises thick-walled cells that are isodiametric, ranging from 40–120 μm in diameter in transverse section and elongate up to 280 μm long in longitudinal section, with cell wall thickness ranging from 30 to 40 μm in the larger cells (fig. 3*d*). The outer sclerotesta possesses between six and 18 rows of cells, with the rows generally becoming thicker and comprising larger cells farther outward (fig. 3*d*, 3*f*). The inner zone ranges from 100 to 250 μm thick, with cells being slightly tangentially elongated in transverse section and elongate in longitudinal section and individual cells ranging from 15 to 20 μm in radial diameter (fig. 3*e*, 3*f*). These cells also have thick walls, although not as thick as those from the outer sclerotesta, and range from 15 to 20 μm thick.

The endotesta forms the innermost layer of the integument, and it is not persistent and best observed apically (fig. 5*a*, 5*b*) where it surrounds the nucellar apex. Here the endotesta is approximately 250 μm thick and comprises thin-walled isodiametric cells of approximately 30–40 μm in diameter. In the central region of the ovule, the endotesta is unusually thickened and can be up to 1.5 mm thick (central bulge in fig. 2*a*). Individual endotesta cells are poorly preserved but are relatively thin-walled parenchymatous cells that are more or less isodiametric (fig. 4*a*, 4*b*). These cells have undergone some taphonomic distortion but are clearly attached to the inner part of the integument (fig. 2*a*) and are absent at the chalaza (fig. 2*b*).

Nucellus, Megaspore, and Nucellar Apex

The nucellus fills the majority of the seed cavity. It is thin, 10–30 μm thick, and fused to the integument only proximally (fig. 2*a*, 2*b*; fig. 4*d*). The nucellus contains a thin seed megaspore membrane that is 10 μm thick (fig. 4*c*), and distally, a small pollen chamber is present (fig. 4*e*, 4*f*). In specimen A, this is small but not well preserved and is located about 1.5 mm below the integumentary apex (figs. 2*c*, 4*e*). However, in specimen B, the pollen chamber protrudes through the commissure (fig. 4*f*), showing the base of the nucellar apex. The nucellar apex comprises a small elliptical-shaped pollen

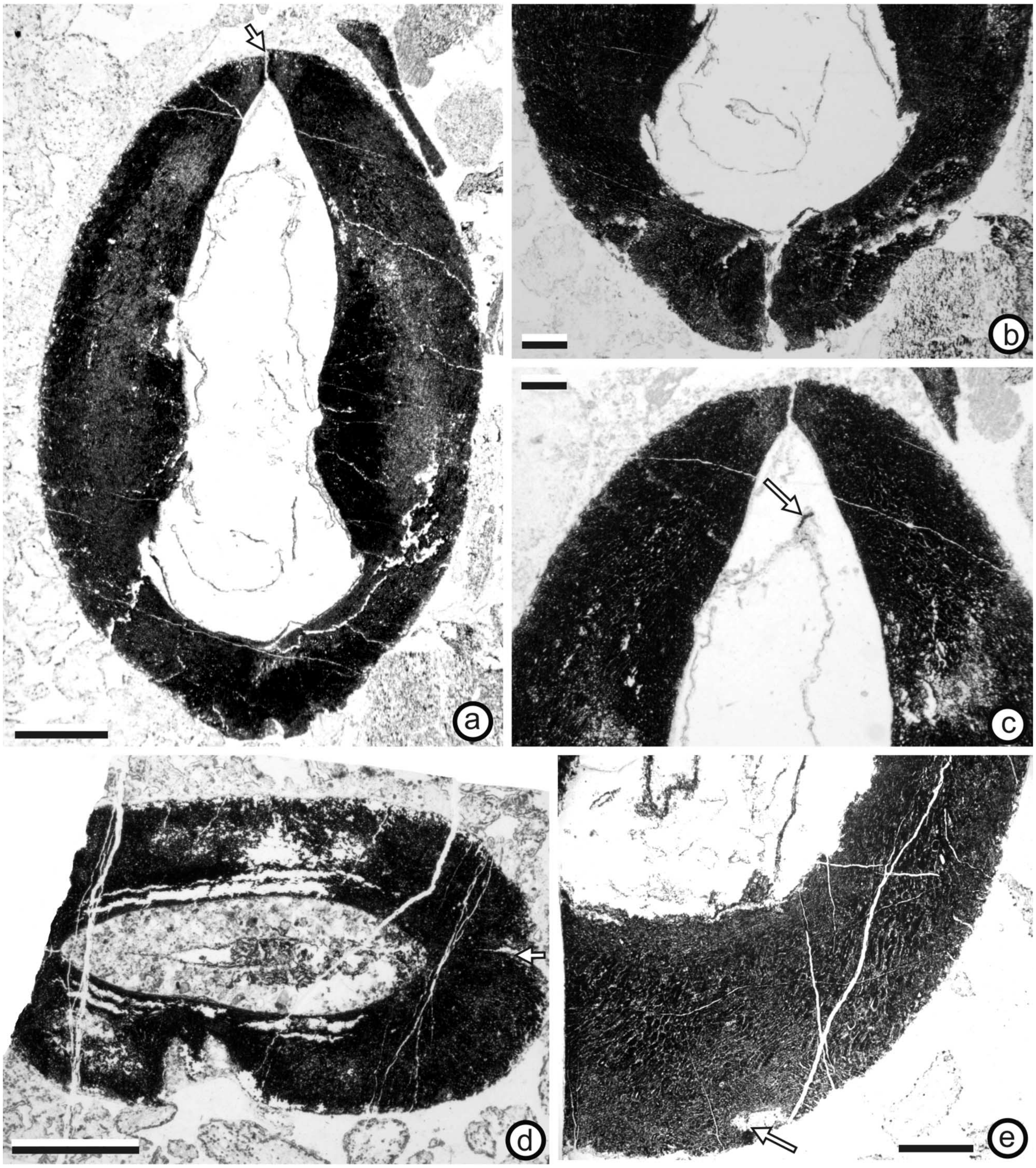

Fig. 2 Gross morphology of *Cardiocarpus huopuensis* sp. nov. All scale bars = 1 mm unless otherwise indicated. *a*, Ovule in near longitudinal section through minor plane, showing characteristic ovate shape, distal commissure (arrow), and central bulge of endotesta. GPP2-0003-F-0, scale bar = 2 mm. *b*, Same ovule as *a* but in higher section, showing rounded chalaza and single nucellar bundle passing through integument. GPP2-0003-F-3. *c*, Enlargement of apex of same ovule from *a* in different section, showing commissure and apex of nucellus indicated (arrow). GPP2-0003-F-3. *d*, Second specimen in near transverse section, showing elliptical shape. Arrow marks position of commissure in major plane. GPP2-0003-I-1, scale bar = 2 mm. *e*, Chalazal portion of same ovule as in *a*–*c* cut to reveal major plane, showing rounded base and with prominent lacunae containing integumentary bundle (arrow). GPP2-0003-K-2/Top-10.

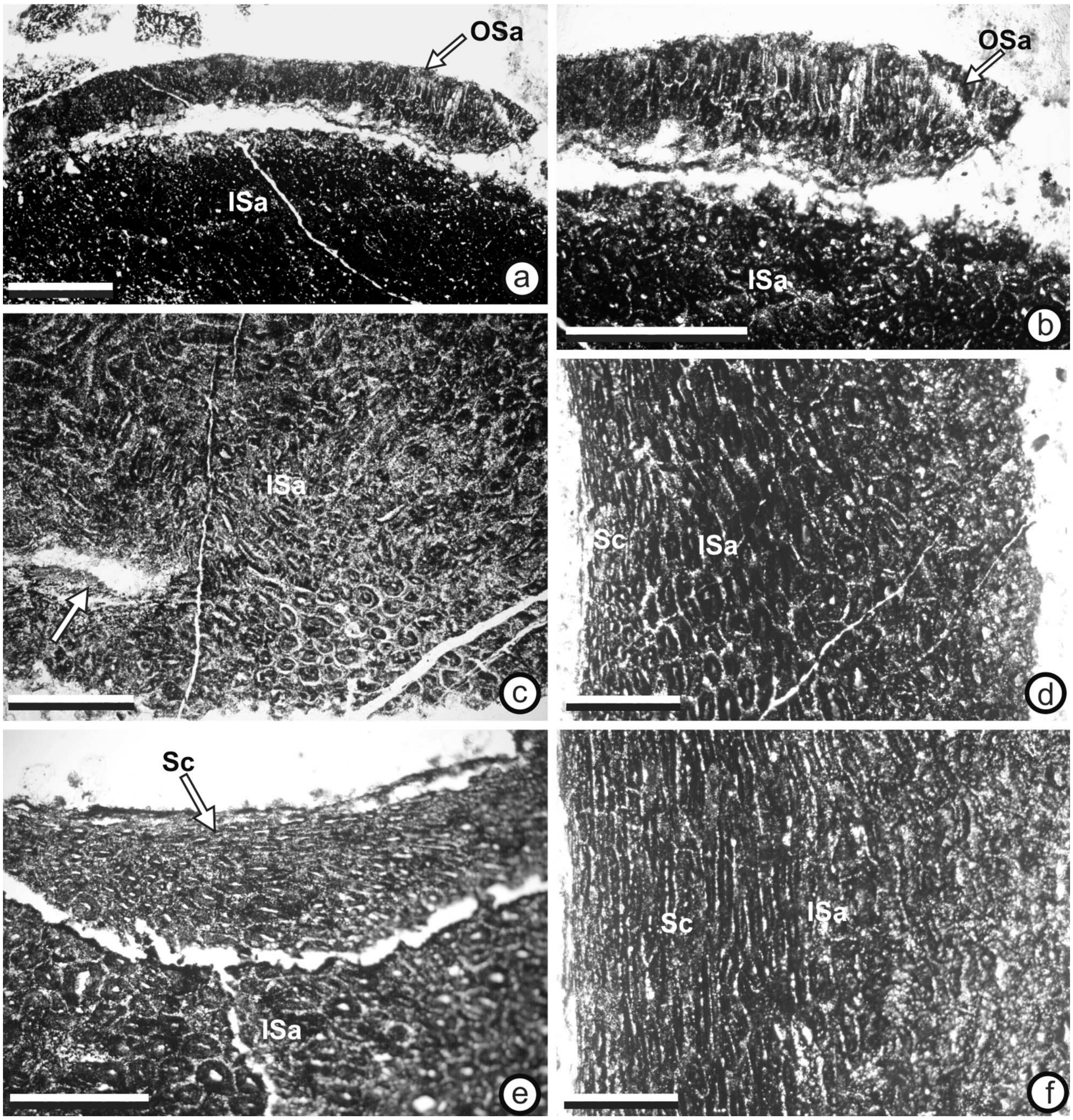

Fig. 3 Integumentary anatomy of *Cardiocarpus huopuensis* sp. nov. *OSa* = outer sarcotesta, *ISa* = inner sarcotesta, *Sc* = sclerotesta. All scale bars = 500 μm. *a*, Longitudinal section in minor plane, showing the outermost part of sarcotesta external to zone of poorly preserved cells. GPP2-0003-E/Bot-2. *b*, Enlargement from *a* of radially aligned thin-walled cells of the outer sarcotesta. *c*, Inner sarcotesta near base of ovule (from same specimen but at different level in same plane as fig. 2*e*) showing thick-walled cells and integumentary bundle (arrow). GPP2-0003-K-2/Top-14 (longitudinal section in major plane). *d*, Integument near chalaza, showing thick inner sarcotesta intergrading with thin sclerotesta. GPP2-0003-E/Bot-4 (longitudinal section in minor plane). *e*, Integument near chalaza, showing thick zone of inner sarcotesta (bottom) comprising thick-walled cells, intergrading upward into thin zone of sclerotesta. GPP2-0003-F-0. *f*, Integument near apex with relatively thick inner sarcotesta, thick sclerotesta, and no endotesta. GPP2-0003-E/Bot-4.

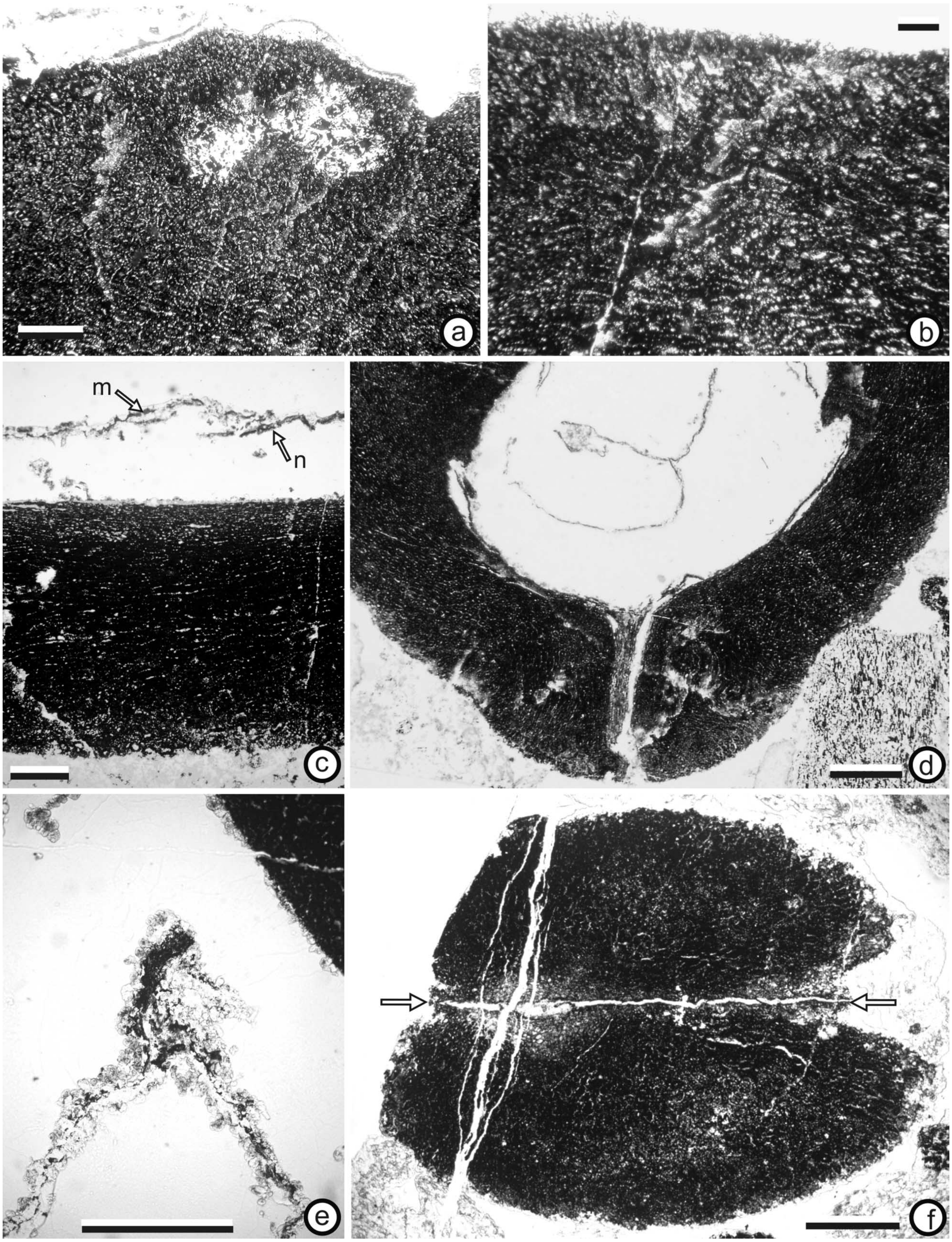

Fig. 4 Integument and nucellus of *Cardiocarpus huopuensis* sp. nov. Scale bars = 500 μm unless otherwise indicated. *a*, Parenchymatous endotesta from central bulge enlarged from fig. 2*a*. GPP2-0003-F-4. *b*, Enlargement of endotesta from *a* in higher section. Scale bar = 100 μm. *c*,

chamber (arrow, fig. 5*a*) with a distally extending narrow apical tube (arrow, fig. 5*b*) approximately 500 μm in diameter. Pollen and other contents are not preserved within the pollen chamber.

Vascular Tissues

A single vascular bundle, 200 μm wide and composed of approximately 10–15 tracheids, enters the base of the ovule at the chalaza and passes through the integument in a straight line to the base of the nucellus (fig. 4*d*; fig. 5*c*, 5*d*), where it forms a small vascular cup approximately 500–600 μm in diameter (fig. 5*c*). Tracheids are poorly preserved such that it has not been possible to measure them individually. We have not observed integumentary bundles departing from the nucellar bundle, but diverging from the chalaza, a prominent lacuna containing a small vascular bundle is observed on one half of the ovule (figs. 2*e*, 3*c*, 5*e*). This runs outward and upward from the chalaza in the major plane of the ovule near the outer surface of the inner sarcotesta. This position infers that it is one of a pair of integumentary bundles situated to either side of the nucellar bundle in the major plane. This integumentary bundle has been observed only in the chalazal region of the ovule, so the distal extent of these bundles is unknown, but they are absent or not preserved in the distal half of the ovule length when seen in transverse section (fig. 2*d*; fig. 5*a*, 5*b*).

Discussion

Comparisons with Other Cardiocarpalean Ovules

The gross morphology of the species described here falls within the traditionally circumscribed cardiocarpalean ovule group (Seward 1917) characterized by 180° rotational symmetry (*sensu* Rothwell 1986; platyspermic *sensu* Seward 1917), an integument fused to the nucellus only toward the chalaza, a small pollen chamber, and the presence of an integumentary commissure that occurs in some (but not all) cardiocarpalean taxa (see Hilton et al. 2003). A number of cardiocarp morphogenera have been recognized. The pattern of chalazal vasularization observed in the specimens described here is distinct from that of the genera *Mitrospermum* Arber and *Rhabdospermum* Seward (Arber 1910; Seward 1917; Taylor and Stewart 1964; see Hilton et al. 2003 summary), in which the integumentary bundles pass the integument twice, but is similar to that observed in the genera *Cardiocarpus* Brongniart, *Taxospermum* Brongniart, *Nucellangium* Darrah, and *Callospermarion* Eggert and Delevoryas. However, in *Nucellangium*, the nucellus is more extensively vascularized, and the ovule lacks a commissure (Stidd and Cosentino 1976; Hilton et al. 2003). The genus *Taxospermum* is incompletely characterized but appears to have its nucellus fused to the integument in the basal third of the ovule and also appears to have its nucellus vascularized below this level (Oliver 1903; Bertrand 1907). In *Callospermarion*, the seed cavity is nearly round in cross section, and a commissure is absent (Rothwell 1980). Both species of *Callospermarion* are also much smaller than the ovules described here (Eggert and Develoryas 1960; Rothwell 1980). The features of the present ovule therefore fit the circumscription of the morphogenus *Cardiocarpus* (see Hilton et al. 2003), to which the ovule is here assigned. However, as Hilton et al. (2003) previously determined, *Cardiocarpus* as currently delimited is not defined on a single diagnostic character or a suite of characters and represents an unnatural (para- or polyphyletic) grade of organization that is the symplesiomorphic condition among several groups of cardiocarp-producing plants. While the name *Cardiocarpus* is unsatisfactory, methods to reliably separate seeds assigned to it into biologically significant entities are not currently available.

Comparisons with Other Morphospecies of Cardiocarpus

The specimens described here are most similar to the morphospecies of *Cardiocarpus* recognized from the Late Carboniferous and the basalmost Permian of France in the St. Etienne and Grand Croix chert assemblages (Brongniart 1874, 1881; Doubinger et al. 1995). From this assemblage a number of large cardiocarpalean taxa have been reported in which ovule length is over 10 mm long, and several of these ovules have a thick integument similar to that of the specimens described here. However, the majority of the French taxa require detailed reinvestigation and taxonomic revision before being fully characterized and before the full diversity of forms in this assemblage is recognized (see Hilton et al. 2003). From information currently available on the French species (Brongniart 1874, 1881; Doubinger et al. 1995), we find that all are distinct from that described here; *Cardiocarpus drupaceous* Brongniart, *Cardiocarpus sclerotesta* Brongniart, *Cardiocarpus tenuis* Brongniart, and *Cardiocarpus orbicularis* Brongniart all have a strongly cordate base and are, in general, wider in the minor plane and have a shorter length : width ratio than *C. huopuensis*. Where known, these ovules also lack a two-layered sclerotesta, as recognized in *C. huopuensis*. From the same assemblage in France, a number other ovules have an overlapping character with *Cardiocarpus*, including *Diplotesta avellana* Bertrand, *Cyclospermum nummulare* (Brongniart) Seward, and *Leptocaryum avellanum* Brongniart. *Diplotesta avellana* is distinguished from the ovule we describe here in possessing a strongly cordate base, and all three of these species are distinct from the ovule described here in possessing a prominent vascular pad at the base of the nucellus.

A number of morphospecies of *Cardiocarpus* have recently been characterized from the Late Paleozoic floras of China. These are exclusively Lower Permian in age, considerably smaller than the species described here, and in each case are distinct

Section through midlevel of ovule in longitudinal section revealing thick sclerotesta, nucellus (*n*), and seed megaspore membrane (*m*) and lacking endotesta. GPP2-0003-E/Bot-4. *d*, Chalazal region of ovule in higher plane of section from fig. 2*b*, showing straight and undivided nucellar bundle. GPP2-0003-F-4, scale bar = 1 mm. *e*, Enlargement of nucellar apex from same specimen as shown in fig. 2*a* but in different section. GPP2-0003-F-3. *f*, Distal region of ovule shown in fig. 1*d*, with commissure in major plane (arrows), thick endotesta, and pollen chamber (enlarged in fig. 5*a*). GPP2-0003-I-3, scale bar = 1 mm.

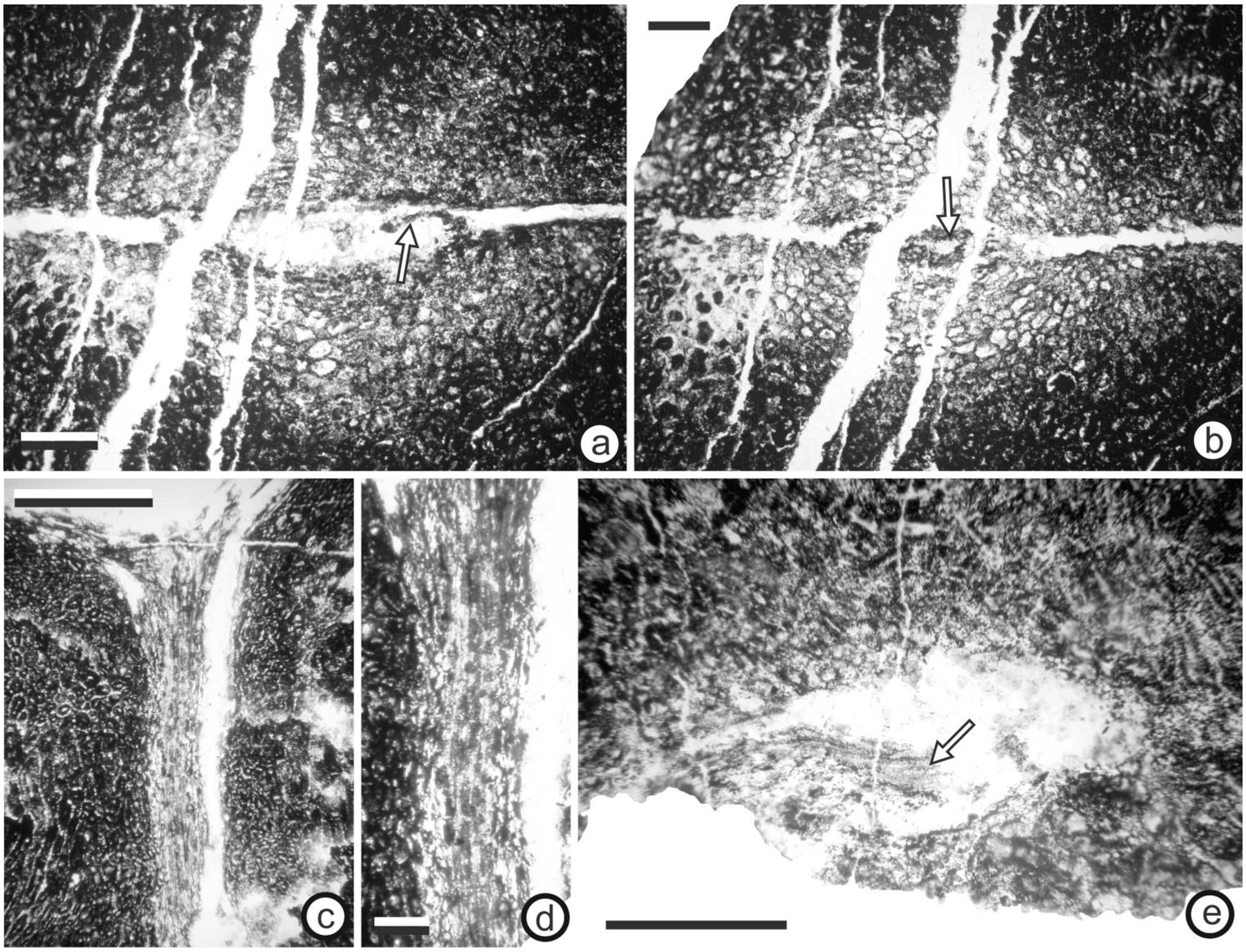

Fig. 5 Nucellar apex and vascularisation of *Cardiocarpus huopuensis* sp. nov. Scale bars = 500 μm unless otherwise stated. *a*, Enlargement from fig. 4*f*, showing well-preserved endotesta surrounding elliptical but broken pollen chamber (arrow). GPP2-0003-I-8. *b*, Same specimen as in *a* but at higher level, showing distally extending tubular extension of the nucellar apex (arrow) surrounded by thick endotesta. GPP2-003-I-9. *c*, Enlargement of apical region of chalazal bundle from fig. 4*d*, where it widens to form a cup at base of the nucellus. GPP2-0003-F-4. *d*, Enlargement of chalazal bundle from fig. 4*d*, showing poorly preserved trachetary elements. GPP2-0003-F-4, scale bar = 100 μm. *e*, Enargement of poorly preserved integumentary bundle (arrow) and surrounding lacuna from same specimen as fig. 2*e* but in higher plane. GPP2-0003-K-2/Top-15.

from the morphospecies described here. In *Cardiocarpus taiyuanensis* (Wang) Hilton et al., the nucellus is more extensively vascularized (Hilton et al. 2003), and *Cardiocarpus samaratus* (Wang and Tian) Wang et al. is distinguished by its bilateral symmetry and also the presence of a small integumentary wing (Wang et al. 2003*b*). *Cardiocarpus tuberculatus* Wang et al. possesses a distinctive tuberculate sarcotesta (Wang et al. 2003*a*) and lacks a commissure. *Cardiocarpus dabiziae* Hilton et al. possesses prominent glands on the exterior of the sarcotesta and lacks a two-part sclerotesta (Hilton et al. 2001*a*). The species described here are therefore established as a new morphospecies, *Cardiocarpus huopuensis* sp. nov.

Comparison with Previously Reported Upper Permian Permineralized Ovules from China

Four permineralized cardiocarpalean ovules have been previously reported from the Upper Permian of China: two unnamed species from the Xuanwei Formation (Hilton et al. 2004), *Cryptonosperma primitiva* Li 1992*b nomen nudum* (=seeds of *Cryptonoclea primitiva* Li 1992*a nomen nudum*) and *Diplotesta* sp. (Li 1992*c*) from the Wangjiazhai Formation. The two species described by Hilton et al. (2004) are distinct from the current species; both are smaller, with one possessing a thin sclerotesta and a variably thick sarcotesta with prominent integumenary glands, while the other has a thinner integument that has a relatively thick sclerotesta and a thin sarcotesta, with integumentary bundles forming ribs on the lateral margins of the ovule. Although *Cryptonoclea* and *Crytosperma* are nomenclaturally invalid, and despite published accounts structurally misinterpreting the morphology and organization of the ovule (see Hilton et al. 2003), published illustrations show the ovule to be cardiocarpalean with a prominent and thick lateral wing that protrudes from the margins of the ovule for approximately 2 mm. The integument contains small isodiametric cells and lacks a two-part sarcotesta and sclerotesta. *Cryptosperma*/*Cryptonoclea* is therefore distinct from the species described here. *Diplotesta* sp., as described by Li (1992*c*), is based on a single ovule from which only a few details of the ovule structure and histology can be determined. The ovule is somewhat smaller than that described here (13 × 8 mm in apparently longitudinal section) and possesses a uniformly thick integument comprising a thin sclerotesta and a thin sarcotesta. The sarcotesta appears to have anastomosing elongated cells toward the exterior. Where known, these features are also dissimilar from the species described here. Collectively, these previously published reports show that the ovules from the Upper Permian of China need detailed reexamination before being adequately characterized, but all are distinct from *Cardiocarpus huopuensis* sp. nov.

Affinities of Cardiocarpus huopuensis *sp. nov. and Relationship to Other Cardiocarpalean Taxa*

Cardiocarpalean ovules referred to as *Cardiocarpus* are produced by a variety of plants (e.g., Hilton et al. 2003; Wang et al. 2003*b*), including cordaitean coniferophytes, conifers, and various pteridosperm groups. Based on the evidence currently available and the absence of information about its parent plant, *C. huopuensis* cannot be assigned to a particular group of seed plants. Although *Cardiocarpus* is often associated with cordaitean coniferophytes (e.g., Rothwell 1988; Hilton et al. 2003), existing evidence demonstrates that cordaiteans are absent from the Xuanwei Formation (Yao et al. 1980; Zhao et al. 1980; Wang 1998), and our preparations from the Huopu tuff show an absence of cordaitean roots, stems, leaves, and fertile shoot systems. The precise affinity of *C. huopuensis* therefore remains unknown. Our only certainty is that it was produced by either a coniferophyte or a seed fern (see Hilton et al. 2003).

The vascular arrangement exhibited in *Cardiocarpus*, with a single nucellar bundle and two integumentary bundles positioned in the major plane, represents the symplesiomorphic condition within ovules of this kind (Hilton et al. 2003). As such, the morphogenus *Cardiocarpus*, which is primarily defined on this vascular arrangement, represents a paraphyletic genus that, although serving a purpose nomenclaturally and taxonomically, is virtually meaningless systematically and phylogenetically. Although adoption of this system of classification is far from ideal, at present no viable alternatives are possible. The prime reason for this is that many of the historically cited and figured specimens, typically those from the Late Carboniferous and Early Permian of France (e.g., Brongniart 1874, 1881; Doubinger et al. 1995), including those species from which the morphogenus *Cardiocarpus* is founded, the type species of the genus *C. drupaceous*, and a number of species that closely resemble the present species, require additional investigation in order to be accurately characterized and diagnosed. Therefore, it is highly probable that any wide-ranging systematic revision undertaken at this time, before reinvestigation of the French specimens, would not survive subsequent taxonomic revisions once the French specimens have been reinvestigated. While this work is urgently needed, it falls outside the scope of this investigation. Our solution is therefore to erect the current taxon as a new morphospecies and in doing so recognize its distinction from other recognized cardicoarpalean ovules. However, we also acknowledge that with future investigations it is likely that the morphogenus *Cardiocarpus* will be revised to exclude at least some of the species assigned to it and that this ovule may be transferred to a more biologically meaningful genus from the non-informative morphogenus *Cardiocarpus*.

Ontogenetic Sarcotestal Exfoliation

Ovules of *C. huopuensis* have retained the radially aligned columnar cells of the outer sarcotesta in only a few places (e.g., fig. 3*a*, 3*b*), and all specimens lack an epidermis. It is therefore possible that what we here consider to be the outer sarcotesta has other tissue layers external to it, making the ovule larger and more structurally complex than considered at this time. However, a growing number of Paleozoic ovules are now recognized as being externally incomplete and lacking their outermost integumentary layers (e.g., Rothwell 1971, 1980; Doubinger et al. 1995; Wang et al. 2003*a*). In many cases the reasons for the absence of sarcotesta are unclear. Rothwell (1971, 1980) reported ontogenetic sloughing off of the outer sarcostesta in ovules of *Callospermarion pusillum* from the Late Carboniferous of North America. In *Callospermarion* cells at the inner margin of the sarcotesta break down with maturation, enabling the sarcotesta to be exfoliated through ontogeny (Rothwell 1971, 1980). The same may be true of *Cardiocarpus huopuensis*, although it is also plausible that these outermost layers were simply not preserved or were degraded by taphonomic processes during transport and deposition within the tuff. Here the presence of a zone of poorly preserved cells at the boundary of the inner and outer sarcotesta that is surrounded by well-preserved cells suggests that these cells underwent selective decay before fossilization. We propose that these cells form an exfoliation zone similar to that observed in *Callospermation undulatum*, but in this case, only the outer part of the sarcotesta is lost rather than the entire sarcotesta as seen in *Callospermarion* (Rothwell 1981). Clearly, a large number of specimens are required before ontogenetic exfoliation can be unquestionably identified in the present species, as similarly noted by Wang et al. (2003*a*). However, we consider that this feature is likely to be systematically informative with the presence and absence of sarcotestal exfoliation and perhaps different positions of sarcotestal exfoliation reflecting different systematic affinities within seed plants.

Systematic Description

Order—Cardiocarpales Seward, 1917

*Morphogenus—*Cardiocarpus *Brongniart, 1881*

*Morphospecies—*Cardiocarpus huopuensis *Wang, Hilton, Liang et Stevens sp. nov. (Figs. 2–5)*

Diagnosis. Ovule with 180° rotational symmetry, ovate in longitudinal section, and elliptical in transverse section, with well-developed commissure. Ovules approximately 15 mm long, 12–15 mm wide in the major plane, and 7–8 mm wide in the minor plane. Integument comprising outer sarcotesta of radially aligned columnar cells, inner sarcotesta of thick-walled cells. Sarcotesta intergrades with sclerotesta. Sclerotesta comprising two zones: outer sclerotesta of large sclereids, inner sclerotesta of smaller sclereids. Endotesta of thin-walled parenchyma cells, thick in central part of ovule and apex. Nucellus free from integument except at base. Nucellar apex comprising basal pollen chamber, with distally protruding tubular projection. Vascular system with single bundle entering ovule at chalaza, dividing in the major plane to produce two integumentary bundles situated between the inner and outer sarcotesta, with nucellar bundle continuing to the base of the nucellus, where it forms a small nucellar cup.

Type locality. Huopu coal mine, Panxian County, Guizhou Province, China.

Geological horizon. Xuanwei Formation.

Age. Wuchiapingian to Changhsingian stages, Upper Permian.

Holotype. Specimen A, comprising serial section of the ovule on slides GPP2-0003-E/Bot-1 to GPP2-0003-E/Bot-12, GPP2-0003-M/Top-1 to GPP2-0003-M/Top-16, and GPP2-0003-F-0 to GPP2-0003-F-4. Figure 2*a*–2*c*, 2*e*; figure 3; figure 4*a*–4*e*; figure 5*c*–5*e*.

Paratype. Specimen B, incorporating serial sections of ovule on slides GPP2-0003-I-1 to GPP2-0003-I-9. Figure 2*d*; figure 4*f*; figure 5*a*, 5*b*.

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Etymology. Specific epiphet refers to the source locality in the Huopu coal mine.

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Literature Cited

Arber A 1910 On the structure of the Palaeozoic seed *Mitrospermum compressum* (Will.). Ann Bot 24:491–509.

Bertrand CE 1907 Les charactéristiques du genre *Taxospermum* de Brongniart. Bull Soc Bot Fr 54:213–224.

Brongniart AT 1874 Etudes sur les graines fossiles trouvées à l'état silicifié dans le terrain houiller de Saint-Étienne. Ann Sci Nat Bot 5: 243–265, pl 21–23.

——— 1881 Recherches sur les graines fossiles silicifieés. Masson, Paris. 93 pp, 21 pl.

Cleal CJ, BA Thomas 1999 Tectonics, tropical forest distribution and global warming in the Late Palaeozoic. Acta Palaeobot, suppl 2, pp 17–19.

Combourieu N, J Galtier 1985 Nouvelles observations sur *Polypterospermum*, *Polylophospermum*, *Colpospermum* et *Codonospermum*, ovules de Pteridospermales du Carbonifere superieur francais. Palaeontogr Abt B Palaeophytol 196:1–29.

DiMichele WA, RW Hook 1992 Paleozoic terrestrial ecosystems. Pages 204–325 *in* AK Behrensmeyer, JD Damuth, WA DiMichele, R Potts, eds. Terrestrial ecosystems through time. University of Chicago Press, Chicago.

DiMichele WA, HW Pfefferkorn, RA Gastaldo 2001 Response of Late Carboniferous and Early Permian plant communities to climate change. Annu Rev Earth Planet Sci 29:461–487.

DiMichele WA, TL Phillips, WJ Nelson 2002 Place vs. time and vegetational persistence: a comparison of four tropical mires from the Illinois Basin during the height of the Pennsylvanian Ice Age. Int J Coal Geol 50:43–72.

Doubinger J, P Vetter, J Langiaux, J Galtier, J Broutin 1995 La flore fossile du bassin houiller de Saint-Étienne. Mem Mus Natl Hist Nat 164. 355 pp.

Eggert DA, T Delevoryas 1960 *Callospermarion*: a new seed genus from the Upper Pennsylvanian of Illinois. Phytomorphology 10:131–138.

Galtier J 1997 Coal-ball floras of the Namurian-Westphalian of Europe. Rev Palaeobot Palynol 95:51–72.

Galtier J, TL Phillips 1999 The acetate peel technique. Pages 70–76 *in* TP Jones, NP Rowe, eds. Fossil plants and spores: modern techniques. Geological Society of London, London.

Glasspool IJ, J Hilton, ME Collinson, SJ Wang 2004 Foliar physiognomy in Cathaysian gigantopterids and the potential to track Palaeozoic climates using extinct plant groups. Palaeogeogr Palaeoclimatol Palaeoecol 205:69–110.

Hilton J, RM Bateman 2006 Pteridosperms are the backbone of seed plant evolution. J Torrey Bot Soc 133:119–168.

Hilton J, CJ Cleal 2003 Fossil floras of the late Carboniferous and Early Permian of North China: implications on extinction patterns and biogeographic realms. Palaeontol Assoc Newsl 54:153.

Hilton J, GW Rothwell, CS Li, SJ Wang, J Galtier 2001*a* Permineralized cardiocarpalean ovules in wetland vegetation from Early Permian volcaniclastic sediments of China. Palaeontology 44: 811–825.

Hilton J, SJ Wang, J Galtier, IJ Glasspool, L Stevens 2004 A Late Permian permineralized plant assemblage in volcaniclastic tuffs from the Xuanwei Formation, Guizhou Province, China. Geol Mag 141:661–675.

Hilton J, SJ Wang, J Galtier, CS Li 2001*b* An Early Permian plant assemblage from the Taiyuan Formation of northern China with compression/impression and permineralized preservation. Rev Palaeobot Palynol 114:175–189.

Hilton J, SJ Wang, B Tian 2003 Reinvestigation of *Cardiocarpus minor* (Wang) Li *nomen nudum* from the Lower Permian of China and its implications for seed plant taxonomy, systematics and phylogeny. Bot J Linn Soc 141:151–175.

Hilton J, SJ Wang, WQ Zhu, B Tian, J Galtier, AH Wei 2002 *Callospermarion* ovules from the Early Permian of northern China: palaeofloristic and palaeogeographic significance of callistophytalean seed-ferns in the Cathaysian flora. Rev Palaeobot Palynol 120: 301–314.

Klavins SD, EL Taylor, M Krings, TN Taylor 2001 An unusual, anatomically preserved ovule from the Permian of Antarctica. Rev Palaeobot Palynol 115:107–117.

Li ZM 1992*a* The reconstruction of a new member of gigantopterids from coal balls of China. Cathaya 4:161–178.

——— 1992*b* Studies on Palaeozoic seeds: *Crytosperma primitiva* gen. et sp. nov. Pages 5–6 *in* Papers for the 3rd symposium of Chinese Palaeobotanical Association, Chinese Palaeobotanical Association. (In Chinese.)

——— 1992*c* Studies on two Palaeozoic seeds from China. Acta Bot Sin 34:790–795, 2 pl. (In Chinese, with English abstract.)

McManus HA, EL Taylor, TN Taylor, JW Collinson 2002 A petrified *Glossopteris* flora from Collinson Ridge, central Transantarctic Mountains: Late Permian or Early Triassic? Rev Palaeobot Palynol 120:233–246.

Nishida H, KB Pigg, JF Rigby 2003 Swimming sperm in an extinct Gondwanan plant. Nature 422:396–397.

Oliver FW 1903 The ovules of older gymnosperms. Ann Bot 17: 451–476.

Phillips TL 1980 Stratigraphic and geographic occurrences of permineralized coal-swamp plants: Upper Carboniferous of North America and Europe. Pages 25–92 *in* DL Dilcher, TN Taylor, eds. Biostratigraphy of fossil plants: successional and palaeoecological analysis. Dowden, Hutchinson & Ross, Stroudsburg, PA.

Phillips TL, RA Peppers, WA DiMichele 1985 Stratigraphic and interregional changes in Pennsylvanian coal swamp vegetation: environmental inferences. Int J Coal Geol 5:43–109.

Retallack GJ, DL Dilcher 1988 Reconstructions of selected seed ferns. Ann Mo Bot Gard 75:1010–1057.

Rothwell GW 1971 Ontogeny of the Palaeozoic ovule, *Callospermarion pusillum*. Am J Bot 58:706–715.

——— 1980 The Callistophytaceae (Pteridosperma). II. Reproductive features. Palaeontographica Abt B Palaeophytol 173:85–106.

——— 1981 The Callistophytales (Pteridospermopsida): reproductively sophisticated Paleozoic gymnosperms. Rev Palaeobot Palynol 32: 103–121.

——— 1986 Classifying the earliest gymnosperms. Pages 137–162 *in* RA Spicer, BA Thomas, eds. Systematic and taxonomic approaches in palaeobotany. Clarendon, Oxford.

——— 1988 Cordaites. Pages 273–297 *in* CB Beck, ed. Origin and evolution of gymnosperms. Columbia University Press, New York.

Rothwell GW, R Serbet 1994 Lignophyte phylogeny and the evolution of spermatophytes: a numerical cladistic analysis. Syst Bot 19: 443–482.

Seward AC 1917 Fossil Plants. Vol 3. Pteridospermae, Cycadofilices, Cordaitales, Cycadophyta. Cambridge University Press, London.

Shao L, P Zhang, P Ren, J Lei 1998 Late Permian coal-bearing successions in southern China: coal accumulation on carbonate platforms. Int J Coal Geol 37:235–256.

Shen G 1995 Permian floras. Pages 127–223 *in* XX Li, ed. Fossil floras of China through the geological ages. Guangdong Science and Technology Press, Guangzhou, China.

Stewart WN, GW Rothwell 1993 Paleobotany and the evolution of plants. Cambridge University Press, Cambridge. 521 pp.

Stidd BM, K Cosentino 1976 *Nucellangium*: gametophytic structure and relationship to Cordaites. Bot Gaz 137:242–249.

Taylor TN, WN Stewart 1964 The Paleozoic seed *Mitrospermum* in American coal balls. Palaeontographica Abt B Palaeophytol 115: 51–58, pl 17–20.

Taylor TN, EL Taylor 1987 Structurally preserved fossil plants from Antarctica. III. Permian seeds. Am J Bot 74:904–913.

——— 1992 Reproductive biology of the Permian Glossopteridales and their suggested relationship to flowering plants. Proc Natl Acad Sci USA 89:11495–11497.

——— 1993 The biology and evolution of fossil plants. Prentice Hall, Upper Saddle River, NJ. 982 pp.

Tian B, SJ Wang, YT Guo, GR Chen, H Zhao 1996 Flora of Palaeozoic coal balls in China. Palaeobotanist 45:247–254.

Tian B, LW Zhang 1980 Fossil atlas of Wangjiazhai mine region in Suicheng, Guizhou. Coal Industry Press, Beijing. 110 pp, 51 pl. (In Chinese.)

Wang SJ 1998 The cordaitalean fossil plants from Cathaysian area in China. Acta Bot Sin 40:573–579. (In Chinese, with English abstract.)

Wang SJ, J Hilton, B Tian 2003*a* A new species of cardiocarpalean ovule from Early Permian coal balls from north China. Rev Palaeobot Palynol 123:303–319.

Wang SJ, J Hilton, B Tian, J Galtier 2003*b* Cordaitalean seed plants from the Early Permian Taiyuan Formation of North China. I. Delimitation and reconstruction of the whole-plant *Shanxioxylon sinense*. Int J Plant Sci 164:89–112.

Wang SJ, SS Li, J Hilton, J Galtier 2003*c* A new species of the sphenophyte stem *Arthropitys* from Late Permian volcaniclastic sediments of China. Rev Paleobot Palynol 126:65–81.

Yao ZQ, JT Xu, ZG Zheng, XH Zhao, ZG Mo 1980 On the biostratigraphy of the Permian and the boundary between the Permian and Triassic in western Guizhou-eastern Yunnan. Pages 1–69 *in* Nanjing Institute of Geology and Palaeontology, Academia Sinica, eds. Late Permian coal bearing strata and biota from western Guizhou and eastern Yunnan. Science, Beijing. (In Chinese.)

Zhao XH, ZG Mo, SZ Zhang, ZQ Yao 1980 Late Permian flora from western Guizhou and eastern Yunnan. Pages 70–122 *in* Nanjing Institute of Geology and Palaeontology, Academia Sinica, eds. Late Permian coal bearing strata and biota from western Guizhou and eastern Yunnan. Science, Beijing. (In Chinese.)