

NEW GLOSSOPTERID POLYSPERMS FROM THE PERMIAN LA GOLONDRINA FORMATION (SANTA CRUZ PROVINCE, ARGENTINA): POTENTIAL AFFINITIES AND BIOSTRATIGRAPHIC IMPLICATIONS

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ABSTRACT – Impression fossils of ovuliferous fructifications from the Permian La Golondrina Formation in Santa Cruz, Argentina, are described, their affinities compared, and finally, assigned to the Arberiaceae (Glossopteridales). Based on morphological differences from the genera in Arberiaceae, a new taxon is established for some specimens, whereas others are allocated to *Arberia madagascariensis* (Appert) Anderson & Anderson. This is the first record of Arberiaceae from the La Golondrina Basin. The biostratigraphic implications of the occurrence of this family in this unit are discussed, and suggest that more evidence other than that provided by the megafloreal elements is needed to resolve the age of the constituent members of the La Golondrina Formation.

Key words: Arberiaceae, Argentina, biostratigraphy, fructifications, Glossopteridales, Gondwana.

RESUMO – São descritos impressões fósseis de frutificações femininas provenientes da Formação La Golondrina, Permiano de Santa Cruz (Argentina), atribuídas a Arberiaceae (Glossopteridales), segundo a comparação de suas afinidades. Com base nas diferenças morfológicas dos gêneros da Família Arberiaceae, um novo táxon é proposto, enquanto as outras amostras são alocadas em *Arberia madagascariensis* (Appert) Anderson & Anderson. Este é o primeiro registro de Arberiaceae na bacia do La Golondrina. As implicações bioestratigráficas fornecidas pela presença deste grupo, nesta unidade, são discutidas e sugere-se que mais provas, além das fornecidas pelos elementos megaflorísticos, são necessárias para restringir os limites de idade do membro da Formação La Golondrina.

Palavras-chave: Arberiaceae, Argentina, bioestratigrafia, frutificações, Glossopteridales, Gondwana.

INTRODUCTION

During the second half of the last century and in recent years, a large number of interesting fructifications from the *Glossopteris* floras across Gondwana has come to light, revealing varied morphologies that imply great diversity amongst glossopterids and their associates. Key studies include those from India (Surange & Chandra, 1975; Banerjee, 1984; Bajpai, 2001; Tewari *et al.*, 2012; Srivastava & Agnihotri, 2013), Australia (Holmes, 1974; Rigby, 1972, 1978; McLoughlin, 1990a,b, 1995, 2012a,b), South Africa (Anderson & Anderson, 1985; Adendorff *et al.*, 2002; Prevec *et al.*, 2008; Prevec, 2011), Antarctica (Ryberg *et al.*, 2012), and South America (Menéndez, 1962; Bernardes de Oliveira & Carvalho, 1981; Bernardes de Oliveira *et al.*, 2000; Rösler *et al.*, 1994; Barreda & Césari, 1995; Iannuzzi, 2010).

The taphoflora from the La Golondrina Formation (Santa Cruz Province, Argentina) is acknowledged as one of the most diverse Permian floras from South America. Fertile remains of glossopterids and sphenopsids and some plants of unknown affinities (Archangelsky, 1960, 1992; Archangelsky & Bonetti, 1963; Cariglino *et al.*, 2009; Cariglino, 2013; Carrizo & Archangelsky, 2013) have enhanced understanding of the

floristic diversity of the region. Despite the recent discoveries, fertile parts of other plant groups, for example lycopsids and cordaitaleans, have remained elusive in this unit.

This paper aims to describe three fructifications hitherto unknown from the La Golondrina Formation. Based on their general structure, the fructifications are compared with those of the Cordaitanthales (*Cordaitanthus*), Peltaspermales (*Autunia*), and Glossopteridales (*Arberia*, *Rigbya*), and their systematic position is clarified. Last, the biostratigraphic implications of these discoveries are also analyzed.

MATERIAL AND METHODS

The fossil specimens were recovered from the middle member of the La Golondrina Formation (Laguna Polina Member), at the Laguna Polina locality (La Golondrina Basin), Santa Cruz Province, Argentina (Figure 1). Stratigraphic and sedimentological descriptions of the area were detailed previously (Jalín, 1987, 1990; Panza, 1994; Archangelsky *et al.*, 1996a,b; Archangelsky, 2006; Gutiérrez *et al.*, 2006), whereas several other works have documented the floral composition in all three members of this unit (Archangelsky, 1959; Arrondo, 1972; Cariglino, 2011, among others).

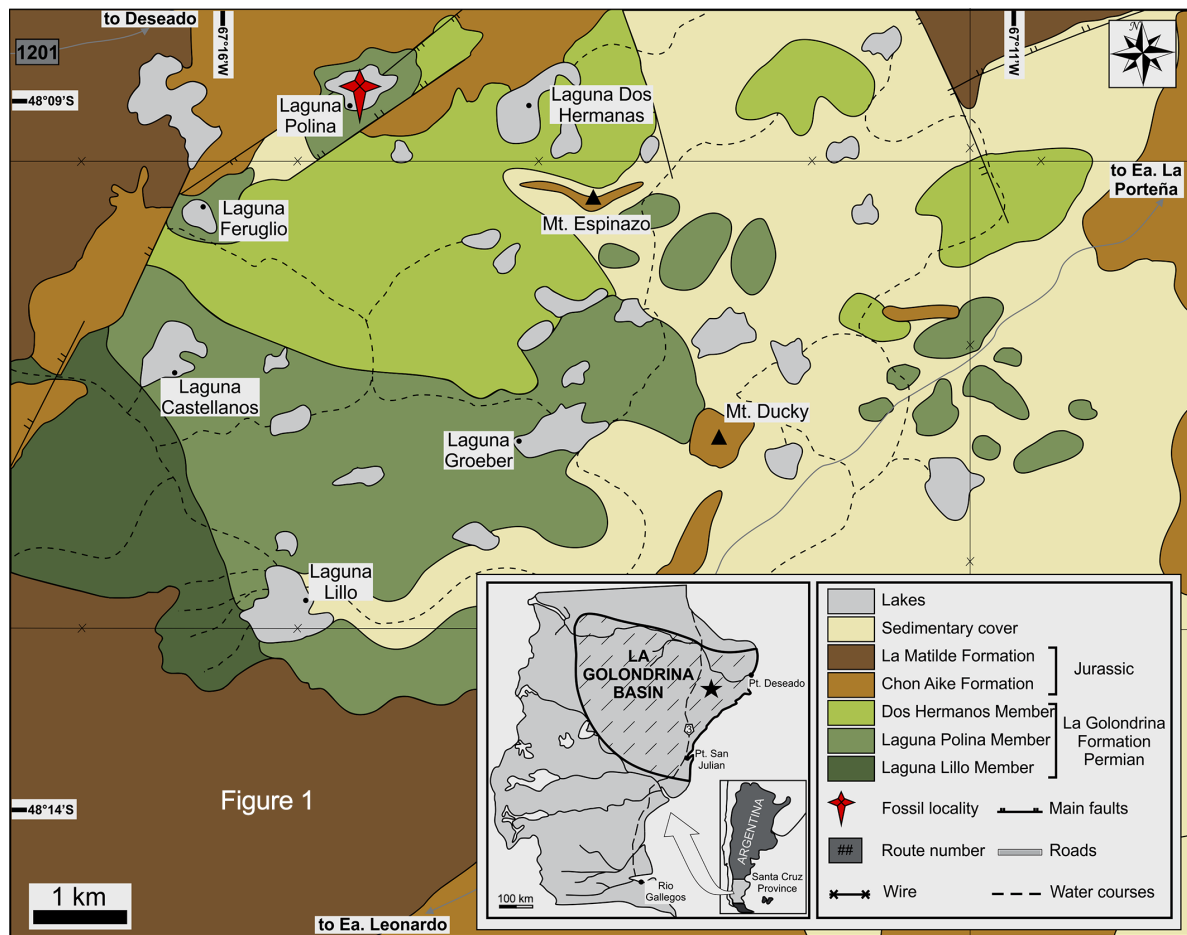


Figure 1. Geological map of the area from where the fossils were recovered.

The specimens described here consist of regular to well-preserved, in some cases fragmented impressions lacking their counterparts; consequently, neither detailed studies of their anatomy or cuticular analyses were possible. Specimens LIL Pb 1975 and LIL Pb 1381 were collected from the Laguna Polina Member by Dr. S. Archangelsky in 1957, and generously ceded to the author for this study. Specimen MPM Pb 4856 on the other hand, was collected on a field trip in 2010 from the same fossiliferous unit by the author. Abundant glossopterids (*Gangamopteris* spp., *Glossopteris* spp.), ferns (*Asterotheca* spp., *Dizeugotheca* spp., *Dichotomopteris* spp., *Damudopteris* sp.), sphenophytes (*Sphenophyllum* spp., *Annularia* sp., *Phyllotheca* sp.) and various other fructifications (*Dictyopteridium* spp., *Plumsteadia* spp., *Eretmonia* sp., ?*Senothea* sp., cf. *Lilpopia* sp.), in addition to other less common elements (*Cordaites* sp, lycophytes, and coniferophytes), are also contained in the Laguna Polina Member (Archangelsky, 1959; Cariglino, 2011, 2013). On the basis of the assemblage in all three members, the La Golondrina Formation is considered to range in age from the latest Cisuralian (Laguna Lillo Member), the Guadalupian (Laguna Polina Member), to the Lopingian (Dos Hermanos Member).

The material was photographed using a Canon Powershot S5IS (8.0 megapixel) digital camera. For detailed analysis

and illustration, specimens were photographed under strong unilateral light at different angles to enhance their surface relief using a Nikon DS-Fi1-U2 digital camera attached to a Nikon SMZ800 stereomicroscope. Measurement of specimens was done with a vernier caliper and using the scale tool in Adobe Photoshop CS3 on digital images. Images were only corrected for contrast.

Fossils under the prefix **LIL Pb** are housed at the Fundación Lillo paleobotany collection in Tucumán Province, whereas those with the **MPM Pb** prefix belong to the Museo Regional Provincial "Padre Jesús Molina" paleobotany collection, in Santa Cruz province.

SYSTEMATIC PALAEOBOTANY

Order GLOSSOPTERIDALES Pant, 1982

Family ARBERIACEAE Rigby, 1972

Golondrinia gen. nov.

Type species. *Golondrinia archangelskyi* sp. nov.; monotypic.

Stratigraphic and geographic range. Guadalupian?-Lopingian of the La Golondrina Formation (Laguna Polina Member), Santa Cruz Province, Argentina.

Etymology. In reference to the name of the estancia hosting the fossil localities (La Golondrina; also name of the basin and geological formation).

Generic diagnosis. Ovuliferous fructifications with a pinnate branching pattern comprising a primary axis bearing two lateral rows of opposite to sub-opposite pairs of branchlets at 90° to the main axis. Main axis robust, stalked, and longitudinally striated. Branchlets short, stalked, finely striated, and expanded distally, ending as a flabelliform scale-like or cup-shaped structure. Ovule scars located on the fertile surface of the scales.

Golondrinia archangelskyi sp. nov.
(Figures 2A-G, 3, 4A-C)

Holotype. LIL Pb 1975 (Figures 2A-G, 3).

Paratype. MPM Pb 4856 (Figures 4A-C).

Type locality. Laguna Polina, Estancia La Golondrina, Santa Cruz Province, Argentina.

Type horizon. Laguna Polina Member.

Etymology. Dedicated to the Argentinian paleobotanist Dr. Sergio Archangelsky, for his pioneering work at the La Golondrina Formation.

Species diagnosis. Polysperm stalked, with a robust primary axis at least 85 mm long and 4.5 mm wide. Main axis with thick longitudinal striate. Lateral branching is pinnate. Branchlets are short (<5 mm), and finely striated; they attach to the main axis at about 90° by a short stalk, and expand distally as a flabelliform scale-like feature that sometimes takes the shape of a cup. Scale features bifacial, with a single ovule attachment on the fertile surface and a striate sterile surface.

Description. The *Golondrinia archangelskyi* gen. et sp. nov. holotype (LIL Pb 1975; Figures 2A-G) is a well-preserved impression of an ovuliferous fructification. Its primary axis is ~85 mm long (top is missing) and varies in thickness from 4.7 mm at the base to 2.0 mm at the top; although the broad basal part may represent a preservational artifact. The axis is longitudinally striate, with a maximum width, taking into account the lateral branchlets, of ~8.0 mm. More than 16 pairs (in some cases unpaired due to preservational issues) of

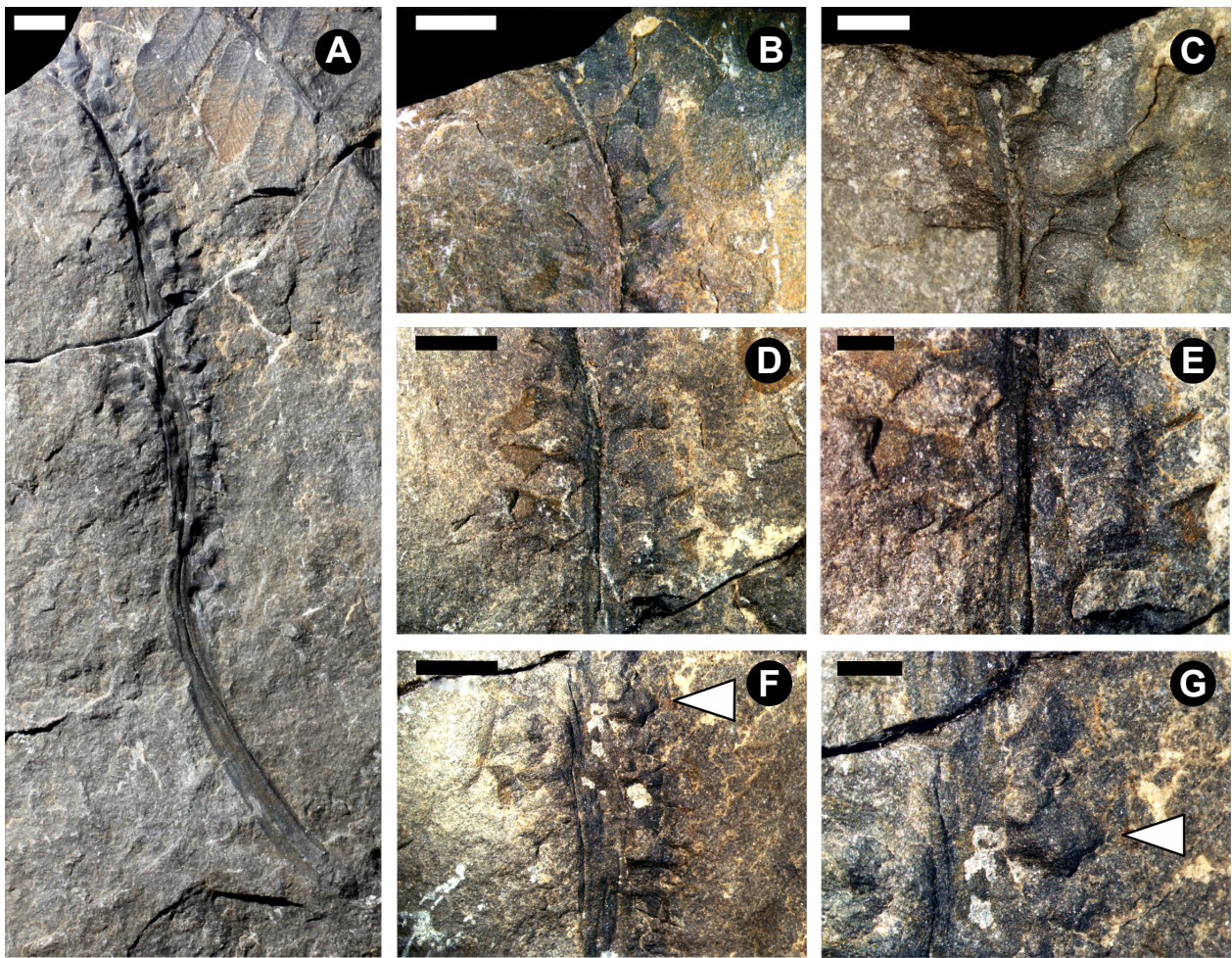


Figure 2. Holotype of *Golondrinia archangelskyi* gen. et sp. nov. (LIL Pb 1975), recovered from the Laguna Polina Member, La Golondrina Formation, Permian of Santa Cruz, Argentina. **A**, preserved specimen; note stalked base; **B-C**, upper part of specimen, showing longitudinal striation of the main axis and finely striated fertile branchlets; **D-E**, middle part of specimen, showing different morphologies of fertile branchlets, sometimes ending in a scale-like structure, in other cases, as a cup-shaped feature; **F-G**, basal part of specimen, showing striated axis, fertile branchlets, and potential terminal ovule (arrow).

striated branchlets are present, separated from each other by 2.0-2.2 mm. Branchlets range from 4.3 to 4.9 mm long, and expand terminally, in some cases as a flabelliform feature, in other cases as an apparent cup-shaped structure (Figures 2D-E). Ovules were not seen directly, but could be inferred in some cases based on the rounded imprint (seed scar) on the fertile surface of the scales in some of the branchlets (Figures 2F-G; arrow).

The paratype (MPM Pb 4856; Figures 4A-C) is regularly preserved and less complete than LIL Pb 1975. The main axis is robust, at least 44 mm long (fragmented at the base and top) and 3.4 mm thick, reaching up to 10.1 mm when including a pair of branchlets. Axis is densely striate longitudinally (Figure 4A). More than 10 pairs of branchlets are present, each separated by 2.0 mm, except at the apex, where they appear clustered (preservational artifact?) (Figure 4B). Branchlets are finely striated, with flabellate termini. Although questionable, faint imprints of solitary oval ovule scars ~2.65 mm long and 1.6 mm wide are located on the surface of the scales in some branchlets on the lower right side of the main axis (Figure 4C; arrows).

Remarks. The features present in *Golondrinia archangelskyi* gen. et sp. nov. seem to combine a mixture of characters represented in Rigbyaceae and Arberiaceae. As previously mentioned, these specimens have an unbranched axis bearing two lateral rows of fertile branchlets. The axis is longitudinally striate, relatively long (>40 mm) and varies in thickness, slightly attenuating at the top. All these characteristics relate these specimens with Arberiaceae. On the other hand, the holotype of *Golondrinia* is basally complete (Figure 2A), showing that these fructifications were stalked, a character shared with both Rigbyaceae and Arberiaceae. Both studied specimens (LIL Pb 1975 and MPM Pb 4856) are referred to the same species based on the presence of an unbranched striated axis, and the two lateral rows of opposite to sub-opposite

branchlets comprising a short, striated and in some cases, slightly expanded base, ending in a flabelliform, scale-like structure that is also longitudinally striate.

Arberia White, 1908

Type species. *Arberia minasica* White, 1908 emend. Rigby, 1972

Arberia madagascariensis (Appert)
Anderson & Anderson, 1985
(Figures 5A-E)

Specimen number. LIL Pb 1381.

Stratigraphic and geographic range. Early Permian, Gondwana.

Description. Two similar, well-preserved impressions of fructifications are adjacent to each other, partially overlapping, but with no obvious organic connection between them or with the underlying *Glossopteris retifera* Feistmantel leaf (Figure 5A). One of the fructifications is ~35 mm long (incomplete at the top) and 10 mm wide (maximum width); the other – upside-down in reference to the former – is 22 mm long and 7 mm wide (the base and apex are lacking). The primary axis is laminar and longitudinally striated; it expands slightly towards the apex and tapers to the base. Forking of the main axis is not evident from the preserved parts. The branching is pinnate; branches arise at varying degrees from the margins (30° to >90°), and are separated by 1.52-[2.41]-3.72 mm (more separated in the basal section, N=7) from each other. The lateral branches are 3.56-[4.46]-5.4 mm long and ~2.0 mm wide (N=6), and bear a conspicuous striae. These branches do not fork, and terminate in a simple scale-like expansion (Figures 5B-E). A small (1.76 mm long and 1.12 mm wide) platyspermic ovate seed with a narrow wing is closely associated with the base of one of the lateral branches in one of the specimens, and potentially pertains to the described polysperms (Figure 5D, arrow).

Remarks. The two polysperms in LIL Pb 1381 differ from *Golondrinia archangelskyi* gen. et sp. nov. by possessing flattened main axes that taper basally. Nevertheless, they share the longitudinal striation and the presence of two lateral rows of fertile branchlets, arising at varying degrees from the axis. Branchlets are also striated, and end in a simple scale-like expansion, as is the case in *Golondrinia* specimens. Ovule scars, and even a closely associated (if not in direct organic connection with) platyspermic seed, are observed at the base of some of the branchlets, adding stronger support for an affinity of LIL Pb 1381 with Arberiaceae (although platyspermic seeds are also associated with Rigbyaceae, see Schopf, 1976).

DISCUSSION

Potential affinities

Fructifications with a basic structural organization consisting of a main axis bearing two or more rows of fertile structures have evolved independently in several plant

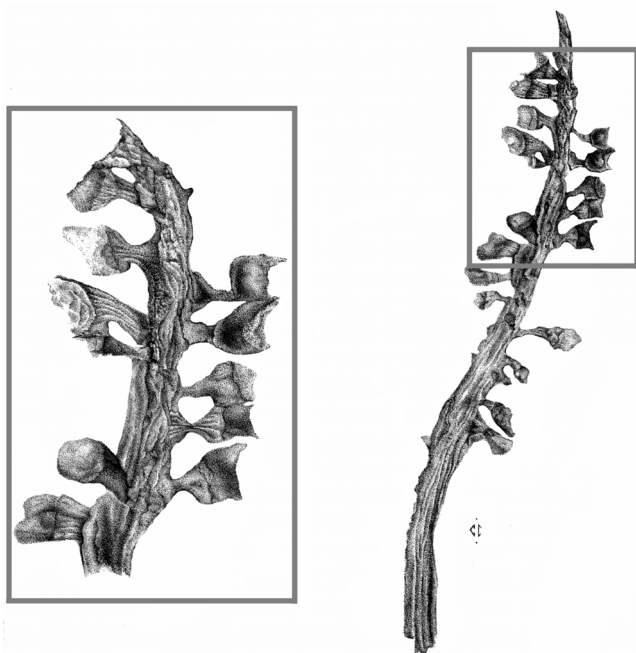


Figure 3. Hand illustration of *Golondrinia archangelskyi* gen. et sp. nov. holotype (LIL Pb 1975). Credits: Carmen Castellano.

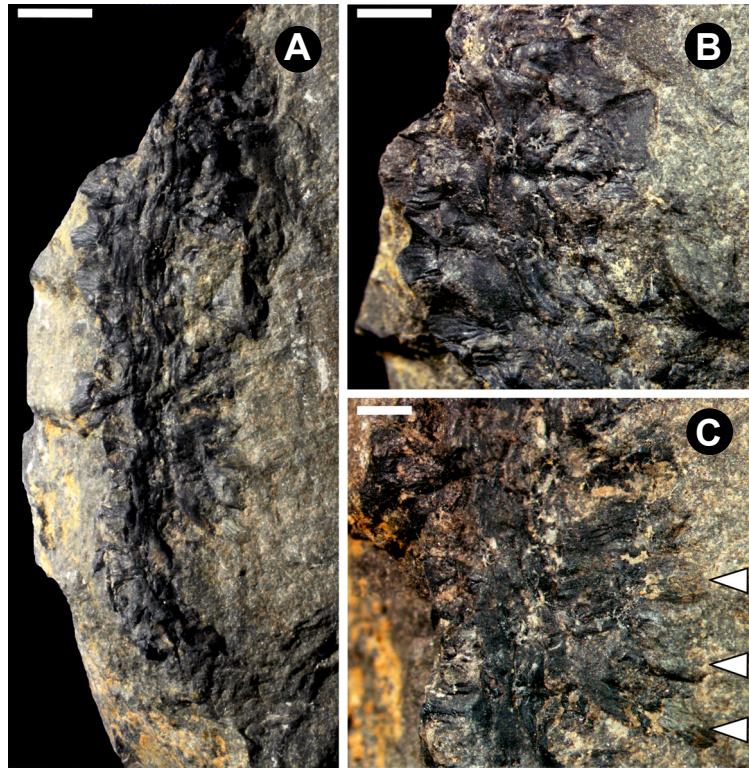


Figure 4. Paratype of *Golondrina archangelskyi* gen. et sp. nov. (MPM Pb 4856) recovered from the Laguna Polina Member, La Golondrina Formation, Permian of Santa Cruz, Argentina. **A**, preserved specimen; **B**, upper part of specimen, showing the finely striated branchlets ending in a scale-like structure; **C**, middle part of specimen, showing longitudinal striation of main axis and fertile branchlets with potential terminal ovules (arrows).

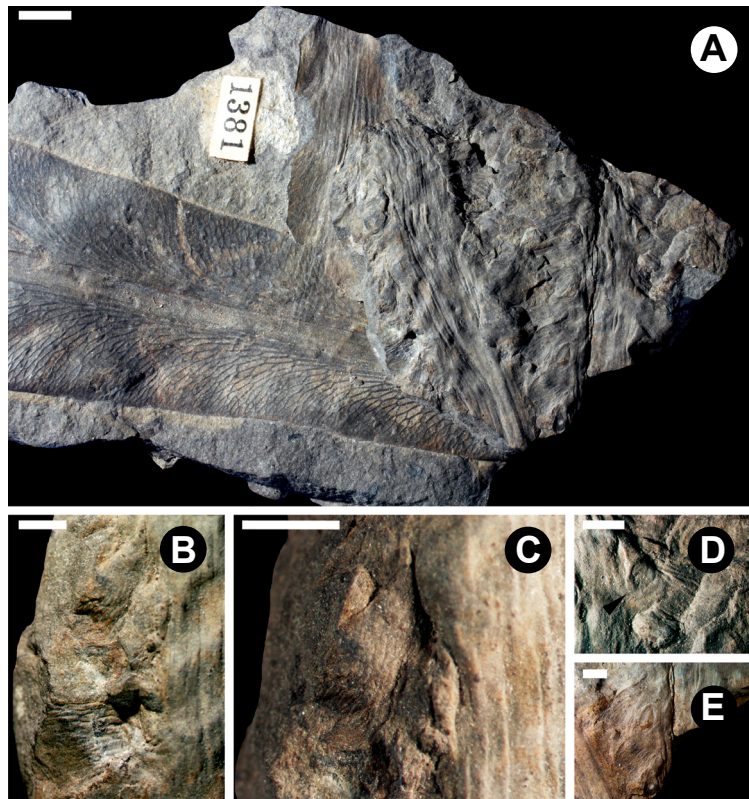


Figure 5. *Arberia madagascariensis* (LIL Pb 1381) recovered from the Laguna Polina Member, La Golondrina Formation, Permian of Santa Cruz, Argentina. **A**, two preserved specimens; the one on the right is upside-down; **B**, fertile branchlets, one showing ovule/seed scar at the base of the scale-like feature; **C**, fine striation of fertile branchlet; **D**, detail of fertile branchlet with platyspermic seed (arrow); **E**, flabelliform, scale-like ends and striation of fertile branchlets.

lineages. There is a wide variety of female reproductive structures that repeat this general morphology, and have been described using generic terms such as “cupules”, “capsules”, “cones”, “megasporophylls” and “strobili”. Although these terms do not necessarily imply homologies between the different forms, all are characterized by being used to describe ovule/seed-bearing structures. Some of the morphological characters exhibited in the fructifications from the La Golondrina are shared with plant taxa from the Cordaitanthales (Meyen, 1984), Peltaspermales (Delevoryas, 1979), and Glossopteridales (Pant, 1982). A discussion of the similarities and differences among them, and the potential affinities of the new material is given below. In order to narrow the comparisons, primary focus was placed on late Paleozoic floras, in particular with those that share elements with the paleoflora of the La Golondrina Formation.

Cordaitanthus-type fructifications from Gondwana were unknown until recently, when Césari & Hünicken (2013) described fructifications associated with *Cordaites bifolius*, and assigned them to *Cordaitanthus* sp. 1 and 2. All other known *Cordaitanthus* species are from Carboniferous and Permian floras of the Northern Hemisphere (Feistmantel, 1876; Grand'Eury, 1877; Florin, 1951; Meyen, 1984; Rothwell, 1977, 1982, among many others). Meyen (1984) and Ignatiev & Meyen (1989) pointed out the problematic use of *Cordaitanthus* as a genus, given it comprised both male and ovuliferous fructifications, disregarding differences in preservational types and quality. Among the many characters that were used by different authors to describe ovuliferous *Cordaitanthus*, it is possible to find various interpretations of these fructifications, including descriptions as a long, unbranched primary axis, bearing two lateral rows of opposite to alternate seeds either in the axils of bracts (*i.e.* Grand'Eury, 1877), on short pedicels composed by two or more sterile scales (Florin, 1951), or even sessile on the axis (Lesquereux, 1880), pointing out the problematic nature (or at least uncertain diagnostic limits) of this genus. At first impression, the presence of an unbranched primary axis, bearing two lateral rows of branchlets (= “secondary shoots”) may fit under the wide definition of ovuliferous *Cordaitanthus*, especially if the branchlets in *Golondrinia archangelskyi* gen. et sp. nov. are considered as some sort of bract-axillary complex, since some of the cup-shaped termini on specimen LIL Pb 1975 could be interpreted as ovuliferous and subtending bracts (Figures 2D-E). Recently, a new taxonomic approach has been taken to define *Cordaitanthus* as a genus, including only compressions/impressions of either male or female lax cones, composed of a primary axis (cone axis), bearing distichous bracts and, in the axil of each bract, a secondary shoot with helically arranged scales that carry distally attached ovules or pollen cones (Ignatiev & Meyen, 1989; Taylor *et al.*, 2009). Thus, upon closer inspection, the gross similarities with the La Golondrina specimens disappear; even if there is a main axis with “secondary fertile shoots”, these do not bear bracts or cones that reveal any affinity with the Cordaitanthales.

Golondrinia archangelskyi gen. et sp. nov. is also comparable to Permian peltasperms described from China and Russia (Wang, 1997; Naugolnykh & Oskolski, 2010). The *Autunia shanxiensis* Wang specimens illustrated from the Permian of China (Wang, 1997, text-figs. 8a-c and e, text-figs. 9a-d) share certain resemblance in their overall morphology: a main striated axis with “megasporophylls” attached at right angles by a slender petiole, terminally ending in a broadly flabelliform head. However, from the species diagnosis, important differences arise: the megasporophylls are spirally attached to the main axis, forming a lax cone, and they are composed of a semi-rounded head with two or more flattened ovules of the *Carpolithus*-type (Kerp, 1988; Wang, 1997; Geng & Hilton, 1999). Similar features are evident in the *Peltaspermum* species illustrated by Naugolnykh & Oskolski (2010, figs. 1a,c), where they depict two impression fossils of fructifications comprising a main axis bearing two lateral rows of “racemose aggregation of seed-bearing discs” (Naugolnykh & Oskolski, 2010, p. 30). The basic arrangement of these polysperms shows some features in common with the specimens from the La Golondrina Formation; however, *Peltaspermum* species are characterized by the presence of peltate discs attached to a main axis, whereas there are no peltate discs in the La Golondrina specimens.

Two ovuliferous fructifications of glossopteridean affinity from India and Africa share similar morphological features with *Golondrinia archangelskyi* gen. et sp. nov. *Khania dhenkanalensis* Chandra & Singh is an ovuliferous fructification consisting of an unbranched, slender main axis, bearing two opposite rows of small stalks carrying seeds marked with vertical grooves (Chandra & Singh, 1988), being the main difference with the specimen from the La Golondrina Formation the absence of a scale-like feature at the end of the branchlets. *Wankiea bondii* Lacey & Huard-Moine is described as a seed-bearing fructification with a longitudinally striated main axis bearing two orders of pinnately arranged branches, the ultimate order of branches forming clusters of 4-6 branchlets bearing ovate seed-like bodies. Although Lacey & Huard-Moine (1966) indicated that the seed attachment was unclear, they suggested that seeds were possibly borne on a peltate expansion or a scale-like extension. *Golondrinia archangelskyi* gen. et sp. nov. shares with *Wankiea bondii* the basic arrangement of a main axis with pinnate branching and the seed attachment on a scale-like feature, although they differ in that in the former, there is only one order of branching.

All three fructifications described in this paper share most features with those of the Glossopteridales. More specifically, strong similarities are evident with fructifications from Arberiaceae and Rigbyaceae. Rigbyaceae polysperms have, in most cases, a long, slender stalk with short, dichotomous branchlets arranged into a flabellate lamina with varying degrees of fusion. Each branchlet bears a single ovule/seed, and ends in a scale-like structure that is longitudinally striate (Adendorff, 2005). Arberiaceae, on the other hand, have polysperms with a main axis, that may be unbranched or branched several times; the last order of branches bearing a single ovule/seed, and terminating in a distal scale-like

structure, similar to those of Rigbyaceae (Rigby, 1972; Adendorff, 2005), but Arberiaceae polysperms do not have a fan-shaped primary axis. Taking into account the general architecture discussed above, both forms are attributed to Arberiaceae.

Golondrinia archangelskyi gen. et sp. nov. presents characteristics that fit well under the Family Arberiaceae (*sensu* Rigby, 1972, and as proposed to be emended by Adendorff, 2005), as it is an ovuliferous fructification comprising a longitudinally striated main axis with two lateral rows of fertile branchlets ending in an expanded scale-like structure. The creation of a new genus and species is justified by the morphological differences the specimens from the La Golondrina reveal with the four known architectural groupings attributed to Arberiaceae, viz., *Arberia* White emend. Rigby, 1972, *Dolianitia* Millan, 1967, '*Arberia*' *leeukuilensis* Anderson & Anderson, 1985 and *Arberiopsis* Bernardes de Oliveira, 1978 (Table 1). *Dolianitia* and *Arberia* are polysperms with a planar primary axis that is usually dichotomously branched, in some cases in multiple planes, characterized by "stocky striate pleiochasial axes with short ultimate branchlets bearing relatively large ovules" (Millan, 1967; McLoughlin, 1995, p. 183). The close similarities

between *Dolianitia* and *Arberia* led several authors to consider them synonymous (Rigby, 1972; Banerjee, 1984; Anderson & Anderson, 1985; McLoughlin, 1993, 1995). '*Arberia*' *leeukuilensis* on the other hand, has a planated axis without dichotomies, bearing two opposite rows of ovuliferous, short, unspecialized branchlets "with rounded, pendulous, slightly expanded and strongly recurved termini" (see Adendorff, 2005, unpubl.). Thus, both '*Arberia*' *leeukuilensis* and *Golondrinia* lack the dichotomous branching typical of *Arberia* and *Dolianitia* species. In addition, '*Arberia*' *leeukuilensis* shares with *Golondrinia* a pinnate branching pattern on an undivided axis, but they differ in that the former has an axis that is planated and oblanceolate to narrowly elliptical, whereas in *Golondrinia* it is more akin to a slender axis. They also differ in that the fertile branchlets in '*Arberia*' *leeukuilensis* are rounded, slightly expanded, and distally recurved, whereas in *Golondrinia archangelskyi* they have a short, striate base that expands distally, normally as a flabelliform feature. Although in neither of these genera the ovules were found attached, it is more likely these were borne on the fertile surface of the scale-like feature in *Golondrinia*, as inferred from the faint imprints of the ovule seed scars. Last, *Arberiopsis* is characterized by a slender rachis that

Table 1. Main morphological features and distribution of Arberiaceae taxa. **1**, this work; **2**, Maithy (1970); **3**, Rigby (1972); **4**, Chandra & Srivastava (1981); **5**, Surange & Lele (1956); **6**, McLoughlin (1995); **7**, Adendorff (2005); **8**, Anderson & Anderson (1985); **9**, Bernardes de Oliveira (1978). **Abbreviations:** EPm, Early Permian; MPm, Middle Permian.

Taxon	Rachis/branching morphology	Ovule placement	Formation (Locality)	Age	Refs.
<i>Golondrinia archangelskyi</i> gen. et sp. nov.	Undivided main axis, pinnate branching, branchlets straight	Ovules attached at the end of each branchlet	La Golondrina Fm. (Argentina)	Late EPm (?) -MPm	1
<i>Dolianitia (Arberia) kaharbariensis</i> Maithy	Striated main axis, multi-dichotomous irregular branching	unknown	Karharbari Fm. (India)	EPm	2
<i>Arberia minasica</i> White emend. Rigby	Thick striated rachis, pinnate or dichotomous branching, very variable	Ovules inserted on expanded cushions	Rio Bonito Fm. (Brazil), Arroyo Totoral Fm. (Argentina)	EPm	3
<i>Arberia indica</i> Feistmantel	Flattened main rachis, pinnate branching	Ovules on flattened tips	Karharbari Fm. (India)	EPm	4
<i>Arberia surangei</i> Chandra & Srivastava	Flattened main rachis, dichotomous branching	Ovules attached on the apex of each branchlet	Karharbari Fm. (India)	EPm	4
<i>Arberia umbellata</i> Surange & Lele	Flattened main rachis, dichotomous branching	Ovules attached on recurved branches	Talchir Fm. (India)	EPm	5
<i>Arberia woolagaensis</i> McLoughlin	Flattened, striated main rachis, tappers basally, unbranched	Ovules sessile or inserted on short stalks along the margin of rachis	Irwin River Coal Measures (Australia)	EPm	6
<i>Arberia hlobanensis</i> Anderson & Anderson emend. Adendorff	Main axis with single major dichotomy, branching in multiple planes	1-2 ovule attachments at the base of the scale-like feature	Vryheid Fm. (South Africa)	EPm	7, 8
<i>Arberia madagascariensis</i> (Appert) emend. Adendorff	Flattened, striated main rachis, pinnate branching	Ovules attachment at the base of the scale-like feature	Madagascar, South Africa, La Golondrina Fm. (Argentina)	EPm/ Late EPm (?) -MPm	1,7
' <i>Arberia</i> ' <i>leeukuilensis</i> And. & And. (see Adendorff, 2005)	Flattened, striated main rachis, pinnate branching with recurved branchlets	Rounded, barely expanded seed attachment points	Vryheid Fm. (South Africa)	EPm	7,8
<i>Arberiopsis boureaui</i> Bernardes de Oliveira	Flattened, striated main axis, with slightly anistomous branching in a plane	Ovules attached terminally to last order branches	Rio Bonito Fm (Brazil)	EPm	9

dichotomizes various times in a slightly anistomous way, the branches of the last order bearing anatropous ovules. The primary difference with *Golondrina* is, once again, that the main axis in the latter is not dichotomized.

Both specimens preserved on LIL Pb 1381 are assigned to *Arberia madagascariensis* since they exhibit many of the diagnostic characters of the species. On contrary to the specimens described as *Golondrina archangelskyi* gen. et sp. nov., the ovules (as indicated by the seed scars) in *A. madagascariensis* are placed at the base of the scales (Figures 5B, D).

The detailed description of *Arberia madagascariensis* provided by Adendorff (2005) and mostly based on the material from Madagascar originally described by Appert (1977), shares almost every qualitative feature with the specimens in LIL Pb 1381. The thorough emended generic and species diagnosis provided by Adendorff (2005) however, mentioned that the main axes are “commonly” bifurcated at the apex. Given that the specimens from the La Golondrina Formation (as well as the Madagascan examples) are apically incomplete, it is not possible to assess this feature. Nevertheless, it is important to point out that some *Arberia* species lack of an apical dichotomy (*A. surangei*, Chandra & Srivastava, 1981), thus the possibility of these specimens not having a dichotomized main axis is feasible; although I consider it unlikely, since all the most complete *Arberia madagascariensis* specimens found (South Africa) exhibit an apical bifurcation. Also, the South African and Madagascan specimens described by Adendorff (2005) are comparatively larger than the specimens from the La Golondrina. The presence of a platyspermic seed organically attached and figured in one of Appert’s (1977) specimens is also seen in one of the two fructifications on LIL Pb 1381, where a seed is closely associated (or in direct contact) with the base of one lateral branchlet (Figure 4D); however, they differ in size, the latter being smaller. These differences in size could be explained as distinct growth stages; perhaps the La Golondrina specimens represent a less mature stage. Or the environmental conditions in which these plants grew were different, causing reduced growth. Regardless these few differences from the South African and Madagascan forms, the features of the specimens in LIL Pb 1381 allow the confident allocation to *A. madagascariensis*.

Thus far, *Arberia madagascariensis* has been found only in Madagascar and South Africa. The new records extend the range of this species to South America. Other *Arberia* species are known from India, South Africa, Australia, Brazil and Argentina (Table 1). *Arberia minasica* (White) emend. Rigby, 1972, and *Dolianitia* (= *Arberia*) *karharbarensis* Pant & Nautiyal, 1965 differ from *A. madagascariensis* in their multi-dichotomous branching. *Arberia umbellata* Surange & Lele, 1956, and *A. surangei* Chandra & Srivastava, 1981 differ from *A. madagascariensis* in having a more widespread apical region from which fertile branches dichotomize one or more times. The obovate primary axis in *Arberia surangei*, however, does not show the typical apical dichotomy, similar to that observed in LIL Pb 1381 specimens. *Arberia indica* (White)

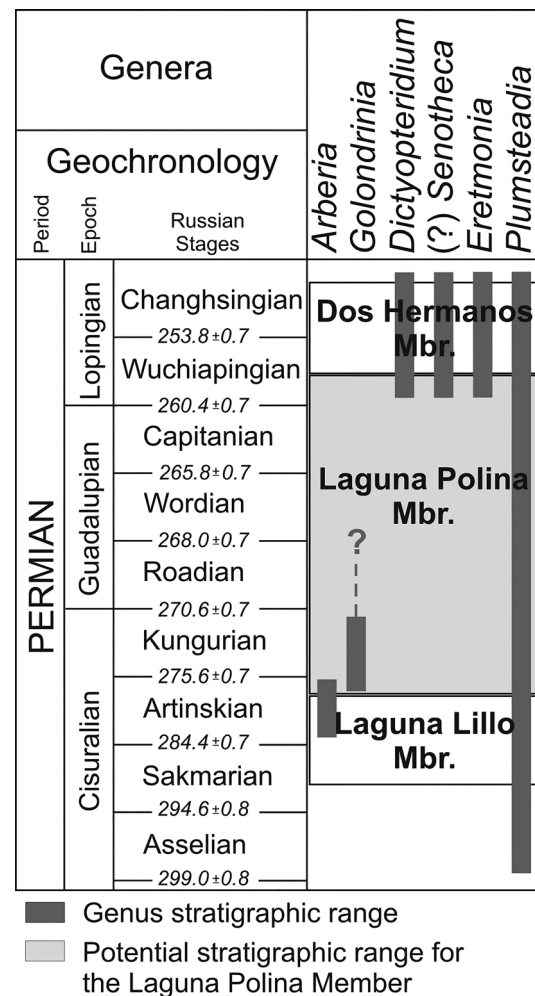


Figure 6. Biostratigraphic ranges of glossopterid ovuliferous genera recovered from the Laguna Polina Member (La Golondrina Formation).

ex Chandra & Srivastava and *A. woolagaensis* McLoughlin, 1995 are different from *A. madagascariensis* in that they bear medium to large seeds sessile or inserted in short stalks (strongly recurved in *A. indica*) along the margins of the planate axis. These two species are, however, most closely comparable to the polysperms in LIL Pb 1381 in their striate, planate main axis without a prominent apical dichotomy, bearing two lateral rows of fertile branchlets. Last, *Arberia hlobanensis* Anderson & Anderson consists of a polysperm with multidimensional branching, distinguishing it from all other *Arberia* species.

Biostratigraphic implications

The biostratigraphic scheme for the La Golondrina Formation has remained unmodified since the original proposal by Archangelsky & Cúneo (1984). According to these authors, the La Golondrina Formation spans the late Cisuralian to the Lopingian. Paleofloristic elements from the lower Laguna Lillo Member were at that time unknown, but recently recovered fossil plants (currently under study), re-confirms an early Permian age for the lower portion of the La Golondrina Formation. On the other hand, the paleoflora

recovered from the Laguna Polina Member has been studied in detail, as outcrops are widely represented in the basin and the lithology is finer, allowing better preservation of the plants. Thus, the majority of the materials collected to date – including those described here – come from this member. Unfortunately, even after the recent discovery of glossopterid fructifications, such as *Dictyopteridium* spp., *Eretmonia* sp. and ?*Senothecca* sp., considered to be useful biostratigraphic indices (Cariglino, 2013), narrowing the age of each member of the La Golondrina Formation based solely on paleofloristic assemblages has proven inconsistent. Thus, the age of the Laguna Polina Member is still broadly defined, as ranging from the Guadalupian to early Lopingian (Archangelsky & Cúneo, 1984; Archangelsky *et al.*, 1996a,b; Andreis & Archangelsky, 1996; Andreis, 2002; Cariglino *et al.*, 2012; Cariglino, 2013) (Figure 6).

The biostratigraphic occurrence of all known Arberiaceae is restricted to the Cisuralian (Artinskian) at all Gondwanan localities (Table 1). In Argentina, *Arberia* is so far only recorded at Sierra de los Llanos in Paganzo Basin (*Arberia* cf. *A. minasica*; Archangelsky & Arrondo, 1973), and the Tepuel Genoa Basin (*Arberia* sp.; Gallego *et al.*, 2008). In this context, the presence of *Arberia* and another new taxon attributed to Arberiaceae in the Laguna Polina Member raises the question about the lower temporal range of this unit. Two possibilities are proposed to explain this dilemma: (i) the stratigraphic range of Arberiaceae should be extended to the middle Permian, or (ii) the lower boundary of the Laguna Polina Member of the La Golondrina Formation should be extended to the upper Cisuralian.

Taking into account that all *Arberia* and related taxa have been found throughout Gondwana in lower Permian strata, the most parsimonious interpretation is to extend the lower limit of the middle member of the La Golondrina Formation to the upper Cisuralian (Figure 6). Moreover, it is noteworthy that “*Arberia allweyensis*” Anderson & Anderson, a poorly preserved singleton, was recovered from the Lawley locality in South Africa, considered Guadalupian in age. However, the recent revision and interpretation of this specimen (see Adendorff, 2005; Shi *et al.*, 2010) places it under *Rigbya*, a genus commonly used as biostratigraphic index for the Guadalupian-Lopingian.

CONCLUSIONS

This study recognized two taxa attributed to Arberiaceae from the La Golondrina Formation; one is assigned to a new taxon, *Golondrinia archangelskyi* gen. et sp. nov., whereas the other is allocated to *Arberia madagascariensis*. The general structure of *G. archangelskyi* gen. et sp. nov. is somewhat similar to that of some Cordaitanthales and Peltaspermales; however, the undeniable presence of fertile branchlets with terminal scale-like structures in all three specimens was diagnostic for its assignment to Arberiaceae. Moreover, the basic morphologic features (*i.e.* non-dichotomized main axis, fertile branches arrangement) in *G. archangelskyi* gen. et sp. nov. are considered sufficiently different from the known

genera in this family to justify the establishment of a new taxon. The polysperms in LIL Pb 1381 were assignable to *A. madagascariensis*, despite the lack of a clear dichotomization of the main axis.

Relationships within the Glossopteridales have long been debated. In view of the fossil record, most researchers consider *Arberia* (and allied genera) to bear ancestral characters of glossopterids, which Schopf (1976) and McLoughlin (1993) considered to be derived from a cordaitalean ancestor. Since Arberiaceae fructifications have never been found attached to their vegetative parts, other authors have suggested that *Arberia* (= *Dolianitia*) could be the fructification of *Cordaites* (= *Noeggerathiopsis*) (Millan, 1967; Bierhorst, 1971; Chandra & Srivastava, 1981), a view nowadays discarded, as there are no doubts these fructifications belong to Glossopteridales (Rigby, 1972; Anderson & Anderson, 1985; McLoughlin, 1993; Adendorff, 2005). However, the idea of a close affiliation between both cordaitaleans and glossopterids is still hypothesized (McLoughlin & Drinnan, 1996). The morphological similarities of *Golondrinia archangelskyi* gen. et sp. nov. with some fructifications closely allied to cordaitaleans may provide some insights into the relationship between these groups. Better-preserved specimens are needed to evaluate this hypothesis.

This is the first record of Arberiaceae (Glossopteridales) from the La Golondrina Formation. The presence of these fructifications poses a dilemma about the age generally attributed to the formation. With this new evidence, the Laguna Polina Member may extend its range at least to the late Cisuralian (Kungurian?), spanning almost all through the Permian to the early Lopingian, and consequently constraining the lower Laguna Lillo Member to the early Permian (Sakmarian?) (Figure 6). It is clear that a more precise dating methodology other than macrofloral biostratigraphy is needed in the basin, since the floral assemblage, although abundant and diverse, provides inconsistent signals. Until then, the more reliable biostratigraphic indices are without question the fructifications of the various plant groups. In general, in any plant group, the discovery of fertile parts tends to be rarer in comparison with the vegetative parts. This is also the case at the La Golondrina Formation; unfortunately, only one specimen of each fertile taxon described so far has been found, and most commonly, these had preservation that precluded the observation of fine details that would help allocating them at the species or even genus level (see Cariglino, 2013). Despite their rarity, the La Golondrina Formation keeps yielding interesting material within each collecting trip. It is expected that both the number of taxa and specimens will keep increasing, helping to elucidate the diversity and phylogenetic relationships of the different glossopterid families, and improving their stratigraphic significance.

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