


## Spontaneous Article

# The ferns in a new Middle Jurassic locality from the Otlaltepec Formation, Puebla, Mexico

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**ABSTRACT:** Mesozoic ferns from Mexico have been the subject of serious academic endeavours since the beginning of the 20th Century, to understand these plants at the time of their peak diversity. Most findings have been made in a set of Middle Jurassic Basins of the Mixtec Terrain in the Oaxaca State. However, fossil ferns are scarce in other assemblages, so further identification of this group has been infrequent. Here we describe six new and recently collected fossil plants from the Middle Jurassic Otlaltepec Formation, Puebla. Based on their fertile and vegetative fronds, we propose the new genus *Paralophosoria* Morales-Toledo, Mendoza-Ruiz & Cevallos-Ferriz, gen. nov. in the Dicksoniaceae, represented by *Paralophosoria jurassica*, Morales-Toledo, Mendoza-Ruiz & Cevallos-Ferriz, sp. nov., and identify the following genera: cf. *Aspidistes*, *Sphenopteris*, *Spiropteris*. A fern with uncertain affinities was also described. This work contributes to the understanding of fern diversity in low latitudes during the Middle Jurassic in Mexico.



**KEY WORDS:** *in situ* spores, pteridophytes, rift basin, venation patterns.

Ferns are a diverse group of land plants that have a worldwide distribution, but the paleontological record of ferns is incomplete. Three evolutionary radiations of homosporous leptosporangiate ferns have been proposed. The first radiation occurred during the Palaeozoic (Rothwell 1999), and the second radiation can be traced back to the early Triassic (Skog 2001), where fossils assignable to modern genera *Osmunda sensu lato* (*s.l.*) were found in the Triassic of Antarctica (Phipps *et al.* 1998). By the Jurassic, all the basal families of living leptosporangiate ferns were produced (Skog 2001; Smith *et al.* 2006; Rothwell & Stockey 2008). The families represented in this radiation encompass Osmundaceae, Gleicheniaceae, Hymenophyllaceae, Dipteridaceae, Matoniaceae, Schizaeaceae *s.l.*, and Cyatheaceae *s.l.* (Smith *et al.* 2006). These families are well represented in different Middle Jurassic floras worldwide (Barale & Ouaja 2002; Wang 2002; Cleal & Rees 2003; Birkenmajer & Ociepa 2008; Mehlqvist *et al.* 2009; Barbacka 2011; Vaez-Javadi 2011; Kostina & Herman 2013; Scanu *et al.* 2015), but their distribution is far from understood in low-latitude regions such as Mexico.

The study of Jurassic ferns in Mexico dates back to the beginning of the last century with Wieland's study of 'The Liasic *Mixteca Alta* Flora' (1914–1916) and later Silva-Pineda (1978) reviewed the material and made several taxonomic refinements. Afterwards, Person & Delevoryas (1982) described a variety of fossil plants in the Middle Jurassic Flora of Oaxaca, Mexico. More recently, further research has reported new findings, though the efforts to understand members of these

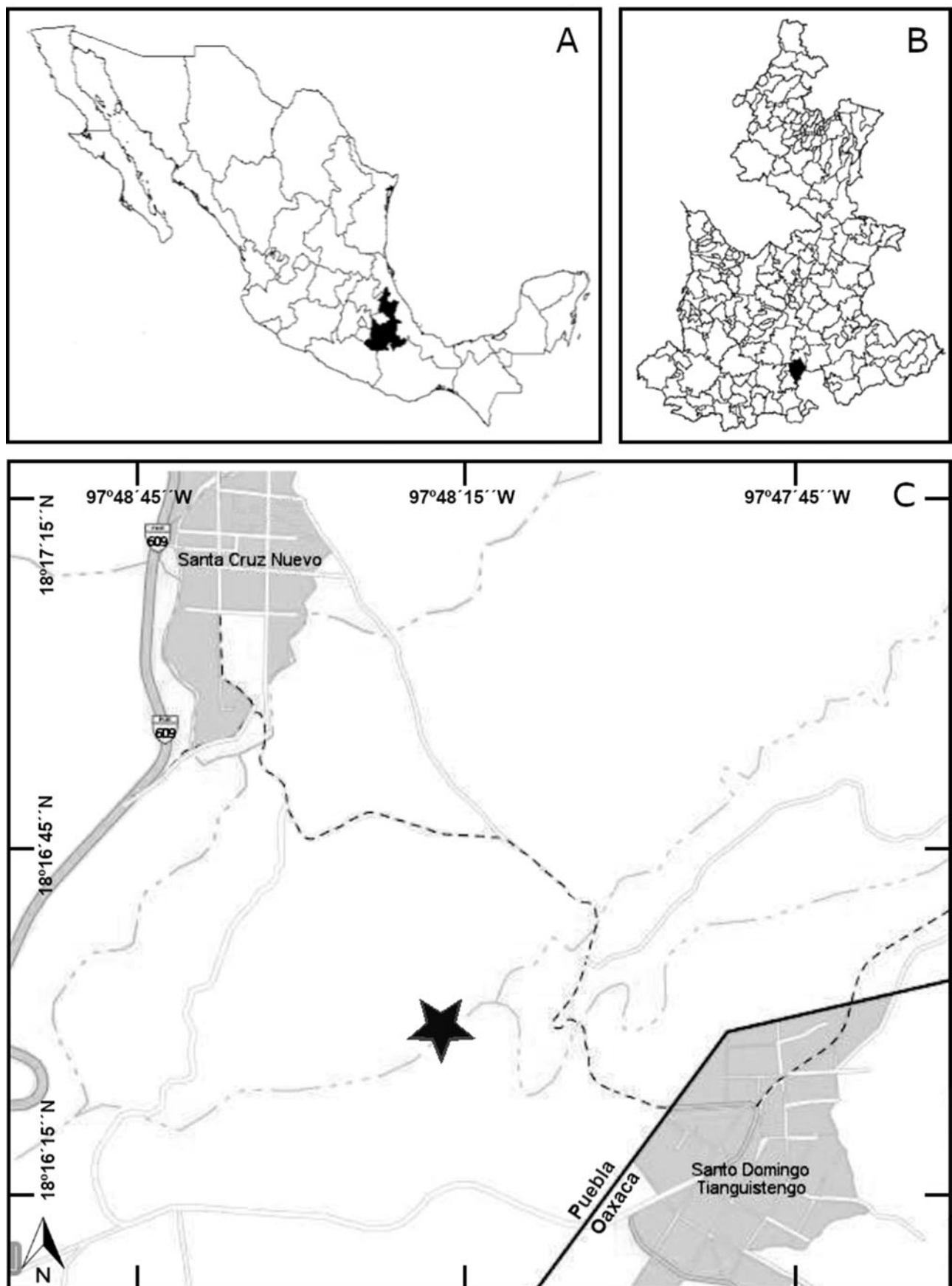
spore-producing organisms are still scarce (Lozano-Carmona & Velasco-de León 2016).

The Middle Jurassic fern fronds from Mexico are *Piazopteris* Lorch, *Cladophlebis* Brongniart and *Coniopteris* Brongniart and other closely related taxa such as *Sphenopteris* Brongniart (Person & Delevoryas 1982). For decades, most studies were carried out in Jurassic localities from Oaxaca State (e.g., Silva-Pineda 1969, 1978; Person & Delevoryas 1982; Lozano-Carmona & Velasco-de León 2016). However, new plant-fossil occurrences were discovered from the Otlaltepec Formation at Santo Domingo Tianguistengo locality in Puebla.

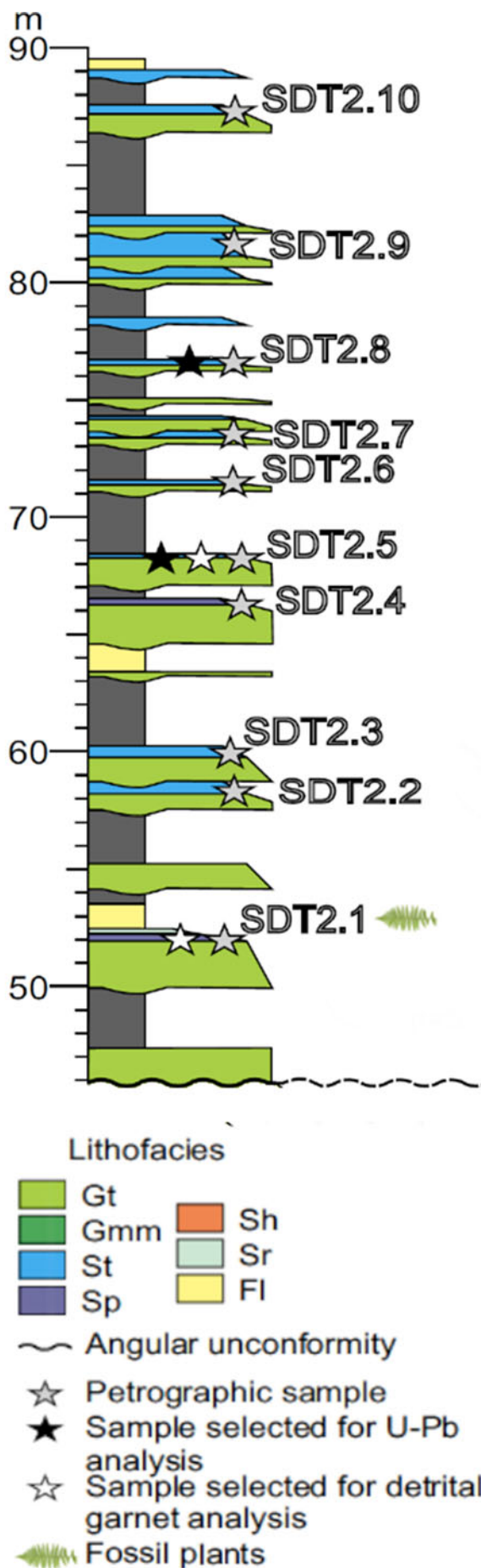
By analysing the morphological and reproductive features of newly collected specimens and comparing them with both extinct and extant species, we aim here to contribute to the knowledge of low-latitude Middle Jurassic floras. This could have implications for understanding the global distributions of families at the end of the second evolutionary radiation of leptosporangiate ferns. Here, we present the first systematic description of the newly collected ferns from the Otlaltepec Formation.

## 1. Material and methods

Specimens were collected from an outcrop located between Santo Domingo Tianguistengo and Santa Cruz Nuevo, in the 'Totoltepec de Guerrero' Municipality, Puebla [18.18°N, 97.40°W] (Fig. 1). The locality is situated in the Magdalena



**Figure 1** The locality of plant fossils of Santo Domingo Tianguistengo, in the Magdalena Creek, Puebla, Mexico. (a) A map of Mexico with Puebla state highlighted in black. (b) Puebla with Toluquepec de Guerrero Municipality highlighted in black. (c) Star pointing the place of the locality where the Otlaltepec Formation outcrops.



**Figure 2** Stratigraphic column representative of the Otlaltepec Formation (modified from Martini *et al.* 2016). SDT - Santo Domingo Tianguistengo. Gt - Scoop-shaped bodies of trough-cross-bedded conglomerate typically cut into each other both laterally and vertically.

Creek where the Otlaltepec Formation crops out. The Otlaltepec Basin fill is composed of a more than 2000-m-thick clastic sedimentary succession (Martini *et al.* 2016). The stratigraphy and structure of the Otlaltepec Basin is poorly defined, but Morán-Zenteno *et al.* (1993) and Verde-Ramírez (2016) divided it into four units – namely, from base to top, the Tianguistengo, Piedra Hueca, Otlaltepec, and Magdalena formations (Martini *et al.* 2016).

The plant fossils are found in the Otlaltepec Formation, which is composed of an alternation of lithofacies including conglomerates, palaeosols, horizontally interlaminated mudstones, siltstones and very fine-grained sandstones, and fine to very coarse-grained sandstone displaying trough cross-bedding (Fig. 2; Martini *et al.* 2016). Detailed information on the lithostratigraphic section is given in Martini *et al.* (2016). Martini *et al.* (2016) analysed the provenance of the sandstones of the Otlaltepec Formation, where the studied fossils were discovered, and determined that the depositional age of the Otlaltepec Formation is constrained between  $163.5 \pm 1$  and  $167.5 \pm 4$  Ma (Late Bathonian–Callovian, late Middle Jurassic age). The ferns from this work were found in the horizontally interlaminated mudstone, siltstone, and very fine-grained sandstone (Fig. 2). In recent years, other fossil plant taxa have been collected from this locality but have not yet been formally described (Morales-Toledo 2016). Among them are abundant foliage and reproductive structures with bennettitalean affinity, as well as conifer shoots, cones, and leaves (Morales-Toledo 2019).

The fossil material consists of stems and moderately well-preserved compressions of sterile and fertile frond fragments. The fossils were studied using a dissecting microscope (Olympus Stemi DV4 and Zeiss Stemi 200-C). The *in situ* spores were obtained by the methods described by Brown *et al.* (1989, 1992). The samples were boiled in 6% Potassium hydroxide (KOH) for 20 min and sieved in a 180  $\mu$ m grid, then they were treated with Hydrofluoric acid (HF) (48%) in a boiling water bath for about 25 min, and finally they were treated in a 1% sodium chloride solution in a boiling water bath for 10 min. The treated samples were mounted in glycerine jelly. Photographs were taken with a digital camera (Canon EOS Rebel T2i), while the detailed structures were obtained with an Axio Zoom.V16 and Discovery.V8 microscope. The fossils and slides are housed in the ‘Colección Paleobotánica del Museo de Paleontología’ (National Paleontological Collection), Instituto de Geología, Universidad Nacional Autónoma de México under the prefix ‘IGM-PB’. The classification used in this work is based on Chase & Reveal (2009) and Christenhusz *et al.* (2011).

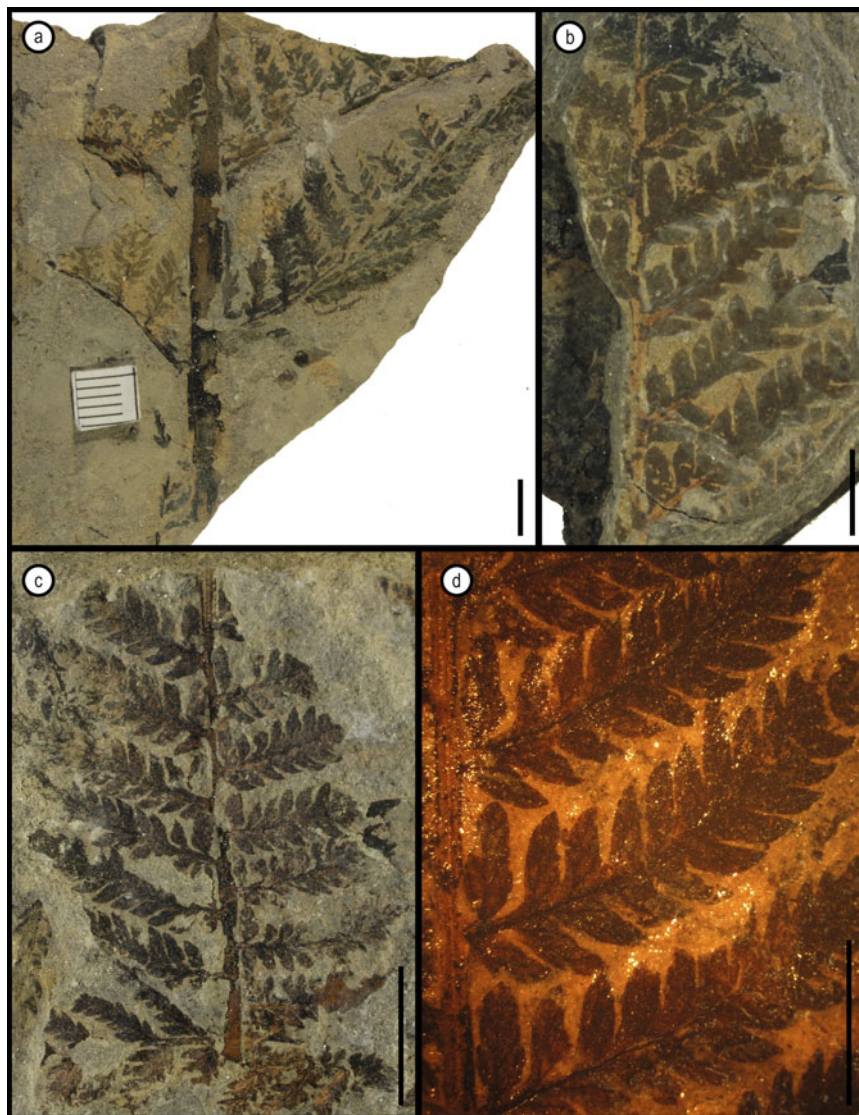
## 2. Systematic descriptions

Order Cyatheales A.B. Frank, 1877

Family Dicksoniaceae M.R. Schomb., 1849

Gmm - Matrix-supported, poorly sorted conglomerate characterized by the lack of clast framework. Beds of this lithofacies have sharp but non-erosional relationship with underlying deposits. St - Fine- to very coarse-grained sandstone displaying trough cross-bedding. Sp - Fine- to coarse-grained sandstone displaying planar cross-bedding. Sh - Very fine- to coarse-grained sandstone with horizontal lamination. Sr - Very fine- to coarse-grained sandstone displaying ripple crosslamination. Fl - Horizontally interlaminated mudstone, siltstone, and very fine-grained sandstone.





**Figure 3** *Paralophosoria jurassica* sp. nov. (a–d) (IGM-PB 118 to IGM-PB 121). (a) Sterile fronds with the number of divisions and arrangement. (b) Distal sterile pinna with pinnules arrangement, and the first acroscopic ultimate segment lobed. (c) Proximal sterile pinna with pinnules arrangement, and acroscopic ultimate segment lobed. (d) Detailed section of a sterile pinna with ultimate segments having the venation pattern. Scale bars = 1 cm (a–c); 0.1 cm (d).

Genus *Paralophosoria* Morales-Toledo, Mendoza-Ruiz & Cevallos-Ferriz, gen. nov.

**Diagnosis.** Similar to the fronds of *Lophosoria quadripinnata* but deeply incised pinnatifid pinnules, the sori are round to kidney-shaped, and the spores are triangular to rounded-triangular in shape with a reticulate perispore.

**Etymology.** From Greek *para* (beside) + *Lophosoria*.

**Discussion.** *Paralophosoria* and *Lophosoria* share bipinnate-pinnatifid fronds with alternate pinnules (Fig. 3a); lobed to pinnatifid, sessile, ultimate segments (Figs 3a–d, 4d, 5a–d, 6a–b); pinnate free veins (Figs 4, 5c–d, 6a–b); and exindusiate sori on a terminal vein (Figs 5a–d, 6b), but they differ in sori and spore shape, and spore ornamentation. *Paralophosoria* has round to kidney-shaped sori (Fig. 5a–e) while *Lophosoria* has round sori (Fig. 6b). Spores differ in that *Paralophosoria* has triangular to rounded-triangular spores (Fig. 5f–k) with reticulate perispore (Fig. 5f, h, k), in contrast to *Lophosoria* spores that are spheroidal, with a prominent equatorial flange, and the distal face is strongly perforate and more or less covered by a granulate perispore deposit.

*Paralophosoria jurassica* Morales-Toledo, Mendoza-Ruiz & Cevallos-Ferriz, sp. nov.

**Holotype.** IGM-PB 1312, Figures 3–5.

**Paratypes.** IGM-PB 118 to IGM-PB 262.

**Repository.** ‘Colección Paleobotánica del Museo de Paleontología’ (National Paleontological Collection), Instituto de Geología, Universidad Nacional Autónoma de México.

**Type locality.** Santo Domingo Tianguistengo locality, located in the Magdalena Creek between the town Santo Domingo Tianguistengo, Oaxaca, and Santa Cruz Nuevo, Puebla, at [18.18°N, 97.40°W].

**Stratigraphic horizon.** Otlaltepec Formation, Middle Jurassic.

**Etymology.** From the Jurassic period.

**Diagnosis.** Frond bipinnate-pinnatifid, adaxial surface glabrous, rachis sulcate, pinnae alternating along the rachis, asymmetric. Deeply incised pinnatifid pinnules with the first acroscopic ultimate segment lobed. Rest of the ultimate segments are sessile, trapezoid shaped with an acute apex. Middle ultimate segments larger than the basal and apical ultimate segments. Pinnate free veins. Sori at the end of the veins, exindusiate, one per ultimate segment, trilete spores, trilete mark surrounded by a labrum.



**Figure 4** *Paralophosoria jurassica* sp. nov. (a–d) (IGM-PB 121 to IGM-PB 122). (a) Sessile ultimate segments of pinnules with pinnate venation. (b) First acroscopic ultimate segment lobed with pinnate venation. (c) Sessile ultimate segments of pinnules with pinnate venation. (d) Schematic drawing of a complete pinnule. Scale bars = 0.1 cm (a, b); 0.2 cm (c, d).

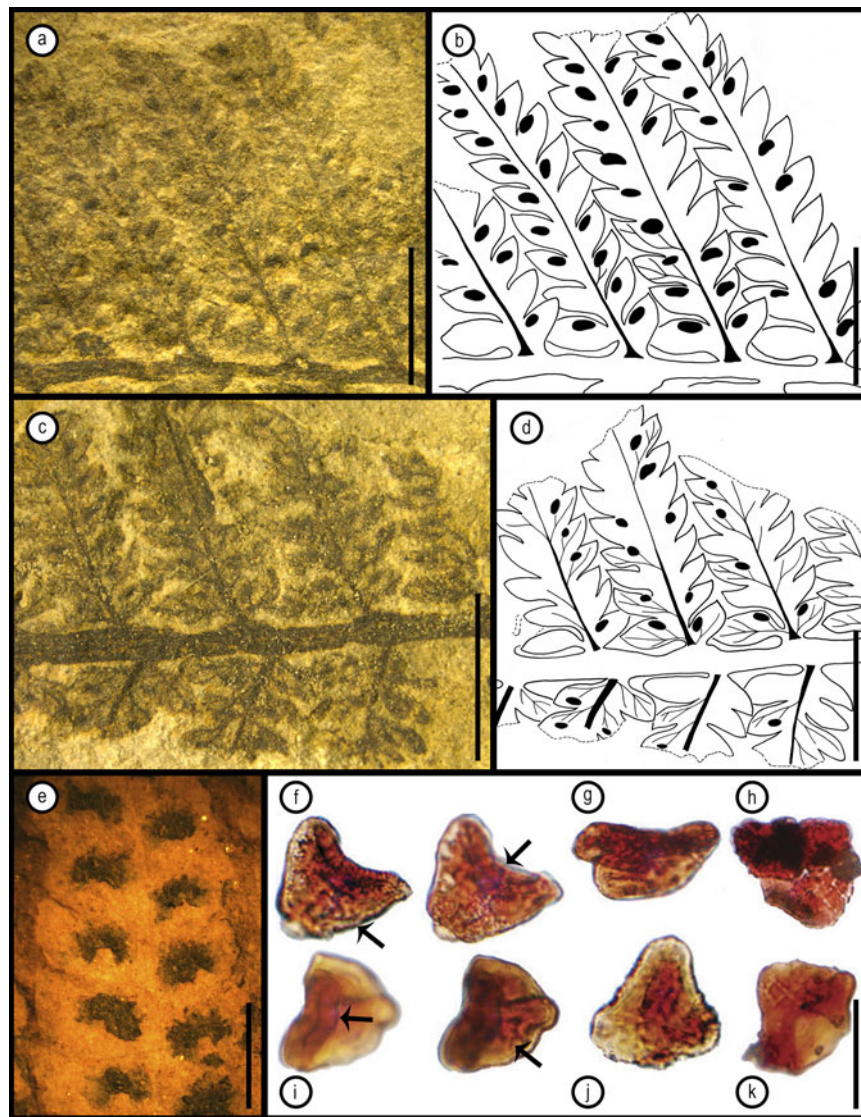
**Description.** The new taxon is represented by fertile and vegetative fronds with no morphological differentiation (Figs 3–5). Fronds bipinnate-pinnatifid (Fig. 3a). Preserved part of the lamina 6 cm long, 9 cm wide. Rachis glabrous, 0.4 cm wide, tapering towards the apex of the lamina. Pinnae pinnate-pinnatifid (Fig. 3b, c), alternate, inserted along the main rachis at 1.5–2 cm of distance each, arising at acute angles (50–65°), 4.5 cm long, 2–3 cm wide. Deeply incised pinnatifid pinnules, alternate, 1–1.5 cm long, 0.3 cm wide, first acroscopic ultimate segment lobed, rest of the ultimate segments are sessile, trapezoid shaped with an acute apex (Figs 3d, 4d, 5a–d). Veins in the ultimate segments pinnate, catadromous (Fig. 4a–d). Sori alternate, exindusiate, abaxial, one per ultimate segment, terminal on a vein, rounded to kidney-shaped (Fig. 5a–e). Spores triangular to rounded-triangular, trilete mark reaching the spore edge, trilete surrounded by a 4- $\mu$ m-wide labrum, triangular in polar view, concave edges, equatorial diameter 21–27  $\mu$ m, reticulate perispore about 1  $\mu$ m wide (Fig. 5f–k).

**Discussion.** The material from the Santo Domingo Tianguis-tengo locality is similar to the vegetative material of *Cladophlebis browniana* (Dunker) Seward from the Middle Jurassic of Oaxaca (Person & Delevoryas 1982), with the exception of specimen IGM\_PB\_406-EIV\_8\_13 (Fig. 6c–i). They share key characters

such as deeply incised pinnatifid pinnules (Figs 3–4, 5a–d, 6c–f), first acroscopic ultimate segment lobed (Figs 3b–d, b, d, 6c–e), and rest of the ultimate segments trapezoid shaped with acute apex (Fig. 3a–c, 6c–f). However, the fertile material of *C. browniana* from the Middle Jurassic of Oaxaca highly contrasts with ours in that it has pinnules with eight to ten pairs of circular-oval soral scars (Fig. 6i), while our material has one rounded to kidney-shaped sori per ultimate segment, at the end of each vein (Fig. 5a–e).

*Cladophlebis* Brongniart is characterised by large bipinnate fronds, the blades are not decurrent, are attached to the rachis by their hole base, and the veins are simple, double-forked, or dichotomously arched (Brongniart 1849; Bodor & Barbacka 2008). The ultimate segments (each pinnule) of *Cladophlebis* possess a prominent and persistent midvein that gives off secondary forked veins (Seward 1898–1919). These *Cladophlebis* diagnostic characters have been reported on other Jurassic *Cladophlebis* species from Bornholm, Denmark (Mehlqvist *et al.* 2009), Sardinia, Italy (Scanu *et al.* 2015), Yorkshire, UK (Harris 1961), Alborz, Iran (Vaez-Javadi 2011), Clarence-Moreton Basin, Australia (Jansson *et al.* 2008), Queensland, Australia (McLoughlin & Drinnan 1995), and Antarctica (Birkenmajer & Ociepa 2008), but are absent in our material





**Figure 5** *Paraloophosoria jurassica* sp. nov. (a–d) (IGM-PB 123 to IGM-PB 125). (a) Fossil fertile frond having the same venation pattern and sori position. (b) Schematic drawing of (a) showing the venation pattern and sori position. (c) Fossil fertile frond showing position, number, and shape of sori. (d) Schematic drawing of (c) showing the venation pattern and sori position (e) Fertile fragment having sori with small leptosporangia. (f) Equatorial view of the trilete spore showing reticulate exine (left arrow) and labrum (right arrow). (g) Deformed spore, showing the labrum. (h) Deformed spore with reticulate exine. (i) Equatorial view of the trilete spore showing labrum (left arrow) and reticulate exine (right arrow). (j) Polar view of the spore showing the trilete surrounded by a labrum. (k) Deformed spore with reticulate exine. Scale bars = 0.5 cm (a–d); 0.2 cm (e); 20  $\mu$ m (f–k).

or the one described by Person & Delevoryas (1982). Therefore, the material should not be referred to *Cladophlebis* but it can be placed within Dicksoniaceae.

The Jurassic fossil record for Dicksoniaceae is known from different floras worldwide (e.g., Barale & Ouaja 2002; Wang 2002; Cleal & Rees 2003; Birkenmajer & Ociepa 2008; Mehlqvist *et al.* 2009; Barbacka 2011; Vaez-Javadi 2011; Kostina & Herman 2013; Scanu *et al.* 2015). We compared the fossil material to extant and extinct genera from Dicksoniaceae and it appears to show a unique combination of features (Table 1). Our material can be distinguished from *Calochlaena* (Maxon) M.D. Turner & R.A. White and *Dicksonia* M.R. Schomb. due the lack of sori with bivalvate or cuplike indusium in a marginal position (Smith *et al.* 2006). It differs from fossil genera such as *Coniopteris* Brongniart and *Eboracia* Thomas due the lack of marginal sori with a cup-shaped indusium (Harris 1961; Li *et al.* 2020). *Kylippteris* Harris has fertile parts reduced to stalked pinnules with a hemispherical cup-shaped indusium (Harris 1961), unlike our fossils, and *Culcitites* Appert has a marginal pocket-shaped indusium (Appert 1973), which is not seen in our material. Finally, our material can be distinguished from *Haydenia thyrsopteroides* Seward due

the lack of a crenate margin on the ultimate segments of fertile material, ultimate segments with forked veins coming from a mid-vein in the non-fertile material (see Appert 1973, Abb. 42–43 and pl. 59, fig. 4, pls. 61–63), or fertile fronds with irregularly lobed pinnules with numerous marginal sori (Seward 1912).

The material shares characters with extant *Lophosoria quadripinnata* C. Presl, such as the number of divisions of the frond (Smith *et al.* 2006) and exindusiate sori that are single and dorsal on the veins (Kramer 1990b; Smith *et al.* 2006). In particular, some foliage characters (e.g., deeply incised pinnatifid pinnules and ultimate segments with pinnate veins) and exindusiate sori at the end of one vein are shared between *L. quadripinnata* C. Presl and *Paraloophosoria jurassica*. Nevertheless, the *P. jurassica* can be distinguished from *L. quadripinnata* because the second species lacks sessile ultimate segments with an entire margin (Fig. 6a, b), and just have round to kidney-shaped sori (Fig. 6b).

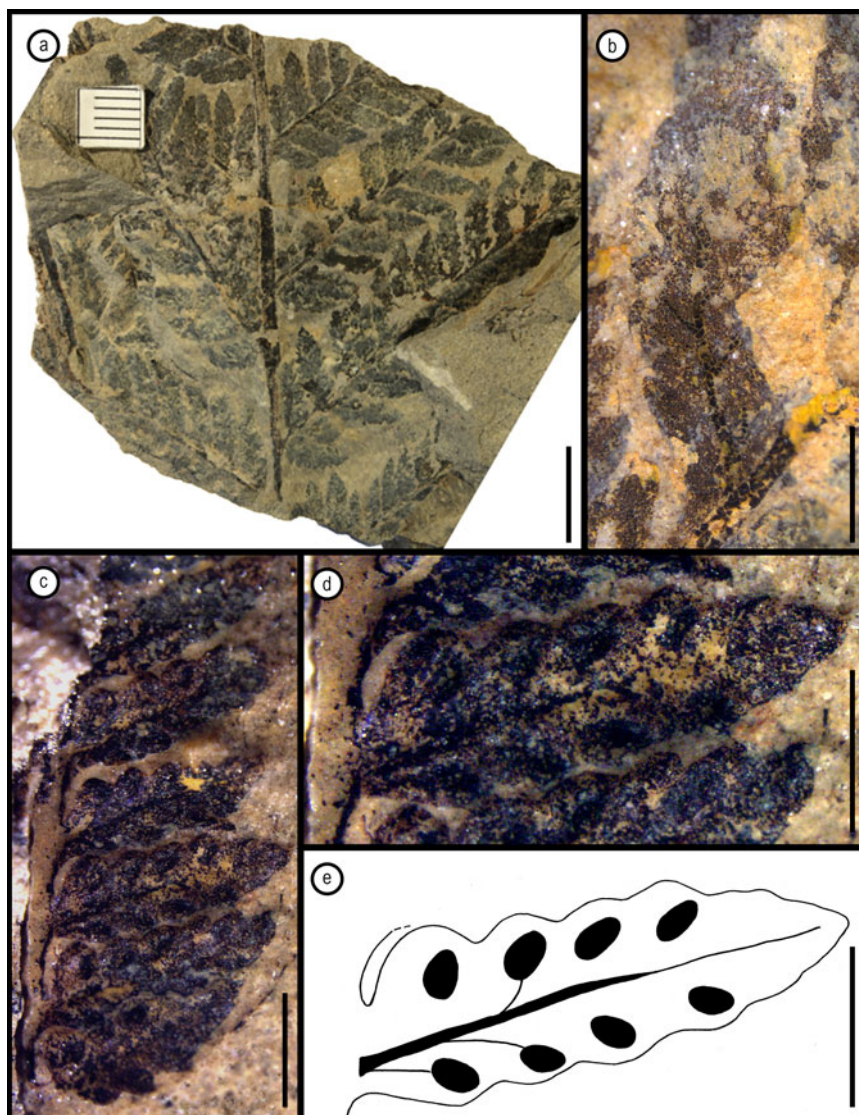
The *in situ* spores of *Paraloophosoria* do not have the conspicuous characters diagnostic of *Lophosoria* (e.g., equatorial cingulum and proximal inter-radial sculpture/protuberances) as reported by Gastony & Tryon (1976). Furthermore, *Paraloophosoria* has triangular to rounded-triangular spores (Fig. 5f–k),





**Figure 6** *Lophosoria quadripinnata* (a, b) and *Cladophlebis browniana* as described in Person & Delevoryas (1982) (c–i). (a) Sterile pinnule with ultimate segments having pinnate venation, Missouri Botanical Garden Herbarium, 6,212,483 (barcode from the specimen). (b) Fertile pinnule with ultimate segments having pinnate venation and sori, Missouri Botanical Garden Herbarium, 04911731 (barcode from the specimen). (c) Vegetative frond showing the number of divisions and arrangement, IGM-PB 401. (d) Vegetative frond showing the shape of the ultimate segments of the pinna, IGM-PB 403. (e) Pinna showing the number of divisions and phyllotaxy, IGM-PB 404. (f) Detailed section of (e), showing the venation pattern. (g) Pinnules showing the ultimate segments' arrangement, IGM-PB 406. (h) Detailed section of (g), showing the venation pattern. (i) Fertile fronds showing the position, number, and shape of sori, IGM-PB 405. Scale bars = 1 cm (a–c, e, g); 0.5 cm (d, i); 0.2 cm (f); 0.1 cm (h).





**Figure 7** *Aspidistes silvapinedae* (a–e) (IGM-PB 263 to IGM-PB 264). (a) Number of divisions and arrangement of sterile fronds. (b) Pinnules with venation pattern. (c) Position, number, and shape of sori of fertile fronds. (d) Closer magnification of (c) showing venation pattern and sori position. (e) Schematic drawing of (d) showing the venation pattern and sori position. Scale bars = 1 cm (a); 0.1 cm (b, c); 0.05 cm (d, e).

as seen in *Coniopteris* (Van Konijnenburg-Van Cittert 1989), but the perispore is granular in the latter and reticulate in our material. A reticulated perispore is present in some members of *Dicksonia* (Tryon & Lugardon 1991) and *Paralophosoria*, whereas perispore is smooth in *Eboracia* and *Kylikopteris* and is thin and granulate in *Calochlaena* (Table 1).

The spores of *Paralophosoria* can be compared with fossil spores from members of Matoniaceae due to the distinct raised laesurae (treated here as a labrum) (van Konijnenburg-van Cittert 1993; Givulesco & Popa 1998; Popa & van Konijnenburg-van Cittert 1999). However, these spores are psilate to faintly granulate or granulate, contrasting with the reticulate perispore from our material, and none of the more 140 specimens have recorded the morphological features of Matoniaceae. Based on the unique combination of pinnae morphology, venation patterns, sori position and shape, and spore surface and shape, we recognise this material as a new taxon within Dicksoniaceae, a family with higher diversity during the Jurassic than today.

*Incertae sedis*

Genus *cf.* *Aspidistes* Harris, 1961

*Aspidistes silvapinedae* Morales-Toledo,  
Mendoza-Ruiz & Cevallos-Ferriz, sp. nov.

**Holotype.** IGM-PB 263, Figure 7.

**Paratypes.** IGM-PB 263 to IGM-PB 265.

**Repository.** 'Colección Paleobotánica del Museo de Paleontología' (National Paleontological Collection), Instituto de Geología, Universidad Nacional Autónoma de México.

**Type locality.** Santo Domingo Tianguistengo locality, located in the Magdalena Creek between the town Santo Domingo Tianguistengo, Oaxaca, and Santa Cruz Nuevo, Puebla, at [18.18°N, 97.40°W].

**Stratigraphic horizon.** Otlaltepec Formation, Middle Jurassic.

**Etymology.** The specific epithet *silvapinedae* honours Dr Alicia Silva-Pineda, whose contributions to the study of the Jurassic palaeobotany in Mexico are far-reaching.

**Diagnosis.** Bipinnate catadromous fronds. Rachis glabrous. Pinnae alternate, width constant towards the lamina apex. First basal acroscopic pinnules are shorter. Pinnules alternate, basally lobed to dentate towards the apex margin, first basal ultimate segment slightly rounded. Venation pinnate, free. Sori round, on medial to supra-medial position, at the end of a vein.

**Description.** Frond bipinnate, catadromous (Fig. 7a). Preserved part of the laminae 5.2 cm long, 5.5 cm wide. Rachis glabrous, 0.2 cm wide, tapering towards the apex of the frond. Pinnae linear, alternately inserted each 1.5 cm along the main rachis,



**Table 1** Useful characteristics that distinguish *Paralophosoria* from other genera within Dicksoniaceae (characters from: Seward 1912; Harris 1961; Appert 1973; Gastony & Tryon 1976; Van Konijnenburg-Van Cittert 1989; Kramer 1990b; Tryon & Lugardon 1991; Smith *et al.* 2006; Li *et al.* 2020).

Fern character	<i>Paralophosoria</i>	<i>Calochlaena</i>	<i>Dicksonia</i>	<i>Lophosoria</i>	<i>Coniopteris</i>	<i>Eboracia</i>	<i>Kylukipteris</i>	<i>Calcutites</i>	<i>Haydenia</i>
Sorus position	Terminal on a vein	Marginal, terminal on a vein	Marginal	Terminal on a vein	Marginal, terminal on lateral vein	Marginal	Reduced to a stalk	Marginal, terminal on a vein	Marginal at the end of a vein
Sorus shape	Round to Kidney	Round	Isodiametric	Round	Round	No information	No information	Kidney	Circular
Indusium	Exindusiate	Bivalvate	Bivalvate	Exindusiate	Cup-shaped	Cylindrical	Hemispherical cup-shaped	Cup-shaped	?
Spore shape	Triangular to rounded-triangular	Globose	Tetrahedral-globose, the lobes sometimes prolonged, with lateral surfaces often depressed between aperture arms	Spheroidal, with a prominent equatorial flange, distal face hemispherical	Rounded, triangular to rounded-triangular	Rounded	Rounded	No information	No information
Spore ornamentation (perispore)	Reticulate	Thin granulate	Plain or coarsely reticulate, with granulate deposit, and rodlets	Proximal face smaller, coarsely tuberculate, the distal face strongly perforate, more or less covered by granulate perispore deposit	Granular	Smooth	Smooth	No information	No information

arising at acute angles (34–57°), 4 cm long, 1.2 cm wide, not overlapping with other pinnae, with first basal acroscopic pinnule shorter. Pinnules alternate, 0.7–0.8 cm long, 0.2 cm wide, constricted acroscopic bases, slightly decurrent basicopic bases, crenate–dentate margins on sterile segments and crenate to rounded margins on fertile segments (Fig. 7b–e). Venation pinnate, free (Fig. 7b, d). Sori round, 0.5 mm in diameter, on medial to supra-medial position, at the end of a vein, eight sori per pinnule (Fig. 7c–e).

**Discussion.** Harris (1961) placed *Aspidistes* in the Aspidiaceae, which is included in Dryopteridaceae by Smith *et al.* (2006). However, Lovis (1975) remarked on the controversial placement of Jurassic material in the Polypodiales Link and discussed that *Aspidistes thomasi* could represent a member of Thelypteridaceae Ching ex Pic. Serm. The only reliable way to decide if our material is in Thelypteridaceae is with the recovery of bilateral spores with monoete scars (as is found in almost all genera of this family), or tetrahedral spores with a trilete scar, as in *Trigonospora* Holttum. Unfortunately, no spores were retrieved from our material, so placement in Thelypteridaceae is tentative.

Our fossil material shares some characters with *Aspidistes*, such as repeatedly pinnate fronds with catadromic branching, diverging branch veins, similar sterile and fertile leaves, and round sori (Harris 1961), but the indusium is not visible in our material. *Aspidistes silvapinedae* can be distinguished from *A. thomasi* Harris from the Jurassic of Yorkshire, UK, *Aspidistes delicatula* Barale & Ouaja from Merbah El Asfer, South Tunisia (Barale & Ouaja 2002), and *Aspidistes sewardi* Watson from the Wealden district in the UK (Watson 1969), by the fertile pinnule margin, number of sori per pinnule, number of sori per lobe, and sori size (Table 2).

Person & Delevoryas (1982) illustrate fertile pinnules attributed to *Cladophlebis browniana* (Dunker) Seward, but we suggest that fertile material does not represent the actual pinnules of *C. browniana* (discussed above). Their material consists of a fragment that bears at least 12 rounded sori (Fig. 6i). Due to the possible presence of *Aspidistes* in the Otlaltepec Formation, we suggest that Person & Delevoryas (1982) material should be reviewed and possibly moved to this taxon.

Genus *Sphenopteris* Sternberg  
*Sphenopteris* sp.  
(Fig. 8a–e)

**Specimens examined.** IGM-PB 108 to IGM-PB 117.

**Description.** Fragments of vegetative fronds with bipinnate-pinnatifid blade, 4 cm long, 3.6 cm wide (Fig. 8a–e). Rachis glabrous, non-sulcate, 0.2 cm wide, tapering towards the apex of the lamina. Pinnae alternate, inserted at intervals about 1 cm along the main rachis, arising at acute angles (65–70°), 2.8 cm long, 1 cm wide (Fig. 8c). Pinnules pinnatifid, alternate, some opposite, with decurrent basicopic and constricted acroscopic margin (Fig. 8d, e), 0.5–0.6 cm long, 0.3 cm wide, tapering towards pinnule apex (lanceolate). Ultimate segments with a rounded or acute apex (Fig. 8a–e). Each ultimate segment with a single vein (Fig. 8a–b, d).

**Discussion.** Wieland (1914–1916) reported similar foliage in Oaxaca, and Person & Delevoryas (1982) assigned them to *Sphenopteris goepperti* Seward. The shared characters between our material and *S. goepperti* from Oaxaca are the lamina division, rachis width, pinnae arrangement, the rounded shape of the ultimate segments ('spatula shaped' in Person & Delevoryas 1982), and the prominent mid veins. However, *S. goepperti* was transferred to *Ruffordia goepperti* by Seward (1894). Seward (1894) describes the venation as being 'of the types *Caenopteridis* and *Sphenopteridis*', but in his plate VI of figure 1a, the venation

**Table 2** Useful characteristics that distinguish *Aspidistes silvapinedae* from other species of the world (characters from: Harris 1961; Watson 1969; Barale & Ouaja 2002).

Fern character	<i>Aspidistes silvapinedae</i>	<i>Aspidistes thomasi</i>	<i>Aspidistes delicatula</i>	<i>Aspidistes sewardi</i>
Fertile pinnule margin	Crenate-dentate	Rounded	Lobed (rounded)	Rounded
Number of sori per pinnule	Eight	Eight	Ten	Not given
Number of sori per lobe	One	One	One	Three
Sori size (mm)	0.5	1.0	Not given	Not given



**Figure 8** *Sphenopteris* sp. (a–e) (IGM-PB 108 to IGM-PB 111) and *Spiropteris* sp. (f) (IGM-PB 266). (a) Pinnate-pinnatifid pinna with venation and constricted bases. (b) Schematic drawing of (a) showing the venation reaching every segment. (c) Vegetative fronds with the number of divisions and phyllotaxy. (d) Ultimate segments with round or acute apex and a decurrent-base pinnule segment. (e) Ultimate segments with round or acute apex and a decurrent-base pinnule segment (barcode from the herbarium). (f) Fragment of a crozier circinate frond. Scale bars = 1 cm.

of a piece of a pinna is shown that differs from our material in having flabellate venation rather than each last segment with a single vein. Furthermore, Mohr *et al.* (2015) described a well-preserved specimen of *R. goepperti* where the main vein of the pinnule emerges from the pinna rachis and ends in the middle of the first lobe division, then free veins diverge and dichotomise several times, reaching the edge of each lobe in a flabellate venation pattern, contrasting with a single vein in each ultimate segment of our material.

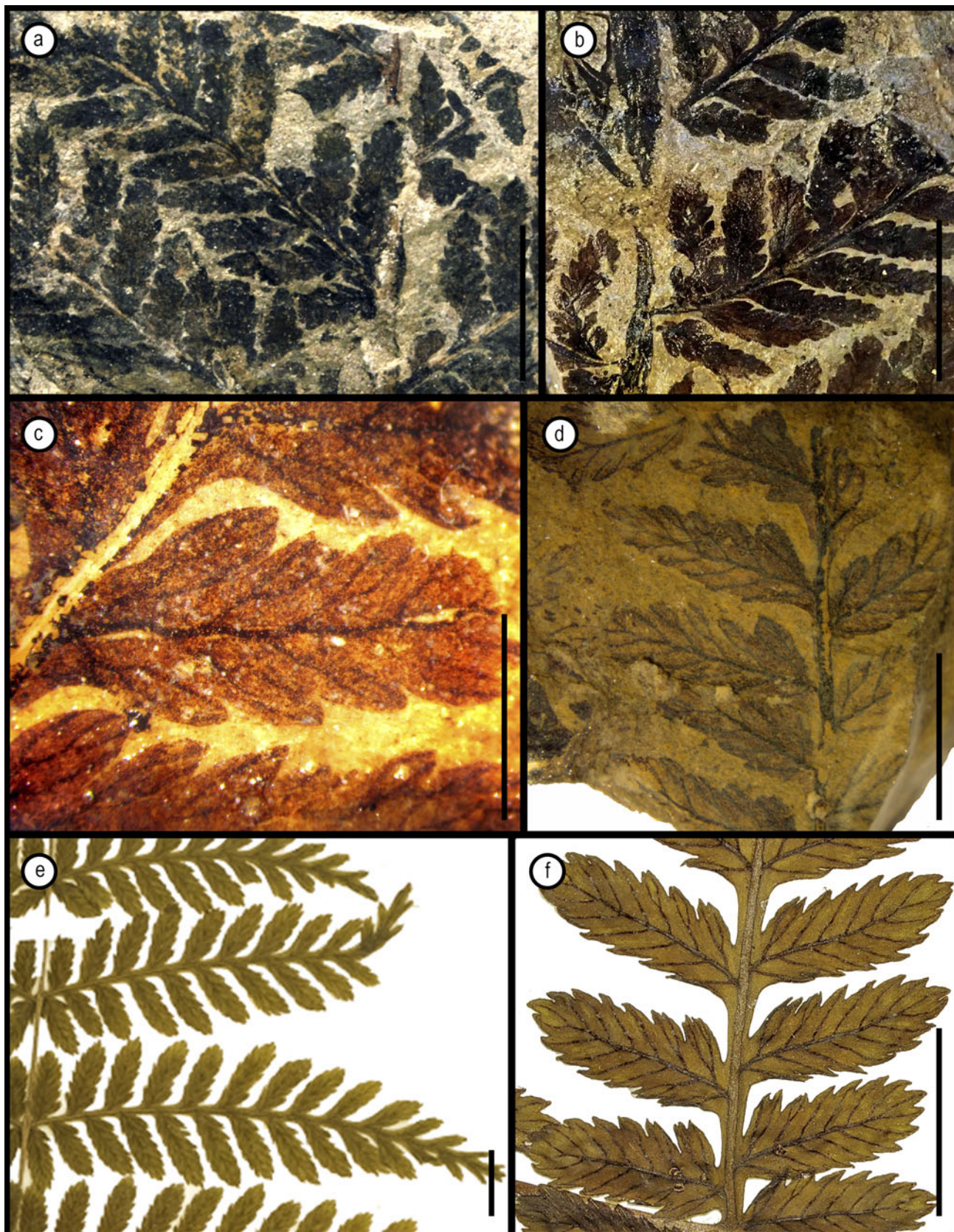
*Sphenopteris* (*s.l.*) is generally characterised by pinnules constricted at the base, with an oval outline and almost entirely margined, or lobed, and are usually decurrent, giving the pinna axes a distinctly winged shape (Taylor *et al.* 2009). Our

material has the characters needed to be placed in *Sphenopteris* but not into *S. goepperti* as reported by Person & Delevoryas (1982) since *S. goepperti* has changed to *R. goepperti* and our material is not a *Ruffordia*. Other genera, such as *Onychiopsis* Yokoyama and *Coniopteris* Brongniart are similar to *Sphenopteris* sp., but fertile structures are needed to justify the placement of our material within any of these Dicksoniaceae genera.

Genus *Spiropteris* Schimper, 1869  
*Spiropteris* sp.  
 (Fig. 8f)

**Specimens examined.** IGM-PB 266 to IGM-PB 269.





**Figure 9** Fern type 1 (a–d) (IGM-PB 104 to IGM-PB 106) and *Leptopteris fraseri* (e, f). (a) Vegetative fronds showing the number of divisions, and pinnae arrangement. (b) Vegetative fronds showing the number of divisions, and pinnae arrangement with veins. (c) Pinnules of (b) showing the venation pattern. (d) Pinnules showing secondary veins forking. (e) Extant fronds showing pinnae arrangement, University of Michigan Herbarium, 1,177,561 (barcode from the specimen). (f) Pinnules of (d) showing the venation pattern. Scale bars = 1 cm (a, b, e, f); 0.2 cm (c); 0.5 cm (d).

**Description.** Fragment of a young frond that shows the laminae rolled from apex to base with the apex in the centre of coil (crossier circinate) (Fig. 8f). Petiole is 3 cm long. Coil about 1 cm in diameter.

**Discussion.** *Spiropteris* is a morphotaxon including distinctive fossil circinate coiled frond tips that could not be assigned to foliage-based genera due to the absence of lamina features (Mehlqvist *et al.* 2009).



**Table 3** The comparison of Otlaltepec Formation fern diversity with other published works from the Middle Jurassic of Mexico (information from: Silva-Pineda 1969, 1978; Person & Delevoryas 1982).

Taxon	Otlaltepec Formation Santo Domingo Tianguistengo	Rosario	Zorrillo	Tecomazuchil Formation				Family
		Formation La Carbonera	Formation Arroyo del Carrizo	Olomatlán	Ayuquila	Texcalpa	Tonalá	
<i>Piazopteris branneri</i>		X		X	X	X	X	Matoniaceae
<i>Cladophlebis browniana</i>		X	X					?
<i>Cladophlebis denticulata</i>				X				Osmundaceae
<i>Sphenopteris goeppertii</i>		X	X					<i>Incertae sedis</i>
<i>Coniopteris arguta</i>		X	X					<i>Incertae sedis</i>
cf. <i>Coniopteris</i> <i>hymenophylloides</i>		X	X					Dicksoniaceae
<i>Paralophosoria jurassica</i> gen. et sp. nov.	X							Dicksoniaceae
cf. <i>Aspidistes silvapinedae</i> sp. nov.	X							Dicksoniaceae
<i>Sphenopteris</i> sp.	X							<i>Incertae sedis</i>
<i>Spiropteris</i> sp.	X							<i>Incertae sedis</i>
Fern type 1	X							<i>Incertae sedis</i>

'Fern type 1'  
(Fig. 9a–d)

**Specimens examined.** IGM-PB 104 to IGM-PB 107.

**Description.** Fragments of vegetative, bipinnate fronds are 4 cm long by 8 cm wide (Fig. 9a, b). Rachis glabrous, 0.3 cm wide, tapering towards the apex. Pinnae alternate, inserted in intervals of about 1 cm along the main rachis, arising at acute angles (50–75°), slightly falcate, contiguous, tapering towards the apex, 2–3.5 cm long, 1.3 cm wide (Fig. 9b). Pinnules alternate, decurrent, pinnatifid, with acute apex, 0.8–1 cm long, 0.3 cm wide. Each pinnule with a persistent primary vein running into the apex, then secondary veins forking two to three times in the first lobule (Fig. 9c), and then twice (Fig. 8d).

**Discussion.** Our material is similar to a single specimen of *Cladophlebis browniana* (Dunker) Seward from the Middle Jurassic of Oaxaca (Person & Delevoryas 1982), which is deposited in the 'Colección Paleobotánica del Museo de Paleontología' under the prefix IGM-PB 406 (Fig. 6g, h). Both have alternate, pinnatifid pinnules with decurrent bases and pinnules with a persistent primary vein with dichotomising secondary veins (Figs 6g–h, 9c–d). In the generic diagnosis of *Cladophlebis* Brongniart (1849), the pinnules are not decurrent, in contrast to the decurrent base of the pinnules from our material (Fig. 9c, d). In considering the venation, *Cladophlebis*, *Todites* Seward emend. Harris, and *Osmundopsis* Harris emend. Harris are all similar in having a thickened midvein and many bifurcating lateral veins (Harris 1961), which also differs from our material that may have trifurcations and bifurcations matching up the teeth of the margin (Fig. 9c, d). Thus, only with fertile structures could this material be assigned confidently to any of these genera.

*Raphaelia* Debey & Ettingshausen is a genus represented by sterile and fertile foliage (Tidwell & Ash 1994) and it is extensively recorded from the Far-East region in Russia and Mesozoic deposits of China, where *Raphaelia diamensis* is the most significant representative (Tian *et al.* 2016). The sterile fronds of *R. diamensis* have pinnules with a primary vein and diverging lateral veins and the pinnules have a cuneate base with entire margins. Even though the pinnule venation of *R. diamensis* and our material are similar, the gross morphology of the pinnules differ. *Phyllopteroides* Medwell is a Cretaceous genus reported in Australia (Cantrill & Webb 1987) and India (Banerji 1987). The pinnules from *Phyllopteroides* are simple, linear-lanceolate

with a prominent midrib, and the base tapers sharply (Cantrill & Webb 1987), in contrast to the morphology from the pinnules presented here.

Though the specimens have characters in common with extant Osmundaceae, they can be distinguished from the sterile leaves of *Osmunda* L. due to its articulate pinnae (Kramer 1990a), which are unlike the decurrent pinnules from our material. *Todea* Willd. ex Bernh. has ultimate tongue-shaped pinnules (ultimate segments) (Kramer 1990a) that are different from the ultimate falcate segments from the Fern type 1 material. *Leptopteris* C. Presl, like the new material, is characterised by bipinnate lamina with dentate to deeply pinnatifid pinnules (Kramer 1990a). Kramer (1990a) does not describe the venation pattern, but it resembles that of *Leptopteris fraseri* (Hook. & Grev.) C. Presl., which bears a middle vein in the ultimate segment from where secondary bifurcated veins run towards the teeth (Fig. 9e, f). This venation pattern is also found in Fern type 1 material. However, sterile foliage alone is not very informative, and without the sporangia it is difficult to confidently assign the material to a species or genus. The gross morphology and the venation patterns of the pinnules suggest that the material can be a member within Osmundaceae, but fertile structures are needed to confirm this hypothesis.

### 3. Discussion

Leaf venation patterns have been widely used to identify fossil plant leaves, principally in the angiosperm group (Hickey & Wolfe 1975; Leaf Architecture Working Group 1999). In other groups such as the ferns it can be a challenging endeavour to use leaf architecture to identify the plants. To identify fossil ferns, reproductive structures that bear unambiguous diagnostic characters for identification are preferred. However, these materials are not always present in the collections, and vein patterns in fern taxonomy have proven to be an important alternative to discriminate between species, genera, and families (Wagner 1979). Recently, fern venation patterns have been discussed and used with confidence as an important taxonomic tool where reproductive organs are lacking (Simpson 2010).

Tuomisto & Groot (1995) pointed out that fern flora and monographic treatments typically describe adult plants and, thus, all identification pteridophytes keys are skewed towards fertile material. This can be seen in important works, such as that of Mexico (Mickel & Smith 2004), where the description of the



venation patterns of ultimate segments of fronds is somewhat superficial, thus hindering character comparison. The description and identification of both extant and fossil ferns is biased towards the fertile material leaving out a lot of valuable information that venation patterns can provide. Here, we have paid special attention to the venation patterns, and their interactions, specifically with their development near the margin in the ultimate segments of the pinnae.

Venation patterns are also important to understand previous records for the Middle Jurassic of Mexico. The case of the specimens described and identified as *Cladophlebis browniana* by Person & Delevoryas (1982) shows that the sterile fronds are actually fronds from *Paralophosoria jurassica* and the fertile fronds are a different unknown species. The venation pattern of the ultimate segments of their material does not correspond to the pattern of *Cladophlebis*, but is clearly similar to the one described for *Paralophosoria*.

In addition, the venation patterns in the ultimate segments of both our material and *Leptopteris fraseri* correspond to comparable morphologies. We suggest that even though fertile material bears key characters that help to identify groups, foliar characters can be useful to identify non-fertile fossil material when more specific descriptions of vein patterns of the ultimate segment(s) are available, and it would be valuable for future researchers to further document pinnule venation.

This study has greatly expanded the diversity of ferns known from the Middle Jurassic of Mexico (Table 3). Previously, six species were identified (Silva-Pineda 1969, 1978; Person & Delevoryas 1982), representing at least three different families (Matoniaceae, Osmundaceae, Dicksoniaceae). The Otlaltepec Formation material shows that the ferns here were more diverse than previously thought by adding new occurrences of five species not found previously in this region. In particular, we expanded the known diversity of Dicksoniaceae, by recognising a new genus for the family and two new species. Overall fern biodiversity during the Middle Jurassic in Mexico is far from understood, but by studying new localities, such as the Santo Domingo Tianguistengo locality, we can provide more evidence to understand fern evolution and taxonomy.

#### 4. Conclusions

This study provides the description and identification of different ferns from a new locality from the Middle Jurassic of Mexico. These new records encompass two new genera (*Paralophosoria* gen. nov., Dicksoniaceae, and *Spiropteris*), two new species (*P. jurassica* sp. nov. and *Aspidistes silvapinedae*), and one previously reported genus (*Sphenopteris*). In addition, a new type of fern with uncertain affinities was also described (Fern type 1). The systematics of previous records from the area were discussed on the basis of new evidence from a bigger sample of specimens, putting an important emphasis on the venation patterns of sterile foliage. Our work contributes to the understanding of fern diversity during the Middle Jurassic in Mexico.

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#### 6. Author contributions

J.M.-T.: investigation, writing – original draft; A.C.M.-R.: supervision, writing – review and editing; S.R.S.C.-F.: resources, writing – review and editing, supervision, project administration, funding acquisition.

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