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Research Article

New genus of Cupressaceae from the Upper Cretaceous of Patagonia (Argentina) fills a gap in the evolution of the ovuliferous complex in the family

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Abstract The conifer family Cupressaceae encompasses seven subfamilies. Five of them were once considered to constitute the family Taxodiaceae, later eliminated because of its paraphyletic nature but remaining as an informal category for early-diverging Cupressaceae lineages. Among the taxodiaceous subfamilies, Athrotaxoideae shows a unique morphology in its ovuliferous complexes (OCs) and a phylogenetically unexplored fossil record. We describe the new genus and species *Patagotaxodia lefipanensis*, based on OC adpressions associated with leafy branches collected at the Maastrichtian section of the Lefipán Formation (Patagonia, Argentina), and we refer it to Athrotaxoideae. We include *Patagotaxodia* in total evidence phylogenetic analysis to test its affinity, and we recover it within the subfamilies Athrotaxoideae or Cunninghamioideae. However, we argue that the characters supporting the athrotaxoid affinity are more meaningful in a taxodiaceous systematic context. This placement is also supported by taxon inclusion-exclusion experiments. We discuss the position of other Cretaceous athrotaxoid records. With basis on the morphological insights provided by the OC morphology of extant and extinct Athrotaxoideae, we study the evolution of the OC morphology in the family in a phylogenetic context and discuss the results in the light of the fossil record of the family. We discuss how and when the different morphologies appeared in the family. Based on phylogenetic, temporal, morphological, and ontogenetic evidence, we conclude that the OC morphology shown by the subfamily Athrotaxoideae is intermediate between two of the most common morphologies within extant and extinct Cupressaceae species, one of which would show adaptative advantages over basal morphologies.

Key words: *Athrotaxis*, Athrotaxoideae, Cunninghamioideae, Cupressaceae Phylogeny, *Elatides*, ovuliferous complex evolution, *Patagotaxodia*, *Protodammara*, seed cone evolution,
Taxodiaceae.

1 Introduction

The conifer family Cupressaceae encompasses 30 genera with extant representatives, within the subfamilies Cunninghamioideae, Taiwanioideae, Athrotaxoideae, Sequoioideae, Taxodioideae, Callitroideae, and Cupressoideae (Gadek et al., 2000; Farjon, 2005; Mao et al., 2012). The subfamilies Cupressoideae and Callitroideae constitute the Cupresaceae *sensu stricto* lineage, whereas Taxodioideae, Sequoioideae, Athrotaxoideae, Taiwanioideae, and Cunninghamioideae form a paraphyletic group that was once considered to be the family Taxodiaceae (Pilger, 1926; Gadek, 2000). Both groups constitute the Cupressaceae *sensu lato*.

The three first diverging subfamilies of the crown group of Cupressaceae (i.e., Cunninghamioideae, Taiwanioideae, and Athrotaxoideae) are currently monotypic (Farjon, 2005); however, they were more diverse in the past as it is evidenced by their abundant fossil record (Hill & Brodribb, 1999; Stockey et al., 2005; LePage, 2009; Shi et al., 2014; Escapa et al., 2016; Herrera et al., 2017; Zhang et al., 2018; Atkinson et al., 2021). Cunninghamioideae, with two extant species within *Cunninghamia* R. Br. ex A. Rich., is restricted today to continental SE Asia and Taiwan Island (Farjon, 2005), and has the most abundant known fossil record by far, including numerous extinct species widely distributed since the Jurassic until the Neogene, many of which have been studied in phylogenetic analyses (Shi et al., 2014; Herrera et al., 2017; Atkinson et al., 2021). Taiwanioideae is represented by the single extant species *Taiwania cryptomerioides* Hayata, restricted to Chinese Mainland, Indochina, and Taiwan Island (Farjon, 2005), and by numerous fossil species recovered from Cretaceous and Cenozoic sediments of the Northern Hemisphere (Stockey et al., 2005; LePage, 2009; Zhang et al., 2018). The Cunninghamioideae and Taiwanioi-

Table 1 Extant and fossil species morphologically comparable to *Patagotaxodia*

Species	Subfamily	Age	Locality	Citation
Elatides bommeri	Cunninghamioideae Athrotaxoideae	Early Cretaceous	Wealden Gp., Belgium	Harris (1953), this study (Fig. 7)
Athrotaxis ungeri (only leaves)	Athrotaxoideae	Early Cretaceous	Anfiteatro del Ticó Fm., Argentina	Archangelsky (1963), Villar de Seoane (1998)
Athrotaxis ungeri	Athrotaxoideae	Early Cretaceous	Kachaike Fm., Argentina	Halle (1913), Florin (1940), Passalia (2007), Del Fueyo et al. (2008)
Athrotaxites yumenensis	Athrotaxoideae	Early Cretaceous	Zhonggou Formation, China	Dong et al. (2014)
Athrotaxites berryi	Athrotaxoideae	Early Cretaceous	Baltimore Gp., Luscar Fm., Bullhead Gp., Hazelton Gp., Canada Kootenai Fm., US; Razdolnaya River Basin, South Primorye, Russia	Bell (1956), Krassilov (1967), Miller & LaPasha (1983)
Protodammara sp.	Athrotaxoideae	Early Cretaceous	Akaiwa Fm., Japan	Kimura & Sekido (1978)
Protodammara speciosa	Athrotaxoideae	Late Cretaceous	Raritan Fm., US	Hollick & Jeffrey (1906, 1909)
Protodammara reimatamoriori	Athrotaxoideae	Late Cretaceous	Tupuangi Fm., Chatham Islands, New Zealand	Mays et al. (2017a), Mays & Cantrill (2019)
Patagotaxodia lefipanensis	**Athrotaxoideae**	**Late Cretaceous**	**Lefipán Fm., Ar**	**This study**
Athrotaxites stockeyi	Athrotaxoideae	Late Cretaceous	Raritan Fm., US	Escapa et al. (2016)
Athrotaxis novae-zeelandiae (only leaves)	Athrotaxoideae	Late Cretaceous	Taratu Fm., Shag Point, New Zealand	Ettingshausen (1887, 1891), Florin (1960), Pole (1995), Hill & Brodribb (1999), Hill (2001)
'*Athrotaxis*' *couttsiae*	Athrotaxoideae	Paleocene–Miocene	Calau Beds, Brandenburg, Germany; Kazakhtan; UK	Mai (1998)
Athrotaxis tasmanica (only leaves)	Athrotaxoideae	Eocene	Buckland, Tasmania, Australia	Townrow (1965, 1967)
Athrotaxis rhomboidea	Athrotaxoideae	Oligocene	Little Rapid River, Tasmania, Australia	Hill et al. (1993)
Athrotaxis mesibovii	Athrotaxoideae	Oligo-Miocene	Lea River, Little Rapid River, and Pioneer, Tasmania, Australia	Hill et al. (1993)
Athrotaxis cf. *laxifolia* (only leaves)	Athrotaxoideae	Pleistocene	Regatta Point, Tasmania, Australia	Hill et al. (1993)
Athrotaxis cupressoides	Athrotaxoideae	Extant	Tasmania, Australia	Farjon (2005)
Athrotaxis laxifolia	Athrotaxoideae	Extant	Tasmania, Australia	Farjon (2005)
Athrotaxis selaginoides	Athrotaxoideae	Extant	Tasmania, Australia	Farjon (2005)
Elatides williamsonii	Cunninghamioideae	Middle Jurassic	Cloughton Fm., UK	Harris (1943)
Elatides harrisi	Cunninghamioideae	Early Cretaceous	Haizhou Fm., China	Zhou (1987), Dong et al. (2013)
Elatides zhoui	Cunninghamioideae	Early Cretaceous	Khukhteeg Fm., Mongolia	Shi et al. (2014)
Sphenolepis kurriana	Cunninghamioideae	Early Cretaceous	Wealden Gp., Belgium	Harris (1953)
Cunninghamia lanceolata	Cunninghamioideae	Extant	Chinese Mainland and Vietnam	Farjon (2005)
Cunninghamia konishii	Cunninghamioideae	Extant	Taiwan Island	Farjon (2005)

Abbreviations under "Locality": Gp., group; Fm, formation.

deae were recovered as a monophyletic group in a few phylogenetic studies that included extant and fossil species (e.g., Escapa et al., 2008), but they are usually recovered as successive sister clades to all other Cupressaceae (e.g., Shi et al., 2014). The subfamily Athrotaxoideae includes the single extant genus *Athrotaxis* D. Don with three modern species, all endemic to Tasmania, and it is the only taxodiaceous subfamily with extant representatives in the Southern Hemisphere (Cullen & Kirkpatrick, 1988; Farjon, 2005). The fossil record of the athrotaxoids is relatively scarce, it comes mainly from Cretaceous and Cenozoic fossil localities of both hemispheres (Hill & Brodribb, 1999; Hill, 2001; Stockey, 2005; Escapa et al., 2016; Table 1) and includes fossil species within *Athrotaxis*, as well as the fossil genera *Athrotaxites* and *Athrotaxopsis* (e.g., Archangelsky, 1963; Miller & LaPasha, 1983; Hill et al., 1993; Dong et al., 2014; Escapa et al., 2016; Table 1). Other Cupressaceae extinct genera have species that resemble *Athrotaxis*, although no formal referrals to the subfamily were proposed in most cases (e.g., Hollick & Jeffrey, 1906, 1909; Harris, 1953; Mays & Cantrill, 2019; Table 1).

Cupressaceae seed cones show an extensive morphological diversity in their ovuliferous complexes (OC) (Takaso & Tomlinson, 1989, 1990, 1992; Farjon, 2005; Jägel & Dörken, 2014, 2015a, 2015b). This diversity is particularly noticeable in the overall shape of the OCs and in their highly variable number of ovules among genera, species, and even among OCs within the same cone (Farjon, 2005; Little, 2006; Schulz & Stützel, 2007). The high variability in the number of ovules per OC in Cupressaceae contrasts with the situation in most extant conifer families, where each OC present either invariably two (i.e., Pinaceae, Farjon, 2010) or one seed (i.e., Podocarpaceae, Araucariaceae, Taxaceae; Farjon, 2010). The Cupressaceae morphological diversity has been rarely studied in phylogenetic contexts in the past (e.g., Schulz & Stützel, 2007), constituting an obstacle for the understanding of its evolution.

In this contribution, we describe a new fossil genus and species, which we refer to Cupressaceae *sensu lato*, based on adpressions of OC found in close association to leafy twigs that resemble the athrotaxoid morphology. The fossils were collected in Upper Cretaceous (Maastrichtian) sediments of the Lefipán Formation, Patagonia, Argentina. We performed a phylogenetic analysis including the new species together with other significant athrotaxoid and cunninghamioid fossil and extant species, and in the light of our results, we discuss the morphological evolution of the OC in the Athrotaxoideae lineage. Moreover, we interpret the OC morphology of extant and fossil athrotaxoids in the context of that of other Cupressaceae subfamilies and provide a novel reconstruction of the evolution of this organ for the family, which is discussed in the light of the fossil record of the group.

2 Material and Methods

2.1 Geologic setting

The Cañadón Asfalto Basin, located in Central Patagonia, comprises sediments accumulated between the Jurassic and the early Paleocene (Cúneo et al., 2013; Figari et al., 2015). The Lefipán Formation corresponds to the last stratigraphic section of the basin infilling (Figari et al., 2015). This formation was deposited in the Paso del Sapo embayment, in a tide-dominated delta, during the latest Cretaceous and earliest Paleocene (Scasso et al., 2012). The Lefipán Fm. is best exposed along the Middle Chubut River Valley (Figs. 1A, 1B) where it overlays outcrops of the Campanian-early Maastrichtian Paso del Sapo Formation (Scasso et al., 2012; Fazio et al., 2013; Figari et al., 2015; Vellekoop et al., 2017; Butler et al., 2020). The age of Lefipán sediments was determined to be Maastrichtian to early Paleocene (Danian) based on molluscs (Medina et al., 1990; Medina & Olivero, 1994; Scasso et al., 2012; Aberhan & Kiessling, 2014), as well as terrestrial (Baldoni, 1992; Baldoni & Askin, 1993; Barreda et al., 2012) and marine palynomorphs (Vellekoop et al., 2017).

Within the Lefipán Fm., the K/Pg boundary was constrained to 4 m of sequence based on biostratigraphic markers (Barreda et al., 2012). However, the limit layer itself is apparently not preserved due to a stratigraphic hiatus caused by a sea-level regression across the K/Pg boundary (Barreda et al., 2012; Vellekoop et al., 2017). The Cretaceous portion of the Lefipán Fm. yields both micro- and macrofossil assemblages of numerous fossil plants, the latter differ in composition among the localities at the south margin of the Chubut River, which are slightly younger in age, and those at its north margin (Cúneo et al., 2008; Wilf et al., 2017; Andruchow-Colombo et al., 2018; Escapa et al., 2018; Martínez et al., 2018; Stiles et al., 2020; Cúneo et al., 2021). Contrastingly, the paleobotanical component of the Danian portion of Lefipán only preserves palynological remains (Barreda et al., 2012). The palynology of Lefipán has been studied in detail for the southern localities (Baldoni, 1992; Baldoni & Askin, 1993; Barreda et al., 2012) showing major changes in the composition of its paleoflora across the K/Pg boundary (Barreda et al., 2012).

The Cañadón del Loro locality of the Lefipán Fm. is located northwest of Chubut Province (Patagonia, Argentina) at the northern margin of the homonymous river (Fig. 1B). The macroflora of Cañadón del Loro is constrained to four fossiliferous levels (NF1–4, Fig. 1C) and it is characterized by an angiosperm flora of low diversity, possibly due to biostratinomic biases (Martínez et al., 2018; Cúneo et al., 2021), conifers of the families Araucariaceae and Cupressaceae (Andruchow-Colombo et al., 2018; Cúneo et al., 2021), and ferns (Cúneo et al., 2021). The specimens here described were collected at the four fossiliferous levels of Cañadón del Loro locality, although the fossiliferous level 1 yield the most fossils (NF1 = *coníferas* site). This material includes numerous isolated OC found in intimate association with leafy twigs.

2.2 Fossil preparation and illustration

The fossil specimens studied are preserved as impressions and compressions. The material was prepared using standard mechanical techniques (i.e., microscribers and 3.0 mm angled slit knives) and photographed with a Canon EOS 7D camera (Canon Corp., Melville, NY, USA) with a Canon EF-S 60 mm macro lens at the Museo Paleontológico Egidio Feruglio (MEF, Trelew, Chubut, Argentina), and with a Nikon DS-Ri2 camera attached to a Nikon SMZ18 stereoscopic microscope at the Gandolfo Lab (L.H. Bailey Hortorium, Plant Biology Section, School of Integrative Plant Science, Cornell

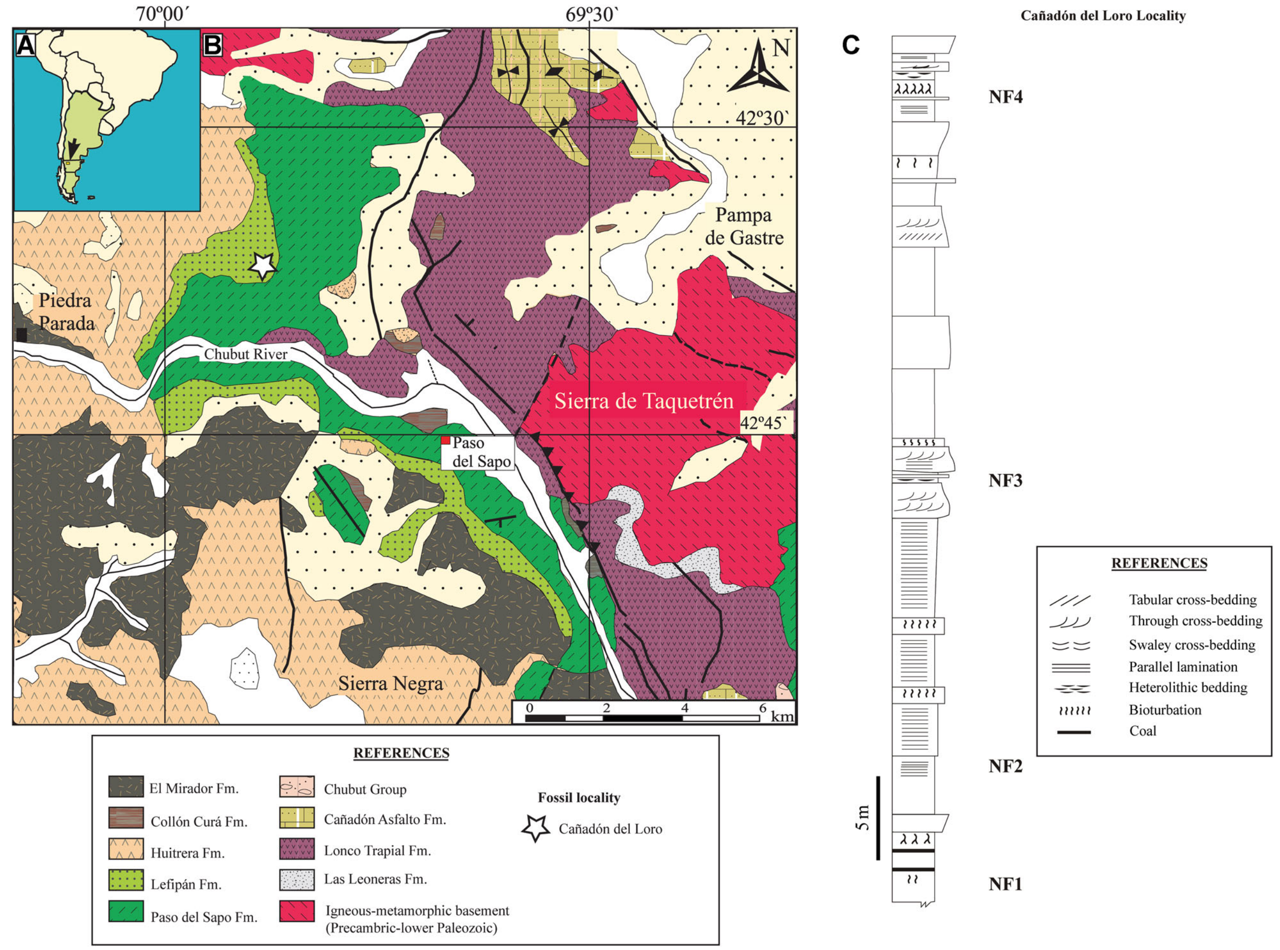

Fig. 1. Geologic map and stratigraphic section of Cañadón del Loro locality, Lefipán Formation. **A**, Localization of the study area. **B**, Detail of the area with the Cañadón del Loro locality (Chubut Province, Argentina) marked with a white star; map modified from Fazio et al. (2013). **C**, Partial stratigraphic section of the lower portion of Lefipan Formation at the Cañadón del Loro locality.

University, NY, USA). Photos were processed with Adobe Photoshop Lightroom Classic 10.2 (Adobe, Mountain View, California, USA) for white balance and micro-contrast enhancing, and with Adobe Photoshop 22.3.1 for plate assembling. Drawings were made in Adobe Illustrator 25.2.1.

The fossil specimens are housed permanently at the Paleobotany Collection of the Museo Paleontológico Egidio Feruglio (repository abbreviation MPEF-Pb), Trelew, Chubut, Argentina.

2.3 Terminology and abbreviations

The abbreviation “OC” refers to “ovuliferous complex,” both of these terms used throughout the text. Following Escapa et al. (2008), we chose the designation “ovuliferous complex” as we agree that the structures identified as “scale” and “bract” in cupressaceous seed cones might not be homologous to those of the typical conifer cone (Florin, 1951). This was discussed by several authors based on ontogenetic and paleontological studies (Cúneo, 1985; Archangelsky & Cúneo, 1987; Tomlinson & Takaso, 2002; Escapa et al., 2008).

To describe the overall morphology of Cupressaceae OCs, we follow those used in previous studies (i.e., foliate, peltate, valvate; Farjon, 2005; Stockey et al., 2005; Shi et al., 2014; Herrera et al., 2017) and we define a fourth OC morphological type denominated “Pseudopeltate” that represents an intermediate form between the foliate and peltate. This interpretation is supported by observations of living and fossil material, as well as by prior ontogenetic studies (e.g., Farjon, 2005), and it is explained in detail in Section 4.6 (evolution of the OC morphology). *Foliate* OCs are bifacially flattened, have a varying degree of lignification with a distal area generally thinner than the main body; in the Cupressaceous foliate OCs, the seeds are distally positioned (e.g., *Cunninghamia*). *Pseudopeltate* OCs show a similar general outline to the foliate OCs but are more tridimensional than the foliate type, tend to have a proportionally longer and thinner stalk, and the seeds are located distally on the widened portion of the complex that is culminated in a generally lignified cap (e.g., *Athrotaxis*). *Peltate* OCs have a well-defined stalk and a pelta perpendicular to it, generally bears multiple seeds at the internal side of the pelta and the adaxial side of the stalk, and peltae become fused together in the post-pollination cone protecting the developing seeds (e.g., *Cupressus*, Farjon, 2005). *Valvate* OCs are characterized by a shell-like, lignified morphology, some presenting interlocking cells located on their edges, and are associated with the presence of multiple seeds per OC (e.g., *Widdringtonia*, Little, 2006). These four OC types are illustrated in Fig. 8. Overall, following the similarities between neighbor states (i.e., foliate-pseudopeltate; pseudopeltate-peltate; peltate-valvate) and ontogenetic studies that show the intermediary condition of the pseudopeltate morphology (Farjon, 2005), these four OC morphologies are interpreted to be sequential stages on a transformational series in the context of the family Cupressaceae (see Section 4.6 Evolution of the ovuliferous complex morphology).

2.4 Phylogenetic analysis

The new Patagonian taxon was included in a combined (i.e., molecular and morphological) matrix to test its affinities within the family Cupressaceae. In our phylogenetic analyses, the newly defined taxon and the associated leaves are being treated as a single terminal (detailed justification for this is provided in the discussion Section 4.3 on the foliage and seed complexes association), which is referred to as the *Patagotaxodia* plant or simply as *Patagotaxodia*. The taxon sampling includes 21 species (Table IA, Appendix I), representing 14 extant and 5 extinct Cupressaceae species, *Sciadopitys verticilata* (Sciadopityaceae), and *Cedrus deodara* (Pinaceae) that was used for rooting the tree. In addition to the new Patagonian fossil taxon, the fossil species included in the analyses are *Elatides williamsonii* (Seward 1900; Harris, 1943), *Elatides zhoui* Shi, Leslie, Herendeen, Ichinnorov, Takahashi, Knopf et Crane (Shi et al., 2014), *Elatides bommeri* Harris (1953), and *Protodammara speciosa* Hollick & Jeffrey, 1906, 1909). While the species *E. williamsonii* and *E. zhoui* have been included in previous phylogenetic matrices (Shi et al., 2014; Herrera et al., 2017), this is the first time that *E. bommeri* and *P. speciosa* are considered in phylogenetic analyses, and were selected here due to their morphological similarities to the new Patagonian fossil species.

The combined matrix comprises 13 386 characters (of which 5.86% are informative for parsimony; Table IA). The new matrix has 11 blocks, the first one with 26 vegetative and reproductive morphological characters (Appendix SI). The characters and character scorings used in the analyses were obtained from combinations and modifications of previously published matrices by diverse authors (Gadek et al., 2000; Farjon, 2005; Escapa et al., 2008; Shi et al., 2014; Herrera et al., 2017; see Appendix I). The remaining 10 blocks of the combined matrix correspond to six molecular markers from the chloroplast (*matK*, *petB-D*, *psbB*, *rbcL*, *rps4*, *trnL-F*, Table IB), two mitochondrial (*atp1*, *coxI*, Table IC), and two nuclear (*18S*, *26S*, Table IC). The DNA sequences were downloaded from *Genbank* (https://www.ncbi.nlm.nih.gov/genbank/; for accession numbers see Supplementary Material: Tables IB, IC, Appendix I) and were aligned and formatted with GB-to-TNT (Goloboff & Catalano 2012), using MAFFT (Multiple Sequence Alignment Software) v7.487 (Katoh et al., 2002; Katoh & Standley, 2013) as the alignment software under default parameters. The combined matrix is available in the supplementary information as a TNT file (Appendix II), and the nexus for the morphological matrix was uploaded to *Morphobank* (https://morphobank.org/) under the project number P4095.

Phylogenetic analyses were conducted on TNT 1.5 (Goloboff et al., 2003, 2008; Goloboff & Catalano, 2016) under maximum-parsimony optimality criterion, with equal weights. All morphological characters were treated as unordered except for one seed cone character (16, mature OC morphology), which was treated as additive (Appendix I; see justification in Section 2.5; the alternative treatment of this character as non-additive is provided in Appendix V). The parsimony analyses were performed as implicit enumerations (i.e., exact search algorithm; Goloboff et al., 2008). Unstable taxa were pruned from the consensus (command *ne//*) to show their alternative positions over the consensus topology. Group synapomorphies (common to all most parsimonious trees) were calculated with the TNT implemented command *apo*. Absolute frequencies of Symmetric Resampling were calculated for group support (Goloboff et al., 2003).

Taxon inclusion–exclusion experiments were performed to test the robustness of the affinity hypotheses of the new species; these consist of the alternative exclusion from the matrix of the fossils recovered within the Cunninghamioideae and Athrotaxoideae lineages, as well as the removal of every fossil from the matrix except for the new species.

2.5 Mapping of the OC morphology

The additive multistate character "mature ovuliferous complex morphology", as defined in the character list (character 16, Appendix I, Supplemental Information), was mapped on a reference topology that was built as a combination of the topologies published by Mao et al. (2012) and Leslie et al. (2018) so it would include all extant genera of Cupressaceae, as well as Sciadopityaceae, Araucariaceae (as a single terminal), and Pinaceae (also as a single terminal, for rooting the tree). The character mapping was performed in TNT 1.5 (Goloboff et al., 2003, 2008; Goloboff & Catalano, 2016). The mapping of this same character treated as unordered is provided as supplemental information.

The mature OC morphology is considered as an additive character with four states (i.e., foliate, pseudopeltate, peltate, and valvate; defined in Section 2.3 on terminology and abbreviations) because (i) the pseudopeltate state presents an intermediate morphology between the foliate and peltate states; and (ii) the valvate morphology appears in three subfamilies consistently recovered as the most nested in the phylogenetic history of the family (e.g., Mao et al., 2012; Leslie et al., 2018), it is the last morphology to be registered in the fossil record (see Section 4.6 on the evolution of the OC morphology), and it presents similarities in the margin morphology and interlocking of OCs with the peltate morphology (Little, 2006).

3 Results

3.1 Systematic paleontology

Order Cupressales Link 1831
Family Cupressaceae Gray 1821
Subfamily Athrotaxoideae L.C. Li 1992

Genus *Patagotaxodia* gen. nov. Andruchow-Colombo
Figs. 2, 3

Type species: Patagotaxodia lefipanensis Andruchow-Colombo

Generic diagnosis: Ovuliferous complexes shed from the cone at maturity; pseudopeltate, sub-rhomboidal to umbrella-shaped, longer than wider, with a prominent distal cap, woody with multiple resin canals; 3–5(–6) seeds located at the widest point of the OC in a single row.

Derivation of name: the first part of the generic name "*Patagotaxodia*" refers to the Patagonian region, where the fossils were collected, while the second part of the name refers to the similarity of the fossils to members of the taxodiaceous Cupressaceae.

Species: Patagotaxodia lefipanensis sp. nov. Andruchow-Colombo*Derivation of name:* the specific epithet refers to the Lefipán Formation where the fossil remains were collected.

Holotype: MPEF-Pb 10862. Figs. 2, 3.

Paratypes: MPEF-Pb 5824, 10851, 10855-10867, 10879-10881, 10884, 10887, 10891, 10892, 10895, 10896, 10906, and 10909-10911.

Type Locality: Fossiliferous level 1 (NF1, *coníferas* site), Cañadón del Loro locality situated on the north margin of the Chubut River, Lefipán Formation, Cañadón Asfalto Basin, central Patagonia, Chubut Province, Argentina.

Stratigraphic occurrence: Fossiliferous level 1–4 at Cañadón del Loro locality, Maastrichtian (Upper Cretaceous), Lefipán Formation.

Specific diagnosis: Pseudopeltate ovuliferous complexes, sub-rhomboidal to umbrella-shaped, longer than wider, 7–11 resin canals at its widest point, sometimes emerging to the surface at the widest point; distal cap of the ovuliferous complex slightly convex to bell-shaped, with a distal prolongation, and multiple resin canals; seeds 3–5(–6) at the widest point of the ovuliferous complex in a single row.

Description: Ovuliferous complexes (OCs) are always found isolated (Figs. 2, 3), although commonly associated in the same fossil sites and even in the same hand specimens. OC pseudopeltate, sub-rhomboidal to umbrella-shaped, longer than wider (Figs. 2, 3), without differentiation between a bract and a scale; 9.1–21.4 mm long (n: 32, mean: 15.3 mm, sd: 3.0 mm), 1.3–4.4 mm wide (n: 34, mean: 2.6 mm, sd: 0.7 mm) at the basal narrow portion of the complex, and 5.4–13.6 mm wide at its widest point (n: 36, mean: 8.9 mm, sd: 2.4 mm). The position of the maximum width of the OC is at 55.5–78.2% (n: 29, mean: 64.8%, sd: 5.8%) of the total length, delimiting the basal narrow portion that is the longest portion of the OC. The OC body is woody in appearance and shows a single -or possibly a few- resin canals entering at its base and dividing into 7–11 resin canals (n: 9, mode: 10) at the widening point of the OC (Figs. 2A, 2F, 2J–L, 3), which is located at approximately 38.4–60.7% (n: 26, mean: 50.1%, sd: 5.6%) of its total length. In some specimens, the resin canals appear to emerge to the surface at the widest point of the complex (Figs. 2F, 2K, 2L, black arrowheads), suggesting the irrigation of multiple seeds in that area. Distally to this line, there is a distal cap (Fig. 2A, black arrowhead); its shape ranges from slightly convex (Fig. 2J) to bell-shaped (Fig. 2I); and in certain specimens preserve a distal prolongation (Figs. 2I, 2K, white arrowheads). The distal cap shows prominent and regular striation, corresponding with resin canals trajectory (Figs. 2A–E, 2I, 2K, 3).

Although seeds are commonly absent on the OC, between three and five or six oval potential seeds or seed scars are found at the widest point of the OC in a single row in a few specimens (Figs. 2A, white arrowheads; 3).

Notes: Because the ovuliferous complexes (OCs) are always found isolated, although intimately associated in the sediments, we interpret that they were shed from the cones at maturity. In most cases, these OCs lack seeds, suggesting that they were likely mature and the seeds were already dispersed.

3.2 Associated foliage

Figs. 4–6

Studied material: MPEF-Pb 8326, 10847, 10852-10854, 10859, 10862, 10871-1876, 10878-10880, 10883, 10885, 10889-10891, 10894, 10903, and 10905.

Description: Leafy branches up to 13.8 cm long and 7.7–15.5 mm wide including leaves. Naked branches are 1.1–6.4(–13.3) mm wide. Leaves are spirally arranged (Figs. 4C, 4D), spreading but overlapping for most of their length (Figs. 4, 5). Leaf insertion angle of 28°–67° in fully developed branches (Figs. 4C–J; mean: 47°; sd: 6°; n: 33), and lower toward the apical shoot region, where the leaves are more densely packed (Fig. 4K). Leaf shape is subulate to linear (Figs. 4A, 4C, 4F, 5B), nearly falcate in lateral view, rhomboidal in cross section near the base and becoming bilaterally flattened toward the middle leaf portion (Figs. 4C–H, 5D–F), and have an acute apex of 17°–40° (mean: 25°; sd: 6°; n: 10). Leaves are 7.1–18.2 mm long (mean: 12.3 mm, s.d: 2,4 mm, n: 24) and 0.8–2.2 mm wide (mean: 1.4 mm; s.d.: 0.3 mm; n: 22); and they are attached through all their base. Leaf base is rhomboidal and expanded (Figs. 4D, 4H, 5B, 5C), 0.8–3.4 mm high (mean: 2.2 mm; s.d.: 0.5; n: 20) and 0.5–2 mm wide (mean: 1.5 mm; s.d.: 0.3 mm; n: 20). Each leaf base has a longitudinal ridge, commonly corresponding to the abaxial leaf keel (Figs. 4D, 5C). At younger branches, the leaf bases are rarely observable because most of the leaves are still intact (Figs. 4A, 4B, 4K); in older branches leaves appear more fragile and it is usual to observe adjacent leaf bases not presenting inter-areas (Figs. 4C, 4D, 4G, 4H, 5C). At the oldest (thickest) branch found, the leaf bases are markedly expanded, rhomboidal to sub-oval in shape, 2.6–3.4 mm high (mean: 3.2 mm; s.d.: 0.4 mm; n: 4 leaf bases of a single specimen) and 2.3-3.1 mm wide (mean: 2.7 mm; s.d.: 0.4 mm; n: 4 leaf bases of a single specimen), and present inter-areas that are 0.9–1.7 mm thick (mean: 1.3 mm; s.d.: 0.3 mm; n: 4 interareas of a single specimen; Fig. 5G). Leaves show two lateral darker bands in their abaxial epidermis, possibly corresponding to stomatal bands (Figs. 6A, 6B) and certain specimens show apparent mummified anatomy, showing a central vascular bundle and probable lateral bands of transfusion tissue (Fig. 6D).

3.3 Phylogenetic analyses

The analysis of the matrix that includes the complete taxon sampling (i.e., including 16 extant and 5 fossil taxa) resulted in three most parsimonious trees (MPT) of 2860 steps, which differ in the position of *Patagotaxodia* plant (i.e., *Patagotaxodia lefipanensis* OC + associated leaves, see Section 4.3 on foliage and seed complexes association), also referred here as *Patagotaxodia*. The strict consensus of the three

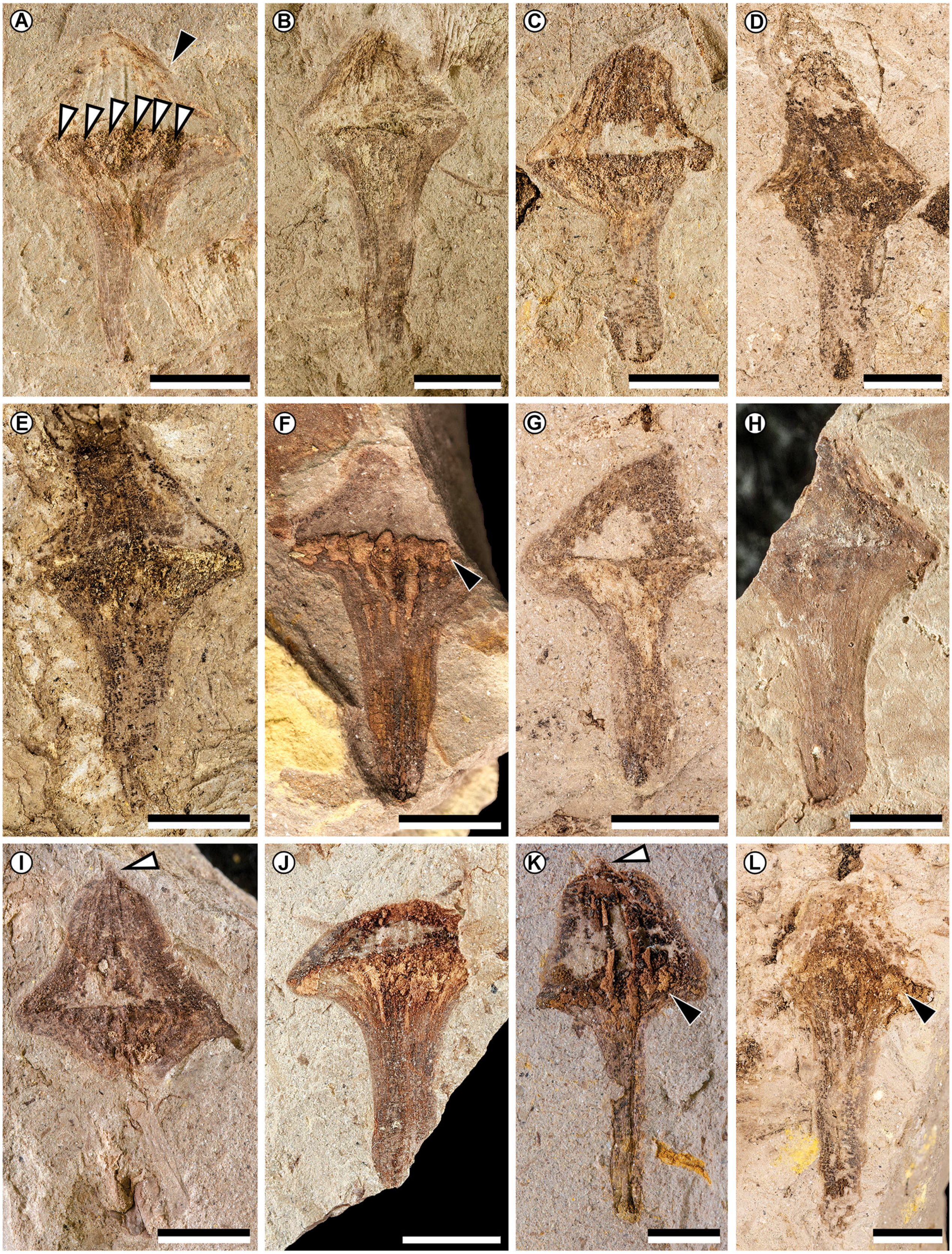

Fig. 2. Continued

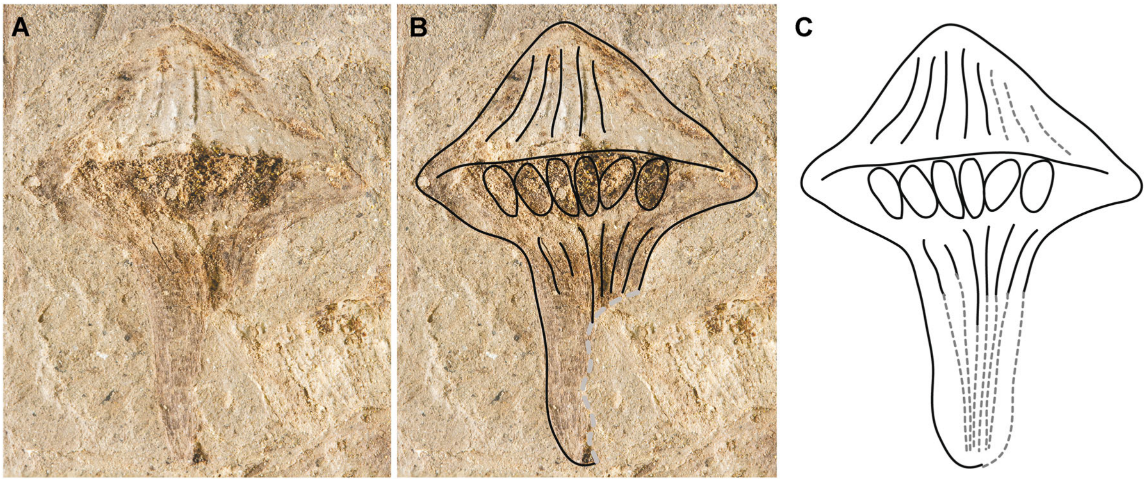

Fig. 3. Morphology of the holotype of *Patagotaxodia lefipanensis* sp. nov. **A,** Holotype of *P. lefipanensis*, MPEF-Pb 10862 as illustrated in Fig. 2A. **B,** Holotype of *P. lefipanensis* with a line drawing overlaid showing the main characters observed: general shape, trajectory of resin canals, and position and morphology of the seeds. **C,** line drawing of the holotype of *P. lefipanensis*, showing the main characters observed (complete, black line), with inferred missing parts of the fossil in gray, dashed lines.

topologies, with the three alternative positions of *Patagotaxodia* indicated with black and white circles, is shown in Fig. 7. In these three topologies, the *Patagotaxodia* plant is recovered either as part of the subfamilies Athrotaxoideae or Cunninghamioideae (Fig. 7, alternative positions marked in gray). Within the Athrotaxoideae, *Patagotaxodia* is recovered as sister to the extinct *Elatides bommeri* or to *Protodammara speciosa* (Fig. 7, white circles). In these two alternative topologies, *Patagotaxodia, E. bommeri,* and *Protodammara speciosa* form a monophyletic group sister to a clade conformed by the three extant *Athrotaxis* species (Fig. 7). Within the Cunningamioideae, *Patagotaxodia* is recovered as sister to a clade that encompasses the extinct *Elatides williamsonii* and *E. zhoui* and the extant *Cunninghamia lanceolata* (Fig. 7, black circle). In all MPT, the genus *Elatides* is recovered as polyphyletic (Fig. 7, white arrowheads), with two species within the Cunninghamioideae lineage (i.e., *E. williamsonii* and *E. zhoui*) and one within the Athrotaxoideae lineage (i.e., *E. bommeri*).

Within the two phylogenetic hypotheses that recover the *Patagotaxodia* plant as a member of the Athrotaxoideae (Fig. 7; white circles), the single synapomorphy supporting the grouping of *Patagotaxodia* and *Protodammara speciosa* is the shedding of the mature OC (character 14, state 0), whereas the synapomorphy supporting its grouping with *E. bommeri* is the falcate shape of adult leaves (character 24, state 0). The synapomorphy of the clade formed by *Patagotaxodia*, *P. speciosa*, and *E. bommeri* (common to the two trees containing this clade) is the absence of seed wings (character 21, state 0), a character scored by *Protodammara* and *Elatides* but not for *Patagotaxodia*. The common synapomorphy for the athrotaxoids is the presence of three seeds per OC (character 18, state 1), and for *Athrotaxis* it is the distribution of the transfusion tissue in leaves in a continuous band across the adaxial side of the xylem (character 25, state 1). Other features that support the placement of *Patagotaxodia* within the subfamily Athrotaxoideae are the mature pseudopeltate OC morphology, the lack of differentiation of the ovuliferous scale in mature seed cones, and the number of ovules associated with each OC (characters 16–18; Appendix III).

Within the phylogenetic hypothesis that recovers the *Patagotaxodia* plant as a member of the Cunninghamioideae (Fig. 7; black circle), the single synapomorphy supporting the grouping of *Patagotaxodia* and the clade that includes *Elatides williamsoni*, *E. zhoui*, and *Cunninghamia lanceolata* is the presence of four to six ovules per OC (character 18, state 2). The synapomorphy of the clade formed by *Elatides williamsoni*, *E. zhoui*, and *Cunninghamia lanceolata* is the small and membranous morphology of the ovuliferous scale in mature seed cones (character 17, state 1).

The analysis that excluded the cunninghamioid fossil species (i.e., *Elatides williamsonii* and *E. zhoui*), but included the athrotaxoid fossils *E. bommeri* and *Protodamara speciosa*

Fig. 2. Morphological diversity of the ovuliferous complexes (OCs) referred to *Patagotaxodia lefipanensis* sp. nov. **A,** Holotype of *P. lefipanensis*, MPEF-Pb 10862, white arrowheads indicate the position of seeds/seed scars, black arrowhead indicates the distal cap. **B,** MPEF-Pb 10861. **C,** MPEF-Pb 10857 b. **D,** MPEF-Pb 10857 a. **E,** MPEF-Pb 10860 b. **F,** MPEF-Pb 10909, black arrowheads are one of the points of emergence of the resin canals to the surface of the OC. **G,** MPEF-Pb 10863 b. **H,** MPEF-Pb 10867 a. **I,** MPEF-Pb 10864, white arrowhead indicates the distal prolongation. **J,** MPEF-Pb 10911. **K,** MPEF-Pb 10851 a, white arrowhead indicates the distal prolongation, black arrowhead indicates one of the points of emergence of the resin canals to the surface of the OC. **L,** MPEF-Pb 10866 a, black arrowhead indicates one of the points of emergence of a resin canal to the surface of the OC. Scale bars A–G, I, J = 5 mm; H, K, L = 2.5 mm.

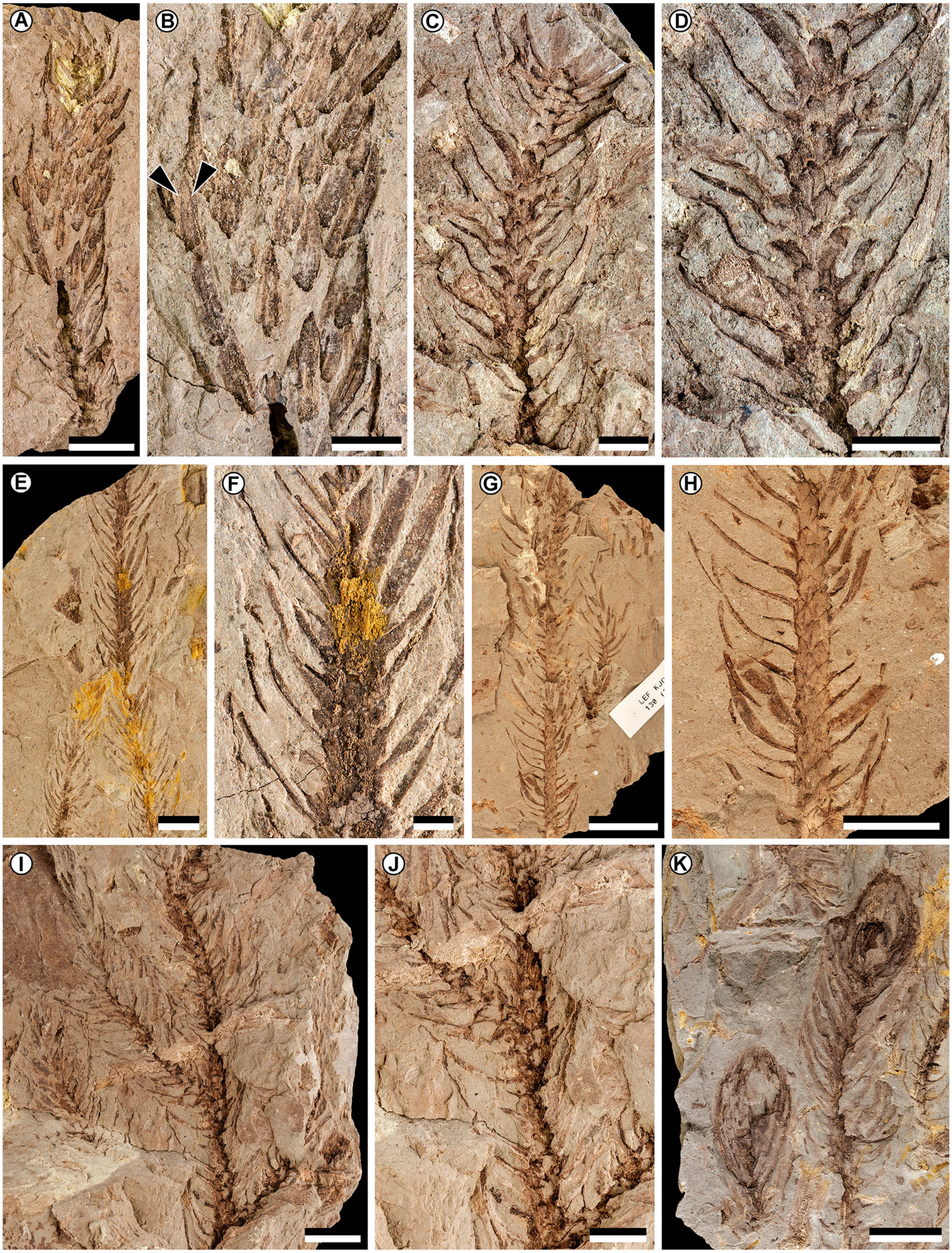

Fig. 4. Continued

as well as the new taxon, recovered two most parsimonious trees. Both trees show *E. bommeri*, *Patagotaxodia*, and *P. speciosa* as part of the Athrotaxoideae clade (Appendix IVA). In these hypotheses, *Patagotaxodia* is recovered as sister to *P. speciosa* or to *E. bommeri* (Appendix IV). The synapomorphies supporting the grouping of [*Patagotaxodia* + *Protodammara*], [*Patagotaxodia* + *E. bommeri*], [*Protodammara* + *Patagotaxodia* + *E. bommeri*], the extant species of *Athrotaxis*, and the total group of the Athrotaxoideae subfamily are the same as recovered for the complete matrix.

Alternatively, the analysis that excluded only the athrotaxoid fossils (i.e., *Elatides bommeri* and *Protodammara speciosa*), but included the cunninghamioid fossils *E. williamsonii* and *E. zhoui*, as well as the new taxon, recovered three most parsimonious trees. In this analysis, the *Patagotaxodia* plant is recovered as part of the cunninghamioid lineage in the same position as the recovered by the analysis of the complete matrix (Fig. 7, black circle; Appendix IVB), or within the athrotaxoid lineage, either as sister to *Athrotaxis selaginoides* or to the clade of extant *Athrotaxis* (Appendix IVB).

Finally, the analysis that excluded all fossils except the *Patagotaxodia* plant recovered the new Patagonian taxon only within the Athrotaxoideae, as sister to *Athrotaxis selaginoides* or to the clade of extant *Athrotaxis* (Appendix IVC).

The analysis of the complete matrix was performed also with character 16 as non-additive and resulted in the same maximum-parsimony topologies as when that character was treated as an additive (Fig. 7; Appendix V).

4 Discussion

4.1 Assignment to Cupressaceae

The ovuliferous complexes of *Patagotaxodia lefipanensis* have several features that link them to the conifer family Cupressaceae. These features include the pseudopeltate overall morphology of the ovuliferous complexes (OCs), the absence of a clear differentiation between a bract and a scale, the presence of multiple seeds per OC, and the seed distal attachment in the OC, all common features within this family, particularly among the "taxodiaceous" Cupressaceae (Farjon, 2005), and markedly differ from other conifer families (Farjon, 2010). The datum that all the OC of *P. lefipanensis* were found isolated strongly suggests that these were dehisced from the cone at maturity, a feature extremely rare in extant Cupressaceae (i.e., only reported for *Taxodium*), being the commonest dehiscence units the seeds or, in certain genera, the complete cone (Farjon, 2005; Contreras et al., 2017). Nevertheless, some Cupressaceae fossils, such as the species of *Protodammara* Hollick et Jeffrey, seem to have dispersed their OCs (Hollick & Jeffrey, 1906, 1909; Mays & Cantrill, 2019), as it is inferred for *Patagotaxodia*.

In the context of determinating the affinity of *Patagotaxodia* with extant conifer families, the leaves intimately associated with it do not provide much information because they are amongst the commonest leaf types within conifers (i.e., subulate to linear, tetragonal in cross section toward its base, with a decurrent and expanded base), being present not only in Cupressaceae but also in Araucariaceae, Pinaceae, and Podocarpaceae (de Laubenfels, 1953; Farjon, 2010).

Another conifer group that might be considered in the comparisons with *Patagotaxodia* is the extinct order Voltziales Andreanszky (1954), which biochron extends from the Pennsylvanian to the Early Cretaceous (Florin, 1951; Miller, 1977; Stewart and Rothwell, 1993; Herrera et al., 2015). *Patagotaxodia* shares with Cretaceous Voltziales species the overall morphology of the OC and the presence of multiple seeds per OC. However, the Cretaceous voltzialean conifers, which are members of the family Krassiloviaceae, produced peltate OCs with multiple spines at their distal area. Moreover, while some Paleozoic Voltziales have a leaf morphology comparable to that of the Patagonian remains (e.g., Stewart & Rothwell, 1993; Hernandez-Castillo et al., 2009), Mesozoic Voltziales are characterized by expanded, multiveined leaves (Escapa et al., 2010; Morel et al., 2011; Bomfleur et al., 2013; Bodnar et al., 2020; Herrera et al., 2020).

4.2 Comparisons

4.2.1 Protodammara and Patagotaxodia

The genus *Protodammara* was erected for small three-ovulated, kite-shaped OC from the Upper Cretaceous Raritan Formation (Staten Island, New York, USA; Hollick & Jeffrey, 1906). Depending on the authors, *Protodammara* was included within Araucariaceae (Hollick & Jeffrey, 1906), the extinct family Volziaceae (Anderson et al., 2007), or Cupressaceae (Miller, 1977; LaPasha & Miller, 1981; Mays & Cantrill, 2019). Hollick and Jeffrey (1906) considered *Protodammara* as belonging to the family Araucariaceae due to its morphological similarity with fossil species previously described under *Dammara* Link (illegitimate synonym of *Agathis* Salisb.), such as *Dammara borealis* Heer (1882), *Dammara microlepis* Heer (1882), and *Damara* (?) *cliffwoodensis* Hollick (1897), and due to the "internal structure" of the remains, although they did not provide any specific anatomical character supporting that statement (Hollick & Jeffrey, 1906). However, *Protodammara* was separated from fossil and extant species of *Dammara*

Fig. 4. Morphological diversity of the foliage associated with *Patagotaxodia lefipanensis*. **A, B,** MPEF-Pb 10894 a, general view and detail of the specimen showing the leaf shape and stomatal bands (black arrowheads in B). **C, D,** MPEF-Pb 10894 e, general view and detail of the specimen showing the profile of the leaves and the leaf bases. **E, F,** MPEF-Pb 10859, general view and detail of the specimen. **G, H,** MPEF-Pb 8326, general view and detail of the specimen showing the morphology of the leaf bases. **I, J,** MPEF-Pb 10890, general view and detail of the specimen with multiple ramifications. **K,** MPEF-Pb 10889, detail of an apical portion of two leafy branches with densely packed leaves. Scale bars G = 20 mm; A, E, H, I, K = 10 mm; B, C, D, J = 5 mm; F = 2.5 mm.

Fig. 5. Morphological diversity of the foliage associated with *Patagotaxodia lefipanensis*. **A, B, C,** MPEF-Pb 10873, general view and detail of the specimen showing the morphology of leaf bases and leaves. **D, E,** MPEF-Pb 10875, general view and detail of the specimen leaf profiles and leaf bases. **F,** MPEF-Pb 10874, general view of a leafy branch. **G,** MPEF-Pb 10876, specimen showing an older (and thicker) branch with laterally expanded leaf bases separated by conspicuous interareas (arrowhead). Scale bars A = 20 mm; D, F, G = 10 mm; B, E = 5 mm; C = 3 mm.

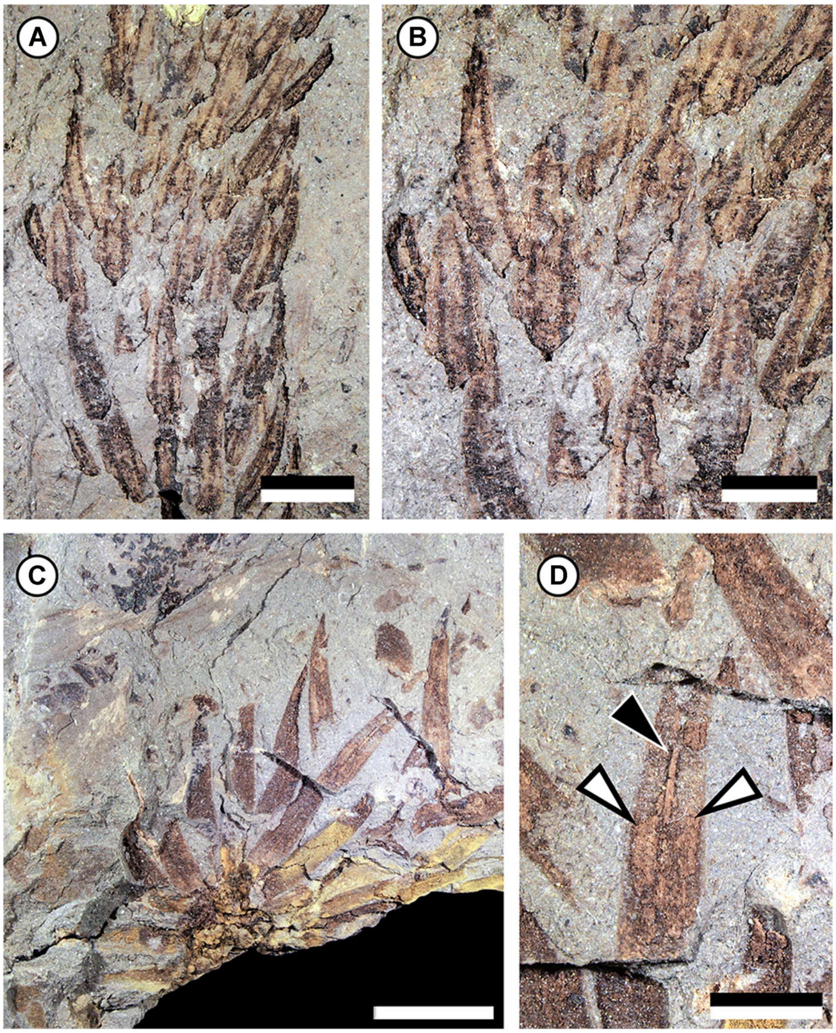

Fig. 6. Morphological details of the leaves associated with *Patagotaxodia lefipanensis*. **A, B,** MPEF-Pb 10894 a, details of the leafy branch shown in Figs. 4A, 4B, showing abaxial side of leaves with lateral stomatal bands. **C, D,** MPEF-Pb 10903a, general view and detail of specimen. **D,** detail of a leaf showing the mummified vascular strand in the middle of the leaf (black arrowhead), and putative remains of transfusion tissue (white arrowheads). Scale bars A = 5 mm; B = 3 mm; C = 7 mm; C = 2.5 mm.

(*Agathis*) based on the presence of three seeds per OC, instead of one as occurs in all known Araucariaceae species (Stockey, 1982, 1994; Escapa & Catalano, 2013; Andruchow-Colombo et al., 2018; Rossetto-Harris et al., 2020), and in the presence of an apical process that is absent in *Agathis* species (Hollick & Jeffrey, 1906). Anderson et al. (2007) treated *P. speciosa* as the last occurrence of the family Voltziaceae (Order Voltziales), but they did not provide a list of characters supporting this taxonomic treatment. However, *Protodammara* differs from the diagnosis of the family Voltziaceae given by Anderson et al. (2007) in the degree of fusion between the bract and the scale, which is incomplete in members of Voltziaceae and would be complete for *Protodammara*, and the lobed morphology of the Voltziaceae scale that is not present in *Protodammara*.

Protodammara was also argued to belong to Cupressaceae (Miller, 1977; LaPasha & Miller, 1981) based on the pattern of vasculature and resin canals, which would suggest a closer affinity to extant *Cunninghamia* according to LaPasha and Miller (1981), and in the presence of multiple seeds per OC. However, the genus *Protodammara* was not formally transferred to Cupressaceae until recently, based on a study of a new *Protodammara* species from the Chatham Islands and the revision of the bibliographical information on the original species performed by Mays & Cantrill (2019). As it is evidenced from its known fossil record, the biochron and distribution of *Protodammara* encompass the Cretaceous of North America, Japan, and Zelandia (Hollick & Jeffrey, 1906, 1909; Berry, 1919; Kimura & Sekido, 1978; Mays & Cantrill, 2019; Table 1), showing that this Cretaceous genus would possibly have been cosmopolitan.

Protodammara shares several morphological traits with *Patagotaxodia*, such as the kite- to umbrella-shaped OC morphology, both resembling the morphology of several extant foliate and pseudopeltate Cupressaceae (Farjon, 2005), the presence of multiple seeds per OC located in a

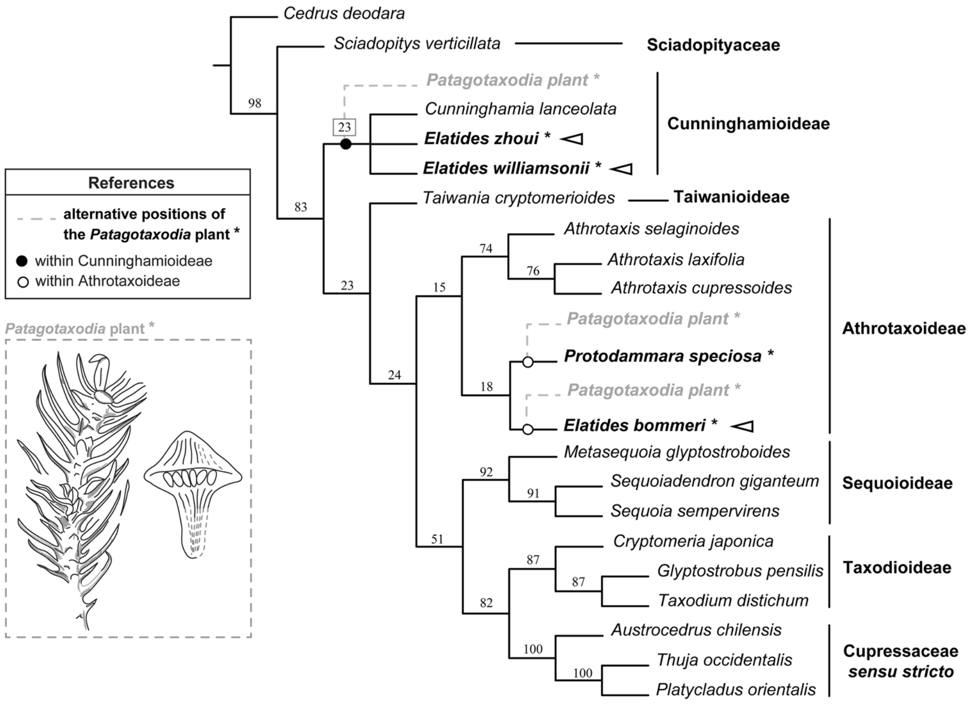

Fig. 7. Strict consensus of the three most parsimonious trees obtained by analyzing the complete matrix. Fossil taxa are indicated in bold typography and have an asterisk. Symmetric resampling values (absolute frequencies) are shown over the branches. The alternative positions of the *Patagotaxodia* plant (i.e., ovuliferous complexes referred to *Patagotaxodia lefipanensis* + associated foliage, see Section 4.3 on foliage and ovuliferous complex association) are indicated with circles, white circles indicate the alternative positions within the Athrotaxoideae subfamily, and the black circle indicates the position within the Cunninghamioideae subfamily. White arrowheads show the positions of the three *Elatides* species included in the analysis, showing the polyphyletic current status of the genus.

single row at the distal area of the complex, and the presence of multiple resin canals (Hollick & Jeffrey, 1906, 1909; Berry, 1919; Kimura & Sekido, 1978; Mays & Cantrill, 2019). However, these two genera differ in several diagnostic characters, including the number and shape of the seeds. *Protodammara* seeds are round and they are invariably three per OC (Mays & Cantrill, 2019), whereas *Patagotaxodia* has 3–5–(6) oval seeds per OC (Fig. 3). Furthermore, the OCs of *Patagotaxodia* have a prominent, convex to bell-shaped, distal cap (Fig. 2) whereas in *Protodammara* the distal cap is reduced (Hollick & Jeffrey, 1906, 1909; Mays & Cantrill, 2019).

4.2.2 Similarities with other Cretaceous cupressaceous conifers

Among other Cupressaceae genera, the extant *Athrotaxis* D. Don. and the extinct *Elatides* Heer show a morphology comparable to *Patagotaxodia* and *Protodammara* (Tables 1, 2), as they all produce woody, either foliate to pseudopeltate or strictly pseudopeltate ovuliferous complexes (i.e., proximally thinner, and enlarging toward its distal portion, intermediate between the two-dimensional foliate, and pronouncedly tridimensional peltate morphologies) and bear multiple seeds per OC (Table 2). However, the OC shape varies among these genera, the distal cap being more triangular in *Athrotaxis* and *Elatides* species than in *Patagotaxodia* (Table 2). The seed number and arrangement in one or two rows also varies among these genera (Table 2).

4.3 Foliage and seed complexes association

The Lefipán ovuliferous complexes and leaves described here were found in close association across different fossiliferous levels (see Section 2), usually co-occurring in certain fossil sites (e.g., "*coníferas* site," fossiliferous level 1) and frequently in the same individual hand specimens. Moreover, the abundance of these two organs relative to those of other species tends to increase and decrease together. Based on these arguments, and even though we have treated leaves and OCs as separate entities in the systematic paleontology section (i.e., Section 3.1), we hypothesize that these two organs belonged to the same biological species, here referred to as the *Patagotaxodia* plant.

Additionally, all the species found as closely related to the *Patagotaxodia* plant in the different topologies recovered by our phylogenetic analyses produce comparable foliage (Fig. 7). *Protodammara speciosa* has been reported in close association with *Brachyphyllum* foliage in Upper Cretaceous sediments of the United States (Hollick & Jeffrey, 1906), which is of a similar shape but shorter (ca. 2 mm) and more adpressed compared to the Lefipán leaves here reported (7.1–18.2 mm). *Elatides bommeri* (Harris, 1953) has leaves of a similar shape to those associated with *Patagotaxodia*, although they are also generally smaller (ca. 7 mm) and tetragonal in cross section across most of their length (Harris, 1953). Within extant *Athrotaxis*, two of the three

Table 2 Morphology of the OC (columns 2–6) and associated leaves (column 7) of extant and fossil species morphologically comparable to *Patagotaxodia*

Species	Distal cap	Number of seeds per OC	OC shed at maturity	Number of resin canals	Shape	Morphology of associated leaves
Elatides bommeri	Reduced	At least 2†	No (Persistent)	1	Kite-shaped	Incurved leaves, rhomboidal in cross section, arising from a raised cushion
Athrotaxis ungeri (only leaves)	-	-	-	-	-	Incurved, rhomboidal in cross section
Athrotaxis ungeri	Reduced	?	No (Persistent)	?	Clavate-spathulate	Scale-like, ovate, with rhomboidal base cushion
Athrotaxites yumenensis	Well-developed	2	No (Persistent)	?	?	Scale-like, closely appressed
Athrotaxites berryi	?	?	No (Persistent)	?	Wedge-shaped	Scale-like, closely appressed
Protodammara sp.	Reduced	3 seeds in 1 row	Yes‡	?	Kite-shaped	-
Protodammara speciosa	Reduced	3 seeds in 1 row	Yes‡	7	Kite-shaped	*Brachyphyllum*-like
Protodammara reimatamori	Reduced	3 seeds in 1 row	Yes‡	3–15	Kite-shaped	-
***Patagotaxodia lefipanensis* and associated leaves**	**Well-developed**	**3–5(–6) seeds in 1 row**	**Yes**‡	**7–11**	**Kite- to umbrella shaped**	**Incurved, subulate to linear, rhomboidal in cross section near the base**
Athrotaxites stockeyi	Well-developed	3	?	ca. 10	Kite-shaped (immature)	?
Athrotaxis novae-zeelandiae (only leaves)	?	?	?	?	?	Scale-like, loosely appressed, imbricate
'*Athrotaxis*' *couttsiae*	Well-developed	?	No (Persistent)	?	Umbrella shaped	Scale-like, appressed, keeled
Athrotaxis tasmanica (only leaves)	?	?	?	?	?	Scale-like, more or less triangular, with rounded apex, not keeled
Athrotaxis rhomboidea	Reduced	5–6	No (Persistent)	?	?	Scale-like, loosely spreading
Athrotaxis mesibovii	Well-developed	?	?	?	Kite- to umbrella shaped	Scale-like, loosely spreading, and strongly keeled
Athrotaxis cf. *laxifolia* (only leaves)	?	?	?	?	?	Imbricate, lanceolate, keeled, apex incurved
Athrotaxis cupressoides	Reduced	2–4	No (Persistent)	**?**	Clavate-peltate	Scale-like, ovate, with rhomboidal base cushion
Athrotaxis laxifolia	Well-developed	2	No (Persistent)	ca. 11§,	Clavate-peltate	Imbricate, lanceolate, keeled, apex incurved
Athrotaxis selaginoides	Well-developed	3–6 in 1 row	No (Persistent)	?	Clavate-spathulate	Incurved leaves, linear lanceolate, keeled
Elatides williamsonii	Well-developed	5	No (Persistent)	?	Slender stalk and triangular head	Incurved leaves, rhomboidal in cross section, arising from a raised cushion
Elatides harrisi	Well-developed	Probably 3	No (Persistent)	1	Slender stalk and triangular head	Incurved leaves, rhomboidal in cross section, arising from a raised cushion
Elatides zhoui	Well-developed	4–6 seeds in 1 row	No (Persistent)	3	Slender stalk and triangular head	Linear lanceolate, straight
Sphenolepis kurriana	Reduced	6 seeds in 2 rows	No (Persistent)	3	Peltate	Short, scale-like leaves

Continued

Table 2 Continued

Species	Distal cap	Number of seeds per OC	OC shed at maturity	Number of resin canals	Shape	Morphology of associated leaves
Cunninghamia lanceolata	Well-developed	3	No (Persistent)	?	More or less triangular	Triangular, long, straight, or incurved
Cunninghamia konishii	Well-developed	2–3	No (Persistent)	?	More or less triangular	Triangular, long, straight, or incurved

Under "OC number of seeds": (†) three seeds per OC according to Zhou (1987). Under "OC shed at maturity": (‡) OC only found detached—never in connection to a cone axis; Under "Number of resin canals": (§) information inferred from microCT in Escapa et al. (2016). Under "Associated leaves": NI, not informed; OC, ovuliferous complexes.

recognized species have similar leaves to those associated with *P. lefipanensis* (i.e., *A. selaginoides* D. Don and *A. laxifolia* Hook.), and the third one, *A. cupressoides* D. Don, has scale-like leaves (Farjon, 2005). In summary, all athrotaxoid species considered in this study are characterized by similar leaf morphology supporting both the association of *P. lefipanensis* with the Athrotaxoideae lineage and adding to the hypothesis of these two organs belonging to the same biological species.

4.4 Phylogenetic analysis

4.4.1 Phylogenetic position of the *Patagotaxodia* plant

The alternative positioning of the *Patagotaxodia* plant within the Athrotaxoideae and Cunninghamioidae clades in all most parsimonious trees responds to the high morphological similarities of these two groups, including the general shape of ovuliferous complexes (see Section 2.3 on terminology and abbreviations for a detailed description of these morphologies) and the presence of multiple and distally located seeds per ovuliferous complex (Farjon, 2005; Herrera et al., 2017). However, if the particular characters supporting the alternative positions of the *Patagotaxodia* plant are considered, the hypothesis of its belonging to the subfamily Athrotaxoideae is favored. Such characters include the shedding of OC, the leaf shape, the mature OC pseudo-peltate morphology, the absence (or extreme reduction) of the ovuliferous scale in mature seed cones, and the number of ovules associated with each OC. The shedding of OC is relatively rare among cupressaceous species, occurring only in the subfamily Taxodioideae and in extinct species of Athrotaxoideae (Farjon, 2005; Hollick & Jeffrey, 1906; Mays & Cantrill, 2019). The exclusively isolated way in which the OCs of fossil athrotaxoids *Protodammara* and *Patagotaxodia* are consistently found in the field (Fig. 2; Hollick & Jeffrey, 1906, 1909; Mays et al., 2017a; Mays & Cantrill, 2019) suggests that these fossil genera shedded their OCs on a normal basis.

The foliage found in association with the OCs of *Patagotaxodia lefipanensis* is highly similar to that of extant and extinct members of the Athrotaxoideae, as was discussed in detail in Section 4.3 (on the foliage and seed complexes association). Conversely, the leaf shape associated with *Patagotaxodia* strongly contrasts with the triangular to lanceolate, expanded leaves of extant *Cunninghamia* and some cunninghamioid fossils (e.g., Shi et al., 2014), although it is similar to the morphology shown by certain fossil members of the cunninghamioid clade (e.g., Harris, 1943). On the other hand, the presence of four to six ovules associated with each OC is recovered as a synapomorphy for the grouping of *Patagotaxodia* with the Cunninghamioideae. Yet, this character state also occurs in extant athrotaxoids and is absent in extant cunninghamioids (Appendix III; Farjon, 2005; Schulz & Stützel, 2007; Jagel & Dörken, 2014), and therefore it also supports the hypothesis that reads *Patagotaxodia* as an Athrotaxoideae.

Furthermore, the taxon inclusion-exclusion experiments performed to test the robustness of each of these hypotheses favor that of the athrotaxoid affinity of *Patagotaxodia*. In these experiments, the *Patagotaxodia* plant is always positioned within the athrotaxoids in at least some of the most parsimonious trees whether or not other fossils of that group were included in the analyses

(Appendix IVA–C). On the contrary, when Cunninghamioideae fossils were excluded from the analyses, *Patagotaxodia* was no longer placed within this group (Appendix IVA, C).

4.4.2 Fossil records recovered within the Athrotaxoideae clade

Three fossil species included in our analysis were recovered as part of a single clade that constitutes the stem group of the subfamily Athrotaxoideae (Fig. 7). These three species are from the Cretaceous and belong to different genera: *Protodammara*, *Elatides*, and *Patagotaxodia*. The *Protodamara* species included in the phylogenetic analysis, *P. speciosa*, was described for the Upper Cretaceous of North America (Table 1, Hollick & Jeffrey, 1906, 1909). The genus *Protodammara* has two other species that were not included in our phylogenetic analyses, *Protodammara* sp. from the Lower Cretaceous of Japan (Kimura & Sekido, 1978) and *P. reimatamoriori* from the Upper Cretaceous of Zelandia (Mays et al., 2017a; Mays & Cantrill, 2019). *Elatides* is a widely distributed genus with more than a dozen fossil species, most of which have been proven to belong to the cunninghamioid Cupressaceae (Shi et al., 2014; Herrera et al., 2017; Atkinson et al., 2021). In our phylogenetic analyses, we included *Elatides zhoui, E. bommeri,* and *E. williamsonii* (Fig. 7); and we recover *Elatides* as polyphyletic, with *E. zhoui* and *E. williamsonii* belonging to the subfamily Cunninghamioideae and *E. bommeri* to the subfamily Athrotaxoideae (Fig. 7). According to these results, *E. bommeri* would constitute part of a different biological genus. In this sense, Harris (1953) described in detail the morpho-anatomy of this species and stated that *E. bommeri* was probably more closely related to *Cunninghamia* than to any other living genera based on characters of the seed cone. However, Harris (1953) also recognized several characters in this fossil species that are not typical of *Cunninghamia*, such as the leaf shape and the stomatal morphology and distribution that partially concur with those observed in athrotaxoid Cupressaceae. Furthermore, certain characters of the OC are here considered to be more similar to those of the athrotaxoids than to other Cupressaceae lineages. Particularly the pseudopeltate morphology of the complex that was described by Harris (1953) as having “a better marked stalk and shorter apical point [with respect to *E. williamsoni*, which was the species used as the parameter to justify the inclusion to *Elatides*].” Although Harris (1953) recognized several differences between *E. bommeri* and other *Elatides* species, he considered that they were not enough to include the species in another genus. This resolution is contradicted by the results of our phylogenetic analyses that indicate that *E. bommeri* would belong to an entirely different subfamily within Cupressaceae than other species included within that genus (e.g., Shi et al., 2014).

As it was exposed in Section 4.2.1 on the comparisons between *Protodammara* and *Patagotaxodia*, several morphological features link these two genera, the former of which by Late Cretaceous was present in North America (Hollick & Jeffrey, 1906; 1909) and Zelandia (Mays et al., 2017a; Mays & Cantrill, 2019). Consistently, our phylogenetic analysis also partially supports the hypothesis of these two genera corresponding to the same extinct lineage within the stem group of the subfamily Atrhotaxoideae (Fig. 7). It remains still an open question if these fossil taxa are actually part of a single lineage widely distributed or if they belonged to different groups that shared an OC morphology. In this sense, it becomes more evident the utility of knowing different organs for these fossil plants that allow to test the affinities suggested by the ovuliferous complexes. In the particular case of *Patagotaxodia lefipanensis* and *Protodammara speciosa,* this comparison was possible due to the presence of associated foliage, which, in both cases, was suggested to belong to the same biological species as the ovuliferous complexes (see Section 4.3 on foliage and seed complexes association), and which added further evidence to the close similarity of these extinct taxa.

4.5 Fossil record referred to the subfamily Athrotaxoideae

As it was already mentioned, there is a wide fossil record that has been associated with *Athrotaxis* and therefore most probably belongs to the Athrotaxoideae lineage (Table 1; Florin, 1940; Dong et al., 2014). This fossil record was referred to the genera *Athrotaxis* D.Don, *Athrotaxites* Unger, and *Athrotaxopsis* Fontaine (e.g., Seward, 1919; Florin, 1940; Dong et al., 2014). The fossil record associated to the athrotaxoids indicates that the lineage would have already originated by the Late Jurassic (Florin, 1960), and became conspicuous and distributed worldwide during the Early Cretaceous (Table 1; Florin, 1960; Miller & LaPasha, 1983; Dong et al., 2014). However, toward the Cenozoic it became restricted to the Southern Hemisphere (Table 1; Florin, 1940; Hill & Brodribb, 1999; Dong et al., 2014), reaching the present time with only three species endemic to Tasmania (Table 1; Farjon, 2005). In particular, the fossil record of the group in Argentinean Patagonia is well documented for the Early Cretaceous (Table 1; Archangelsky, 1963; Villar de Seoane, 1998; Passalia, 2007; Del Fueyo et al., 2008). In addition, there is a single Cenozoic record from Santa Cruz Province (Patagonia, Argentina) referred to *Athrotaxites ameghinoana*, based on a leafy branch and a putative seed cone associated, neither of which were clearly described or illustrated (Spegazzini, 1924). The characters listed by Spegazzini (1924) in the description of this scale-leaved species occur in most conifer families (de Laubenfels, 1953), and thus this record for the subfamily is unreliable. Consequently, *Patagotaxodia lefipanensis* constitutes the first Late Cretaceous record of the subfamily Athrotaxoideae in Patagonia and South America, possibly corresponding to its last known representative in the region to date.

4.6 Evolution of the ovuliferous complex morphology

Previous morphological phylogenetic studies of the Cupressaceae recognized and defined three ovuliferous complex morphologies for the family (i.e., foliate, peltate, and valvate; Farjon, 2005; Shi et al., 2014; Herrera et al., 2017; Fig. 8). Nevertheless, based on the *Patagotaxodia* OC morphology and some extant and extinct members of the family (e.g., *Athrotaxis*), we recognize a fourth state, which is intermediate between the foliate and peltate morphologies (i.e., pseudopeltate; Fig. 8).

Foliate OCs are bifacially flattened, show a varying degree of lignification, and have a distal area generally less woody than the main body (Farjon, 2005; Herrera et al., 2017). OCs with foliate morphology in Cupressaceae and Sciadopityaceae bear multiple ovules distally arranged in one or more rows (Table 2; Farjon, 2005; Jagel & Dörken, 2014; Herrera et al., 2017). Extant genera of Cupressaceae with foliate OC morphology include *Cunninghamia* and *Taiwania* (Fig. 8). A similar type of OCs is present in the Araucariaceae (Stockey, 1982; Farjon, 2010; Andruchow-Colombo et al., 2018), Pinaceae (Farjon, 2005; Matsunaga et al., 2021), and some members of the Podocarpaceae (e.g., *Saxegothaea*; Andruchow-Colombo, 2021), but in these families, each OC bears a single (Araucariaceae and Podocarpaceae) or two (Pinaceae) seeds. We here defined the pseudopeltate OC morphology as more tridimensional than the foliate and tending to have a proportionally longer and thinner stalk, with seeds positioned in a distal widened portion of the complex that culminates with a generally lignified cap (Hollick & Jeffrey, 1906, 1909; Harris, 1953; Farjon, 2005; Mays & Cantrill, 2019; Figs. 2, 3). Pseudopeltate ovuliferous complexes are only present in two extant cupressaceous genera, *Athrotaxis* and *Cryptomeria* (Fig. 8). The peltate morphology has a well-defined stalk and a pelta perpendicular to it (Fig. 8), these OCs generally bear multiple seeds that are located at the internal side of the pelta and on the adaxial side of the stalk; the peltae become fused together in the post-pollination cone, protecting the developing seeds (Farjon, 2005). This OC morphology is observed in nearly a third of the extant genera of Cupressaceae (Fig. 8). The valvate OC morphology is the most common among extant genera of the family, being present in more than half of them (Fig. 8); it is characterized by a shell-like, lignified morphology, in some genera presenting interlocking cells located on its edges, as it occurs with the peltate morphology, and it is associated with the presence of multiple seeds per OC (Farjon, 2005; Little, 2006; Jagel & Dörken, 2015a, 2015b). We propose these four OC morphologies (i.e., foliate, pseudopeltate, peltate, and valvate) to be sequential stages on a transformational series in the systematic context of the family Cupressaceae. Therefore, we treated the "OC morphology" character as ordered for the total evidence phylogenetic analysis (Fig. 7) and for the character mapping over a molecular tree showing the relationships among the extant genera of the Cupressaceae (Fig. 8).

According to the reconstruction of the evolution of the OC morphology in Cupressaceae shown in Fig. 8, the ancestral morphology for the crown group of Cupressaceae is the foliate morphology. This morphology appears in the subfamilies Cunninghamioideae and Taiwanioideae, which are successive sister taxa to the clade formed by all other Cupressaceae (Fig. 8). Previously published phylogenetic analyses that included a large diversity of cunninghamioid fossil species within their taxon sampling showed that the foliate OC morphology is a characteristic not only of the extant species of the subfamily Cunninghamioideae but also of its stem lineage (Shi et al., 2014; Herrera et al., 2017; Atkinson et al., 2021). There are no fossil species recovered as part of the Taiwanioideae in published phylogenetic analyses, but it has been discussed that the taxa *Austrohamia* and *Stutzeliastrobus*, which produced foliate OCs (Escapa et al., 2008; Herrera et al., 2017), would belong to that lineage (Herrera et al., 2017). In this sense, *Austrohamia* has been recovered in a polytomy with *Taiwania* in some phylogenetic studies (Escapa et al., 2008; Shi et al., 2014; Atkinson et al., 2021), which is partially compatible with the Taiwanioideae affinity hypothesis of that fossil taxon.

The pseudopeltate OC morphology occurs in fossil and extant members of the subfamily Athrotaxoideae and in the genus *Cryptomeria* (one of the three extant genera of the subfamily Taxodioideae). The appearance of the pseudopeltate morphology in the athrotaxoid lineage is here reconstructed as an intermediate state in the evolution of the ovuliferous complex in the family (Fig. 8). Instead, the appearance of the pseudopeltate morphology in *Cryptomeria* is recovered as a reversion from a peltate ancestor (Fig. 8; Appendix III, mapping of character 16). The common mapping of this character over the phylogeny including fossil species also shows that the total group (i.e., clade formed by the stem and crown groups) of the subfamily Athrotaxoideae has a pseudopeltate morphology as well (Appendix III, mapping of character 16). Extant Sequoioideae members only show the peltate morphology whereas within the Taxodioideae all three extant genera show different OC morphologies (i.e., pseudopeltate, peltate, and valvate; see Fig. 8). Within Cupressaceae *sensu stricto*, the genera of the subfamily Callitroideae uniformly produce valvate OCs, but within the Cupressoideae there is an unfixed morphology since the genera and suprageneric subclades within that subfamily vary between the valvate and peltate morphologies (Fig. 8). The pattern of evolution of the OC morphology reconstructed using a phylogeny with all extant genera of the Cupressaceae (Fig. 8) concurs completely with the reconstruction over the topology obtained in our analysis, which has fewer extant genera represented but includes several extinct genera (Appendix III).

There is a clear distribution pattern of the OC morphologies across the phylogeny of Cupressaceae. In this pattern, the foliate morphology is dominant toward the basal nodes, particularly when considering the fossil record of the earlier divergent lineages (Fig. 8; Appendix III, mapping of character 16; Herrera et al., 2017). The pseudopeltate morphology appears first in Athrotaxoideae (Fig. 8; Appendix III, mapping of character 16), and then as an apparent reversion in part of the Taxodioideae (Fig. 8), two groups for which the positions of their fossil species have been scarcely explored. Finally, the peltate and valvate morphologies are reconstructed as showing a relatively reversible connection between them (Fig. 8), particularly within the subfamily Cupressoideae, evidencing a higher degree of homoplasy, possibly driven by a close identity between these two morphological types.

The distribution pattern of these OC morphologies across the phylogenetic tree is also consistent with the appearance of each one of them as conspicuous elements in the fossil record of the family. In this sense, there are extensive reviews of the fossil record of the Cupressaceae subfamilies worldwide (Hill & Brodribb, 1999; Stockey et al., 2005; Atkinson et al., 2021). Following these mentioned reviews, and posteriorly published works, it becomes evident that the foliate morphology was already present by the Early Jurassic (Escapa et al., 2008; Contreras et al., 2019). The first records of the pseudopeltate morphology appear toward the end of the Early Cretaceous (Tables 1, 2; Harris, 1953; Kimura & Sekido 1978; Dong et al., 2014), whereas the peltate morphology has its earliest records by the beginning of the

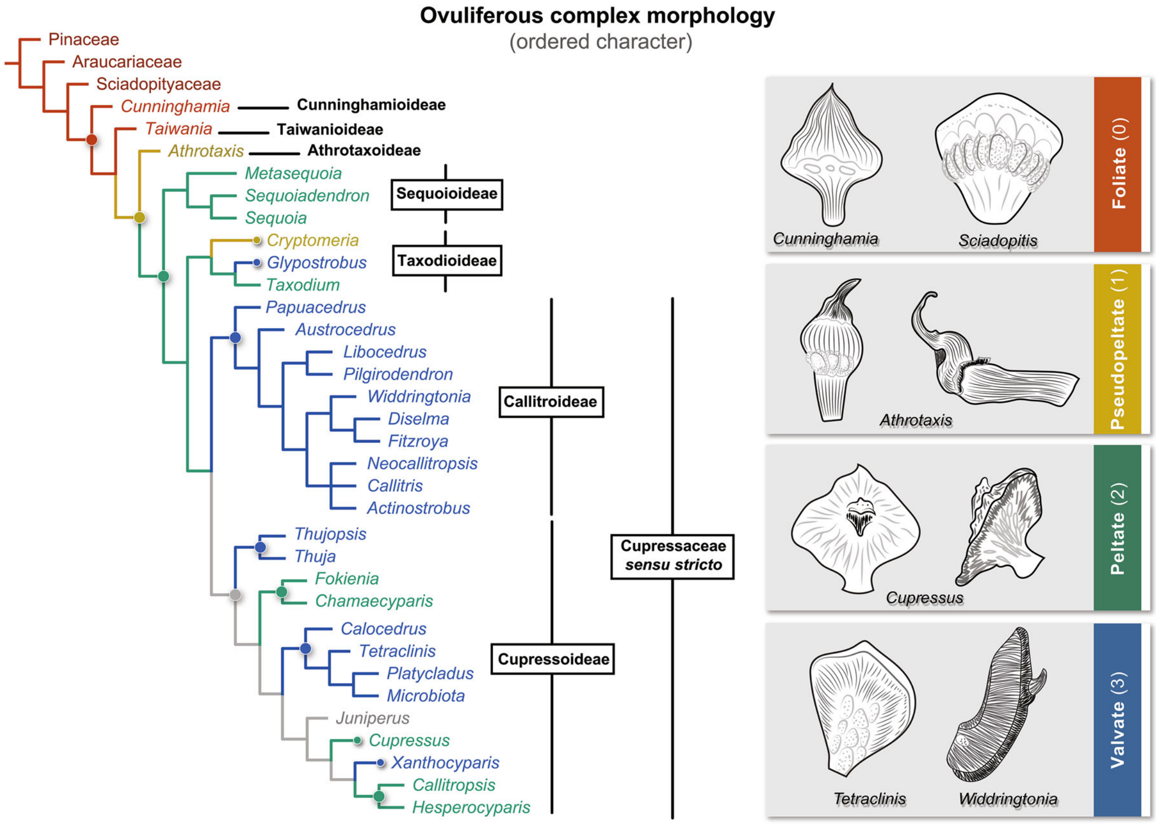

Fig. 8. Mapping of the additive character *Ovuliferous complex morphology* over a topology with genera as terminals that results from the combination of the molecular topologies of Mao et al. (2012) and Leslie et al. (2018). In the right column, the four character states are shown as follows: 0. Foliate, 1. Pseudopeltate, 2. Peltate, and 3. Valvate, with extant examples for each morphology, and the color in which the character state is mapped on the tree. Adaxial views of the OC are provided for *Cunninghamia*, *Sciadopitys*, *Athrotaxis* (left), and *Tetraclinis*; lateral views are provided for *Athrotaxis* (right) and *Widdringtonia*; for *Cupressus* the views provided are external or apical (left) and internal to lateral (right). The basal node of the Cupressaceae is marked with an orange circle, which also indicates that the reconstructed basal morphology for the family is foliate. All other circles mark nodes and terminals where character transformations occur (i.e., yellow: pseudopeltate, green: peltate, blue: valvate, gray: ambiguous between valvate and peltate).

Late Cretaceous (Peters & Christophel, 1978; LePage et al., 2005; Mays et al., 2017b). The close appearance of the pseudopeltate and peltate morphologies in the fossil record suggests a rapid transformation, which is consistent with the low number of species (extant and fossils) that show a pseudopeltate morphology. Such rapid transformation could be justified in the adaptative advantage that would represent having a peltate morphology over the foliate and pseudopeltate morphologies. Such advantage is represented by the complete closure of the ovuliferous cone, by means of the interlocking of adjacent peltae, that occurs after pollination and during the maturation of the seed (Farjon, 2005; Little, 2006). Considering the morphological evidence in both temporal and phylogenetic contexts, the interpretation of the pseudopeltate morphology as intermediate between the foliate and peltate becomes clearer, as the pseudopeltate OC shows a thinning of the basal stalk, a consequent further differentiation of the distal cap, and an apparent stronger lignification with respect to the foliate morphology, but it does not show a differentiation of the distal cap into a pelta perpendicular to the stalk as happens in the peltate morphology. This intermediate condition of the ovuliferous complexes of *Athrotaxis* has been also noted in comparative ontogenetic studies in the family. Farjon (2005) observed that the intercalary growth that occurs during the maturation of the OC, and causes the thickening of the proximal end of the bract of *Athrotaxis*, is more pronounced in taxa that give rise to peltate morphologies. In this scenario, peltate OCs would be peramorphic with respect to the pseudopeltate. Finally, the valvate OC morphology also appears in the fossil record during the early part of the Late Cretaceous (Bell, 1957; McIver, 2001), as was mentioned for the peltate OCs, adding to the hypothesis of the close identity shared by these two morphologies. The valvate OCs also interlock with each other in certain genera, providing protection to the developing seeds (Little, 2006).

5 Conclusions

We describe a new extinct genus and species of the Cupressaceae *s.l.*, *Patagotaxodia lefipanensis* from Late

Cretaceous (Maastrichtian) Lefipán Formation (Chubut Province, Patagonia, Argentina), based on impressions and compressions of ovuliferous complexes found in close association with leafy branches that, although they are not formally included within *P. lefipanensis*, are proposed to belong to the same biological species, here referred to as the *Patagotaxodia* plant. Based on the preserved morphological characters, the new species is placed within the subfamily Athrotaxoideae, a previously unexplored lineage of Cupressaceae in terms of the phylogenetic history of its fossil representatives. This placement was tested using total evidence phylogenetic analyses that recovered the *Patagotaxodia* plant alternatively within the subfamilies Athrotaxoideae and Cunninghamioideae; however, we argue that the characters supporting the athrotaxoid affinity are more significant in the systematic context of the taxodiaceous Cupressaceae. Such characters include the shedding of OC, leaf shape, mature OC pseudopeltate morphology, absence (or extreme reduction) of the ovuliferous scale in mature seed cones, and the number of ovules associated with each OC. The placement of *Patagotaxodia* within the athrotaxoids is also supported by taxon inclusion-exclusion experiments performed in this study to test the robustness of each of the affinity hypotheses.

Two other Cretaceous records were included here for the first time in a phylogenetic context, *Protodammara speciosa* and *Elatides bommeri*. *Protodammara* is a genus with an erratic taxonomic history, only recently formally referred to the Cupressaceae, and is here linked to the Athrotaxodioideae. *Elatides* has always been considered as a genus from the subfamily Cunninghamioideae, but we recovered it as polyphyletic in our phylogenetic analysis, thus concluding that *Elatides bommeri* would possibly belong to a different natural genus, within Athrotaxoideae. Together, *Patagotaxodia*, *Protodammara speciosa*, and *E. bommeri* constitute the first phylogenetically corroborated fossil taxa of the subfamily Athroraxoideae.

Based on fossil and modern species, including the newly erected taxon, we define a new morphology of ovuliferous complexes in Cupressaceae, the pseudopeltate, which is added to the three morphologies previously recognized for the family (i.e., foliate, peltate, and valvate), and allow us to introduce a hypothetical transformational series for Cupressaceae ovuliferous complexes. This transformational series is used to reconstruct the evolution of the ovuliferous complex morphology over a phylogeny of Cupressaceae that includes all extant genera, as well as over the total evidence phylogeny here obtained, which we contrast with the evidence provided by the earliest appearance of each morphology in the fossil record. We found that the foliate OC morphology would represent the ancestral state for the crown group of Cupressaceae, it is present in extant and fossil members of the early divergent subfamilies Cunninghamioideae and Taiwanioideae, and it is the one appearing earliest in the fossil record of the family. The pseudopeltate morphology appears twice within the family, as a transitional morphology in the Athotaxoideae, and then as a reversion in *Cryptomeria*. The peltate and valvate morphologies, dominant among extant genera, appeared the latest in the phylogeny of the family (i.e., in more nested nodes with respect to the other two morphologies) and in the fossil record of the group. Finally, we found that the close appearance of the pseudopeltate and peltate morphologies in the fossil record and in the phylogeny suggests a rapid transformation between these two states, justified here in the adaptative advantage that would represent having a (peramorphic) peltate morphology over the foliate and pseudopeltate, due to the complete enclosure of the ovuliferous cone after pollination in peltate (and valvate) morphologies.

Finally, this contribution strengthens the importance of integrating information from extant species (e.g., DNA, ontogeny, and morphological data) and fossil taxa (e.g., morphologies not observable in modern taxa, as the shedding of OC in *Patagotaxodia*) to interpret the morphological evolution in different groups, as they provide alternative lines of evidence that can be combined to build more robust hypotheses.

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Author Contributions

A.A.-C.: Collected, prepared, studied, and described the material. Compiled, modified, and analyzed the data matrix. Led the discussion and writing of the manuscript. M.A.G.: Provided funding for the project; collected material; contributed to the discussion of the data and correction of the manuscript. I. H. E.: Contributed to the discussion of the data. Correction of the manuscript. N.R.C.: Provided funding for the project. Collected material. Correction of the manuscript.

Conflict of Interest

The authors have no conflicts of interest to disclose.

Disclaimer

As required by the journal, we changed "Taiwan" to "Taiwan Island" and "China" to "Chinese Mainland."

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Supplementary Material

Appendix I. Taxon sampling for the phylogenetic analyses (Table IA), Character list (morphology), Genbank accession numbers for chloroplast (Table IB), mitochondrial and nuclear (Table IC) sequences included in the total evidence analysis.

Appendix II. Total evidence matrix (combined morphology + DNA and fossil + extant species) as a TNT file. The morphological matrix is also uploaded as a nexus file to Morphobank (https://morphobank.org/) under the project number P4095.

Appendix III. Character mapping over the most parsimonious trees that include *Patagotaxodia lefipanensis* as part of the Athrotaxoideae subfamily.

Appendix IV. Topological results of the inclusion-exclusion experiments performed.

Appendix V. Phylogenetic analysis and character mapping treating character 16 as unordere.