Monotypic colonies of *Clathropteris meniscioides* (Dipteridaceae) from the Early Jurassic of central Patagonia, Argentina: implications for taxonomy and palaeoecology

by

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With 6 plates, 3 text-figures and 1 table

Abstract

A collection of over 130 specimens of the fossil dipterid fern *Clathropteris meniscioides* (BRONGN. 1825) BRONGN. 1828 from in-situ colonies in the Lower Jurassic of Chubut, Argentina, provides evidence for population-level morphological variation within the species and palaeoecology of the site. Characters such as angle of insertion of secondary veins, tertiary vein arrangement and tooth depth were observed to vary between specimens, and the total range of variation captured by this population was found to overlap and intergrade with the descriptions of several previously identified *Clathropteris* species. This suggests that species delimitations based on minor differences in such characters should be regarded with skepticism, and that the current number of species ascribed to this genus may be artificially inflated. Abundant *C. meniscioides* fossils at different development stages buried together in a single, thick bed of sheet-flood deposits provide evidence for the species having formed large, pure colonies in open, disturbed floodplain areas. The characteristic and extremely high leaf-vein densities would have allowed for greater carbon assimilation and rapid growth rates. Altogether, this suggests that the species was a fast-growing pioneer species of floodplains, a prominent part of the Early Jurassic vegetation in Gondwana, and a likely food source for large herbivorous dinosaurs common at that time.

Key words: Jurassic; Dipteridaceae; taxonomy; palaeoecology; in-situ ferns

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1 Introduction

The Dipteridaceae SEWARD 1900 is an early-diverged leptosporangiate fern lineage (SCHUETTPELZ & PRYER 2007; LEHTONEN 2011). It contains about 11 extant species in two genera, *Dipteris* REINW. 1825 and *Cheiropleuria* C. PRESL 1851 (KRAMER et al. 1990; KATO et al. 2001). The two genera share a characteristic venation pattern with many orders of veins that are highly reticulated and form a dense meshwork of areoles with included free-ending veinlets (HOLTUM 1954; KRAMER et al. 1990; KATO et al. 2001). *Dipteris* and *Cheiropleuria* occur in warm tropical to sub-tropical regions of Asia, Australia and Polynesia (CORSIN & WATERLOT 1979; KRAMER et al. 1990), where they are generally found at higher altitudes in open exposed areas (HOLTUM 1954; KRAMER et al. 1990). Whereas the Dipteridaceae is only a minor component of today's vegetation, the family has an extensive fossil record and was an important element of many Late Triassic and Early Jurassic floras across the globe (SEWARD & DALE 1901; CORSIN & WATERLOT 1979; WING & SUES 1992; TIDWELL & ASH 1994; CANTRILL 1995; SKOG 2001; VAN KONIJNENBURG-VAN CITTERT 2002).

The earliest fossils with the distinctive venation pattern of Dipteridaceae are from the Middle Triassic (WEBB 1982; TIDWELL & ASH 1994; CANTRILL 1995; KUSTATSCHER & VAN KONIJNENBURG-VAN CITTERT 2011), suggesting that the origin of the family likely dates back into the Early Triassic or the Late Paleozoic (TIDWELL & ASH 1994). Dipteridaceae fossils have been found in Mesozoic deposits on all continents (e.g., ZEILLER 1903; NATHORST 1906; BERRY 1918; OISHI & YAMASITA 1936; FREGUELLI 1941; HARRIS 1961; CORSIN & WATERLOT 1979; WEBB 1982; STOCKEY et al. 2006; BOMFLEUR & KERP 2010; WANG et al. 2014), and include six commonly recognized genera: *Dictyophyllum* LINDL. & HUTTON 1834, *Clathropteris* BRONGN. 1828, *Camptopteris* C. PRESL 1838, *Goeppertella* OISHI & K.YAMASITA 1936, *Hausmannia* DUNKER 1846, and *Thaumatopteris* GOEPP. 1841. The Dipteridaceae reached its greatest generic diversity in the Early Jurassic (CORSIN & WATERLOT 1979; TIDWELL & ASH 1994; CANTRILL 1995), mainly occupying moist localities in the temperate-warm and subtropical zones (VAN KONIJNENBURG-VAN CITTERT 2002). Increasing aridity brought about during the onset of the Late Jurassic and Cretaceous is believed to have contributed

to the decline in diversity of the family (SKOG 2001; VAN KONIJNENBURG-VAN CITTERT 2002); the Cretaceous and Paleogene fossil record of Dipteridaceae is sparse and consists only of various species of *Hausmannia* (CANTRILL 1995; STOCKEY et al. 2006).

Whereas *Clathropteris* has long been considered one of the most common ferns in the Upper Triassic and Lower Jurassic of Eurasia (SEWARD & DALE 1901; CORSIN & WATERLOT 1979), its record from Gondwanan continents is sparse (CORSIN & WATERLOT 1979) and seemingly restricted to a few sites in Argentina and Antarctica (HERBST 1966; WEBB 1982; YAO et al. 1991; REES 1993; BOMFLEUR & KERP 2010). Here, we describe remarkable (par)autochthonous mass occurrences of an unusually large *Clathropteris* species in the Lower Jurassic of Cerro Bayo, Argentina (Text-fig. 1). Our collection includes fertile and sterile material, as well as fronds at different developmental stages. This provides a valuable opportunity to re-examine the taxonomy of the genus. The Cerro Bayo site also has an interesting geological setting, with *Clathropteris* fossils varying in relative abundance between the different depositional beds. These observed patterns offer insights into the palaeoecology of this Jurassic site, and the ecological role *Clathropteris* may have played.

2 Geological setting

The Cerro Bayo locality is situated near Gastre in the northwest part of Chubut Province, Argentina (Text-fig. 1) and has been described in detail in previous works (ESCAPA et al. 2014; ELGORRIAGA et al. 2015). Plant horizons at this locality belong to an unnamed unit of fluvially reworked, volcanoclastic deposits, which are overlain by agglomerates and lavas of the Lonco Trapial Formation and by lacustrine deposits of the Cañadón Asfalto Formation. Previous radiometric studies have dated the site into the Early Jurassic (most likely Pliensbachian) (CÚNEO et al. 2013; ESCAPA et al. 2014).

Most of the dipterid fossils described here were collected from three thick (~1 m) beds of volcanoclastic siltstone extensively exposed at numerous sites in the Cerro Bayo area. The fossils are of a single *Clathropteris* species. The low diversity in these *Clathropteris* beds, the common preservation of almost complete fronds and upright stipes, and the occurrence of fronds preserved at different developmental stages (including croziers) together indicate in-situ burial of

Text-fig. 1. Location and geology of the Cerro Bayo locality where the *Clathropteris meniscioides* fossil material was collected.

large colonies during catastrophic depositional events. These thick *Clathropteris* beds are succeeded by thin beds of partially silicified sediments that contain a taphocoenosis dominated by conifers and ferns (ESCAPA et al. 2014; ELGORRIAGA et al. 2015), including a few specimens of *Clathropteris*. Species that have been described from this site include *Austrohamia minuta* ESCAPA, CÚNEO & AXSMITH 2008 (Cupressaceae; ESCAPA et al. 2008), *Todites cacerei* ESCAPA & CÚNEO 2012 and *Osmundopsis rafaelii* ESCAPA

& CÚNEO 2012 (Osmundaceae; ESCAPA & CÚNEO 2012), *Marattiopsis patagonica* ESCAPA, BOMFLEUR, CÚNEO & SCASSO 2014 (Marattiaceae; ESCAPA et al. 2014), and *Equisetum dimorphum* ELGORRIAGA 2015 (Equisetaceae; ELGORRIAGA et al. 2015). Additional sporadic finds of seed ferns (e.g., Caytoniales) and of another member of Dipteridaceae are still awaiting detailed systematic treatment (ESCAPA et al. 2014).

3 Material and methods

The material comprises about 135 specimens that are housed in the Museo Paleontológico Egidio Feruglio Palaeobotanical Collection in Trelew, Argentina (hereafter **MPEF-Pb**). Most specimens occur in the form of well-defined, conspicuous, rust-coloured impressions of vegetative and fertile fronds; stipes are commonly preserved as compressions and casts. Photographs of specimens were taken with a Canon EOS 7D camera equipped with a Canon EF-S 60 mm macro lens; additional extension tubes were used in order to obtain higher magnifications. In order to obtain greater depth of focus for high-magnification images, we used an image-stacking technique (BERCOVICI et al. 2009) in which one well-focused image is obtained via merging several individual photographs captured at slightly different focal planes. Images were checked and edited for the presence of artifacts related to the stacking process, edited for colour balance, and cropped for publication using Adobe Photoshop. Thin sections of compressed stipes that showed evidence of partially preserved internal anatomy were also prepared. Fine details of the compression/impression specimens and the thin sections were studied using a Zeiss MC80DX stereoscope microscope. Selected fertile specimens were additionally examined using a scanning electron microscope (JEOL JSM-6460) without prior coating.

4 Terminology

All members of Dipteridaceae share the same basic architectural plan (Text-fig. 2). The stipe dichotomizes into two axes (herein termed ‘rachial arms’) to form a bilaterally symmetrical frond (OISHI & YAMASITA 1936; HOLTUM 1954). Each rachial arm subsequently dichotomizes catadromously to give rise to lamina segments that—depending on the degree of lamina dissection—have been referred to as pinnae (e.g., OISHI & YAMASITA 1936), lobes (e.g., HOLTUM 1954), frond members (e.g., REES 1993), or primary segments (e.g., NATHORST 1906). We have chosen to apply the descriptive term ‘primary segment’ (Text-fig. 2) as it is independent from the degree of lamina dissection and can thus be used consistently across different Dipteridaceae. Frond venation is another important character in the Dipteridaceae. In particular, shape and size of the areoles bounded by the secondary and tertiary veins have been used to distinguish genera (OISHI & YAMASITA 1936). We refer to the areoles bounded by the highest-order veins as ultimate areoles, and specify the surrounding vein orders when referring to larger areoles (e.g., areoles bounded by secondary and tertiary veins; Text-fig. 2).

Text-fig. 2. Illustration of terminology used. **A.** Diagram showing Dipteridaceae frond architecture with the stipe (brown), rachial arms (red), primary veins (black), and one primary segment (*) highlighted. **B.** Close up of a primary segment showing the areoles formed by the secondary veins (blue) and tertiary veins (green). **C.** Close up showing the meshwork of higher order veins and an ultimate areole (highlighted in grey).

5 Systematic description

Family Dipteridaceae SEWARD 1900

Genus *Clathropteris* BRONGN. 1828

1828 *Clathropteris* BRONGN., p. 62

Type species: *Clathropteris meniscioides* (BRONGN. 1825) BRONGN. 1828; by original designation.

*Clathropteris meniscioides*¹ (BRONGN. 1825) BRONGN.
1828

Plates 1–6

1825 *Filicites meniscioides* BRONGN., p. 218; pl. 11.

1828 *Clathropteris meniscioides* (BRONGN.) BRONGN., p. 62

Specimens examined: MPEF-Pb 1564–1565, 1732, 1771, 1784, 1857, 2214, 2669, 2691, 2696, 2703, 2707–2708, 2713, 2732, 2735, 2742, 2744, 2749, 2755, 2758, 2762, 2766, 2773, 2780, 2794, 2801, 2808, 2811, 2814–2815, 3400–3406, 3411–3412, 3417–3418, 3422–3423, 3425–3426, 3428–3430, 3436, 3443, 5055–5058, 5272–5277, 5331–5334, 5337–5339, 5352–5353, 5355–5358, 5382–5391, 5394–5398, 5513–5514, 5516, 5518, 5621, 5624, 5667–5672, 5678, 5680, 5683, 5688, 5692, 5695–5696, 5727, 5729–5732, 5735–5740, 5744–5745, 5748–5749, 6435–6437, 6544, 6566, 6584, 6587, 6596, 6599, 6950, 6970, 6997–6999.

Description: Stipes are up to 3 cm wide (Pl. 2, Fig. 2). Their complete length is unknown, but the longest stipe fragment is 12.5 cm long and 0.5 cm wide (Pl. 1, Fig. 1). Stipes are generally subterete in cross section, with a pronounced central longitudinal groove on the adaxial surface and two smaller, parallel longitudinal grooves on the abaxial surface (Pl. 5, Fig. 6); the grooves commonly appear as longitudinal ridges in compressed specimens (Pl. 1, Fig. 2; Pl. 5, Fig. 4). The stipe surface is otherwise smooth. Stipe vasculature comprises in cross section a single C-shaped bundle with incurved tips (Pl. 5, Fig. 6).

The fronds are large, bilaterally symmetrical, and flabellate (Pl. 1, Fig. 1; Pl. 2, Fig. 1). The precise maximum size is unknown, but is probably exceeding 1.5 m in diameter. Lamina is regularly incised to more than 2/3 of the total length, typically forming 12 (but possibly up to 16) about equally sized, lanceolate to oblanceolate primary segments (Pl. 1, Fig. 1; Pl. 2, Figs 1–4; Pl. 3, Figs 1–2; Pl. 4, Figs 1–3) that are separated by

wide sinuses (Pl. 3, Fig. 2). Primary segments probably reached up to 70 cm in length, the largest specimen of a complete primary segment having a length-to-width ratio of ~6:1 (22.3 cm in length and 3.8 cm at its widest point) (Pl. 2, Fig. 1) and the largest incomplete segment being 12 cm wide and over 34 cm long (Pl. 3, Fig. 1). Frond lamina glabrous and the margin of the primary segments is serrate (Pl. 3, Figs 1–3; Pl. 4, Figs 2–3; Pl. 5, Figs 1–2). Teeth occur at intervals of 9–17 mm and are incised to 4–10 mm depth, corresponding to ~20–40% of the length of the secondary vein that enters the tooth (Pl. 3, Figs 1–3; Pl. 5, Fig. 2). Each tooth is triangular to slightly falcate, with a straight to slightly concave acroscopic margin and a convex basiscopic margin. The tooth apex is inclined apically at an angle of ~20–45° to the primary vein of the segment (Pl. 3, Figs 1–3; Pl. 5, Fig. 2).

The base of the frond blade is composed of two equal, opposite rachial arms up to 8 mm thick (Pl. 2, Figs 2–4). Each rachial arm undergoes a series of 5 (or occasionally 6 or 7) catadromous dichotomies (the final dichotomy being more or less isodromous) at intervals corresponding to 2–4 times the basal width of the rachial arm (i.e., 4.5–20 mm) (Pl. 2, Figs 2–4; Pl. 4, Fig. 1). Acroscopically, the dichotomies give rise to 6–8 primary veins, which depart at angles of 30–60° (rarely up to ~80°), the angle of insertion generally decreasing with each successive dichotomy giving the architecture a flabellate appearance (Pl. 2, Figs 2–4; Pl. 4, Fig. 1). Each primary vein forms the main axis of a primary segment (Pl. 3, Figs 1–2; Pl. 4, Figs 1–3). Primary veins are simple and straight, up to 3.5 mm wide at the base and tapering to ~0.1 mm at the apex of the primary segment (Pl. 2, Figs 1–4; Pl. 3, Figs 1–2; Pl. 4, Figs 1–3). Secondary veins are (sub)opposite to alternate, and depart at angles between 55–80° (typically ~70°) and at regular intervals of 6–18 mm, depending on the size of the frond (Pl. 3, Figs 1–3; Pl. 4, Figs 4–5). Secondary veins are simple, straight, and ~0.2–0.6 mm wide (Pl. 3, Figs 1–3; Pl. 4, Fig. 5; Pl. 6, Fig. 1). In the fused basal portion of the frond lamina, secondary veins become confluent at varying angles (Pl. 4, Fig. 4), whereas in the separate primary segments, each secondary vein terminates in a tooth

Most authors have adopted the spelling '*meniscoides*' instead of the original '*meniscioides*'. However, it is clear from the original description that BRONGNIART (1828) chose this name to indicate the similarity of the type material with extant *Meniscium* (now a subgenus of *Thelypteris*); hence, like NATHORST (1906), we propose that the original spelling '*meniscioides*' (i.e., 'resembling *Meniscium*') should be preferred over of the more commonly used '*meniscoides*' (i.e., 'resembling a crescent'; see HITCHCOCK 1855).

at the lamina margin (Pl. 3, Figs 1, 2; Pl. 5, Fig. 1–2); very rarely, secondary veins also converge in the free primary segments (Pl. 5, Fig. 3). Tertiary veins are generally opposite, ~ 0.1 – 0.2 mm in width, and departing from secondary veins at ~ 70 – 100° (typically 85°) at regular intervals between 3–8 mm (Pl. 3, Figs 1–3; Pl. 4, Fig. 5). In the free, distal ends of the primary segments, most tertiary veins are monopodial, connecting to adjacent secondary veins in straight or slightly outward-curving lines to form a regular latticework of orthogonal areoles with the secondary veins (Pl. 3, Figs 1–3; Pl. 4, Fig. 5); tertiary veins are very rarely sympodial or forming a zig-zag pattern (Pl. 4, Fig. 6). In the fused basal portion of the frond, the arrangement and general appearance of the tertiary veins is irregular; they may appear sympodial, are sometimes indistinct from secondary veins, and generally form polygonal areoles (Pl. 4, Fig. 4). Across the lamina, the tertiary and higher-order veins depart at an angle of $\sim 90^\circ$ to form a fine reticulate mesh of square or rectangular ultimate areoles (Pl. 4, Fig. 7). Each ultimate areole is ~ 0.2 – 1.0 mm² in area, and most ultimate areoles enclose a single vein that dichotomizes to form two free-ending veinlets (Pl. 4, Fig. 7).

In fertile fronds, sori are scattered across the lamina surface without any apparent association with the major veins, although they become more dispersed towards the frond margins (Pl. 6, Fig. 1). Each sorus is positioned in an ultimate areole (although adjacent sori can become confluent and appear to take up more than one areole; Pl. 6, Figs 1–5), round, 0.5–1 mm in diameter, exindusiate, and composed of at least 8 (probably between 10–15) sporangia that do not seem to be arranged in any regular order (Pl. 6, Figs 5–6). Sporangial capsules measure 200–300 μ m in diameter (Pl. 6, Figs 6–7) and have a ring-like annulus that is composed of more than 12 cells (probably 25–30 cells) ~ 50 μ m in width (Pl. 6, Figs 7–8).

Comparisons: The new material from Cerro Bayo falls into the range of variation seen in the type species *C. meniscioides* (Table 1). This is evident by its very large size, lanceolate to oblanceolate shape of primary segments, moderately developed teeth (incised to up to 30% of the secondary-vein length), and mainly monopodial tertiary-vein architecture (Table 1). Similarly large fronds of *Clathropteris* have previously been described from Germany (GOEPPERT 1846), eastern North America (e.g., FONTAINE, 1883), and Vietnam (ZEILLER 1903), under the name *C. platyphylla* (GOEPP. 1846) BRONGN. 1849 (Table 1).

In Patagonia, several fragments of large *Clathropteris* fronds from Neuquén province, Argentina, were described as *C. ingens* FRENG. 1941 (FRENGUELLI 1941). FRENGUELLI (1941) also reported a second *Clathropteris* species (*C. kurtzii* FRENG. 1941) from the same site that differs from *C. ingens* merely in its smaller size. Additional material of *C. kurtzii* was subsequently described from coeval deposits at other sites in Chubut province, Argentina (BONETTI 1963). In a review of the Patagonian fossils, HERBST (1966) considered both *C. kurtzii* and *C. ingens* to be insufficiently distinguishable and placed both in synonymy with *C. obovata* OISHI 1932. Our specimens are indistinguishable from the fragmentary specimens of *C. ingens*, and we are of the opinion that *C. kurtzii* is likely a juvenile form of *C. ingens*. However, whereas we agree with HERBST's (1966) decision to consider the two species as conspecific, we disagree with synonymizing the two species with *C. obovata*, as the type of the latter differs by deeper teeth and obovate primary segments. Instead, we consider *C. ingens* and *C. kurtzii* to be conspecific with *C. meniscioides*.

6 Discussion

The generic status of *Clathropteris*

Clathropteris was established in 1828 with the description of *C. meniscioides* from Höör, southern Sweden (BRONGNIART 1828), based on a detailed treatment of material earlier described under the name *Filicites meniscioides* BRONGN. 1825. BRONGNIART (1828) characterized the genus as being pinnatifid; having strong primary veins that extend to the extremities; and having many simple, parallel, secondary veins perpendicular to the primary vein and traversed by tertiary veins to form a meshwork of square areoles. However, not a single additional fossil has since been found to show the hierarchical pinnatifid architecture as illustrated by BRONGNIART (1825). Instead, the primary segments in all known fossils are disposed in a pedate manner (e.g., GOEPPERT 1846; OISHI 1932; FRENGUELLI 1941). NATHORST (1906) discussed the original description in detail and concluded that the illustration of *C. meniscioides* was inaccurate in its depiction of gross morphology since it was based merely on a sketch of the fossil as seen by the author on site during a field excursion led by Mr S. NILSSON (NATHORST 1906). Based on entries in S. NILSSON's field-book notes, NATHORST (1906) further argues that the original specimen was then later re-

moved from the quarry and brought to the geological collection of Lund University. The specimen was subsequently transferred to the Swedish Museum of Natural History in Stockholm, where it is housed today. NATHORST (1906) then synonymized *C. platyphylla* with *C. meniscioides*, as these two species were considered identical apart from the misinterpreted simply-pinnate frond architecture of the latter. NATHORST's (1906) reinterpretation of the structure of the type species *C. meniscioides* is widely accepted and many authors have since described similar fossils from various localities worldwide as *C. meniscioides* (e.g., OISHI & YAMASITA 1932; KON'NO 1968; CORNET & TRAVERSE 1975; SCHWEITZER et al. 2009; BOMFLEUR & KERP 2010; WANG et al. 2015).

Past authors have held differing views on the taxonomic rank of *Clathropteris* and its relationship with *Dictyophyllum*. Both genera are similar in gross morphology and differ mainly in their venation pattern, with *Dictyophyllum* lacking the regular orthogonal latticework of tertiary and higher-order veins seen in *Clathropteris* (SEWARD & DALE 1901; NATHORST 1906; OISHI & YAMASITA 1936; HERBST 1992); the numbers and sizes of sporangia have been considered as further delimiting features (OISHI & YAMASITA 1936). These boundaries are not always entirely clear, as the variation in all these characters appears to overlap and intergrade between species and even individual specimens (KON'NO 1968; CANTRILL 1995). Nevertheless, many authors – including, e.g., NATHORST (1906), BERRY (1918), and OISHI & YAMASITA (1936) – consider the variation in characters as significant and sufficiently useful to separate these taxa at the rank of genus, and the genus *Clathropteris* is widely used today (e.g., WANG 2002; SCHWEITZER et al. 2009; BOMFLEUR & KERP 2010). Other authors, by contrast, advocate merging *Clathropteris* as a subgenus into *Dictyophyllum* (SEWARD & DALE 1901; HERBST 1992).

Delimitation of *Clathropteris* species

The orthogonal venation pattern of *Clathropteris* is highly distinctive, making genus identification even of small fossil fragments easy. It is therefore unsurprising that a relatively large body of literature on this genus exists. Over 20 species of *Clathropteris* have been described (see JONGMANS 1959; DIJKSTRA 1967; BOERSMA & BROEKMEYER 1986; ZHOU et al. 2015). Characters commonly used for species diagno-

ses include the number, size, and shape of primary segments (OISHI 1932; FRENGUELLI 1941; ASH 1970); tooth shape (OISHI 1932); the angle of insertion of secondary veins (HEER 1877; ZHOU et al. 2015); the 'distinctness' of tertiary and quaternary veins (OISHI 1940; SCHWEITZER et al. 2009); and the size and number of sporangia per sorus (ASH 1970). A further character that is sporadically mentioned in the discussion of species boundaries, but is rarely used as a diagnostic character, is tertiary vein appearance (HERBST 1966; KON'NO 1968). However, inadequate descriptions, ambiguous features, incomplete preservation of type specimens, poor knowledge about the diagnostic significance of morphological features, and the high morphological variability of *Clathropteris* species renders the delimitation of many species difficult or impossible. As a result, many earlier-described species have since been merged into one of the two common and broadly defined species, *C. meniscioides* and *C. obovata* (e.g., JONGMANS 1959; HERBST 1966; KON'NO 1968; LITWIN 1985; SCHWEITZER et al. 2009; BOMFLEUR & KERP 2010).

The large collection from Cerro Bayo is valuable as it captures the morphological variation found within a single colony, allowing for an objective assessment of some of the quantitative characters that are commonly used for species diagnoses. For instance, based on our short survey of several *Clathropteris* specimens, including the type specimens of 8 species (Table 1), only two reported specimens, *C. pekingensis* (see ZHOU et al. 2015) and *C. obovata* (WANG et al. 2015) have angles of insertion of secondary veins that fall outside the range observed in the Cerro Bayo specimens. Notably, while HARRIS (1961) stressed that a smaller insertion angle was diagnostic of *C. obovata*, photographs from the original species protologue (OISHI 1932) show the type specimen to have insertion angles comparable to *C. meniscioides*.

Another highly variable character among the Cerro Bayo specimens is tooth depth: the total range in variation overlaps with all the published specimens we surveyed (Table 1) except for the type specimen of *C. obovata*, which has significantly deeper teeth (OISHI 1932; OISHI & YAMASITA 1936). However, other specimens of *C. obovata* (e.g., HERBST 1966; WANG et al. 2015) have much shallower laminal teeth.

The current records on the number of sporangia per sorus also appear to be too variable to be useful. In addition, based on our knowledge on the biology of extant *Dipteris*, it is a character that is difficult to

Table 1. Comparison table of a selection of *Clathropteris* specimens. Non-italicized entries represent observations made by the original authors; italicized entries indicate previously unpublished observations made from the photographs and illustrations available in the original publications.

Specimen	Source	Location & Age	Primary segment			Angle of 2° vein	Tooth shape	Tooth depth	Sorus diameter	No. of sporangia per sorus	Sporangial diameter
			Number	Shape	Max. size						
<i>Clathropteris meniscoides</i> (BRONGN.) BRONGN.	This study	Chubut, Argentina; Early Jurassic	12(–16)	Lanceolate – ob lanceolate	L: > 35 cm W: 12 cm	55–80°	Triangular to slightly facate	19–40%	0.5–1 mm	8(–15)	200–300 µm
<i>C. meniscoides</i> (BRONGN.) BRONGN. (type)	BRONGNIART 1825; BRONGNIART 1828	Höör, Scania, Sweden; Early Jurassic	–	–	–	60–70°	–	–	–	–	–
<i>C. meniscoides</i> (BRONGN.) BRONGN.	KON'NO 1968	Sarawak, Malaysia; Late Triassic	–	Lanceolate	W: 3.5 cm	40–60°	Coarse, short, triangular, acutely pointed	18–34%	0.4–0.5 mm	>10 (–15)	200–270 µm
<i>C. meniscoides</i> (BRONGN.) BRONGN.	BOMFLEUR & KERP 2010	North Victoria Land, Antarctica; Early Jurassic	–	Lanceolate	L: > 6 cm W: 4 cm	70–90°	–	–	–	up to 13	240–350 µm
<i>Polypachylus stormensis</i> X.YAO, T.N. TAYLOR & E.L. TAYLOR (type)	YAO et al. 1991	Queen Alexandra Range, Antarctica; Middle Jurassic	–	–	–	70–85°	–	–	–	10 to 13	275–375 µm
<i>C. elegans</i> OISHI (type)	OISHI 1932; OISHI 1940	Nariwa, Japan; Late Triassic	14–18	–	L: 10 cm W: 2 cm	60–70°	Subacutely or obtusely pointed	<33%	–	–	–
<i>C. walkeri</i> DAUGHERTY (type)	ASH 1970; LITWIN 1985	New Mexico, USA; Late Triassic	6–10	Lanceolate	L: > 15 cm W: 2–3 cm	40–50°	Falcate	~25%	–	7–9 (ASH) 5–15 (LITWIN)	50–210 µm (ASH); 180–280 µm (LITWIN)
<i>C. obovata</i> OISHI (type)	OISHI 1932	Nariwa, Japan; Late Triassic	–	Obovate	L: 12 cm W: 6–8 cm	~70°	Subacutely and deeply lobed, triangular	40–50%	–	–	–
<i>C. obovata</i> OISHI	HERBST 1966	Neuquen, Argentina; Early Jurassic	7(–?)	<i>Lanceolate – ob lanceolate</i>	L: 15 cm W: 8 cm	40–60°	Triangular lobes, acute apex	~25%	0.5–0.6 mm	–	160–180 µm
<i>C. obovata</i> OISHI	WANG et al. 2015	Sichuan Province, China; Late Triassic	–	Obovate	L: > 12 cm W: 5 cm	40–50°, rarely over 60°	Lobed margin	~20%	0.5–1.5 mm	10–20	140–300 µm
<i>Clathropteris</i> sp. cf. <i>C. obovata</i> OISHI	POTT 2012	Svalbard, Norway; Upper Triassic	–	–	L: > 6 cm W: 3 cm	60°	Lobate margin, teeth more acute (hook-like) towards apex	~15–40%	–	–	–

Table 1. Continued.

Specimen	Source	Location & Age	Primary segment			Angle of 2° vein	Tooth shape	Tooth depth	Sorus diameter	No. of sporangia per sorus	Sporangial diameter
			Number	Shape	Max. size						
<i>C. kurtzii</i> FRENG. (type)	FRENGUELLI 1941	Neuquen, Argentina; Early Jurassic	-	-	L: 3.6 cm W: 3 cm	65–90°	Falcate	<33%	-	-	-
<i>C. kurtzii</i> FRENG.	BONETTI 1963	Chubut, Argentina; Middle Jurassic	14–20	Lanceolate	L: > 5 cm W: 2.5 cm	60–65°	Triangular	<20%	-	-	-
<i>C. ingens</i> FRENG. (type)	FRENGUELLI 1941	Neuquen, Argentina; Early Jurassic	-	-	W: 13 cm	60°	-	-	-	-	-
<i>C. platyphylla</i> (GOEPP.) BRONGN. (type)	GOEPPERT 1846	Keuper, France; Triassic	4–5 (8–10?)	Broadly oblong	"Large"	50–80°	Triangular	<20%	-	-	-
<i>C. platyphylla</i> (GOEPP.) BRONGN.	ZEILLER 1903	Tonkin, Vietnam; Late Triassic	10–30	Lanceolate	L: 20–80 cm	~90° 60–80°	-	<25%	-	5–12	-
<i>C. platyphylla</i> var. <i>expansa</i> FONTAINE (type)	FONTAINE 1883	Virginia, USA; Early Mesozoic	>6	Oblong	L: > 30 cm W: 8–10 cm	Acute – right angle	-	-	-	-	-
<i>C. reticulata</i> KURR.	HEER 1877	Switzerland	-	Lanceolate	W: 5 cm	~55°	-	-	-	-	-
<i>C. pekingensis</i> LEE & SHEN	ZHOU et al. 2015	Inner Mongolia, China; Jurassic	-	Lorate, lanceolate	L: > 20 cm W: 8–10 cm	40–45°	Triangular (Serrate)	-	-	-	-

measure and should be regarded with caution. Each sorus of *D. conjugata* REINW. 1825 is known to be composed of many sporangia that have mixed maturation (SEWARD & DALE 1901; ARMOUR 1907), so a count at any single moment in time is likely to be an underestimate. At the same time, even though *D. lobbiana* (HOOK. 1853) T. MOORE 1857 is reported to have simultaneous sporangial maturation (ARMOUR 1907), determining the number of sporangia is still difficult because the sori are covered in a gummy substance before maturity (HOOKER 1853). The diameter of sporangial capsules is a more promising diagnostic character. However, the current paucity of records does not allow for clear distinctions to be made between different taxa. The few well-preserved sporangia from our specimens fall within the full range of all the fossils that have been ascribed to *C. meniscioides*. Interestingly, the *Clathropteris* specimens from Neuquén, Argentina, described by HERBST (1966) also have relatively small sporangia, suggesting that they are more closely aligned with our specimens than specimens of *C. meniscioides* found elsewhere.

Three characters, that are probably diagnostic but can be difficult to determine in fossil material, are the maximum size of fronds, number of primary segments per frond and shape of each primary segment. Our fully-intact specimens from Cerro Bayo are fairly regular in having 12 lanceolate primary segments per frond with only little variation. However, the Cerro Bayo collection is rather unusual in having a large number of intact fronds preserved. These characters are less useful for fragmentary material. The maximum size of fronds is especially difficult to determine from collections where no fertile material is present. In these cases, it is almost impossible to distinguish between mature and juvenile fronds, and maximum size estimates are likely to be underestimates.

Our specimens and the short comparative survey of various *Clathropteris* specimens suggest that many *Clathropteris* species cannot be adequately subdivided based on the available morphological features alone. Perhaps a much larger study including many more *Clathropteris* fossils and additional morphometric tools would be able to further partition the total amount of variation. If so, it would likely result in an overhaul of the taxonomy *Clathropteris*, or at the very least, require the assignment of epitypes to the current species descriptions to resolve differences between the type species.

Palaeoecology of *Clathropteris meniscioides*

The Dipteridaceae is one of three families in the Gleicheniales, a clade that comprises mostly pioneering species of open, disturbed landscapes (HOLTUM 1954; KRAMER et al. 1990; WING & SUES 1992). Fossil evidence from Cerro Bayo provides support for *Clathropteris meniscioides* having occupied a similar ecological niche in the Early Jurassic of Patagonia. The presence of monotypic assemblages of *C. meniscioides* at different developmental stages in thick beds of presumable sheet-flood deposits, overlain by finer-grained lacustrine beds that contain a much richer and more diverse plant taphocenosis (ESCAPA et al. 2008; ESCAPA & CÚNEO 2012; ESCAPA et al. 2014; ELGORRIAGA et al. 2015), suggests that *C. meniscioides* formed large, prominent colonies in floodplains, and was largely absent in the more mature vegetation types. This is comparable to the ecological niche of *Dipteris lobbiana*, an extant rheophytic species that forms thickets in open areas along streams that are liable to sudden flooding (HOLTUM 1954; CHOO pers. obs.).

Venation characters provide further evidence for the palaeoecology of *Clathropteris meniscioides*. The Dipteridaceae is one of the few non-angiosperm lineages that independently evolved a reticulate hierarchical network with internally directed veinlets (BOYCE 2005). The family is also noteworthy in having one of the highest vein densities ($\sim 5 \text{ mm mm}^{-2}$) outside of the angiosperm clade (mean $\sim 8 \text{ mm mm}^{-2}$, but up to 25 mm mm^{-2}), and more than double the vein density of other ferns (mean $\sim 1.5 \text{ mm mm}^{-2}$; BOYCE et al. 2009). This character is significant as venation density is highly correlated with transpiration and carbon assimilation rates (BRODRIBB et al. 2007; BOYCE et al. 2009). Thus, in environments where light and water availability were not limiting, such as open marshes and floodplains, it is likely that *C. meniscioides* would have been much more productive and grow significantly faster than other lineages. One disadvantage of highly irrigated leaves is a susceptibility to drying out in conditions where water is scarce. This may explain why extant Dipteridaceae species are only found in humid, tropical to subtropical regions (KRAMER et al. 1990), and why the family fossil record declines during the later part of the Jurassic, when climatic conditions became drier overall (SKOG 2001; VAN KONJENBURG-VAN CITTERT 2002).

In their review of Mesozoic ecology, WING & SUES (1992) noted that massive herbivorous dinosaurs were common in Gondwana from the Middle Triassic, becoming dominant ecological players in the Jurassic. These megaherbivores must have had high calorific requirements, indicating in turn that the associated vegetation must have provided large amounts of leafy material and have had a capacity for rapid regrowth (WING & SUES 1992; GEE 2011). Some authors have suggested that ferns in large marshlands were probably a major food source, especially for megaherbivores with low browsing ranges, such as the stegosauria (KRASSILOV 1981; WING & SUES 1992; HUMMEL et al. 2008). GEE (2011) compared the likeliness of different Mesozoic plant groups as potential food sources for the large sauropod dinosaurs, and concluded that *Equisetum* L. 1753, which was thought to have grown fast and formed large colonies in open areas, was one of the likely food sources. The two fern groups examined by GEE (2011; i.e. Osmundaceae BERCHTOLD & J. PRESL 1820 and Marattiaceae KALF. 1824) were ranked as less likely food sources for the sauropods, despite having high energy contents, in part due to their preference for closed-canopy habitats, making them less accessible to the sauropods (GEE 2011). Certain osmundaceous ferns were noted to form dense thickets, and were considered as a possible minor part of the sauropod diet in mesic habitats (GEE 2011). In contrast, the slow growth and propagation of living Marattiaceae suggested that the Mesozoic relatives would have had a poor response to intense herbivore feeding pressures (GEE 2011). Interestingly, *Equisetum*, Osmundaceae and Marattiaceae fossils are all found in the Cerro Bayo site (ESCAPA & CÚNEO 2012; ESCAPA et al. 2014; ELGORRIAGA et al. 2015).

In terms of growth habit and preferred habitat, *Clathropteris meniscioides* is more similar to *Equisetum* than either Osmundaceae or Marattiaceae. While we do not have detailed information on the rhizome structure of *C. meniscioides* from Cerro Bayo, *Clathropteris* material from Sweden as well as fossils of *Thaumatopteris* and *Hausmannia*, as well as all extant Dipteridaceae, are known to have horizontal, branching rhizome systems (RICHTER 1906; NATHORST 1906; NATHORST 1907; CHANDRA & KAUR 1993). This low branching system would have allowed *C. meniscioides* to proliferate quickly on the floodplains, forming dense thickets (Text-fig. 3). Having multiple rhizome growth apices at ground level would reduce long-term damage incurred by browsing. Vein density

Text-fig. 3. Artist reconstruction of a *Clathropteris meniscioides* colony, with the silhouette of a person for scale.

evidence also suggests that *C. meniscioides* was likely to have much higher carbon assimilation rates than other lineages, including Osmundaceae and Marattiaceae, which are both free-veined lineages with relatively low vein densities ($1.5\text{--}2.5\text{ mm mm}^{-2}$; BOYCE et al. 2009). This capacity for fast regrowth and high levels of production of leafy material makes *C. meniscioides* a prime candidate as fodder for megaherbivores.

Altogether, the presence of large colonies of *C. meniscioides* at Cerro Bayo suggests that the area was an open, flood-prone marshland during the Early Jurassic. *Clathropteris meniscioides*, with its very large fronds and fast-growing colonizing habit, was a prominent component of the vegetation and may have provided an important food source for local megaherbivores.

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Plates 1–6 and explanation of plates

Plate 1

Single specimen of *Clathropteris meniscioides* (BRONGN. 1825) BRONGN. 1828. The specimen is composed of two counterparts and shows the relative positions of the frond and stipe. (Scale bar = 2 cm)

- Fig. 1. Top view of the specimen, showing two halves of the bilaterally symmetrical frond.
Fig. 2. Side view of one half of the specimen, showing the upright stipe, branching pattern of one rachial arm and one half of the frond.

Plate 1. CHOO et al.

Plate 2

Various sized specimens of *Clathropteris meniscioides* (BRONGN. 1825) BRONGN. 1828 showing the rachial arm architecture.

- Fig. 1. Near-complete frond with the largest complete primary segment of the entire collection indicated (arrowhead).
 (Scale bar = 6 cm)
- Fig. 2. Specimen with the largest stipe. (Scale bar = 5 cm)
- Figs 3–4. Specimens showing catadromously branching rachial arm. (Scale bars = 1 cm)

Plate 2. CHOO et al.

Plate 3

Primary segments of *Clathropteris meniscioides* (BRONGN. 1825) BRONGN. 1828

- Fig. 1. Largest (incomplete) primary segment. Lamina teeth are found throughout the length, indicating that this fragment is from the distal, free end of the frond. (Scale bar = 2 cm)
- Fig. 2. Specimen showing the basal region of a frond where the lamina between primary segments is fused. (Scale bar = 2 cm)
- Fig. 3. Fragment of a primary segment showing laminal teeth. (Scale bar = 2 cm)

Plate 3. CHOO et al.

Plate 4

Frond lamina and venation details of *Clathropteris meniscioides* (BRONGN. 1825) BRONGN. 1828

- Fig. 1. Specimen showing rachial arm architecture and disposition of primary segments. (Scale bar = 2 cm)
- Fig. 2. Lanceolate to oblanceolate primary segment. (Scale bar = 2 cm)
- Fig. 3. Near complete frond showing toothed, lanceolate primary segments. (Scale bar = 2 cm)
- Fig. 4. Details of venation in the fused portion of the lamina. The secondary and tertiary vein paths are irregular and sometimes indistinguishable, and the areoles formed between secondary and tertiary veins are irregular polygons. (Scale bar = 1 cm)
- Fig. 5. Free portion of a primary segment showing the orthogonal areoles formed by the secondary and tertiary veins. (Scale bar = 1 cm)
- Fig. 6. Details of tertiary vein paths between two secondary veins. Most tertiary veins are monopodial; an occasional sympodial tertiary vein is indicated with arrowheads. (Scale bar = 5 mm)
- Fig. 7. Close up of two areoles formed by secondary (vertical) and tertiary (horizontal) veins. Mesh of squarish ultimate areoles formed by higher order veins visible (Scale bar = 2 mm)

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Plate 5

Details of *Clathropteris meniscioides* (BRONGN. 1825) BRONGN. 1828

- Fig. 1. Secondary veins ending in marginal teeth. (Scale bar = 1 cm)
- Fig. 2. Apex of a primary segment. (Scale bar = 1 cm)
- Fig. 3. Rare occurrence of secondary veins anastomosing (indicated by arrowhead). (Scale bar = 1 cm)
- Fig. 4. Close up of the abaxial surface of the stipe, showing two parallel longitudinal grooves. (Scale bar = 2 mm)
- Fig. 5. Large structure that is either a stipe or creeping rhizome. (Scale bar = 2 cm)
- Fig. 6. Cross section through a stipe, showing a single C-shaped vascular bundle with the incurved tips. (Scale bar = 0.5 mm)
- Fig. 7. Crozier. (Scale bar = 1 cm)

Plate 5. CHOO et al.

Plate 6

Reproductive characters of *Clathropteris meniscioides* (BRONGN. 1825) BRONGN. 1828

- Figs 1–2. Circular sori scattered across frond lamina of primary segments. (Scale bar = 1 cm)
Fig. 3. Sori becoming more dispersed towards frond margin. (Scale bar = 6 mm)
Fig. 4. Close up of lamina showing sori positioned within ultimate areoles. (Scale bar = 2 mm)
Fig. 5. Sori showing individual sporangia. (Scale bar = 1 mm)
Fig. 6. Close up of lamina showing impressions of several sporangia with prominent annuli. (Scale bar = 0.3 mm)
Fig. 7. Close up of a sporangium showing uniseriate annulus. (Scale bar = 0.3 mm)
Fig. 8. SEM photograph of a sporangium with part of the annulus visible. (Scale bar = 0.1 mm)