

EVIDENCE FOR POLYMORPHISM OF PALAEO FLORA FROM JURASSIC BEDS IN THE TABBOWA BASIN SRI LANKA

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ABSTRACT

Sedimentary rocks of Jurassic age are found in few small, faulted, basins in the crystalline rock terrain of Sri Lanka, in the northwestern part of the country. Presence of plant fossils in some of the sedimentary rocks in those basins are well known and therefore, the present study was carried out mainly in one of these sedimentary basins; Tabbowa, focusing identification of the morphology of macrofossils in view of determining their systematic affinity to palaeo-environment. The observed characteristic features based on the characteristic venation distribution, pinnule margin and shapes of pinnules, were compared with those of local and international type specimens and with published literature, pertaining to various palaeo-climates. The fossil record of *Cladophlebis* sp. belonging to the family Osmundaceae are known as one of the oldest plant group since Permian period and as representing high diversity in the Early Jurassic. Detailed observations indicated that a many of the *Cladophlebis* spp. are assigned to different species belong to Jurassic: *C. zeylanica* Sitholey 1944, *C. indica* (Oldham & Morris) Sahni and Rao 1933, *C. australis* (Morris) Seward 1904 and *C. antarctica* Halle 1913 even in different countries. However, varying formats of description, varying terminology and the lack of systematic uniformity have often hampered identification of those species correctly. The present study and its identification of morphological and, (though limited) taxonomical features of the studied samples suggest that all species are closely related and possibly originated from one classic species, *Cladophlebis denticulata* Brongniart (1828) Fontaine 1889, known as a polymorphisms or intra-specific variability of its evolutionary process. In addition, this paper provides the morphological characters *vis a vis* taxonomic assignment and palaeoecological significance of the genus *Cladophlebis*.

Key words: *Cladophlebis denticulate*, Jurassic beds, Plant fossils, Polymorphisms, Tabbowa Sri Lanka

INTRODUCTION

About 10% of the landmass of Sri Lanka consists of sedimentary rocks and at few localities, belonging to Jurassic age. Found in some faulted, basins in the Northwestern part of the country. Tabbowa basin is the most known among those. Presence of plant fossils, that are present in some of the rocks in Tabbowa basin are less studied though some workers have studied

geology, mineralogy and geochemistry (Kehelpannala, 1997; Cooray, 1984; Pitawala *et al.*, 2003; Ratnayake and Sampei, 2015; Chang *et al.*, 2017) at several times. Of the studies on Palaeobotany and Palynology, Seward and Holtum (1922), Wayland, (1925), Deraniyagala (1939) and Sitholey (1944) have made significant descriptions on the basic knowledge of fossil plants within the basin. However, since 1944, there had been no recorded

systematic investigations on Palaeobotany or Palynology of the Tabbowa basin with a few exceptions by Edirisooriya and Dharmagunawardhane in 2013, 2014, 2016 and 2017.

In view of the above, the present work is an integrated approach to study the plant fossils in Tabbowa sedimentary basin of Sri Lanka and to investigate the mode of deposition, their features in relation to intra-specific variability in view of reconstructing the environments and climate during the period when these flora were prevailing.

During Early Jurassic the Gondwana beds were dominated by ferns represented by four families as Osmundaceae, Matoniaceae, Dipteridaceae and Dicksoniaceae (Barbacka and Bodor, 2008). One of the well-known species, *Cladophlebis* Brongniart (1828) of the family Osmundaceae is common in Gondwana beds of Sri Lanka, India, Australia and Antarctica (Taylor *et al.*, 1983).

The family Osmundaceae is most primitive among the ferns of the Filicales, dating back to Late Paleozoic in the geological history (Bomfleur *et al.*, 2017). Foliage of the fossil Osmundaceae, however, is not well known. The absence of fertile structures attached to foliage particularly in ferns makes it difficult to separate taxonomically. Therefore, many fossil leaves of Osmundaceae have been placed by the investigators in *Cladophlebis*; a form genus of sterile *Osmunda*-like foliage (Brongniart, 1849). However, Osmundaceous foliage did not morphologically change in the Jurassic period but their fertile fronds have changed mostly in pre-Jurassic period (Harris, 1969).

This family is taxonomically important because morphological investigation of these fossil plants indicated more than one form of individual species in a single species or in the single population, which is known as polymorphism. Evidence for the polymorphism of *Cladophlebis* was found in the Tabbowa plant fossils for the first time, in this study. This paper reports the evidences found, discusses the environment of deposition and the fossil records bridging the gaps of fossil evidence from Sri Lanka in support of its position in the Gondwana. However, the diversity and distribution pattern of this family is yet to be investigated.

GEOLOGICAL BACKGROUND OF THE AREA

Around 90% of the bedrock in Sri Lanka consists of Precambrian crystalline rocks. Jurassic, Miocene and Quaternary strata are largely confined to a thin belt of exposures in the north and northwest of the island (Herath, 1986; Figure 1a). The fossiliferous strata sampled in this study are exposed close to the spillway of an irrigation reservoir – the Tabbowa Tank (8° 04' 21" N, 79° 56' E) - within the Tabbowa Basin (Figure 1b). The Tabbowa Basin is a small graben previously considered to host only Jurassic strata. The basin extends over an area of only a few square kilometers in the Northwestern Province of Sri Lanka (Wayland, 1925; Cooray, 1984). The graben developed in a crystalline basement terrain and hosts nearly 1000 m of strata consisting mostly of grey to reddish shales, mudstones, siltstones and arkosic sandstones (Cooray, 1984).

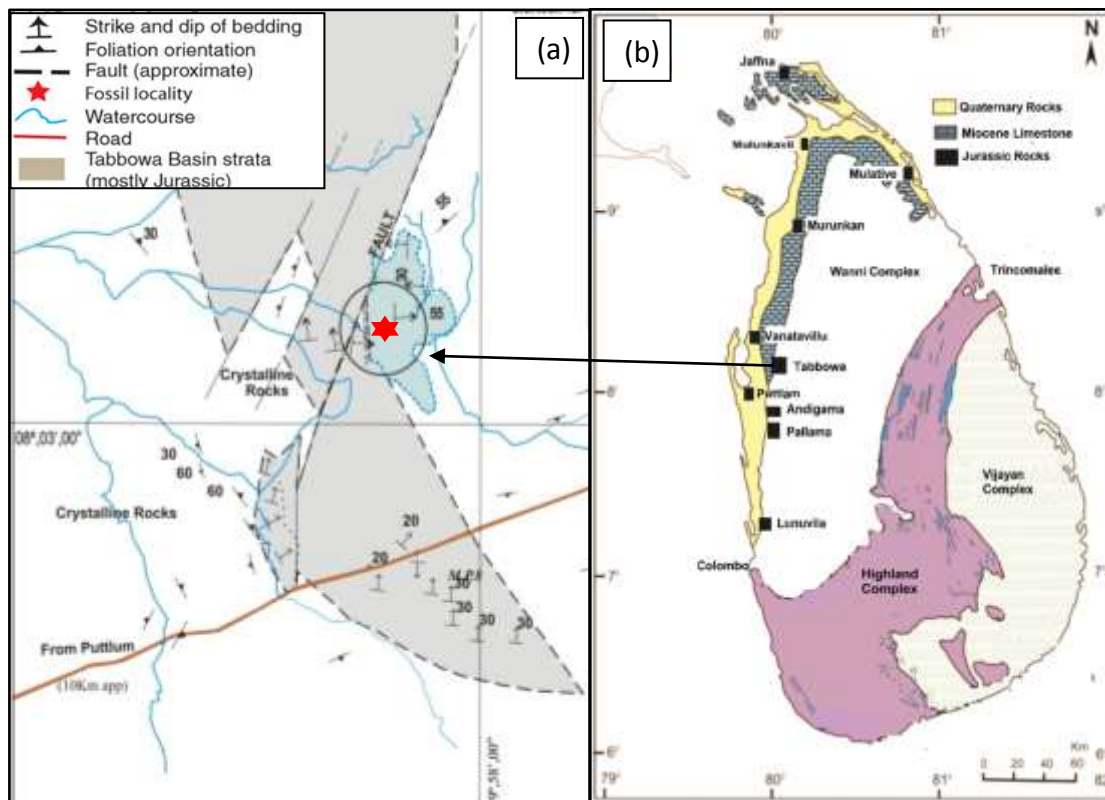


Fig. 1. (a) Generalized map showing major Geological units of Sri Lanka (b) the sample location near to Tabbowa tank (Modified after Wayland, 1925; Cooray, 1984; Cooray and Vitanage, 1991).

MATERIALS AND PROCEDURES

Some of the fern fossil specimens of genus *Cladophlebis* were collected from the Early Jurassic deposits in the Tabbowa basin (Figure 1). The specimens were preserved in Mudstone. The frond fragments were preserved as impressions and small amounts of organic material were occasionally observed but cuticles were not observed. The morphological features of most of the preserved specimens were well defined. Samples were observed under low power microscope under incidence light and the specimens were photographed using standard macro-photographic techniques with low angle illumination. Fossil specimens were identified based on morphological features and specific comparisons were made with the material stored in the Natural History Museum of London,

Victoria National Museum, Melbourne and the specimens recorded from Australia, India and Antarctica.

Morphological terminology used by Seward (1900), Sitholey (1944), Douglas (1969) were followed and classifications and amendments as proposed by Harris (1961) were used in the present study. Wherever complete leaves were preserved the length and the width, thickness of rachis, were measured and the length /width relationship was calculated. All illustrated Sri Lankan specimens were lodged in the Herbarium, National Botanical Department, Royal Botanical Garden, Peradeniya, Sri Lanka (PDA - type) and at Museum, Department of Geology, University of Peradeniya (GMU- holo type), for future reference. Specimens were numbered as - Tabbowa Mudstone Collection-

SL/TB/PDA/T-J/2014/*Clado.*/A-D.

Holotype:SL/TB/GMU/T-

J/2014/*Clado.*/a-c.(*Abbreviations.*- SL -Sri Lanka, TB - Tabbowa, PDA.- Peradeniya National Botanical Department, T-J - Triassic – Jurassic, 2014 - Published year, *Clado.* - Plant name (Genus), GMU - Geology Museum, University of Peradeniya A-D- Collection No).

SYSTEMATIC DESCRIPTION OF PALAEOBOTANY

Order : Osmundales

Family :Osmundaceae Berchtold and Presl.1820

Genus :*Cladophlebis* Brongniart 1828

1. **MORPHOTAXON:** *Cladophlebis zeylanica* Sitholey 1944

MATERIAL

SL/TB/PDA/Triassic- Jurassic / 2014 / *Clado*/ A-D, Near Tabbowa Tank.

Holotype. - SL/TB/GMU/T-J/2014/*Clado*/a-d.

EXAMINED:

All are stored in a Museum, Department of Geology and Peradeniya Royal Botanical Garden, Department of Agriculture. Specimen No. A – TBCI 3, B - TBCI 4, C -TBCI 9, D – TB CI 11. as follows Figure 2 A-D.

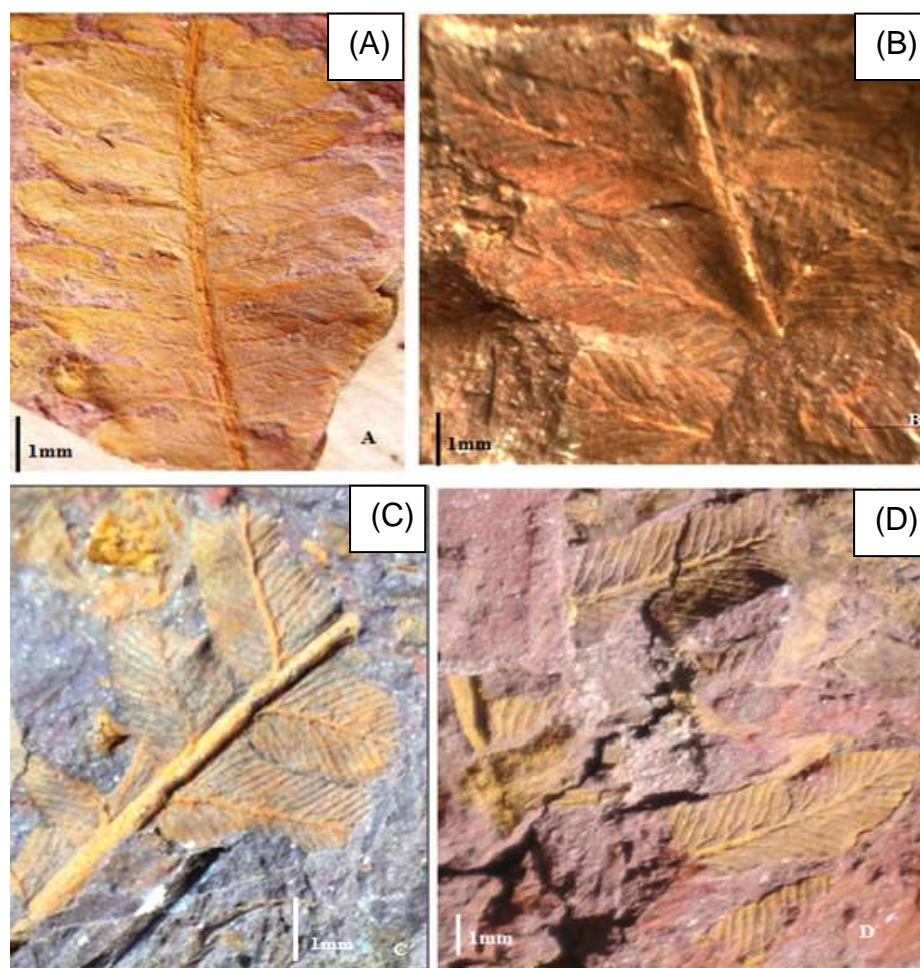


Fig. 2. *Cladophlebis zeylanica*. (A)-(D) specimens of present study found from Tabbowa basin, Sri Lanka. (A) Sterile frond showing pinnule attachment by prominent midrib to upper surface of rachis. (B) Portion of sterile frond showing serrate marginal falcate pinnules. (C) Showing twice bifurcation of most basal vein (X). (D) Showing imprint of detach pinnules.

Description: Portion of the frond (Figure 2a) compound and once pinnate. Length of the frond is 8.5 mm and the width is about 6.0 mm. Length of the whole frond unknown. Frond is sterile (Figure 2a, c). Length of the rachis 8.5 mm and up to 1.0 - 1.5 mm wide. Rachis is distinctly thick, smooth, and rounded, bears alternate nine pairs of pinnules (Figure 2a) though distal most apical pinnules bear sub-opposite. Frond shape is deltoid, occasionally lanceolate.

Pinnules are typically alternate or sub-opposite (Figure 2b), katadromic branching arrangement (Figure 2a, c), arising on basiscopic side of the rachis at an angle of 60° - 70° .

Pinnules straight (Figure 2a) to falcate (Figure 2b) in shape, tapering slightly towards the apex. Pinnule margins prominently dentate or serrate or cuneate but in some cases can be entire (Figure 2a, b) in the upper part or whole pinnule. Margins near parallel in first 2/3 of distance from base to apex then converging to acute apex. Pinnule apices are generally acute (Figure 2b) to sub-acute or blunt (Figure 2a) but occasionally obtuse. Pinnules are attached by entire width of their basiscopic base (Figure 2a-c). Pinnule lamina contiguous near base while rest of the pinnule is separated. Acroscopic base of pinnule is usually expanded. Basiscopic base of pinnule is slightly decurrent, therefore pinnule base is asymmetrical. Pinnule length varying from 4.5 mm to 12 mm, basal width 2.0 mm to 5.0 mm. Pinnule length to basal width ratio is 2.8-3.5.

Midrib is prominent extending up to apex and strongly attached to rachis upper-surface. Primary veins are straight arising on rachis at an angle to 60° - 62° . In basal region primary veins are opposite and in apical region alternate

(alt.) or sub-opposite (rarely). Secondary veins are arch arise making an angle of approximately 35° - 40° to midrib. Secondary veins in apical region of pinnule remaining simple, un-forked (distal most two or three pairs of veins). Vein density varies from 16 to 20 (Figure a-c) on one half of the pinnule and number of secondary veins at the margin is 10-12 pairs.

2. MORPHOTAXON: *Cladophlebis indica* (Oldham and Morris (1863) and Sahni and Rao (1933)

(Pl. I, figs 4, 7; pl. II, figs 5, 6; text-fig. 2)

SELECTED SYNONYMS

1863 *Pecopteris (Alethopteris) indica*, Oldham Morris, P.47

1877b *Alethopteris indica*, Feistmantel, p.89

1877c *Alethopteris (Cladophlebis) indica*, Feistmantel, p.169

1879a *Alethopteris indica* Feistmantel, p.205

1933 *Cladophlebis indica*, Sahni & A.R. Rao, P.189

MATERIAL EXAMINED: Specimen No. (Victoria Museum, Melbourne) A-182046, B -182046, C -181761, D-165769 (61966) as follows: Figure 3 A-D.

Description: Sterile pinna fragments with rather stout pinna axis up to 1-1.5 mm wide. Length of the rachis 7 mm and up to 1.0 -1.5 mm wide. Rachis is distinctly thick, smooth, and rounded, bears alternate pinnules or sub-alternate. Frond shape is lanceolate. Pinnules are typically alternate, or sub-opposite (A-D), katadromic branching arrangement arising on basiscopic side of the rachis at an angle of 40° - 50° . Pinnules straight to falcate or deltoid in shape, tapering slightly towards the apex. Pinnule margins distinctly entire but in some cases can be serrate (C).

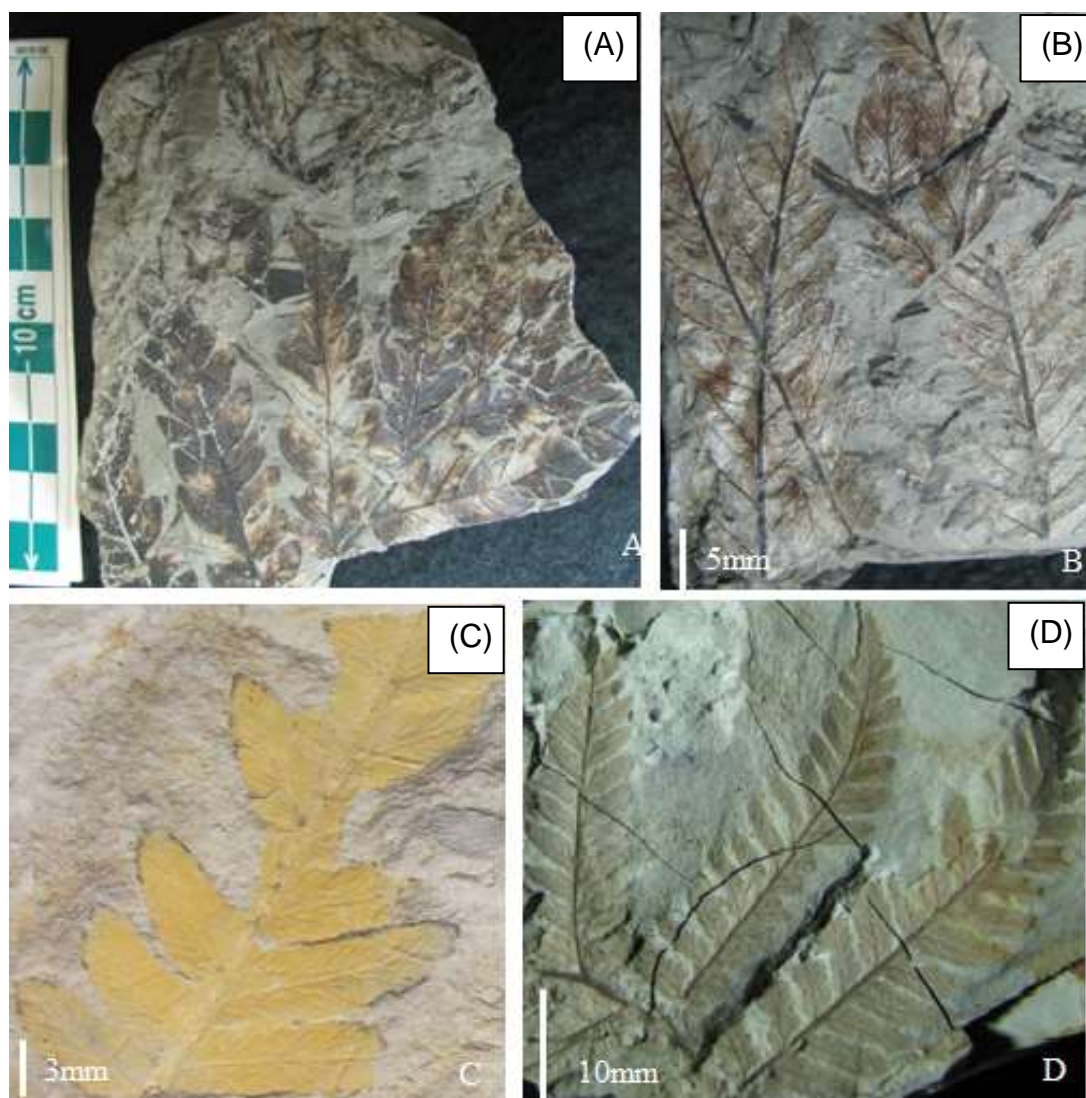


Fig. 3. *Cladophlebis indica* (Oldham and Morris, 1863) and Sahni and Rao (1933) found from Rajmahal India. **A, B, D** - Portions of a large sterile bipinnate and tripinnate fronds showing katadromic branching pattern with alternative pinnules, **C**- upper part of sterile frond showing serrated margin of pinnules and their attachment to the upper surface of grooved rachis.

Pinnule apices are generally acute to sub-acute or blunt but occasionally obtuse. Pinnules are inserted laterally to the rachis by entire width of the base. Pinnule lamina contiguous near base while rest of the pinnule is separated. Acroscopic base of pinnule usually expanded. Basiscopic base of pinnule is slightly decurrent. Pinnule length varying from 10 mm to 11 mm, basal width 1 mm to 3.0 - 5.0 mm. Pinnule length to basal width ratio is 3:1 or less than 3.0.

Midrib is prominent extending up to apex and strongly attached to rachis lateral side or upper-surface. Primary veins are straight arise on rachis at an angle to 60° - 75° . Secondary veins are arising an angle of approximately 30° - 48° to midrib. Secondary veins in apical region of pinnule remaining simple, un-forked. Vein density varies from 8-9 pairs on one half of the pinnule.

3. MORPHOTAXON: *Cladophlebis australis* (Morris) Seward 1904 (Pl.16,

pl.17, figs. 1-4, pl.18, figs.2-3, figs.7, 1-3)

SELECTED SYNONYMS

1845 *Pecopteris australis* (Morris) In Strzelecki, p.248, figs.1, 2 sp.

1874 *Pecopteris australis* (Morris) McCoy, p.16, pl.14, fig.3, 3A (First Victorian figured)

1890 *Alethopteris australis* (Morris). Feistmantel, p.109, pl.27, figs. 3,3A

1900 *Alethopteris australis* (Morris). McCoy, in Stirling p.3., pl.2. figs. 3,3A

1904 *Cladophlebis denticulata* Brongniart var. *australis* (Morris). Seward. P. 171-174, figs.25-27

1954a. *Cladophlebis australis* (Morris) Seward. Medwell.p.84.

1967 *Cladophlebis australis*, Jain and Delevoryas, p.568, pl.88, figs.1-4, pl.89, fig.1

MATERIAL EXAMINED: Specimen No. A -P160557 B.M. (N.H), B-V11607 BM (N.H)-1925, C- 181759, D- V.1579. All are stores at British Natural History Museum. Geology Department, as follows Figure 4. A-D.

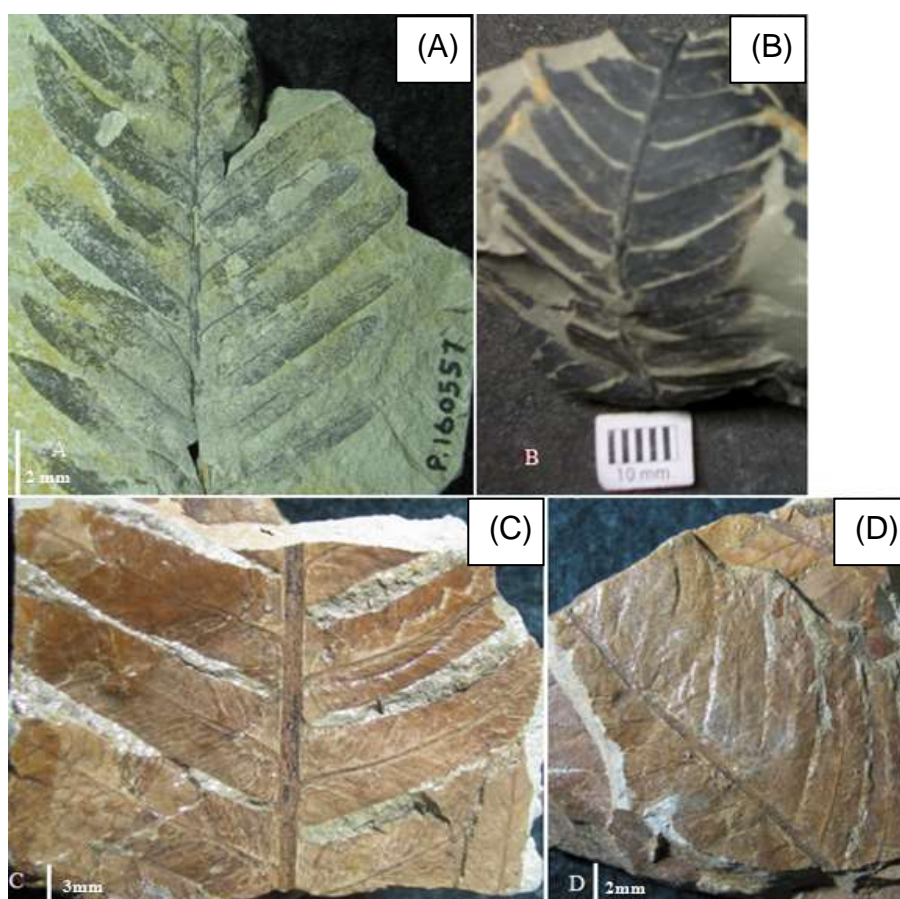


Fig. 4. *Cladophlebis australis* (Morris) Seward, Upper Jurassic, sterile found from Boola Boola forest, Victoria, Australia. **A.** Lower part of sterile leaf, showing pinnule attachment to the upper surface of rachis. **B.** Sterile frond showing upper part with pinnule attachment to rachis. **C, D-** *C.australis* (colle-1910) - middle region of sterile fronds showing elongated form of pinnules.

Description: Portion of the frond large (A, B & C) compound and bipinnate.

Length of the frond variable, incomplete and actual size unknown.

Fronds are sterile (A, B, C & D). Rachis is distinctly thick, smooth, and rounded, bears alternate pinnules though distal most apical pinnules bear sub-opposite (A). Frond shape is conical- lanceolate, apex long pointed – rounded.

Pinnules are typically alternate, katadromic branching arrangement arising on basiscopic side of the rachis at an angle of 45° to 70° - 80° . Pinnules straight (A) to falcate (B, C & D) in shape, tapering slightly towards the apex. Pinnule margins distinctly entire (A & B) but in some pinnules can be serrated (B & D) in the whole pinnule. Pinnule apices are generally long, narrow point (A & B) to blunt (C & D) or occasionally obtuse.

Pinnules are inserted lateral to the rachis by entire width of their basiscopic base (A-D). Pinnule margins indented, rarely overlapping. Acroscopic base of pinnule usually expanded. Basiscopic base of pinnule is slightly decurrent, making asymmetrical base. Pinnule length varying from 3 mm to 15 mm, basal width 3 mm to 5 mm.

Midrib is prominent extending up to apex and strongly attached to rachis lower-surface. Primary veins are straight arise on rachis at an angle to 45° . Secondary veins usually branching near midrib making small angle and in apical region of pinnule remaining simple, un-forked. Vein density varies from 10 to 12 per 10 mm (A-D) on one half of the pinnule.

4. MORPHOTAXON: *Cladophlebis antarctica* Halle, 1913

(Plate 6, figure 2, Plate 7, Figure 3, and Text-figure 3C)

SELECTED SYNONYMS

1913 *Cladophlebis antarctica* Halle, pl.1, fig 15-23, pl.3, fig.6

1947 *Cladophlebis antarctica* Halle, Frenguelli, text-fig.5a-d

1963 *Cladophlebis cf. antarctica* Halle, Bonetti, pl.1, fig.2

1964b *Cladophlebis antarctica* Halle, Herbst, pl.1, fig.8, pl.2, fig.16.

1981 cf. *Cladophlebis antarctica* Halle, Jefferson, pl.4.5, fig.1-2,

1989 *Cladophlebis antarctica* Halle, Gee, pl.2, fig.15, pl.3, fig.24

MATERIAL EXAMINED: A- Collected 1910, Ref. No. V 15735, B- D8941.5A Botany Bay from Antarctica, as follows: Figure.5, A-B. All are stored at British Natural History Museum.

Description: Sterile frond fragment, compound and once pinnate. Length of the incomplete frond is up to 6 mm and the width is about 2.5 mm. Length of the rachis 6.5 mm and up to 1.0 -1.5 mm wide. Rachis is thick, smooth, and prominent, bears alternate pinnules though distal most apical pinnules bear sub-opposite. Frond shape is lanceolate.

Pinnules are typically alternate at the basal region and sub-opposite at the apical region. Pinnules are katadromic arising on basiscopic side of the rachis at an angle of 50° - 70° . Pinnules falcate or cuneate in shape, tapering slightly towards the apex. Pinnule margins distinctly serrate / denticulate but in some cases can be entire in the upper part. Margins near parallel base to acute apex. Pinnule apices are generally acute to sub-acute. Pinnules are inserted laterally to the rachis and typically connected by lamina. Acroscopic base of pinnule usually expanded. Basiscopic base of pinnule is slightly decurrent or contracted therefore pinnule base is asymmetrical. Pinnule length varying from 8.0 mm to 12 mm, basal width 0.8 mm to 1.0 mm. Pinnule length to basal width ratio is 2.9-4.0

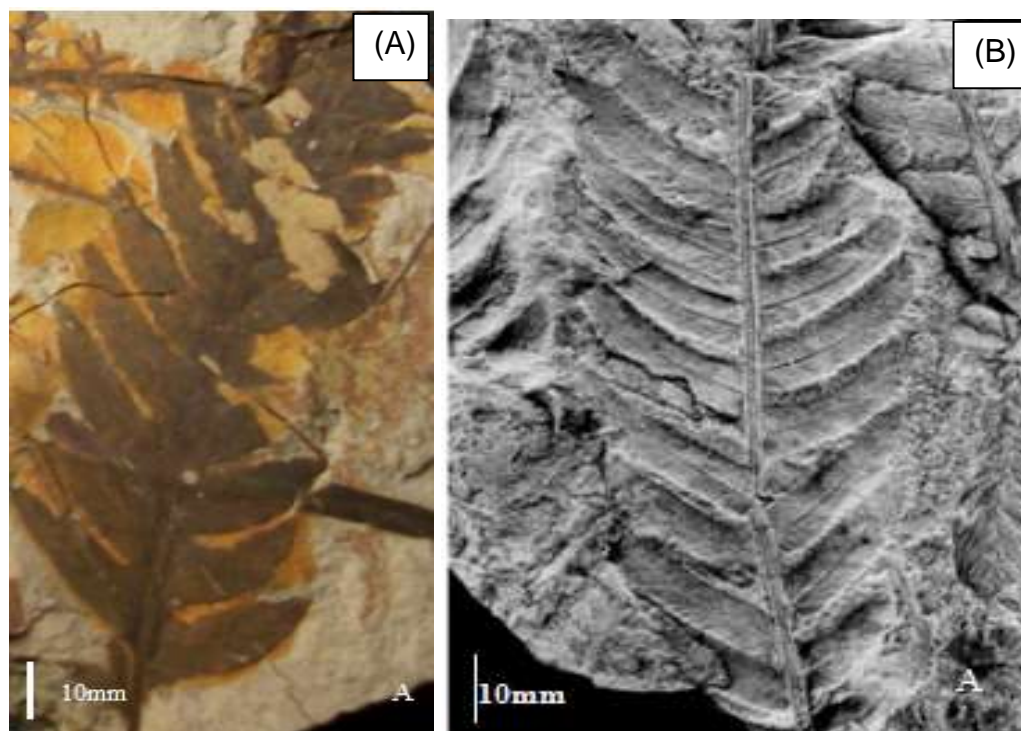


Fig. 5. *Cladophlebis antarctica* Halle found from Botany Bay sedimentary basin .Antarctica. **A**-sterile frond fragment showing pinnule attachment to the main rachis (British.Museum: collected 1910, Ref. No. V 15735), **B** – sterile frond fragment collected from Botany Bay, Antarctica (D.8941, Rees and Cleal, 2004).

Midrib is prominent extending up to apex and strongly attached to rachis lower-surface, slightly sunken on upper surface. Primary veins are straight arise on rachis at an angle to 40° - 46° in central region of pinnule. Secondary veins typically forking once. Secondary veins in apical region of pinnule remaining simple, un-forked (distal most two or three pairs of veins). Vein density varies from 10 to 12 on one half of the pinnule (5-8 pairs).

5. MORPHOTAXON: *Cladophlebis denticulata* (Brongniart 1828) Fontaine 1889 (Pl.2, figs.5-9)

SELECTED SYNONYMS

- 1828 *Pecopteris denticulata* Brongniart, p. 301, pl 98, figs 1, 2.
 1828 *Pecopteris phillipsi* Brongniart, p.304, pl. 109, fig. 1.

- 1876 *Cladophlebis denticulata* (Brongniart) Nathorst, p. 19.
 1889 *Cladophlebis denticulata* (Brongniart) Fontaine 1889, p. 71 pl. 7 figs 7, 7a.
 1905 *Cladophlebis denticulata* (Brongniart) Nathorst; Ward, p. 68, pl.11, figs 1-7.
 1911 *Cladophlebis denticulata* Brongniart; Seward, p. 668, pl. 2, figs 31-36, 38, pl. 6, figs 8, 9, pl. 8,fig. 29.
 1913 *Cladophlebis antarctica* Halle, p. 14, pl. 1, figs 15-23, pl. 3, fig. 6.
 1959 *Cladophlebis denticulata* Brongniart; Kimura,sp. 13, pl. 3, fig. 4; pl. 4, figs 3,6, pl.5, fig.1, pl. 12, fig. 10, text-fig. 8.
 1959 *Cladophlebis* sp. A, Kimura, p. 20, pl. 4, fig. 1.

1989 *Cladophlebis antarctica* Halle;
Gee, p. 166, pl. 2, fig. 15, pl. 3,
fig. 23.

1989 *Cladophlebis denticulata*
(Brongniart) Fontaine 1889
emend. Harris; Gee, p. 166, pl.
2, fig. 14, pl. 3, fig. 25.

1997 *Cladophlebis denticulata*
(Brongniart) Fontaine 1889;
Popa, pl. 2, fig. 3, text-fig. 31.

1997 *Cladophlebis denticulata*
(Brongniart) Nathorst;

2004 *Cladophlebis denticulata*
(Brongniart) Fontaine 1889
emend. Harris; Rees & Cleal, p.
26, pl. 6, fig. 4, pl. 7, figs 1, 2,
text-fig. 3D.

MATERIAL EXAMINED: Specimen No.
A-TB Cl 1, B- TB Cl 2 , TBCl 1 as
follows : Figure 6, A-B All are stored in
a Museum, Department of Geology .

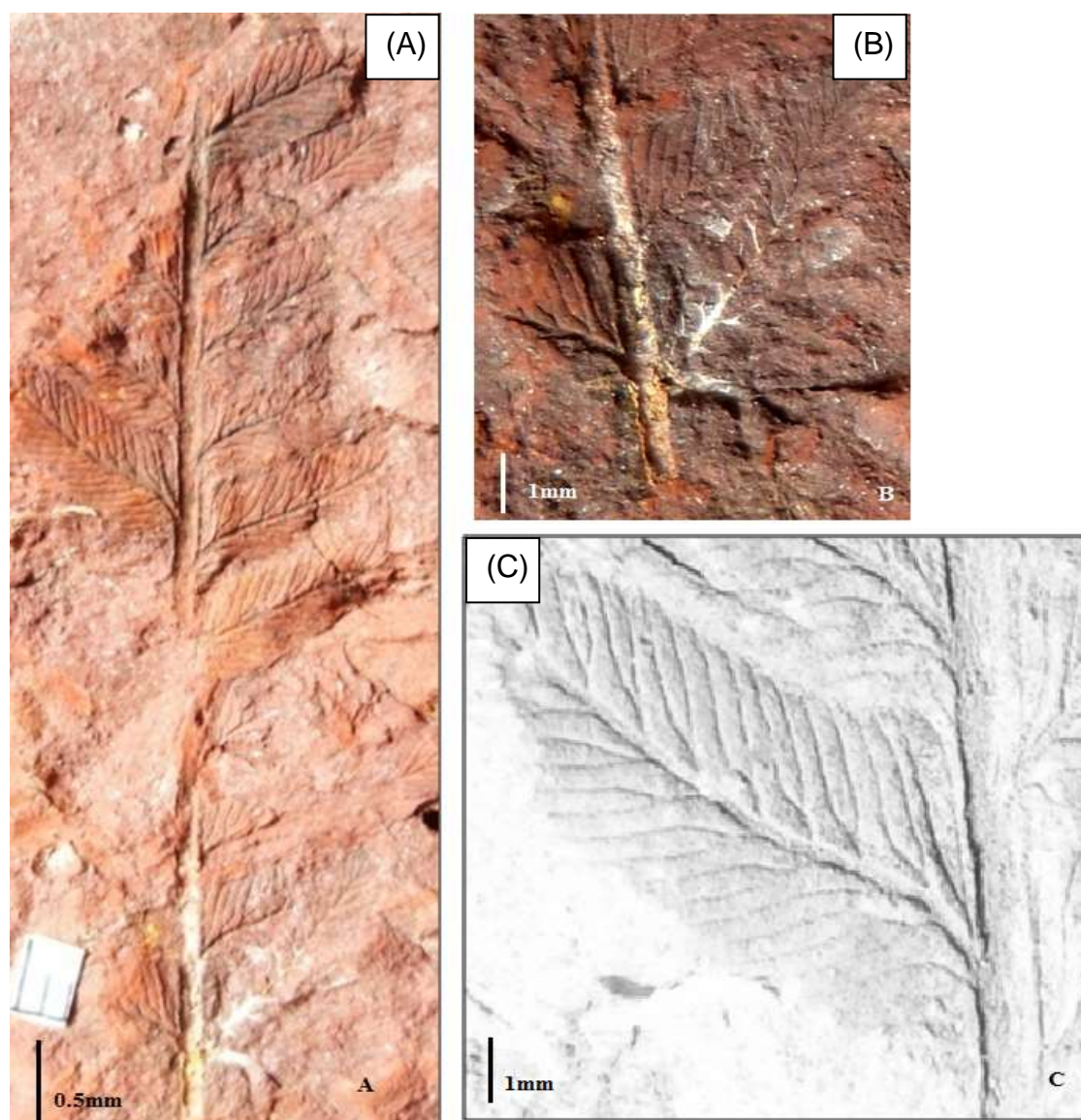


Fig. 6. *Cladophlebis denticulata* (Brongniart, 1828) Fontaine 1889 found from Tabbowa beds, Sri Lanka. **A- B:** sterile frond fragment showing pinnule attachment to the main rachis and **C:** shows the details of close-up of pinnule attachment to the rachis and variation distribution of pinnule.

Description: A well preserved bipinnate, fragmented sterile pinnae. 21.3 mm long, contains nearly 10 complete pinnules. The rachis up to 1.5–2.5 mm wide and smooth.

Pinnules are arise at 45° - 65° angle on pinna rachis. They are typically alternate (A & B) or sub-alternate. Also elongated pinnules are triangular shaped with acute or sub-acute apex, and relatively wide bases, or rarely rectangular pinnules with rounded apex. The adjacent pinnule bases are in contact with each other. Pinnule bases expanded acroscopically and slightly contracted basiscopically. Therefore pinnule base is being asymmetrical.

Margins are serrate or entire. Margins are near- parallel distance from base apex then converging to acute apex. Pinnules are cuneate or falcate can be seen at the middle of pinnae and straight towards the pinnae apex. Width of the largest pinnule at the base is about 6.0 mm to 3.0 - 4.0 mm. Their length ranges from 6 to 17.5 mm and the basal width ranges from 2.8 to 6.5 mm. Ratio of pinnule length to basal width 2.1 to 2.7 (typically 1.5 to < 3 (Rees and Cleal, 2004).

Venation is distinct, pectopterid type, the midrib straight, persisting nearly to apex of the pinnule; Primary veins straight and reaching to the margin. Then secondary veins arise 30° - 35° angle at one third of distance from primary veins. Secondary veins are forking once symmetrically, keeping 0.3-0.4 mm interval between secondary veins.

Lowermost secondary vein arising on basiscopical side of pinnule, typically forking twice. The number of secondary veins (twin) varies from 9 to 10 on one half of the pinnule, most specimens have 10-12 veins, and vein

density at the pinnule margin is 5–9 /cm, (typically 5–6/cm).

In particular, morphological data showing comparative features of different species indicates that *Cladophlebis denticulata* in all probability is an ancestral taxon of the four species, *C. zeylanica*, *C. indica*, *C. australis* and *C. antarctica*. All specimens are recognized as *Cladophlebis* by its shape, relatively narrow and elongated pinnules with dentate, serrate, or entire margins, comparatively thick main rachis, *Cladophlebis* venation pattern, secondary veins once forked, Katadromic pinnule arrangement. Pinnule length to basal width ratio between 5-3.

COMPARISON AND DISCUSSION

Present study describes *Cladophlebis denticulata* (Brongniart 1828) Fontaine 1889 from the Tabbowa basin, based on fossil plant specimen, noted that there were a several taxa of *Cladophlebis* characterized by, falcated shape and slightly dentate or serrate pinnule margins and venation distribution such as *Cladophlebis C. indica* Oldham & Morris) Sahni and Rao 1933, *C. antarctica* Halle, 1913, *C. zeylanica* Sitholey, 1944 and *C. australis* (Morris) Seward 1904 (Table 1 and Figure 7).

Cladophlebis denticulata (Brongniart, 1828) Fontaine 1889 is a very common species in the Early Jurassic and well distinguishable due to its elongated pinnules with dentate margins, acute or sub-acute apices, and rachis ridges. From super-gondwana cluster countries including Sri Lanka, all specimens were found in a large number, enough to show the variability within this species. The most variable characteristics are the shape, size of

pinnules, ratio of pinnules and the pinnule arising angle. The genus *Cladophlebis* contains numerous species distinguished on morphological differences.

Cladophlebis denticulata var. *C. zeylanica* and *C. indica* has the smallest pinnules of all species. It corresponds to the dentate/serrate forms of *C. denticulata* from *zeylanica* and *indica* (Figure 2-B and Figure 3-C) in its rounded apices, sub-alternate or sub-opposite arrangement of the pinnules, serrate pinnule margins, and number of bifurcations of secondary veins. Other morphological features slightly differ in these taxa, such as pinnule length /width and number of secondary veins at the pinnule margin

The difference between *Cladophlebis antarctica* and *C. denticulata* is very slight. The material from Antarctica has slightly lower density of secondary veins (5-8) and a larger angle of arising of secondary veins (usually 50°–80°),

whereas the way of bifurcation of secondary veins, length/ width ratio, and the margins, apex, and base of pinnules correspond in the two taxa. Although *C. australis* bifurcation of secondary veins once only at the most basal veins. Halle (1913) noticed very close similarity between *Cladophlebis denticulata* (Brongniart) Fontaine 1889 and *C. Antarctica* Halle. Therefore, he left these species separate, but Rees and Cleal (2004) suggested that *C. antarctica* Halle and *C. denticulata* (Brongniart, 1828) Fontaine 1889 were not different species, they suggested a fusion of species with emended diagnosis. However, the emended diagnosis given earlier by Harris (1961) seems to be sufficient. The differences between *C.denticulata* (Brongniart) Fontaine 1889 compared with *C. antarctica* Halle is presented in Table 1 fit into the range given by Harris (1961). The number (or density) of secondary veins and their bifurcations in the examined material also show intermediate forms.

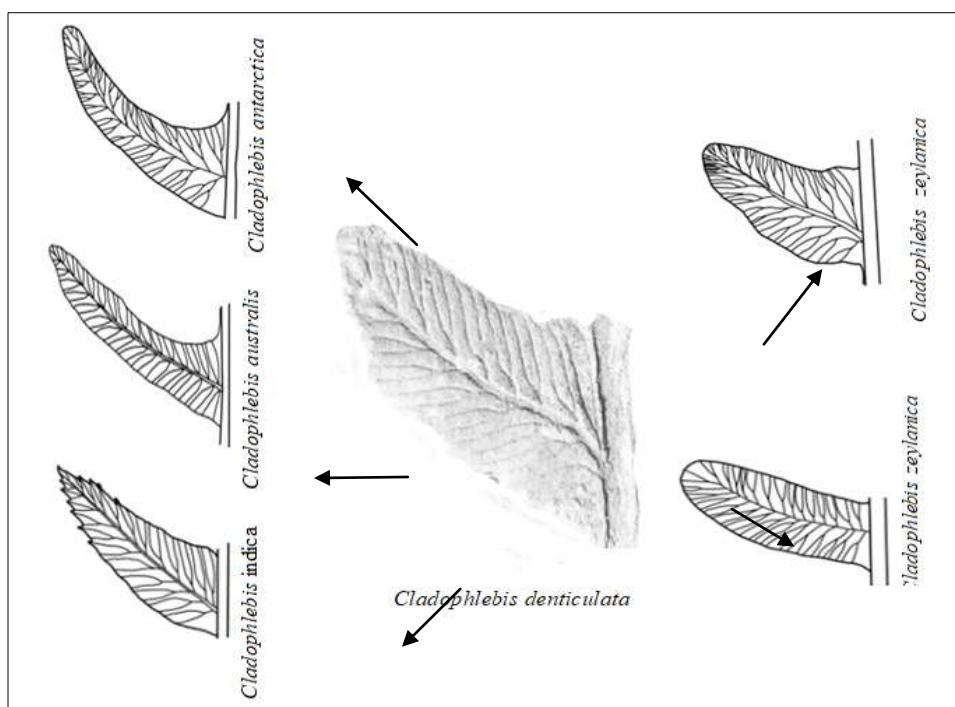


Fig. 7. Schematic drawing of sterile pinnules of different Osmundaceous ferns from Sri Lanka, India, Australia and Antarctica (Sources: Jarzynka, 2016).

Table 1. Showing comparative similarity of characters in different species of *Cladophlebis*

Species Features	<i>Cladophlebis zeylanica</i>	<i>Cladophlebis indica</i>	<i>Cladophlebis australis</i>	<i>Cladophlebis antarctica</i>	<i>Cladophlebis denticulata</i>
Arrangement of pinnules	Alternate/ Opposite, Katadromic	Alternate	Alternate	Alternate	Alternate
Pinnule shape	Falcate / straight	Falcate / Deltoid	Falcate /straight	Falcate	Falcate/ elongated
Base of pinnule	Decurrent	Decurrent	Decurrent	Decurrent	Decurrent
Pinnule apex	Acute / Blunt / Obtuse	Acute / Blunt / Obtuse	Acute / Blunt / Obtuse	Acute / Blunt /Obtuse	Acute/sub acute
Margin of pinnule	Entire / Serrate/ Cuneate	Entire / dentate / Cuneate	Entire /Serrate	Entire / Serrate	Dentate or rarely entire
Pinnule Insertion Angle	60 ⁰ -70 ⁰	40-50 ⁰	45-80 ⁰	50-80 ⁰	27-65 ⁰
Length of Pinnule (mm)	4.5- 12.0	10.0 -11.0	3.0 -15.0	At least 8.5	7-8
Width of Pinnule (mm)	2.0 - 5.0	3.0 - 5.0	3.0-5.0	About 2.5	3-9
Ratio Length/width of pinnule	2.25 – 2.4	3 or less than 3	3.0	3.4 or	1.25
Width of the rachis (mm)	Primary rachis 4.5, 2 ^{ry} rachis 1-1.5	Primary rachis 4.5, 2 ^{ry} rachis 1-1.5	Primary rachis 4.5, 2 ^{ry} rachis 1-1.5	Primary rachis 4.5 and 2 ^{ry} rachis 1-1.5	Primary rachis 4.0 and 2 ^{ry} rachis 1-3
Number of secondary veins at the margin of pinnule (one side)	10-12 pair	8-9 pairs	10-12 pairs	5-8 pairs	4-12 pairs
Vein density/1mm	2 -4 per mm	2 - 4 per mm	2-5 per mm	1-3 per mm	3-9 per mm
Bifurcation of the secondary veins of the pinnule	1mm distance to the midrib. Once or twice only at the most basal vein	1mm distance to the midrib. once or twice only at the most basal vein	1mm distance to the midrib. once only at the most basal vein	One third of distance to the margin. once or twice only at the most basal vein	One third of distance to the margin. once or twice only at the most basal vein

However, high morphological variability of this *C. denticulata* and suggested that *Cladophlebis zeylanica* might be a “naked” form of *C. denticulata* or small form of *C. indica*. The differences between them details of the pinnule margins and the secondary veins (Table 1 and Figure 7); other morphological features of all these taxa resembled, such as the length /width ratio, type of bifurcation, and angle of arising of secondary veins. The specimens described by Figure 2, 3 and 4 are similar to range of features observed in *C. denticulata*. The entire margin in *C. denticulata* corresponds to *C. zeylanica* (Figure 2, A, C), *C. indica* (Figure 3A, B), and *C. australis* (Figure 4A), though the entire and serrate margins both occur even within the same pinnule. Some of the difference between alternate pinnae and the opposite pinnae, value of length and the width, ratio values, apex types, these features do not consider as a truly taxonomical features as they highly variable in taxa according to the position of pinnules, age of the taxon and conditions can be changed by the preservation (Bodor and Barbacka, 2008).

Halle (1913) described *C. antarctica* including to the “group *denticulata*”, suggested that “it is better to separate distinct smaller species than to keep one large collective species” (Barbacka and Bodor, 2008). However, in this reason there were numerous form of species with very similar, sometimes almost the same morphology. This effects as a problem with the identification of a new taxon, which may show slight differences, thus again justify creating as a new species. For the above four species also the same situation has been faced. In such similar forms as mentioned above should be considered as one species with differences that are the result of natural intra-species polymorphism of the genus *Cladophlebis*.

It is worth noticing that all discussed forms usually occur in the same localities

with *C. denticulata* (Brongniart, 1828) Fontaine 1889 and their easily identifiable morphology may be the result of environmental circumstances. Present study suggests that species of *Cladophlebis* distributed in Sri Lanka, India, Australia and Antarctica e. g. *C. zeylanica* Sitholey, 1944 (Sri Lanka), *C. indica* (Oldham and Morris) Sahni and Rao 1933 (India), *C. australis* (Morris) Seward 1904 (Australia) and *C. antarctica* Halle, 1913 (Antarctica) are closely related with the species, *C. denticulata* Brongniart (1828) Fontaine 1889 although they have their own specific characters. Different features are examined in relation with intra-specific variability commonly observed in ferns. We have concluded that many characteristics which are used for species determination of this genus are inter related with classic species *Cladophlebis denticulata* distributed in Early Jurassic beds of Sri Lanka, India, Antarctica and Australia. The significance of these plant fossils have also been discussed in relation to palaeoecological and palaeoenvironmental conditions during Early Jurassic.

PALAEOECOLOGY AND PALAEO-ENVIRONMENTAL SIGNIFICANCE

The state of preservation of macro-remains, collectively proves that most of them are autochthonous in origin and the conditions were suitable for preservation of plant fossils. The dominance of large undamaged fragments, fronds preserved in branching state, relatively large fragments of leaves, occurrence of underground rhizomes with thin roots in growing positions demonstrate in *situ* preservation of plant fossils. It is widely believed that osmundaceous ferns preferred usually wet habitats in the vicinity of riverbanks, lake banks, and marshes or understory of forests growing in swampy areas (Gee, 1989; Barbacka and Bodor 2008). These sites were periodically flooded and were characterized by higher moisture.

Moreover, the low degree of frond fragmentation suggests relatively undisturbed and stable conditions, and short transport to the sedimentary basin.

The Tabbowa sediments where the *C. denticulata* and *C. zeylanica* collected are mostly fluvial fresh water deposits with a significant amount of terrestrial higher plants (Edirisooriya and Dharmagunawardhane, 2013, Ratnayake and Sampei, 2015).

Different *Cladophlebis* species with uniform morphological characters show similar patterns of preservation. Especially *Cladophlebis denticulata* has relatively narrow and elongated pinnules with dentate margins. Though these types of comparatively variable morphological characters (polymorphism) are results of their micro-habitat which must have been a harsher or dry environment.

CONCLUSION

Present study reveals that comparative morphological features of all five *Cladophlebis* species known from Early Jurassic sediments of Gondwanaland viz., *C. zeylanica* (Sri Lanka), *C. indica* (India), *C. australis* (Australia) and *C. antarctica* (Antarctica) demonstrate that they are all closely related ally of the species *C. denticulata* (Sri Lanka) found in Tabbowa basin, Sri Lanka. However, taxonomical significance could not be revealed clearly due to limited number and poor status of preservations of the fossils. Morphological variations in the four species *Cladophlebis* may have possibly developed due to the effect of environmental conditions in their micro habitat in the Early Jurassic during their evolution. Observed morphological characters can be attributed to the result of polymorphism of *Cladophlebis denticulata*. As such *Cladophlebis denticulata* may be considered as the classic form of the family *Osmundaceae* and survived with morphological variation

and adaptation during Early Jurassic in the Gondwanaland. However, further studies with a larger number of samples and solid statistical analysis are required for firm confirmation.

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