A new fern, *Cladarastega burmanica* gen. et sp. nov. (Dennstaedtiaceae: Polypodiales) in mid-Cretaceous Burmese amber

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Abstract

A new fern, *Cladarastega burmanica* gen. et sp. nov. (Dennstaedtiaceae: Polypodiales) is described from a fertile pinnule in Burmese amber. The new species has dentate margins with acute apices, furcated 1 and 2 forked free veins angled toward pinnule apex, elongate, multicellular and glandular hairs on the epidermis, epidermal peltate scales, sori roundish, apical and subapical on abaxial surface of fronds near vein endings and paraphyses. There are both inner and outer cup-shaped indusia. The inner indusium is initially solid but then disintegrates while still attached to the sorus. The sporangium is stalked with a vertical or slightly oblique annulus. The spores are tetrahedral trilette. Related topics discussed are phyllogenetic studies on ages pertaining to the origin of the Dennstaedtiaceae in comparison to the age of the fossil, associations with competing angiosperms and insect herbivores of ferns.

Keywords: Mid-Cretaceous fern; Dennstaedtiaceae; Myanmar; morphology; herbivores; angiosperms.

1. Introduction

Ferns comprise a group that is second only to the flowering plants, with a diversity greater than that of gymnosperms (McElwain 2011). The fossil record of ferns extends back to the Devonian and their origin is inferred to have been in the mid–late Silurian (Testo & Sundue 2016) in the Palaeozoic over 400 Mya, thus revealing their ecological success over time. They continued to prosper and were able to maintain their diversity during the rise of the angiosperms that made their appearance in the Early Cretaceous (Friis & Endress 1990).

The mid-Cretaceous was an extremely important period in the development of ferns and flowering plants. Both groups were evolving and competing for space, sunlight and nutrients with various established gymnosperms. Representatives of five fern families (Dennstaedtiaceae, Cystodiaceae, Lindsaeaceae, Thyrsopteridaceae and Pteridaceae) are currently known to have been part of the flora of the Burmese amber forest (Table 1). Both ferns and angiosperms had to contend with invertebrate and vertebrate herbivores. Ferns had a much longer period to adjust to insect herbivores than angiosperms and that may be why today, there are fewer insect groups attacking ferns than angiosperms.

The purpose of the present paper is to describe a new fern of the family Dennstaedtiaceae in Burmese amber, to compare it with extant ferns as well as those previously described from this source, to discuss the presence of a possible herbivore and to suggest interactions that probably occurred between mid-Cretaceous ferns and evolving angiosperms.

2. Material and methods

The specimen originates from the Noije Bum 2001 Summit Site mine first excavated in the Hukawng Valley in 2001 and located southwest of Maingkhwan in Kachin State (26º20ʹN, 96º36ʹE) in Myanmar. Based on palaeontological evidence this site was dated to the late Albian of the Early Cretaceous (Cruickshank & Ko 2003: fig. 1), placing the age at 97–110 Ma. A later study using U-Pb zircon dating determined the age to be 98.79 ± 0.62 Ma, at the Albian/Cenomanian boundary (Shi et al. 2012). A more recent zircon U-Pb and trace element analyses of amber from different locations in northern Myanmar confirmed an age of around 100 Ma for amber from the Hukawng Valley as well as an age range of 72–110 Ma for amber from other sites in northern Myanmar (Xing & Qui 2020: fig. 1). Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noije Bum 2001 Summit Site indicate an araucarian tree source of the amber (Poinar et al. 2007).

Observations and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 800 X. Helicon Focus Pro X64 was used to stack photos for better depth of field.

3. Systematic description

The fossil represents two terminal fragments of a fertile pinna, which together contain some 25 sori with developing sporangia and spores. One of the fragments is shown in Fig. 1. Syninclusions include the remains of an immature blattoid.
**Table 1.** Ferns described from Burmese amber.

| Taxon                        | Family                   | Reference               |
|------------------------------|--------------------------|-------------------------|
| Cretacifilix fungiformis     | incertae sedis          | Poinar & Buckley (2008) |
| Krameropteris resinatus      | Dennstaedtiaceae         | Schneider et al. (2016) |
| Cystodium sorbifolioides     | Cystodiaceae             | Regaldo et al. (2017a)  |
| Unnamed                     | Lindseaeae               | Regaldo et al. (2017b)  |
| Thyssopteris cretacea        | Thyssopteridaceae        | Li et al. (2019)        |
| Heinrichsia cheilanthoides   | Pteridaceae              | Regaldo et al. (2019)   |
| Proodontosoria myanmarensis  | Lindseaeae               | Li et al. (2020)        |
| Cladarastega burmanica       | Dennstaedtiaceae         | Present study           |

**Table 2.** Characters of other genera in the Dennstaedtiaceae that differ from *Cladarastega burmanica* gen. et sp. nov. (after Yañez et al. 2014; Brownsey 1998; Smith et al. 2006).

| Genus                        | Differing features                                                                 |
|------------------------------|-----------------------------------------------------------------------------------|
| Dennstaedtia Bernh.          | Indusia formed from inner indusium and a modified marginal lamina flap; epidermal scales absent. |
| Oenotrichia Copel.           | Reniform indusia opening towards pinna, epidermal scales absent.                    |
| Hypolepis Bernh.             | False indusium formed from modified recurved lamina margin. Spores monolete.         |
| Leptolepia Prantl.           | Reniform indusia opening toward segment apices; spores monolete, echinate.           |
| Microlepia C. Presl.         | Indusium reniform, half-cup or cup-shaped, semicircular, flap opening towards pinna margin. Spores smooth, verrucate or echinate. |
| Histiopteris (J. Agardh) J. Sm. | Scales only on stipe and rachis; sporangia in ± continuous sori around margins of lamina, spores monolete. |

**Class Polypodiopsida Cronquist, Takhtajan & Zimmermann 1966**

**Order Polypodiales Link 1833**

**Suborder Dennstaedtiineae Schwärzburd & Hovenkamp 2016**

**Family Dennstaedtiaceae Lotsy 1909**

**ETYMOLOGY:** The generic name is from the Greek “kladaros” = frial and the Greek “stego” = cover, regarding the fragile inner indusia.

**Type genus:** *Cladarastega* gen. nov.

**Type species:** *Cladarastega burmanica* gen. et sp. nov., monotypic.

**Diagnosis:** Segments with divided blade; margins dentate with apices acute; venation furcated, 4 times forked, veins free, angled toward pinna apex, epidermis with elongate, multicellular and glandular hairs; peltate scales present; sori rounded, marginal or submarginal on abaxial surface of fronds near vein endings; paraphyses present; with inner and outer indusia, both cup-shaped, inner indusium initially solid, later disintegrating while still attached to sorus; sporangia stalked, annulus vertical or slightly oblique; spores tetrahedral trilete, with perispore ropy and ridged.

*Cladarastega burmanica* gen. et sp. nov.

Figs. 1–5

**ETYMOLOGY:** The species epithet refers to the origin of the fossil.

**Holotype:** Deposited in the Poinar amber collection (B-P-33) maintained at Oregon State University.

**Type locality and horizon:** Kachin (Hukawng Valley) of northern Myanmar; lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

**Diagnosis:** As for genus (monotypy).
though members of the genus that separate them from Cladarastega are listed in Table 2. Typi-
long; short papillary structures lining inner walls of sporangia (Fig. 4); stoma distinct, lip cell present (Fig. 4C), 46 µm
250 µm, and widths from 117–135 µm. Vertical or slightly
(Fig. 3). Sporangia variable in shape, with diameters from 190–
µm; periscope ropy, ridged, but lacking spines (Fig. 5).
Spores tetrahedral trilete, with long axis 32–37
µm; periscope ropy, ridged, but lacking spines (Fig. 5).

**Remarks:** Members of the family Dennstaedtiaceae, which are quite diverse morphologically, are terrestrial, pan-
tropical ferns, often with long creeping rhizomes. While their
fronds are monomorphic, they can vary from 1 to 5 pinnate and
be hairy or glabrous. The veins can be free, forked or 2–3 or
more pinnate, with surfaces hairy. The sori can be round or elong-
ate, marginal or submarginal, positioned at or near vein end-
ings or on marginal connecting veins. Linear, cup-shaped or half-cup-shaped indusia are usually present. Spores are tetra-
中铁, trilet or monolete (BROWNSEY 1998; SMITH et al. 2006; PUNT et al. 2007).

Similar extant genera in the Dennstaedtiaceae and features that separate them from Cladarastega are listed in Table 2. Typi-
cally, epidermal scales are absent in the Dennstaedtiaceae, even
though members of the genus Histiopteris (J. AGARDH) J. SM. pos-
sess scales on the stipe and rachis (BROWNSEY 1998). This feature in Cladarastega associates it with members of the family Sac-
colomataceae (LUONG et al. 2015; SMITH et al. 2006). However,
members of this family typically lack articulate hairs like those
found on the fossil and on other members of the Dennstaedti-
aceae (SMITH et al., 2006). While Cladarastega falls between
these two families, it is retained in the Dennstaedtiaceae since

it shares the presence of paraphyses with this family (paraphy-
theses are rare or absent in the Saccolomataceae (LUONG et al. 2015;
SMITH et al. 2006)) and the presence of scales with Histiopteris in
the Dennstaedtiaceae, even though scales of the latter genus
are only found on the stipe and rachis (Table 2).

It is likely that the branched trichomes, some of which
reached 2.1 mm from the tips of the outstretched strands, were
from the frond of Cladarastega (Fig. 2B). In newly formed sori
of Cladarastega, both indusia are tightly attached but later the
inner one begins to disintegrate, sometimes collapsing around
the entire stalk (Fig. 3A) or from only one side of the cap (Fig. 3B).

The short papillary structures lining the inner walls of the
sporangia are curious and have not been mentioned in other spe-
cies of Dennstaedtiaceae (Fig. 4A, B) (BROWNSEY 1998; SMITH et al.
2006).

**4. Discussion**

Presently, seven genera of ferns from five families have
been described from Burmese amber (Table 1). Cretacif-
lix fungiformis POINAR & BUCKLEY (2008) possessed oval-
shaped monolete spores, reniform indusia, embossed sori,
and sporangia with a short annulus, which distinguishes it
from Cladarastega. The sori of Krameropteris resina-
tus SCHNEIDER, SCHMIDT & HENDRICKS (2016) in the family
Dennstaedtiaceae lack indusia, which differs from Clada-
rasega. Cystodium sorbifoliioides REGALADO, SCHMIDT,
SCHNEID, KRINGS & HENDRICH (REGALADO et al. 2017a), in
the family Cystodiaceae lacks scales, which separates it
from Cladarastega. Thyropteris cretacea LI & MORAN
(LI et al. 2019) in the family Thyrsopteridaceae possesses
terminal sori with cyathiform indusia, which distin-
guishes it from Cladarastega. Heinitrichsia cheilan
hoides REGALADO, SCHMIDT, KRINGS & SCHNEIDER (REGALADO et al.
2019) in the family Pteridaceae has a pseudoindusium
that separates it from the present fossil. A member of
the Lindseaeaceae was also reported from Burmese amber
(REGALADO et al. 2017b). The sori follow a continuous line
in the upper margin of the segments, which distinguishes it
from Cladarastega. Another member of the same family
was described as Proodontosoria myanmarensis LI & MORAN
(LI et al. 2020). It possesses linear sori, which separ-
ates it from Cladarastega.

The mid-Cretaceous age of Burmese amber (~100 Mya)
approaches the 113.993 Mya estimated molecular age of the
dennstaedtioides as determined by SCHNEIDER et al. (2004).
Divergence time estimates for the Dennstaedtiaceae based
on rbcL DNA sequence data and analysis carried out in
BEAST shows the clade appearing some 90 MYA with
the genus Microlepia appearing between 30 and 40 Mya.
Using relaxed clock estimates and the assignment of the
Krameropteris fossil to the split between the Monacho-
sorum clade and Hypolepidioideae clade using Yule
parameter and other analyses (further details provided
by SCHNEIDER et al. 2016), average ranges of 95 Mya to

Fig. 1. Terminal fragment of frond with sori of Cladarastega
burmanica gen. et sp. nov. in Burmese amber. Bar = 1.2 mm.
Fig. 2. Leaf appendages of *Cladarastega burmanica* gen. et sp. nov. in Burmese amber. **A** – Elongate multi-segmented epidermal hair. Bar = 90 µm. Insert shows detail of short portion of hair. Bar = 25 µm. **B** – Trichomes adjacent to pinnule. Bar = 0.6 mm. **C** – Simple setae on veinlet. Bar = 80 µm. **D** – Epidermal gland. Bar = 63 µm.
Fig. 3. Indusia of *Cladarastega burmanica* gen. et sp. nov. in Burmese amber. 

**A** – Disintegration of the inner indusium (arrows). Bar = 170 µm. 

**B** – Outer indusium (left arrow) and inner indusium (right arrow). Bar = 180 µm. 

**C** – Partial outer indusium (right arrow) and inner indusium (left arrow). Bar = 200 µm. 

**D** – Detail of partial outer indusium (arrow). Arrowheads show paraphyses. Bar = 10 µm.
Fig. 4. A – Sporangium of Cladarastega burmanica gen. et sp. nov. in Burmese amber. Arrow shows papillate structures lining inside wall of lip portion of sporangium. Bar = 48 µm. B – Detail of papillate structures (arrowheads). Bar = 8 µm. C – Two sporangia of Cladarastega burmanica in Burmese amber. Arrowheads show spores. st= stoma; lc= lip cell. Bar = 103 µm. D – Two peltate scales on epidermal surface of pinna of Cladarastega burmanica in Burmese amber. Bar = 33 µm.
Ferns and angiosperms were competing for space, sunlight and nutrients in the Burmese Amber forest. It has been suggested that the spread of flowering plants in the terrain resulted in the formation of new niches in forests that could be occupied by lepto sporangiate ferns, allowing them to further diversify (Schuettpelz & Pryer 2009). Both ferns and angiosperms had to contend with herbivores. Many flowers recovered from Burmese amber show definite signs of insect damage (Chambers & Poinar 2020) and in some cases, the actual insect herbivore is entombed with the flowers (Poinar & Chambers 2018). Very little is known about insect herbivores of fossil ferns. That is why the partial remains of an immature blattoid adjacent to the pinna of Cladarastega is interesting (Fig. 5E). What relationship this insect had with Cladarastega is not known, however, Late Palaeozoic cockroaches were speculated to have fed on fern spores (Scott & Taylor 1983) and Blaberus giganteus (L.) was attracted to the axillary nectaries of extant bracken ferns in North America (Douglas 1983).

Certainly, some of the present day fern herbivores, such as sawflies (Tenthredinidae: Hymenoptera), gall gnats (Cecidiomyiidae: Diptera) and aphids (Aphididae: Hemiptera) (Poinar 2016) that have a fossil record extending back at least to the Early Cretaceous (Rasnitsyn & Quicke 2002) could have fed on Burmese amber ferns.

Aside from herbivorous insects, herbivorous dinosaurs also probably influenced the evolution of various fern lineages. Early Cretaceous sauropods were considered to be the dominant herbivores that fed on ferns as well as angiosperms (Ryan 1997). Tiffney (1997) suggested that large sauropods could have fed in “fern prairies” that provided a disturbance-tolerant and high quality food source. Ferns are fascinating plants and those found in Burmese amber represent some of the most detailed fossil representatives available for study.

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Fig. 5. A – Polar view of perispore 1 of Cladarastega burmanica gen. et sp. nov. Bar = 19 µm. B – Polar view of perispore 2 of Cladarastega burmanica. Bar = 19 µm. C – Lateral view of perispore 3 of Cladarastega burmanica. Bar = 12 µm. D – Lateral view of perispore 4 of Cladarastega burmanica. Bar = 13 µm. E – Partial remains of immature blattoid adjacent to pinnule of Cladarastega burmanica. Bar = 0.6 mm.
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