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

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

George Poinar Jr.

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 trilete. Related topics discussed are phylogenetic 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, Lindsaeacea, 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 (26º20′N, 96º36′E) 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	Regalado et al. (2017a)
Unnamed	Lindsaeaceae	Regalado et al. (2017b)
Thyrsopteris cretacea	Thyrsopteridaceae	Li et al. (2019)
Heinrichsia cheilanthoides	Pteridaceae	Regalado et al. (2019)
Proodontosoria myanmarensis	Lindsaeaceae	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
Schwarstburd & 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 roundish, 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).

Description: Apical fragments of pinna lobulate to pinnatifid, 7.6 mm in length, divided into pinnules with mostly pointed margins (Fig. 1). Abaxial surface of pinnules mostly glabrous. Epidermal structures include long multicellular hairs, ranging from 270-355 µm in length (Fig. 2A,), glandular hairs with a length of 128 µm and swollen gland tip width of 106 µm (Fig. 2D) and peltate scales (Fig. 4D). Sori are marginal and submarginal (Fig. 1), ranging from 570–800 µm in width; paraphyses present (Fig. 3D), stalk length 130–250 µm, stalk width, 92-110 µm; with inner and outer cup-shaped indusia; both initially solid, but then inner indusium disintegrates

Fig. 1. Terminal fragment of frond with sori of *Cladarastega burmanica* gen. et sp. nov. in Burmese amber. Bar = 1.2 mm.

(Fig. 3). Sporangia variable in shape, with diameters from 190–250 µm, and widths from 117–135 µm. Vertical or slightly oblique annulus composed of some 16–18 equally spaced radial walls (Fig. 4); stoma distinct, lip cell present (Fig. 4C), 46 µm long; short papillary structures lining inner walls of sporangia (Figs. 4 A, B). 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, pantropical 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 elongate, marginal or submarginal, positioned at or near vein endings or on marginal connecting veins. Linear, cup-shaped or half-cup-shaped indusia are usually present. Spores are tetrahedral, trilete 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. Typically, epidermal scales are absent in the Dennstaedtiaceae, even though members of the genus *Histiopteris* (J. Agardh) J. Sm. possess scales on the stipe and rachis (Brownsey 1998). This feature in *Cladarastega* associates it with members of the family Saccolomataceae (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 Dennstaedtiaceae (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 (paraphyses 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 begans 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 species 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). *Cretacifilix 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 resinatus* Schneider, Schmidt & Hendriks (2016) in the family Dennstaedtiaceae lack indusia, which differs from *Cladarastega*. *Cystodium sorbifolioides* Regalado, Schmidt, Schneid, Krings & Hendrichs (Regalado et al. 2017a), in the family Cystodiaceae lacks scales, which separates it from *Cladarastega*. *Thyrsopteris cretacea* Li & Moran (Li et al. 2019) in the family Thyrsopteridaceae possesses terminal sori with cyathiform indusia, which distinguishes it from *Cladarastega*. *Heinrichsia cheilanthoides* 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 Lindsaeaceae 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 separates 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 Monachosorum clade and Hypolepidioideae clade using Yule parameter and other analyses (further details provided by Schneider et al. 2016), average ranges of 95 Mya to

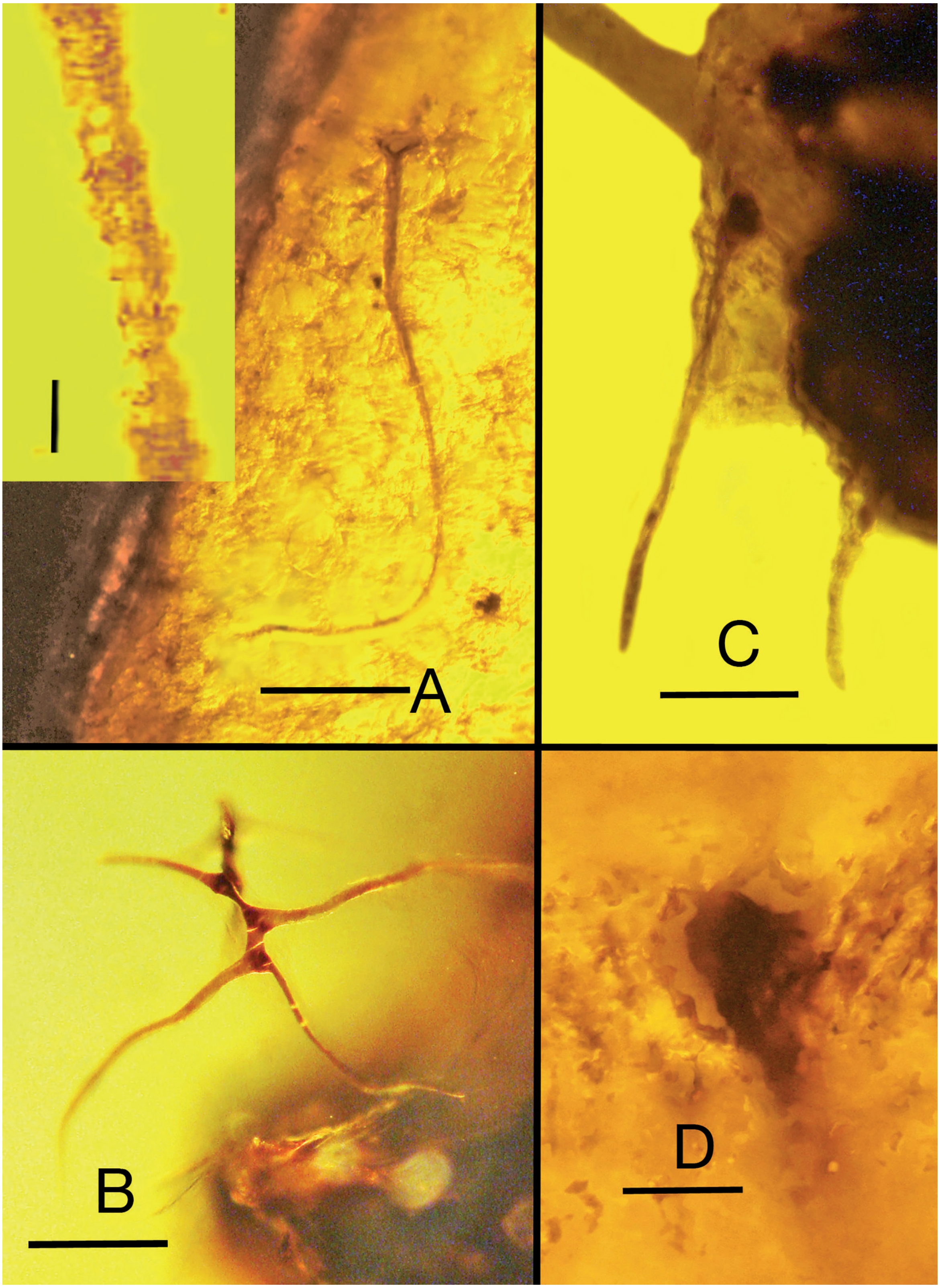

Fig. 2. Leaf appendages of *Cladarastega burmanica* gen. et sp. nov. in Burmese amber. **A** – Elongate multi-segmented epidermal hair. Bar = 90 µm. Insert shows detail of short portion of hair. Bar= 25 µm. **B** – Trichomes adjacent to pinnule. Bar= 0.6 mm. **C** – Simple setae on veinlet. Bar = 80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

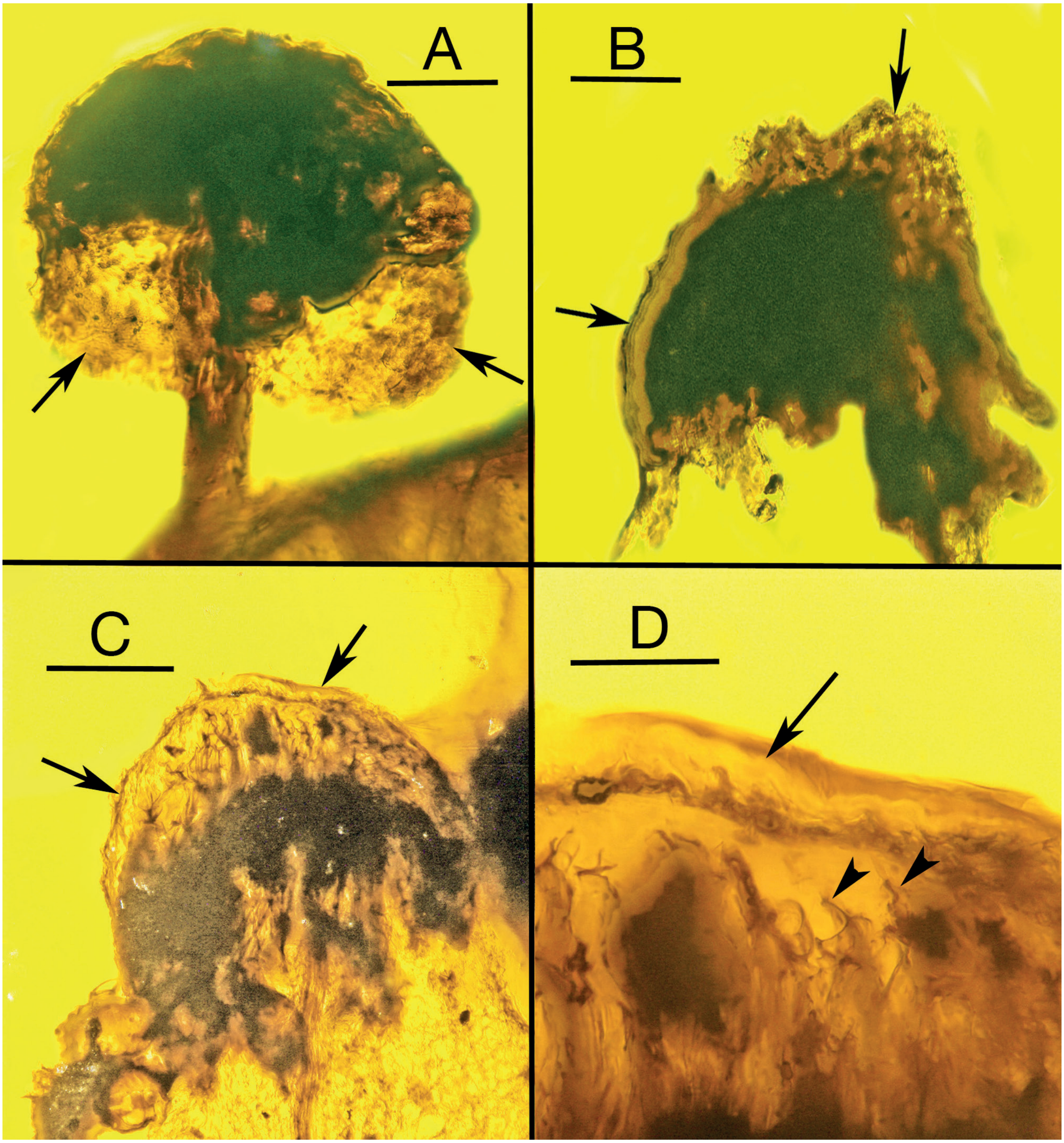

Fig. 3. Indusia of *Cladarastega burmanica* gen. et sp. nov. in Burmese amber. **A** – Disintegrtion of the inner indusium (arrows). Bar = 170 µm. **B** – Outer indusium (left arrow) and inner indusium (right arrow). Bar = 180 µm. **C** – Partial outer indusium (right arrow) and inner indusium (left arrow). Bar = 200 µm. **D** – Detail of partial outer indusium (arrow). Arrowheads show paraphyses. Bar = 10 µm.

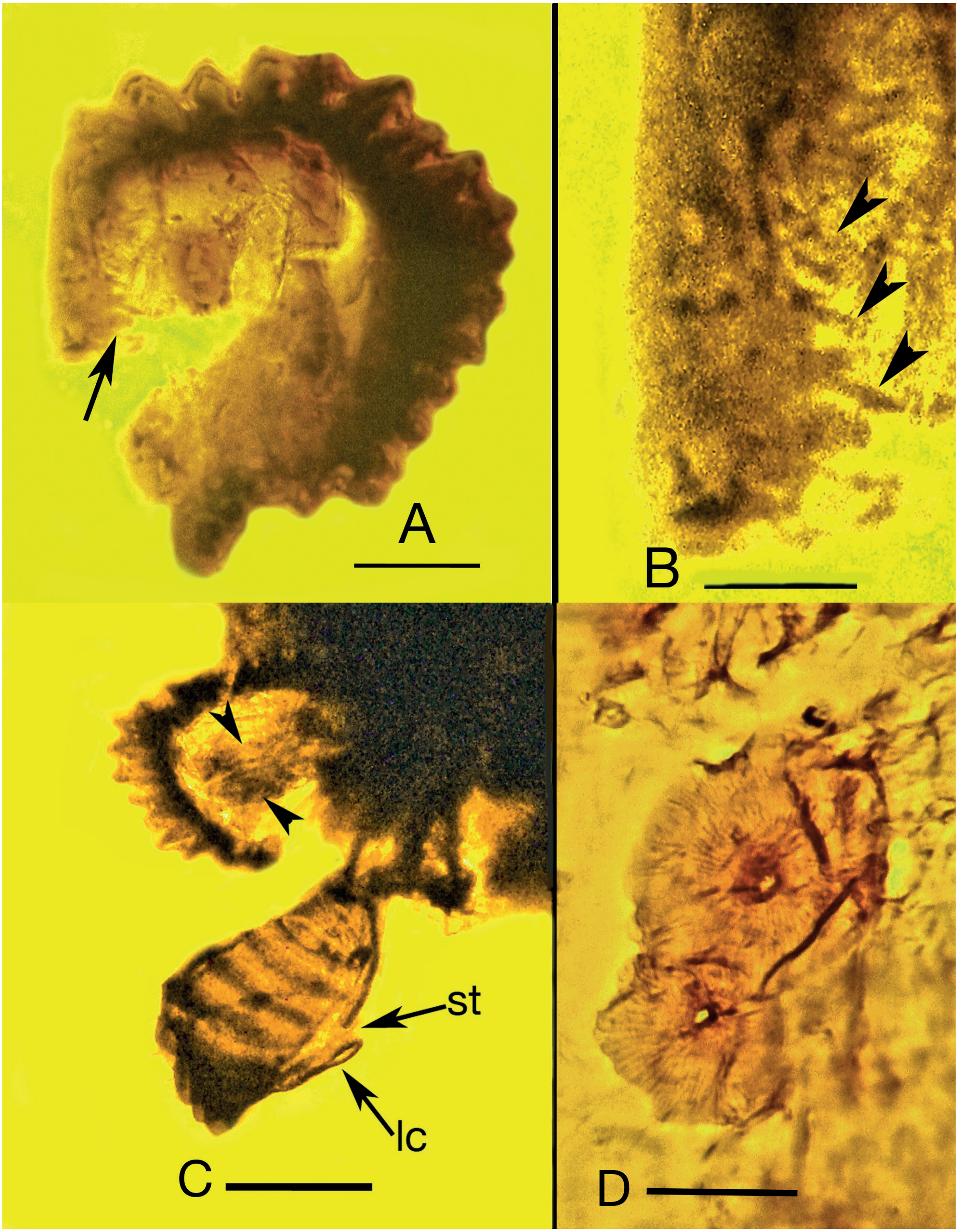

Fig. 4. A – Sporangium of *Cladarastega burmanica* gen. et sp. nov. in Burmese amber. Arrow shows papillate structures lining inside wall of lip portion of sporangium. Bar = 48 µm. **B** – Detail of papillate structures (arrowheads). Bar = 8 µm. **C** – Two sporangia of *Cladarastega burmanica* in Burmese 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.

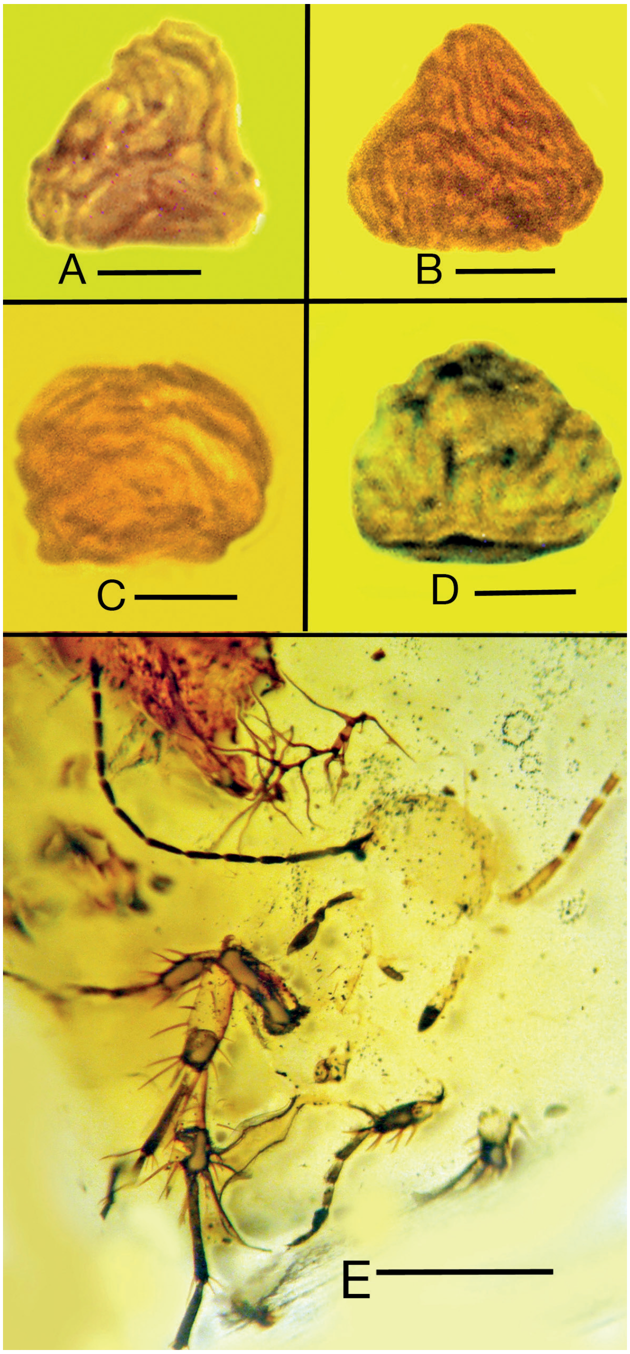

Fig. 5. A – Polar view of perispore 1 of *Cladarastega burmanica* gen. et sp. nov. Bar = 19 µm. **B** – Polar view of perispore 2 of *Cladarastega burmanica*. Bar = 19 µm. **C** – Lateral view of perispore 3 of *Cladarastega burmanica*. Bar = 12 µm. **D** – Lateral view of perispore 4 of *Cladarastega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

137 Mya were presented for the appearance of the family Dennstaedtiaceae (Schneider et al. 2016).

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 leptosporangiate 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 (Ceccidiomyiidae: 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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