

Taxonomic status of the *Cycas pectinata* complex

Jibankumar Singh Khuraijam & Rita Singh

ABSTRACT

The *Cycas pectinata* is a taxonomically complex, confused entity distributed naturally in Northeast India, Bhutan, Bangladesh, Nepal, Southwest China, Myanmar, Thailand and Vietnam. A detailed morphometric analysis of taxonomically distinct vegetative and reproductive structures of *Cycas* populations in India revealed differences among populations supporting their separation into two species: *Cycas pectinata* is confined to the western part of the Indo Burma Range (IBR), and to the east of the IBR, a Southeast Asian taxon which is described and illustrated here as a new species, *Cycas divyadarshanii*. The new species is distinguished from *Cycas pectinata* by its long narrow microsporophylls and lack of a thickened protrusion on the adaxial surface which is prominent in *C. pectinata*. Anatomical characters and pollen structure of both the species also differ. The separation of these taxa is also supported by their association with different putative beetle pollinators.

Keywords

Cycas pectinata, *Cycas divyadarshanii*, morphology, India, Southeast Asia.

Jibankumar Singh Khuraijam

Botanic Garden Division, CSIR-National Botanical Research Institute, Rana Pratap Marg, Lucknow-226001, Uttar Pradesh, INDIA

✉ Email: jskhuraijam@yahoo.com

Rita Singh

University School of Environment Management, GGS Indraprastha University, Sector 16C, Dwarka, New Delhi-110078, INDIA

✉ Email: rsinghipu@gmail.com

PROCEEDINGS

10th International Conference on Cycad Biology, 2015 Medellín, Colombia

Edited by Cristina López-Gallego, Michael Calonje, M. Patrick Griffith & J. S. Khuraijam

Available online at <http://www.cycadgroup.org/>

INTRODUCTION

Cycas pectinata Buch.-Ham. was described from Assam in north-eastern India and has been reported from adjoining countries, Nepal, Bangladesh, China, Myanmar, Thailand and Vietnam making it the second most widely distributed *Cycas* L. species, the first being an insular species *C. rumphii* Miq. Such vast distribution may have resulted from the expansion of distribution or migration of the genus *Cycas* during Pleistocene (Mankga et al., 2020). The genus *Cycas*, with 117 species (Calonje et al., 2020), is the most rapidly diversified clade in the cycad group (Yessoufou et al., 2017; Mankga et al., 2020). Tang (2004) suggested continental drift triggered cycad migration, theorizing that ancestral *Cycas* may have originated in southern Pangea and rode to Asia on one of the many travelling continental arks. Fossil evidence points to Asia as the origin of the genus (Hill, 1995; Xiao and Möller, 2015). The presence of *C. pectinata* in India and adjoining countries like Nepal, Bhutan and Bangladesh suggest that the localities where they occur may be the last limit of the distribution of the species with deeply pectinate megasporophylls. Yang and Merrow (1996) also pointed out that *C. pectinata* complex is comprised of *C. pectinata*, *C. siamensis* Miq. and five to seven undescribed taxa in southern Asia. Recently, Nagalingum et al. (2011) distinguished two undescribed species of *C. pectinata* complex as *C. pectinata* A and *C. pectinata* B based on their positions in the phylogeny. However, Nagalingum et al. (2011) did not include Indian plants in the study. This clearly indicates that there are still many more undescribed species within the *C. pectinata* complex.

As *Cycas* species generally dwell in warm, high rainfall, hilly regions, most of the cycad localities of South Asian and Southeast Asian countries are confined to the warm tropical forest and are endemic to areas of occurrence restricted to a few localities. The isolated and scattered, allochthonous populations adapting to different landscapes and climatic conditions might have led to parallel speciation. In the last few decades, many new species have been described from this region. Recently, Mankga et al. (2020) also suggested that *Cycas* from Indochina may have diversified and occupied its current ranges through vicariance and dispersal events.

Taxonomic history

Cycas pectinata was described by a Scottish naturalist, Francis Buchanan-Hamilton (1762–1829) from Kamrup (at that time part of Myanmar but currently within the state of Assam in India). As Buchanan-Hamilton did not cite any specimens in the protologue, De Laubenfels & Adema (1998) designated a specimen collected by Hooker in 1855 as lectotype of *C. pectinata*, a designation to be corrected to neotype as the specimen was not from the original material. Even this neotypification was invalid. In the absence of type and to maintain nomenclature stability, Khuraijam et al. (2018) proposed to conserve the name *C. pectinata* with a new type consisting of specimen collected from Kamrup (Assam), the single locality mentioned by Buchanan-Hamilton in the protologue.

The taxon here treated as *C. pectinata*, was also described by many authors based on material from the same region (Kamrup) as *C. pectinata* Griff, *Cycas jenkinsiana* Griff and *C. circinalis* var. *pectinata* (Griff.) Schuster. Griffith (1854) gave the same specific name, *C. pectinata* and *C. jenkinsiana* to plants growing in the same region but did not mention Hamilton's earlier use of the specific epithet, *C. pectinata*. Pant (2002) opined that the *C. pectinata* Buch.-Ham. has priority and *C. pectinata* Griff. is a synonym based on erroneous attribution of the specific epithet to Griffith by Kurz (1877), Thiselton-Dyer (1890) and many subsequent authors (Pant, 2002; Pant *et al.*, 1994). Pant *et al.* (1994) also pointed out that *C. pectinata* Buch.-Ham. is a distinct species and not a form of *C. circinalis* L. as claimed by Schuster (1932) or a variety of *C. siamensis* Miq. as suggested by Thiselton-Dyer (1890).

***Cycas pectinata* complex in India**

Pant (2002) in his monumental monograph on *Cycas* considered *C. pectinata* as the least studied species among the Indian cycads. A perusal of literature revealed several reports on the occurrence of *C. pectinata* in Assam (Kanjilal and Bor, 1940; Kanjilal *et al.*, 1940; Sahni, 1990; Kar and Borthakur, 2008), Manipur (Deb, 1958; Sahni, 1990), Meghalaya (Sahni, 1990; Roy and Joshi, 2002), Mizoram, Sikkim (Hooker, 1854; Srivastava, 1993; Hajra and Verma, 1996) and Tripura (Deb, 1983). However, none of these authors have done critical taxonomic studies on the species. Interestingly, Yang and Merrow (1995) used a plant sample of *C. pectinata* from Assam, India provided by Prof. D.D. Pant of University of Allahabad (pers. comm.) in their study to suggest that *C. pectinata* found in Southeast Asia is a complex species. Our study spanning more than ten years of extensive field surveys, herbarium consultation and taxonomic studies, has led us to decipher and understand the *C. pectinata* complex in India. Field expeditions to neighbouring countries Bhutan, Myanmar, Thailand and consultation of virtual specimens and literatures pertaining to *C. pectinata* complex in Thailand, Vietnam, Nepal, Bangladesh and China have resulted in the description of a new species, *Cycas divyadarshanii* from the north eastern state of Manipur, India.

Materials and methods

The present work provides a detailed study on morphology and present distribution of the *C. pectinata* complex in the Southern and Southeast Asia with special emphasis in north-eastern part of India. For taxonomic and phylogenetic interpretation, the first-hand observations and measurements were carried out (irrespective of the prior information available) on *Cycas* growing naturally in Northeast India. Morphological parameters laid down by Lindström (2004) for determining species boundaries in *Cycas* were used in the study. Morpho-anatomical and pollen morphological studies were done on materials collected from the several populations to assess the similarities and differences between and among the populations in order to assign weight to these characters to critically resolve the taxonomy of the species.

Taxonomy

Cycas pectinata Buch.-Ham. In Mem. Wern. Nat. Hist. Soc. 5: 322. 1826.

Type: India, Assam, Kamrup, 2008, *Rita Singh & Khuraijam 36106* (♀)(LWG No. 102998!) [typ. cons. prop. 2653, *Taxon* 67(6): 1213, 2018]

Cycas circinalis L. subsp. *vera* var. *pectinata* (Griff.) Schuster. Pflanzenr. 99: 68. 1932.

Cycas pectinata Griff. Not. Pl. Asiat. 4: 10. 1854.

Type: Icones Plantarum Asiatarum 4: Plate 360, fig. 3. (1854)

Cycas jenkinsiana Griff. Not. Pl. Asiat. 4: 9-10, pl. 360, figs. 1-2, pl. 362, fig. 1. 1854.

Lectotype (designated by Lindström & Hill): India, Assam., *Jenkins s.n.* (K000961259!); isolect. L 0050752!

Description

Stems arborescent, tall, up to 16 m in height, branched or unbranched. Leaves dark green, 90–264 cm long, 100–230 pairs of pinnae, 6–10 mm apart, glabrous. Petiole 18–58 cm long with 11–30 spines on either side. Median pinnae 130–220 mm long, 6–12 mm wide, tapering into a minute apical spine. Pinnae base decurrent, attached to the rachis at 40°–55° on adaxial side, margins beak shaped in cross section. Emergent pinnae covered with yellow trichomes which are shed subsequently with their maturation. Male cones cylindric-ovoid having spirally arranged broad microsporophylls with upturned green apical spines covered with brownish rammenta, cone yellowish green till the dehiscence subsequently turns brownish yellow at maturity, 24–62 cm long, 12–24 cm in diameter. Microsporophyll deltoid 45–60 mm long, 20–32 mm wide at expanded distal portion; fertile zone 33–55 mm long, 18–28 mm wide; sterile apex portion deltoid, with upcurved apical spine attenuate, 20–35 mm long, green in young cones, sterile apex raised towards median adaxial side up to ¼ of the fertile zone. Megasporophylls tightly arranged in a compact and vertically compressed (laterally flattened) cone, innermost megasporophylls are mostly sterile. Megasporophylls 110–250 mm long, densely yellowish-brown silky throughout, lamina 70–150 mm wide, deeply pectinate, 14–30 lateral spines on either side, strong subulate apical spine, 22–70 mm long. Ovules 1–5, glabrous, laterally attached. Seed ovoid or obovoid, 3.4–5.2 × 3.2–4.7 cm, sarcotesta yellowish when young turns dark yellow-orange to orange red at maturity, sarcotesta 3–4 mm thick, fibrous layer present, sclerotesta stony, endotesta scaly and papery, spongy layer absent. Mature seeds platyspermic, tapering towards chalazal end, cryptocotylar.

Distribution:— India (Assam, Meghalaya, northern West Bengal, Sikkim, Bihar), Nepal, Bhutan, Bangladesh

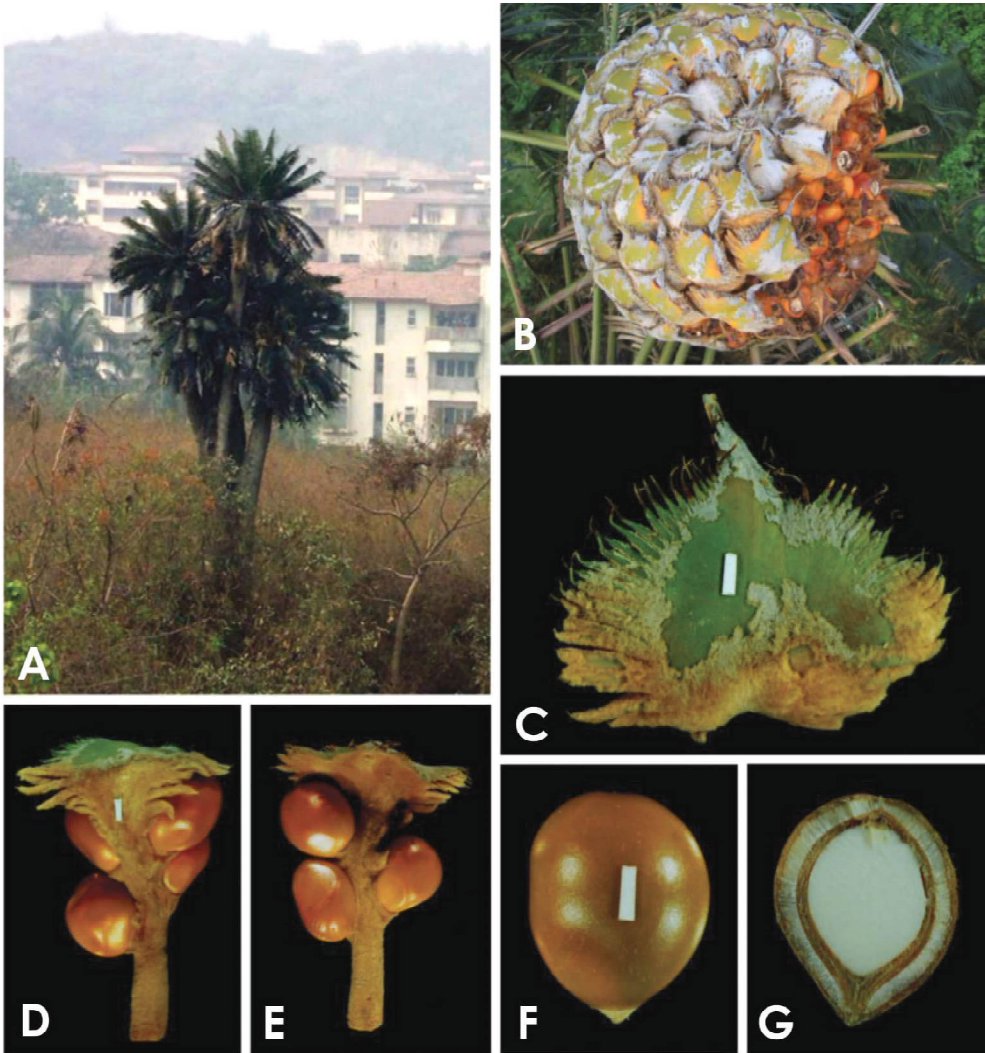


Figure 1. *Cycas pectinata* Buch.-Ham. A. Tall, robust trunk, B. Compact female cone, C. Top view of Hooded pectinate lamina of sterile apex of megasporophyll, D. Back and E. Front view of megasporophyll with mature orange coloured ovules. F. Fertilized ovule. G. Median longitudinal section of a fertilized ovule.

Habitat: — The species grow in warm deciduous forest at an elevation of 52-250 msl. In Bhutan, it grows on hill slopes along with pines sometime reaching up to maximum elevation of 1300 msl. In Nepal, it grows in Sal (*Shorea robusta*) forest at altitude 300-730 msl.

Conservation status:— Vulnerable

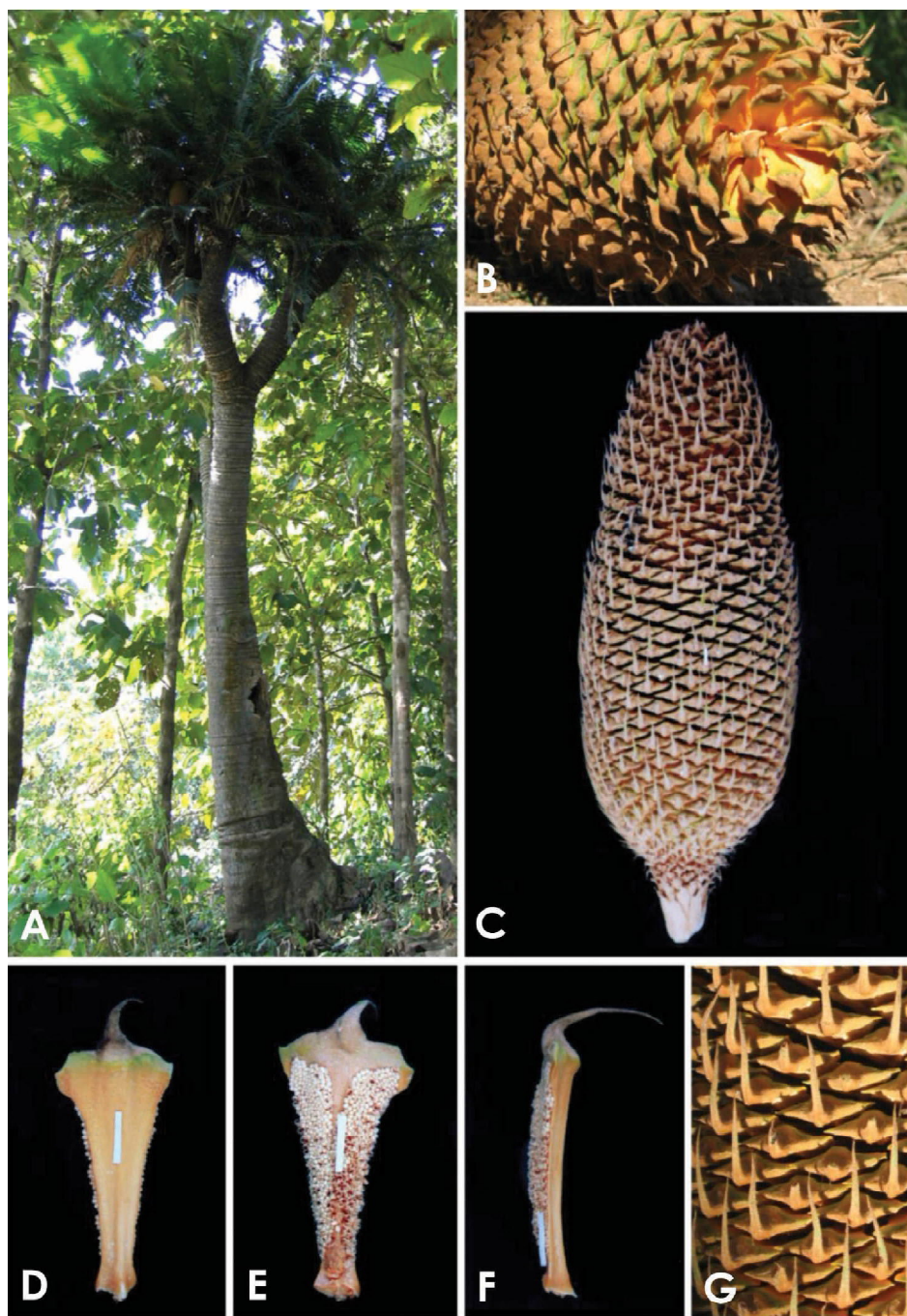


Figure 2. *Cycas pectinata* Buch.-Ham. A. Tall male plant on the bank of Brahmaputra River, B-C. Male cone, D-F. Microsporophylls, adaxial surface, abaxial surface and lateral view, G. A portion of male showing the long apical spine.

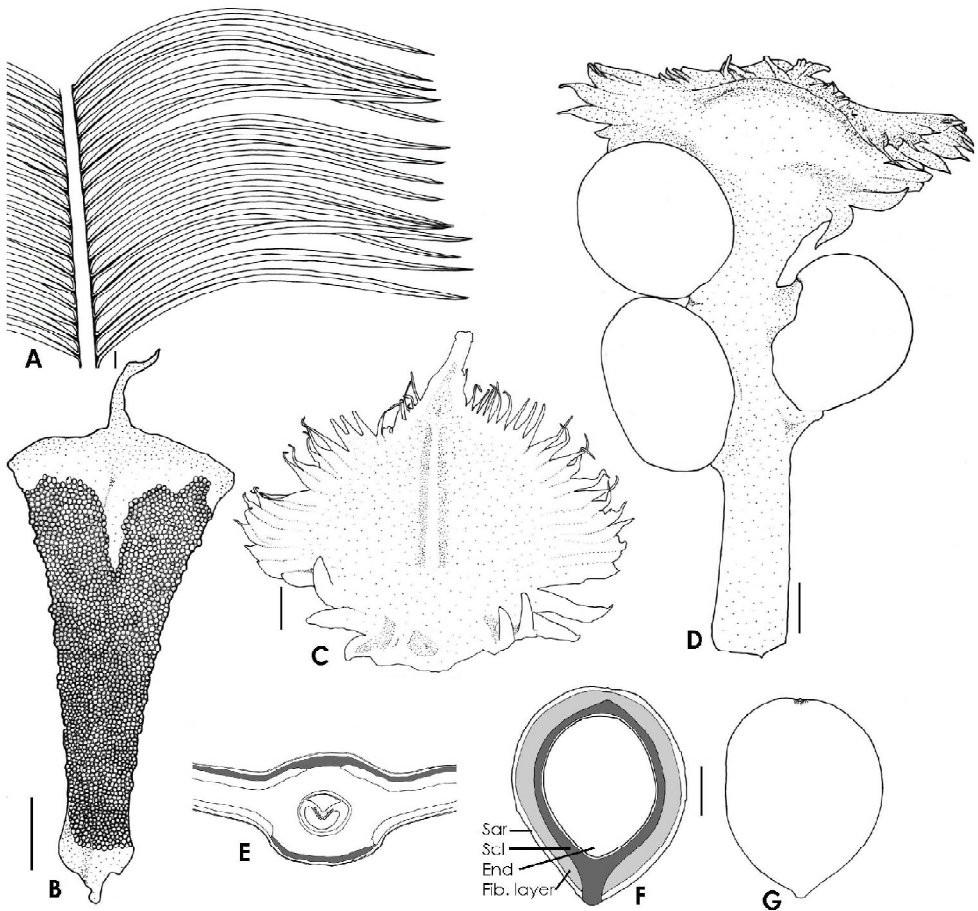


Figure 3. *Cycas pectinata* Buch.-Ham. A. A portion of leaf showing falcate leaflets, B. Microsporophylls; abaxial view with microsporangia, C. Lamina of megasporophylls showing pectinate lateral spines, D. Megasporophyll with ovoid shape ovules attached laterally, E. Section of median portion showing internal structure, F. Cross section of ovules showing prominent fibrous layer (Sar: Sarcotesta, Scl: Sclerotesta, End.: Endotesta, Fl.: Fibrous layer), G. Ovule. Scale bar: 1 cm.

Vernacular names:—*Nagphal*, *Nagchampa*, *Ak Phal* (Assam), *dieng-sia-goda* (Khasi, Meghalaya); *Khu-tha* (Tharu, Bihar); *Thakal* (Sikkim); *Jaggar* (Nepal), *Bango-shing* (Bhutan)

Specimens examined:—INDIA. Assam: *Singh*, *Radha & Khuraijam* 36101 to 36105, March 2007; *Singh & Khuraijam* 36106 to 36114, June. 2007; *Khuraijam* 36115 to 36131, Nov. 2007; *Khuraijam* 36132-36145, March 2009, *Khuraijam* 36146 to 36154, Sept. 2009; Meghalaya: *Hooker & Thomson*. s.n. (K001328056); Sikkim: *Khuraijam* 35901 to 33912, Sept, 2009; *Hooker* s.n. (K001328059); West Bengal: *Khuraijam* 3541-3548, 2009; Bihar: *Haines* 3983 (K001273051, K001273052) Nov. 1916; BANGLADESH.

Chittagong: *Hooker & Thompson* 595 (K001273047); BHUTAN. Mongar: *Balakrishnan* 44604 Nov. 1965; Trashigang: *Grierson & Long* 2357 (K001328057, K001328058) June 1979.

Cycas divyadarshanii Khuraijam & Rita Singh. *sp. nov.*, figs.4,5

Holotype: India, Manipur, Sadar Hills, *Khuraijam* 38522 (♂) November 2007, Indraprastha University Herbarium (IPUH)

Description

Stems arborescent, cylindric, up to 10 m in height, branched or unbranched. Leaves dark green or bright green, 100–220 cm long, 100–230 pairs of pinnae, 6–10 mm apart, glabrous. Petiole 17–36 cm long with 12–22 spines on either side. Median pinnae straight to falcate, 160–230 mm long, 6–9 mm wide, tapering into a minute apical spine. Pinnae

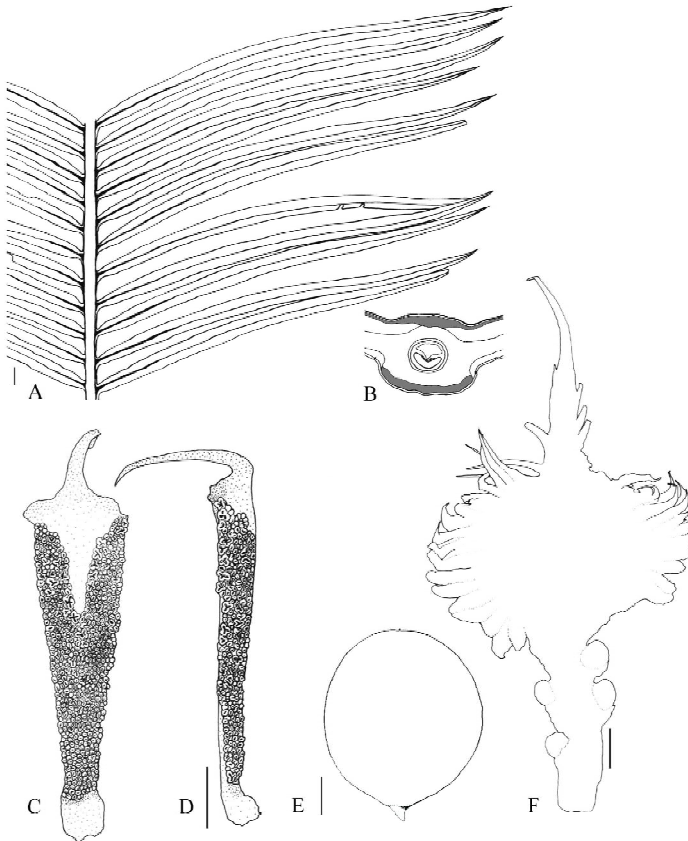


Figure 4. *Cycas divyadarshanii* Khuraijam & Rita Singh *sp. nov.* A. A portion of leaf, B. Cross section of a pinna (midrib region), C-D. Microsporophylls, E. Seed, F. Megasporophyll having long appendiculate apical spine and deeply pectinate lamina. Scale bar: 1 cm.

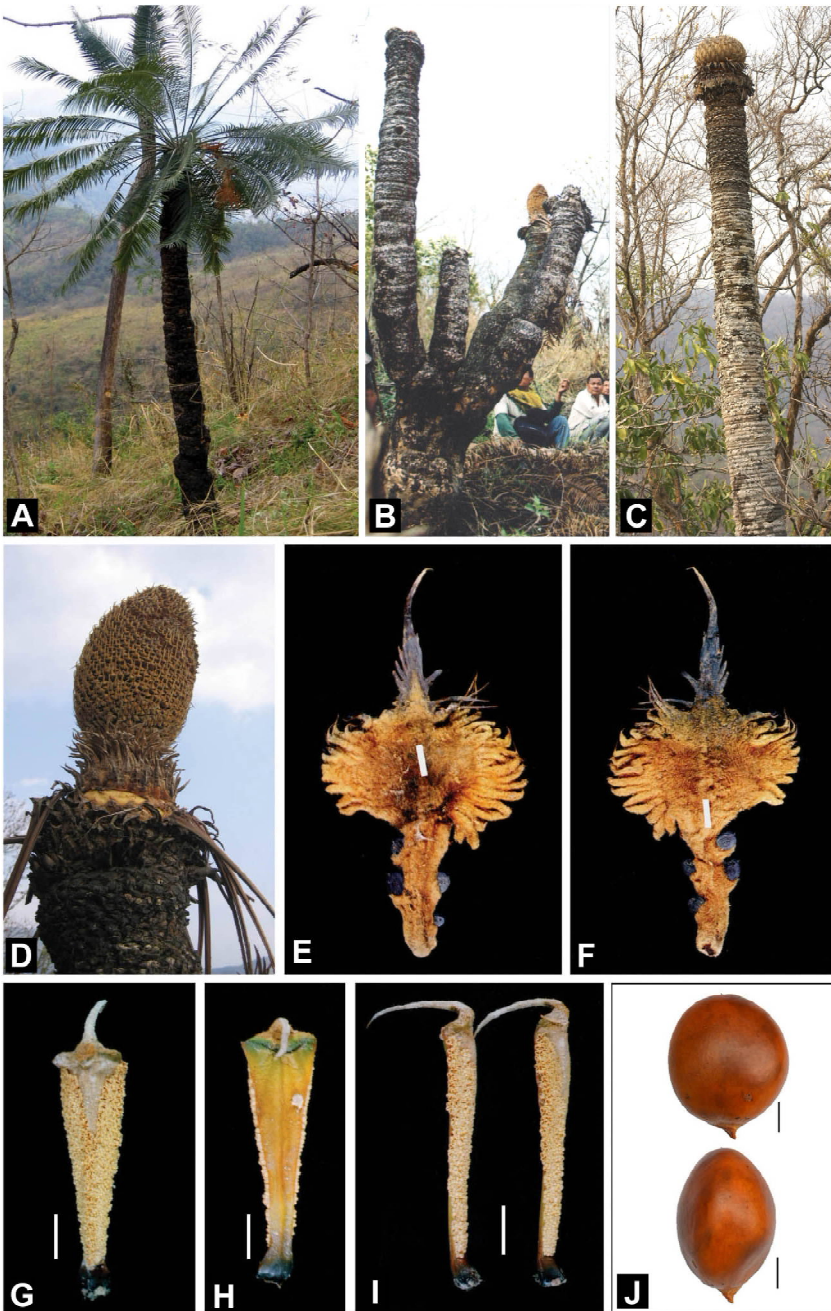


Figure 5. *Cycas divyadarshanii* Khuraijam & Rita Singh *sp. nov.* A. A slender tree, B. A branched male plant with male cone, C. An unbranched female plant, D. A mature male cone, E-F. Megasporophyll with long apical spine and deeply pectinate woolly lamina and stalk with aborted ovules, G-I. Microporophylls with inflexed apical spine, J. Mature seeds. Scale bar: 1 cm.

longitudinally inserted at 50–60° to rachis, base decurrent, margin recurved or revolute in cross section. Cataphylls narrowly triangular, 3–5 × 1.2–2 cm, brown tomentose, apex soft. Male cones cylindric-ovoid, fusiform, yellow or green (young) in colour, 26–50 cm long, 15–19 cm in diameter. Microsporophyll deltoid not dorsiventrally thickened, 50–62 mm long, 17–24 mm wide at expanded distal portion; fertile zone 48–55 mm long, 15–21 mm wide; with inflexed apical spine, 20–42 mm long, sterile apex flat towards median adaxial side up to ¼ of the fertile zone. Megasporephylls compactly arranged, densely tomentose, 14–20 cm long, stalk 4–7 cm; sterile blade deltoid-ovate or suborbicular, 5–9 × 8–10 cm, margin deeply pectinate, with 23–34 lateral lobes, apical spine 3–6 cm long. Seeds 2–6, yellow when young and orange to dark brown on maturity, often obovoid, compressed, 3.6–4.6 × 3.9–4.5 cm; sclerotesta smooth, sarcotesta with thick fibrous layer, spongy layer absent. Seeds platyspermic tapering towards chalazal end, cryptocotylar.

Distribution:— India (Manipur), Myanmar, China, Thailand, Vietnam

Habitat:— In Manipur, the species grows in dry open deciduous forest at elevations ranging from 770 to 1400 msl.

Etymology:— The specific epithet is in honour of Prof. Divya Darshan Pant (1919–2001), the renowned cycadologist and paleobotanist.

Conservation status:— Vulnerable

Distinguishing characters:— large cylindrical ovoid male cone with long narrow microsporophylls with long apical spines, deeply pectinate wooly megasporephylls with appendiculate apical spine.

Vernacular name:— *Yendang* (Manipuri), *Mondang* (Burmese)

Discussion

Cycas pectinata Buch.-Ham has been considered widespread in distribution and has been frequently misidentified. It belongs to the Section Indosinenses which is characterised by deeply pectinate megasporephylls. Members of this section resemble each other and are difficult to identify in vegetative stage. The smooth trunk of mature *C. pectinata* can be confused with those of *C. clivicola* K.D. Hill. Even though, *C. pectinata* shared many similarities with other species in the section, the species has unique features that have been neglected by previous workers. Most of the available literature on the taxonomy of the species are from China, Thailand and Vietnam (Hill and Yang, 1999; Hill, 2004, 2008; Osborne *et al.*, 2007; Wang, 1996). However, the morphological information available in these references are uniform and almost similar. Literature on Indian plants is more limited and only scattered information is available in floristic survey reports and books. While revising the *Cycas* of India, Lindström and Hill (2007) also gave details about *C. pectinata* however, measurements of many of the morphological characters

given in the description are coincidentally similar or same to those described from the plants of China, Thailand and Vietnam.

C. pectinata is geographically separated from Southeast Asian *C. divyadarshanii* by Barak Valley and Brahmaputra Valley. The ecological trap of *C. pectinata* between the Himalaya and Indo Burman Range can also be correlated with the beetle discovered from the *C. pectinata* of Kamrup, *Cycadophila* (*Strobilophila*) *assamensis* Skelley, Xu & Tang which is specific to *C. pectinata* of Assam (Skelley et al. 2017). Similarly, *Cycadophila* (*Cycadophila*) *yunnanensis* (Grouvelle) which is found in Southeast Asian *Cycas* was also reported from the plants of Manipur, which indicates the affinity of *C. divyadarshanii* with Southeast Asian species. The long and narrow microsporophylls of *C. divyadarshanii* is a distinctive character that separates the species from other members of *Cycas pectinata* complex (Figs. 6). Microsporophylls of *C. pectinata* have a thickened protrusion on the adaxial surface which is lacking in *C. divyadarshanii* (Fig. 7). Osborne et al. (2007) pointed out that Vietnamese *C. pectinata* (here *C. divyadarshanii*) is distinguishable from its allies in *C. pectinata* group in having very large, ovoid male cones with long narrow microsporophylls with long apical spines.

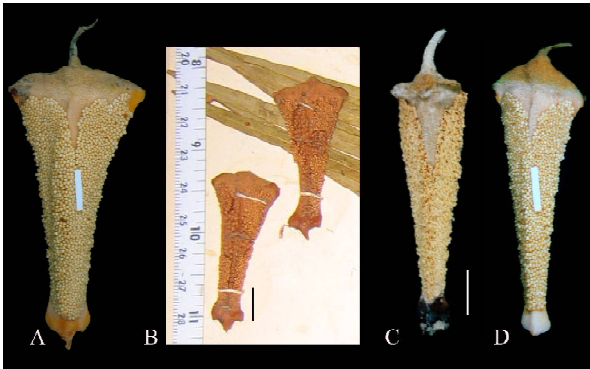


Figure 6. Microsporophylls of *Cycas pectinata* (A, B) and *C. divyadarshanii* (C,D), B. A portion of *Kanjilal 5146*, ASSAM. Reproduced with permission from the Director of the Botanical Survey of India.

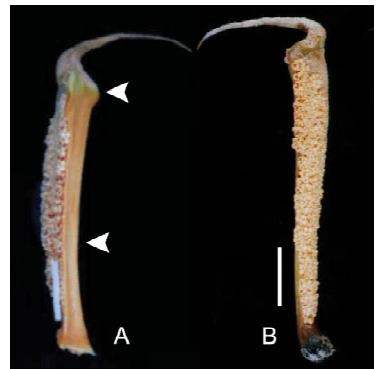


Figure 7. Lateral view of microsporophylls of *Cycas pectinata* (A) and *C. divyadarshanii* (B)

Anatomical characters of leaflets/pinnae of both the species are of taxonomic significance. Like all members of *C. pectinata* group, mucilage canals below or adjacent to the vascular bundle are conspicuously absent in both the species. Idioblasts are uniformly distributed in the midrib region in *C. pectinata* however, in *C. divyadarshanii* they are less and irregularly scattered. Lamina straight in *C. pectinata* and slightly revolute in *C. divyadarshanii* with beak shaped margin in cross section (Fig. 8).

In epidermal peel of pinnae of these two species, the epidermal cells on the adaxial surface are arranged in irregular profiles which are longer than broad, usually each profile has larger cells in the middle and smaller ones either at both the ends or at one end. In

C. pectinata, the pits are more or less circular or oval. *C. divyadarshanii* has circular pits and are scattered and almost crowded on the surface of the epidermal wall and also arranged near the anticlinal walls. On abaxial side of the pinnae, epidermal cells at the laminar region are more sinuous compared to the adaxial epidermis. Both the adaxial and abaxial epidermis has one-two celled hair bases. Pinnae in both species are hypostomatic. Guard cells are either one- or two-celled sunken in *C. pectinata* but is one-celled deep in *C. divyadarshanii* with characteristic polar and lateral lamellae.

Table 1. Micromorphological details of pinnae of *Cycas pectinata* and *Cycas divyadarshanii*.

Characters	<i>Cycas pectinata</i>	<i>Cycas divyadarshanii</i>
Palisade cells size in μm (adaxial surface)	78-100 \times 13-17	130-164 \times 13-21
Shape of vascular bundle	Elliptic to spherical	Elliptic
Stomatal index	6.7-7.4	8
Guard cells size (μm)	48.5 \times 24	49 \times 21.5

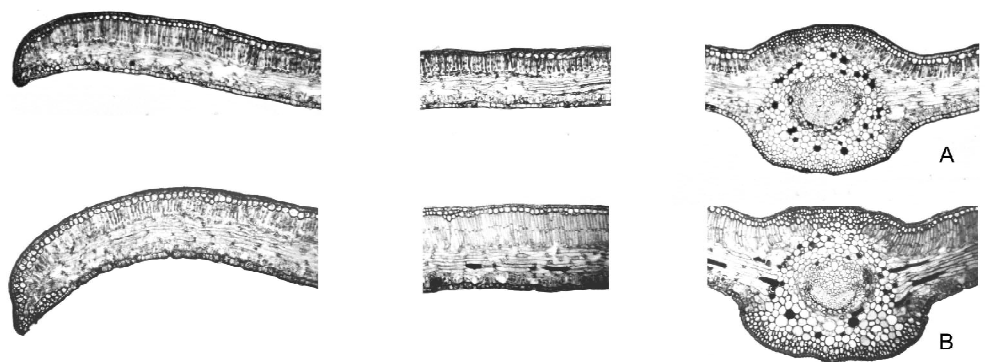
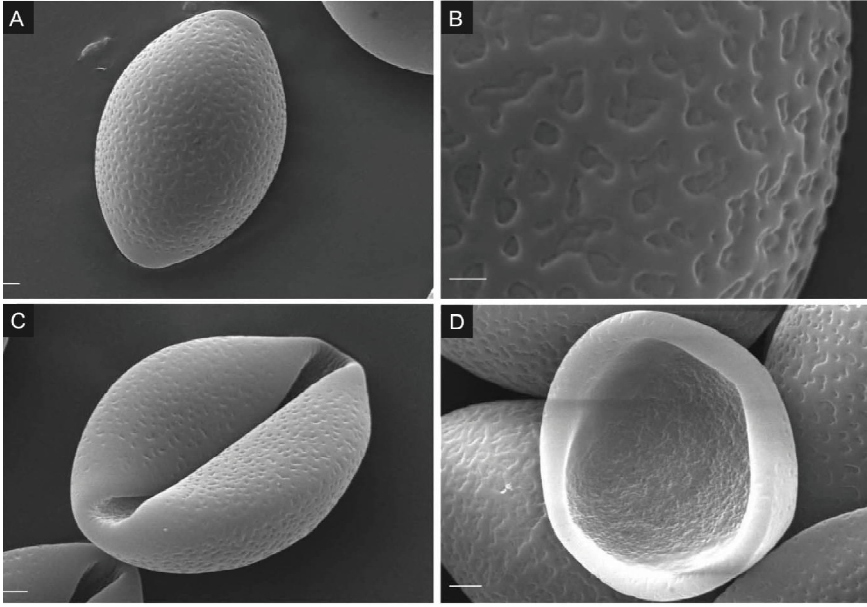


Figure 8. T.S. of a median pinna ($\times 50$). A. *Cycas pectinata* Buch.-Ham. B. *Cycas divyadarshanii* Khuraijam & Rita Singh *sp. nov.*

Pollen grains of the species of *Cycas* are boat shaped, monocolpate, bilaterally symmetrical, anisopolar having a distal colpus and range from widely elliptical or sub-circular or subprolate (Agashe, 2006). The ornamentation ranges from fossulate to foveolate. Exine ornamentation is more prominent towards the proximal surface and is less ornamented towards the brim between the two surfaces. The distal side is totally devoid of exine. Taxonomically, the pollen morphology can be used to identify geographical groups of *Cycas* and infrageneric taxonomic relationships. Pollens of *C. pectinata* and *C. divyadarshanii* are ellipsoidal (boat shaped), monosulcate and bilaterally symmetrical. Pollens of *C. pectinata* are usually broadly elliptic ($24.8 \times 21 \mu\text{m}$) while those of *C. divyadarshanii* are elliptic ($25.2 \times 20.2 \mu\text{m}$). Proximal surface convex and exine foveolate. Exine of distal surface of oblate pollen grain has fossulate surface. Enlarged view of proximal surface revealed coarsely faveolate exine with bigger cavity in *C. pectinata* compared to *C. divyadarshanii*.

Cycas pectinata



Cycas divyadarshanii

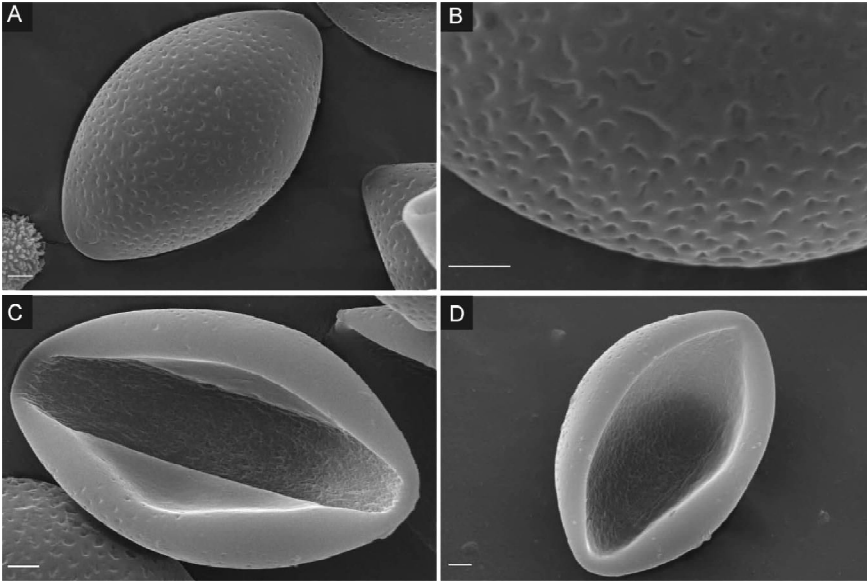


Figure 9. SEM micrograph of pollen grain (*Cycas pectinata* Buch.-Ham. and *Cycas divyadarshanii* Khuraijam & Rita Singh *sp. nov.*). A. Proximal view (scale = 2 μ m), B. Enlarged portion of proximal surface showing foveolate to irregular reticulate exine sculpturing (scale = 2 μ m), C. Distal view showing colpus (scale = 1 μ m), D. Enlarged portion of distal surface showing colpus (scale = 2 μ m).

***Cycas pectinata* complex migration route**

Diversification of *Cycas* in Southeast Asia and Northeast India may have resulted from the ecological traps and geographical barriers. The Northeast India lies at the easternmost part of India stretching from the Eastern Himalayas to the sub-Himalayan region bordering Bangladesh towards its southwest and Myanmar in the southeast. The region was created 40 million years ago when the Indian subcontinent collide with the Asian landmass to form the earth's youngest mountain range (Favre et al., 2015). Tectonically the Himalayan extension of Northeast India comprises of two main regions a) the Himalayan mountain ranges in the north and a) the Indo Burman Range in the east (Westerweel et al., 2019). The states of Sikkim and Arunachal Pradesh along with the neighbouring country Bhutan form the Eastern Himalayas mountain belt. Foredeep Folded Belt in the Indo Burman Range (IBR) comprises the low-lying hills of Nagaland, Manipur, Mizoram and Tripura. The physiography of the Northeast comprises of four main regions: a) the Himalayan mountain belt in the North, b) the Indo Burman Range in the east, c) Shillong Massif Plateau in the south and c) the Brahmaputra Valley forming the extensive Assam plains between East Himalayas and Shillong Plateau and Indo Burman Range. The periodic orogenic events in the region led to physiographic and environmental changes and served as key drivers of the newly evolving ecosystems resulting in geographical isolation of taxa, vicariance, and evolutionary divergence of life forms (Pandit, 2017; Manish and Pandit, 2018). As the region lies at the confluence of Indo Malayan, Indo Chinese, and Indian biogeographical realms, the region experiences a predominantly humid sub-tropical climate with hot, humid summers, severe monsoons and mild winters. Owing to unique land formations and climatic condition, the region is very rich in biodiversity and harbours a great number of endemic species both flora and fauna (Tiwari et al., 2017). The region is centre of diversity of many species. Northeast India has the highest diversity of *Citrus*, *Musa* and has been regarded as centre of diversity of these genera (Gogoi and Häkkinen, 2013; Govind and Yadav, 1999). The region comes under major migration route of mammals like Rhinoceros, Cats, Cervids which had vast distribution in the past and now confined to few areas and become endemic and even some have become extinct (Tougard, 2001). Interestingly, distribution of *Cycas* in Southeast Asia and Himalayan region have apparently similar migration route. It seems the species in Section *Indosinenses* diversified in Yunnan Province in China and Shan Province of Myanmar, and followed multiple routes to enter a) Himalayan and sub-himalayan region after crossing Indo Burman Range, b) towards southern Myanmar and Thailand, and c) Vietnam (Fig. 10). Presence of plants allied to *C. divyadarshanii*, *C. siamensis* and *C. clivicola* in Myanmar clearly indicate the potential migration route of the *Indosinenses* through Myanmar into Indian subcontinent and Thailand. Xiao and Möller (2015) and Mankga et al. (2020) proposed potential colonization routes of the genus *Cycas* from China and Indochina region to Malay archipelagos and then diversification to Africa and Australia. However, both the studies omitted colonization route to Myanmar and Indian sub-continent.

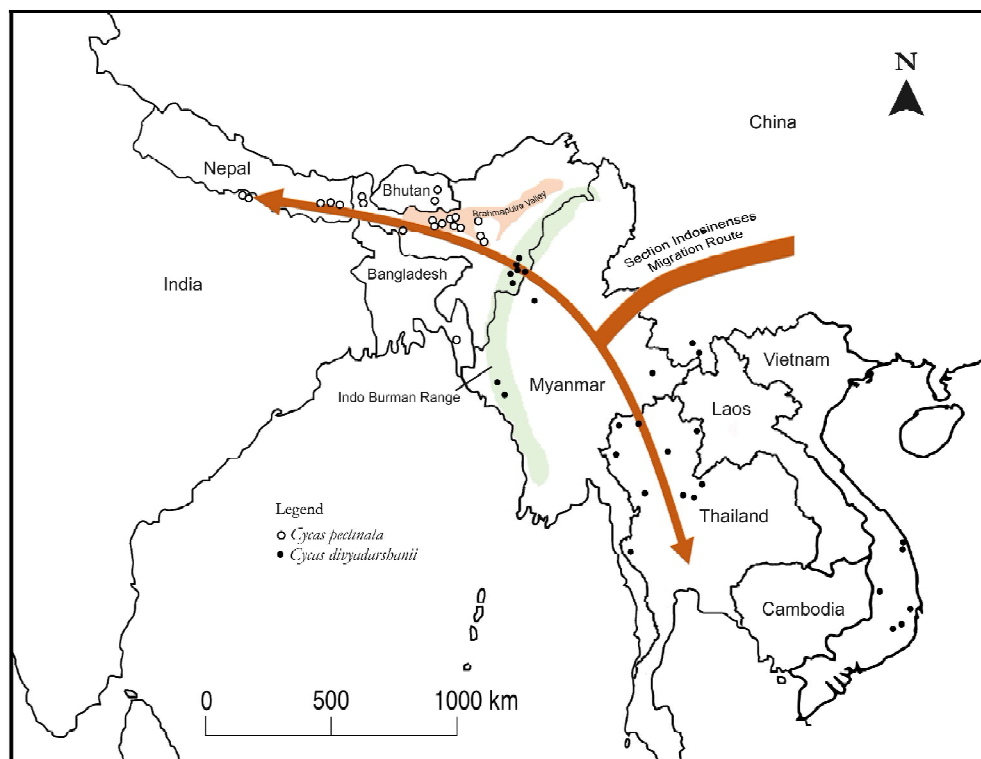


Figure 10. Distribution of *Cycas pectinata* Buch.-Ham. and *Cycas divyadarshanii* Khuraijam & Rita Singh *sp. nov.*, with probable migration route of members of Section Indosinenses in South Asia and Southeast Asia.

ACKNOWLEDGMENTS

The authors thank Curators of Kew Herbarium, CNH and ASSAM for help in the herbarium consultation. The authors are grateful to MoEF& CC, Government of India for funding under the aegis of All India Coordinated Project on Taxonomy [AICOPTAX-No. J-22018/54/2000/CSC (BC)], State Forest Departments for their support and help during the field surveys. The authors thank William Tang for supporting in fieldwork in Southeast Asian countries and Anders Lindström for allowing to study the live specimens of *Cycas* at Nong Nooch Tropical Botanical Garden, Thailand. JSK thank GGS Indraprastha University for Research Fellowship and Director, CSIR-NBRI for support and encouragement.

LITERATURE CITED

- Agashe, S.N. 2006. Palynology and its applications. Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi.
- Buchanan-Hamilton, F. 1826. Commentary on *Cycas pectinata*. *Memoirs of the Wernerian Natural History Society* 5(2): 322–323.

- Calonje, M., Stevenson, D. W., and R. Osborne. 2020. The World List of Cycads, online edition [Internet]. 2013-2020. [cited 2020 Oct 08]. Available from: <http://www.cycadlist.org>.
- de Laubenfels, D. J., and Adema, F. A. 1998. Taxonomic revision of the genera *Cycas* and *Epicycas* gen. nov. (Cycadaceae). *Blumea* 43: 351–400.
- Deb, D. B. 1958. Endemism and outside influence on the flora of Manipur. *Journal of Bombay Natural History Society* 55: 313–317.
- Deb, D. B. 1983. *Flora of Tripura* State. Vol. 2. Today and Tomorrow Printer and Publisher, New Delhi.
- Favre, A., Päckert, M., Pauls, S. U., Jähmig, S. C., Uhl, D., Michalak, I., and A. N. Muellner-Riehl. 2015. The role of the uplift of the Qinghai-Tibetan Plateau for the evolution of Tibetan biotas. *Biological reviews of the Cambridge Philosophical Society* 90(1): 236–253. doi: 10.1111/brv.12107
- Gogoi, R. and M. Häkkinen. 2013. *Musa puspanjaliae* (Musaceae) sp. nov. from Arunachal Pradesh, India. *Nordic Journal of Botany* 31: 473–477.
- Govind, S., and D. S. Yadav. 1999. Genetic resources of Citrus in North Eastern Hill region of India. In S. Singh, and S. P. Ghosh [eds.] *Hi-Tech Citrus Management*, 38–46. ISC, ICAR, NRCC, Nagpur.
- Griffith, W. 1854. *Notulae ad Plantas Asiaticas*, Vol. 4. Bishops College Press, Calcutta.
- Haines, H.H. 1924. *The Botany of Bihar and Orissa*. Part V-VI. Adlard, London.
- Hajra, P. K., and D. M. Verma. 1996. *Flora of Sikkim*. Botanical Survey of India, Calcutta.
- Hill, K. D. 1995. Infrageneric relationships, phylogeny and biogeography of the genus *Cycas* (Cycadaceae). In P. Vorster et al. [ed.], *CYCAD 93*, The 3rd International Conference on Cycad Biology, Proceedings, 139–162. Cycad Society of South Africa, Stellenbosch.
- Hill, K. D. 2004. The genus *Cycas* (Cycadaceae) in Vietnam. *The Botanical Review* 70 (2): 134–193.
- Hill, K. D. 2008. The genus *Cycas* (Cycadaceae) in China. *Telopea* 12 (1): 71–118.
- Hill, K. D., and Yang, S. L. 1999. The genus *Cycas* (Cycadaceae) in Thailand. *Brittonia* 51: 48–73.
- Hooker, J. D. 1854. *Himalayan Journals*. vol. 2. John Murray, London.
- Kanjilal, U. N., and N. L. Bor. 1940. *Flora of Assam*. Vol. 4. Botany Survey of India, Calcutta.
- Kanjilal, U. N., Kanjilal, P. C., De, R. N., and A. Das. 1940. *Flora of Assam*. Government of Assam.
- Khuraijam, J. S., Singh, R., Calonje, M., and J. Mazumdar. 2018. (2653) Proposal to conserve the name *Cycas pectinata* (Cycadaceae) with a conserved type. *Taxon* 67(6): 1213. doi: 10.12705/676.22

- Kurz, S. 1877. Forest Flora of British Burma, 2. Office of the Superintendent of Government Printing, Calcutta.
- Lindström, A. 2004. Morphological characters useful in determining species boundaries in *Cycas* (Cycadaceae). In T. Walters and R. Osborne [eds.] *Cycad Classification. Concepts and Recommendations*, 23–44. CAB International Publishing, Wallingford, Oxfordshire, UK.
- Lindström, A. J., and K. D. Hill, K. D. 2007. The genus *Cycas* (Cycadaceae) in India. *Telopea* 11(4): 463–488.
- Manish, K., and M. K. Pandit. 2018. Geophysical upheavals and evolutionary diversification of plant species in the Himalaya. *PeerJ*, 6, e5919. <https://doi.org/10.7717/peerj.5919>
- Mankga, L. T., Yessoufou, K., Mugwena, T., and M. Chitakira. 2020. The cycad genus *Cycas* may have diversified from Indochina and occupied its current ranges through vicariance and dispersal events. *Frontiers in Ecology and Evolution* 8:44. doi: 10.3389/fevo.2020.00044
- Nagalingum, N. S., Marshall, C. R., Quental, T. B., Rai, H. S., Little, D. P., and S. Mathews, S. 2011. Recent synchronous radiation of a living fossil. *Science* 334: 796–799. doi: 10.1126/science.1209926
- Osborne, R., Hill, K. D., Nguyen, H. T., and L. Phan Ke, L. 2007. *Cycads of Vietnam*. Roy Osborne, Brisbane and Wynand van Eeden, Cape Town.
- Pandit, M. K. 2017. *Life in the Himalaya: an ecosystem at risk*. Harvard University Press; Cambridge.
- Pant, D. D. 2002. *An Introduction to Gymnosperms, Cycas and Cycadales*. Birbal Sahni Institute of Palaeobotany, Lucknow.
- Pant, D. D., Singh, R. and D. V. Chauhan. 1994. On *Cycas pectinata* Hamilton from North-East India. *Encephalartos* 38: 17–30.
- Sahni, K. C. 1990. *Gymnosperms of India and adjacent countries*. Bishen Singh Mahendra Pal Singh, Dehradun.
- Schuster, J. 1932. Cycadaceae. In A. Engler [ed.] *Das Pflanzenreich* 99 (IV): 86–103.
- Singh, K. P., and V. Mudgal. 1997. Gymnosperms. In V. Mudgal and R.K. Hajra [eds.], *Floristic diversity and conservation strategies in India*. vol 1: Cryptogams and Gymnosperms. Botanical Survey of India, Calcutta
- Skelley, P., Xu, G., Tang, W., Lindström, A. J., Marler, T., Khuraijam, J. S., Singh, R., Radha, P., and S. Rich. 2017. Review of *Cycadophila* Xu, Tang & Skelley (Coleoptera: Erotylidae: Pharaxonothinae) inhabiting *Cycas* (Cycadaceae) in Asia, with descriptions of a new subgenus and thirteen new species. *Zootaxa* 4267(1): 1–63.
- Srivastava, R. C. 1993. Gymnosperms of Sikkim, India. *Asia Life Sciences* 2(1): 71–87.

- Tang, W. 2004. Continental drift and the evolution of Asian *Cycas*. *Encephalartos* 80:23–28.
- Thiselton-Dyer, W. T. 1888. Cycadaceae. In W. J. Hooker [ed.] Flora of British India, vol. 5. 655–658. Reeve, London.
- Tiwari, A., Upreti, Y., and S. K. Rana. 2019. Plant endemism in the Nepal Himalayas and phytogeographical implications. *Plant Diversity* 41(3): 174–182.
- Tougard, C. 2001. Biogeography and migration routes of large mammal faunas in South East Asia during the Late Middle Pleistocene: focus on the fossil and extant faunas from Thailand. *Palaeogeography, Palaeoclimatology, Palaeoecology* 168: 337–358. doi: 10.1016/S0031-0182(00)00243-1
- Wang, D. Y. 1996. Taxonomy of *Cycas* in China. In F. X. Wang and H. B. Liang [eds.] *Cycads in China*, 33–142. Guangdong Science and Technology Press, Guangdong.
- Wang, D. Y. 1996. Taxonomy of *Cycas* in China. In F. X. Wang, and H. B. Liang [eds.], *Cycads in China*, 33–142. Guangdong Science and Technology Press, Guangdong.
- Westerweel, J., Roperch, P., Licht, A., Dupont-Nivet, G., Win, Z., Poblete, F., Ruffet, G., Swe, h.h., Thi, M.K., and Day Wa Aung. 2019. Burma Terrane part of the Trans-Tethyan arc during collision with India according to palaeomagnetic data. *Nature Geoscience* 12: 863–868. doi: 10.1038/s41561-019-0443-2
- Xiao, L. Q., and M. Möller. 2015. Nuclear ribosomal ITS functional paralogs resolve the phylogenetic relationships of a late-Miocene radiation cycad *Cycas* (Cycadaceae). *PLoS One* 10: e0117971. doi: 10.1371/journal.pone.0117971
- Yang, S. L., and A. W. Meerow. 1996. The *Cycas pectinata* (Cycadaceae) complex: genetic structure and gene flow. *International Journal of Plant Sciences* 157: 468–483. doi: 10.1086/297364
- Yessoufou, K., Daru, B. H., Tafirei, R., Elansary, H. O., and I. Rampedi. 2017. Integrating biogeography, threat and evolutionary data to explore extinction crisis in the taxonomic group of cycads. *Ecology and Evolution* 7: 2735–2746. doi: 10.1002/ece3.2660