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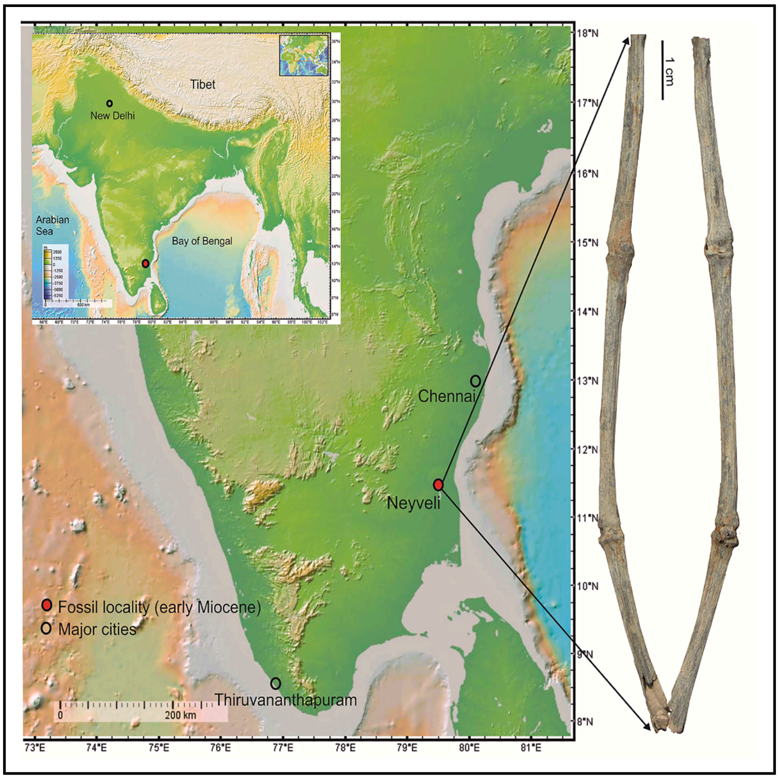
Early Miocene ventricose bamboo from south Asia with implications for evolutionary ecology and biogeography

Graphical abstract



Authors

Harshita Bhatia, Purushottam Adhikari, Poonam Verma, Yogesh Pal Singh, Tao Su, Gaurav Srivastava

Correspondence

gaurav_jan10@yahoo.co.in

In brief

Earth sciences; Paleontology; Evolutionary biology; Paleobiology

Highlights

- Fossil showcase seldom-preserved features–ventricose (swollen) nodes and nodal buds
- Earliest bamboo fossil from Neyveli lignite mine (southern India)
- Supports the hypothesis of a Gondwanan lineage for Asian bamboos
- Suggests a warm, humid tropical climate in the region during the early Miocene

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Early Miocene ventricose bamboo from south Asia with implications for evolutionary ecology and biogeography

Harshita Bhatia,[1,2] Purushottam Adhikari,[3,4] Poonam Verma,[1,2] Yogesh Pal Singh,[1] Tao Su,[5] and Gaurav Srivastava[1,2,6,*]
[1]Birbal Sahni Institute of Palaeosciences, 53 University Road, Lucknow 226007, India
[2]Academy of Scientific and Innovative Research (AcSIR), Ghaziabad 201002, India
[3]Department of Geology, Birendra Multiple Campus, Tribhuvan University, Bharatpur, Chitwan, Nepal
[4]Central Department of Geology, Tribhuvan University, Kirtipur, Kathmandu, Nepal
[5]State Key Laboratory of Oil and Gas Reservoir Geology and Exploitation & Institute of Sedimentary Geology, Chengdu University of Technology, Chengdu 610059, China
[6]Lead contact
*Correspondence: gaurav_jan10@yahoo.co.in
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SUMMARY

The evolutionary history of bamboo has remained elusive, primarily due to the scarcity of fossils that exhibit varied morphological traits, often lacking detailed features. In this study, we introduce a remarkable fossil find, a bamboo culm from the early Miocene sediments of the Neyveli lignite mine in India. This fossil is distinguished by its nodal buds and notably ventricose (swollen) nodes—features rarely preserved in the fossil record. This unique specimen stands alone to showcase such specific morphological characteristics and is the earliest known bamboo fossil from southern India. Its discovery is a significant breakthrough in the study of bamboo diversity, offering fresh insights into the morphological evolutionary history of bamboo and lending support to the hypothesis of a Gondwanan origin for Asian bamboos. Furthermore, this fossil is crucial for reconstructing past environments, suggesting that ancient bamboos likely evolved in warm, humid climatic conditions.

INTRODUCTION

Bamboos, distinguished for their rapid growth and robust woody stems, play a vital role in rural economies and global environmental conservation efforts. These tall, mostly evergreen, tree-like grasses, characterized by resilient rhizome networks and rare flowering events, are versatile renewable resources capable of thriving in diverse climatic and soil conditions.[1] Their adaptability underpins their significant economic impact, fostering various industries, including the production of fuels, chemicals, and biomaterials.[2]

Bamboos are indispensable, utilized in construction, the manufacture of farm implements, and household utensils. They contribute significantly to erosion control, biodiversity conservation, riverbank protection, carbon sequestration, and overall forest health. The economic impact of bamboo is profound, earning it monikers such as "Green Gold," "Cradle to Coffin Timber," and "Poor Man's Timber," reflecting its broad utility and economic potential.[3]

According to the Food and Agriculture Organization, bamboo covers approximately 35 million hectares across Africa, Asia, and the Americas.[4] The majority of bamboo forests are concentrated in Asia and the Pacific.[5] India ranks second globally in bamboo genetic resources, following China, with these two countries together accounting for around 70% of the world's bamboo wealth. Approximately 25% of global bamboo species are found in India, predominantly in the Western Ghats (South India) and North-East India.[6] India possesses significant bamboo diversity, with 125 indigenous and 11 exotic species[7] belonging to 23 genera, covering approximately 15.69 million hectares of forest and non-forest areas.[3]

Classified under the subfamily Bambusoideae of Poaceae, bamboos encompass 136 genera and approximately 1,698 species[8] belonging to three tribes: Arundinarieae (temperate woody bamboos), Bambuseae (tropical woody bamboos), and Olyreae (herbaceous bamboos).[9] Native to all continents except Antarctica and Europe, bamboos are found between latitudes 50°30′ N and 47°S, from sea level up to altitudes of 4,300 m.[10]

Due to the varied habitat range and disjunct distribution patterns among extant bamboo species, their evolutionary ecology remains poorly understood. Most fossil bamboos have been reported in forms such as culms, leaves, rhizomes, pollen, and phytoliths.[11] The earliest records of bamboo macrofossils originate from the Oligocene of Italy and northeast India, with further discoveries in Neogene sediments across continents including North America, South

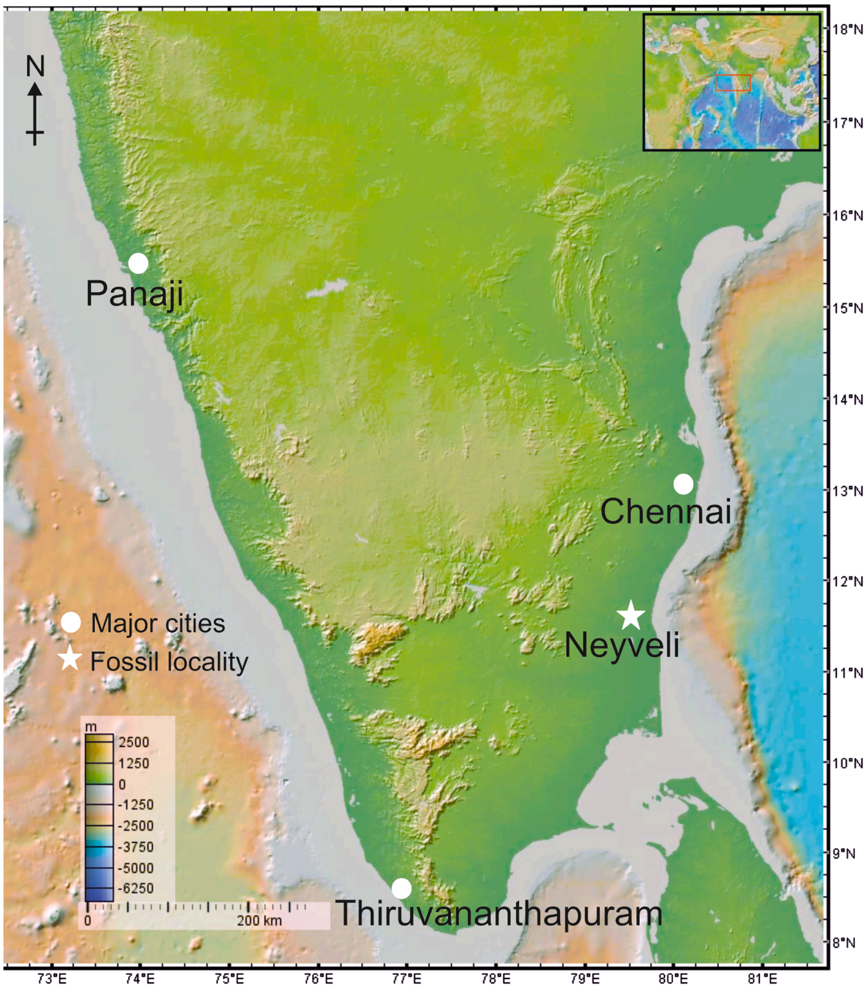

Figure 1. Map showing the fossil locality marked by a white star

Figure made with GeoMapApp (www.geomapapp.org).

America, Europe, Asia, Australia, and New Zealand.[11–14] Typically preserved as culms and leaves, these macrofossils exhibit limited morphological diversity, often lacking detailed features. Consequently, the evolutionary trajectory of bamboo morphology remains poorly understood due to the scarcity of fossils showcasing varied morphological traits. Here, we report a fossil bamboo culm from early Miocene sediments at Neyveli lignite mine, India (Figures 1, 2, and 3), distinguished by nodal buds and notably swollen nodes. These morphological features are rarely preserved in fossilized specimens, making such finds exceptionally valuable. This finding provides new insights into the evolutionary and ecological history of the bamboo during the Miocene time in South Asia.

RESULTS

Systematic paleontology

Order: Poales Small.

Family: Poaceae Barnhart.

Subfamily: Bambusoideae Luerssen

Genus: *Ventriculmus* H. Bhatia et G. Srivastava gen. nov.

Type species: *Ventriculmus neyveliensis* H. Bhatia et G. Srivastava gen. et sp. nov. (Figures 4, 5, and 6).

Holotype: Specimen no. BSIP 42329.

Type locality: Neyveli lignite mine, Tamil Nadu, India.

Stratigraphic age: Early Miocene.

Repository: Birbal Sahni Institute of Palaeosciences (BSIP), Lucknow.

Generic diagnosis

Bamboo culm with distinct nodes and internodes, nodes are ventricose or swollen or bulged out, supranodal ridge and nodal bud present with a nodal line.

Etymology

The genus name *Ventriculmus* is derived from the Latin roots: "Ventri-" (swollen) and "culmus" denotes either bamboo culm or branch. The name describes a fossil resembling a bamboo culm or branch with notably swollen nodes, highlighting its key morphological features.

Specific diagnosis

Bamboo culm or branch with distinct nodes and internodes, preserved internode length and diameter ranging from 3.4 to 4.6 cm and 3.2 to 3.8 mm respectively, nodal line and supranodal ridge present, nodal diameter 4.7 to 5.6 mm, two oval to round shaped nodal buds present, nodes prominently bulged out or swollen.

Etymology

The specific epithet '*neyveliensis*' represents the Neyveli lignite mine from where the fossil was excavated.

Description

Well-preserved petrified bamboo culm or branch, maximum preserved length is 12.2 cm with two distinct nodes, and one complete and two half-complete internodes (Figure 4), the distance between two nodes (internode) is 4.6 cm, other preserved internodes length are 3.4 cm and 3.5 cm, diameter ranges between 3.2 and 3.8 mm (Figure 4), internode seems to be hollow (Figures 4 and 6A). A distinct nodal line has a diameter ranging from 4.7 to 5.6 mm (Figures 5A–5F). Two oval to round nodal buds are present at the nodes (Figures 5D–5F, 6A–6C, and 6E), probably preserved with prophylls (Figures 5E and 5F; Figure 6E). The buds are 1.6 mm and 2.1 mm in length, and 1.7 mm and 2.4 mm in width (Figures 5E, 5F, 6C, and 6E). A supranodal ridge is present

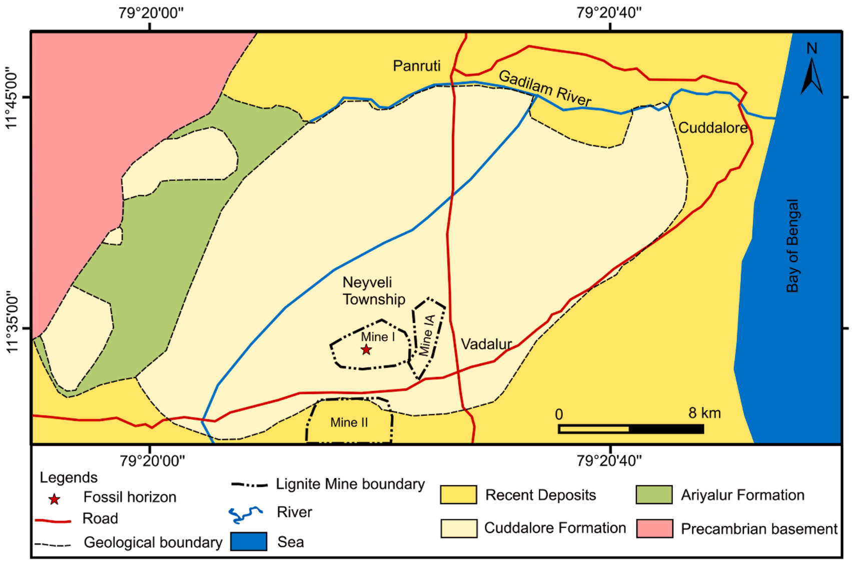

Figure 2. Geological map of the fossil locality

(Figures 5B, 5E, and 6D) and nodes are prominently swollen or bulged out (Figures 5A, 5B, 5D, 5F, 6A, and 6D). The bulging or swelling is observed just above or along the supranodal ridge and just below the nodal area and we have termed it here as ventricose nodes.

DISCUSSION

Comparison with extant and fossil species

The characteristic features of the fossil, such as distinct nodes and internodes, a prominent supranodal ridge, and a nodal line with nodal buds, clearly place it within the subfamily Bambusoideae of the family Poaceae. It is still a challenge to identify extant bamboo species due to their taxonomic complexity and unique reproductive cycle, which mostly occurs once in their lifetime. Consequently, fossil bamboos are difficult to assign to their nearest living relatives (NLR) due to limited preserved morphological characters. Based on its preserved morphological features such as nodes, internodes, and nodal buds, the fossil can be identified as a bamboo culm, branch, or rhizome (Figures 7A–7I and 8A–8G). In bamboo culms and branches, the internodes are typically elongated, with nodal buds often present at alternate nodes. These nodes are characterized by a nodal line and supranodal ridges. In contrast, rhizomes have shorter internodes that are closely spaced, forming compact segments, often with rhizome hairs, and the internodes are not very smooth (Figure 8F), which makes it different from the present fossil. Given that culms and branches share similar morphological features, distinguishing between the two is challenging. While several bamboo species have culms with small diameters comparable to the present fossil, they often lack features such as swollen nodes, whereas others possess swollen nodes but have diameter ranges that do not align with the fossil, further complicating precise identification.

Extant bamboo species such as *Brachystachyum densiflorum* (Rendle) Keng, *Chimonobambusa* sp., *Phyllostachys* sp. and *Sinobambusa tootsik* (Makino) Makino ex Nakai of Tribe Arundinarieae, *Bambusa bambos* (L.) Voss, *Bambusa ventricosa* McClure and *Bambusa vulgaris* Schrad. ex J.C.Wendl. of Tribe Bambuseae exhibit similarities to the fossil in terms of swollen nodes. However, specific distinguishing characteristics—such as thorns in *Bambusa bambos*, while nodes often present with a narrow ring of roots and covered with hairs in *Bambusa vulgaris*, shorter and swollen internodes in *Bambusa ventricosa*, and grooves or sulci on culms and branches in *Phyllostachys*—set these species apart. Within the genus *Chimonobambusa* Makino, species such as *C. quadrangularis* (Franceschi) Makino are notable for their nodal thorns, while others have culm diameters exceeding 10 mm, such as *C. tumidissinoda* Ohrnb. Other species of *Chimonobambusa*, such as *C. angustifolia* C.D. Chu & C.S. Chao, *C. brevinoda* Hsueh & W.P. Zhang, *C. damingshanensis* Hsueh & W.P. Zhang, *C. gracilis* (W.T. Lin) N.H. Xia, *C. hsuehiana* D.Z. Li & H.Q. Yang, *C. leishanensis* T. P. Yi, *C. pubescens* T.H. Wen, and *C. unifolia* (T.P. Yi) T. H. Wen, have culm diameters less than 10 mm (Guadua Bamboo: https://www.guaduabamboo.com/blog/chimonobambusa-species-list), comparable to the fossil. Similarly, *Brachystachyum densiflorum* also has swollen nodes with a culm diameter of approximately 10 mm while *Sinobambusa tootsik* has swollen nodes but have culm diameter usually more than 10 mm.

Similarly, species from genera such as *Pseudosasa* Makino ex Nakai and *Yushania* Keng f. of the tribe Arundinarieae, and *Chusquea* Kunth of the tribe Bambuseae exhibit culm diameters in the range of the fossil but lack swollen nodes traits. For instance, *Pseudosasa gracilis* S.L. Chen & G.Y. Sheng, *P. owatarii* (Makino) Makino ex Nakai, and *P. pubiflora* (Keng) Keng f. have small culm diameters (3–5 mm) but lack swollen nodes. Species of *Yushania*, such as *Y. andropogonoides* (Hand. -Mazz.) T.P. Yi, *Y. baishanzuensis* Z.P. Wang & G.H. Ye, *Y. basihirsuta* (McClure) Z.P. Wang & G.H. Ye, *Y. brevis* T.P. Yi, *Y. glandulosa* Hsueh f. & T. P. Yi, *Y. microphylla* (Munro) R.B.Majumdar, *Y. qiaojiaensis* Hsueh f. & T.P. Yi, and *Y. tenuicaulis* T.P. Yi & J.Y. Shi, also show small culm diameters (3–5 mm). Among *Chusquea* species, examples such as *C. anelythra* Nees, *C. angustifolia* (Soderstr. & C.E.Calderón) L.G. Clark, *C. arachniformis* L.G. Clark & Londoño, *C. argentina* Parodi, *C. bambusoides* (Raddi) Hack., *C. capituliflora* Trin., *C. decolorata* Munro ex L.G. Clark, *C. delicatula* Hitchc., *C. leptophylla* Nees, *C. linearis* N.E.Br., *C. neurophylla* L.G. Clark, *C. nana* L.G. Clark, *C. renvoizei* L.G. Clark, *C. sellowii* Rupr., and *C. smithii* L.G. Clark display culm diameters ranging from 2 to 6 mm.

Other genera, such as *Ochlandra* Thwaites, endemic to the Western Ghats, *Cephalostachyum* Munro, *Dendrocalamus*

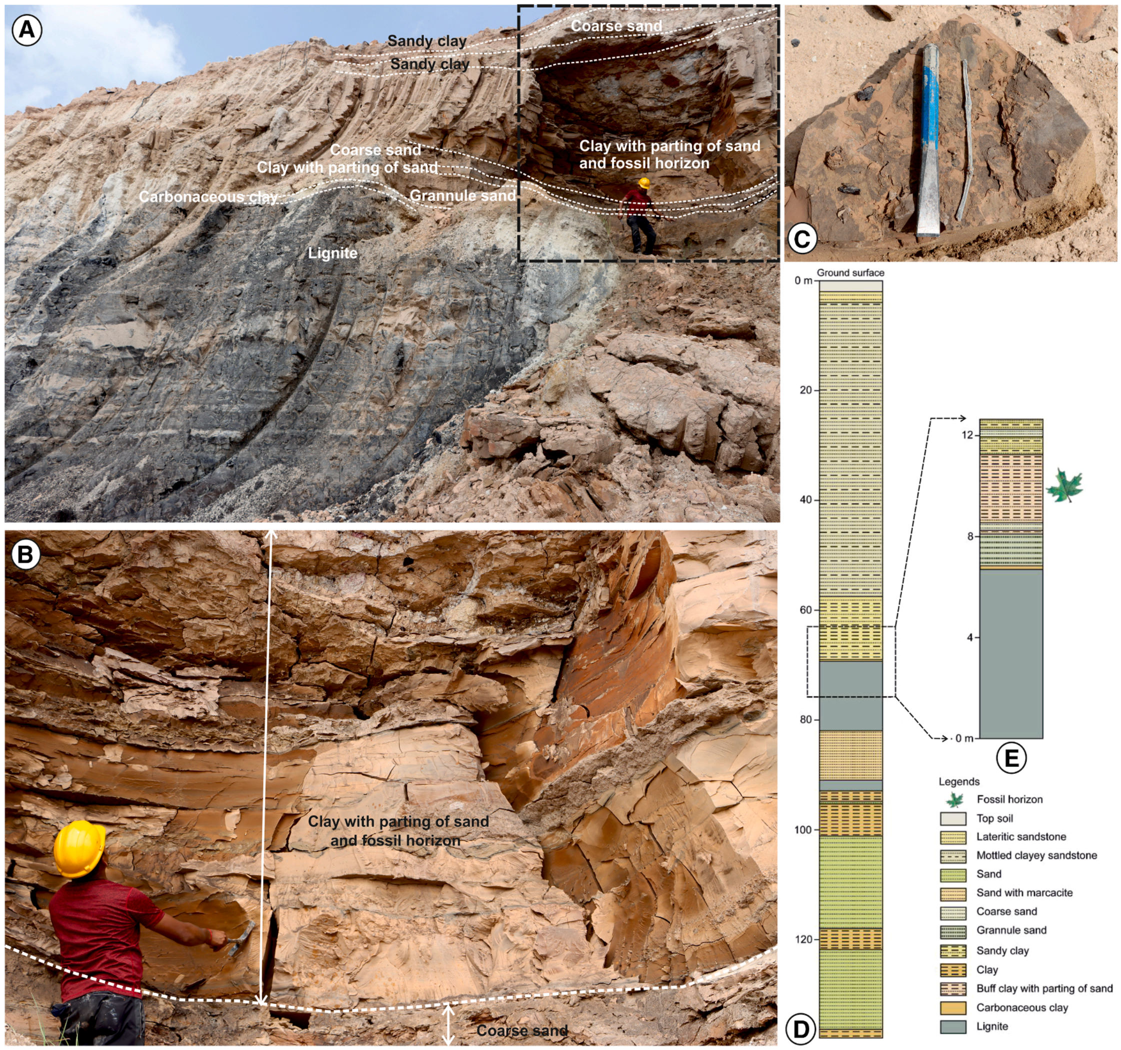

Figure 3. Figure showing the field photographs, fossil horizon and lithological details of the Neyveli lignite mine I

(A) Field photograph of the exposed sections at Neyveli lignite mine I, with the inset highlighting the specific section where the fossil was collected.
(B) Enlarged view of the inset in (A), indicating the fossil horizon.
(C) Field photograph of the fossil bamboo specimen.
(D) Generalized lithological details of mine I.
(E) Observed lithological details from where the fossil was collected.

Nees, *Dinochloa* Buse, *Guadua* Kunth, *Gigantochloa* Kurz ex Munro, *Melocanna* Trin., *Melocalamus* Benth., *Oxytenanthera* Munro, *Pseudostachyum* Munro of the tribe Bambuseae and *Himalayacalamus* Keng f., *Pleioblastus* Nakai, *Sarocalamus* Stapleton, *Schizostachyum* Nees and *Thamnocalamus* Munro of the tribe Arundinarieae and *Olyra* L. of the tribe Olyreae differ further in terms of nodal morphology.

These observations suggest that the fossil may represent either a culm or a branch. Based on the above comparison, the present fossil shows some similarity with the sp. of *Chimonobambusa, Sinobambusa, or Brachystachyum*. Different morphological features of extant bamboo culms, branches, and rhizomes are illustrated in Figures 7 and 8, emphasizing the morphological diversity in extant bamboo species and highlighting the challenges of identifying the fossil to its nearest living relatives. Consequently, the fossil is identified here as a bamboo culm or a branch. For ease of discussion, the terms "culm" and "branch" with respect to the present fossil are collectively referred to as "culm" herein.

The fossil record of bamboo culms is sparse. An early Eocene *Chusquea* culm from Argentina once considered the oldest bamboo fossil,[15] was recently reclassified as belonging to the Podocarpaceae family.[14] Other significant discoveries include *Chusquea* culms from Cenozoic sediments of Colombia,[16] *Bambusiculmus tirapensis* from the late Oligocene sediments of Assam, India,[13] *Phyllostachys* from the late Miocene sediments of Japan,[17] *Bambusiculmus latus* and *B. angustus* from the middle Miocene sediments in Yunnan, China,[18] a bamboo culm from the

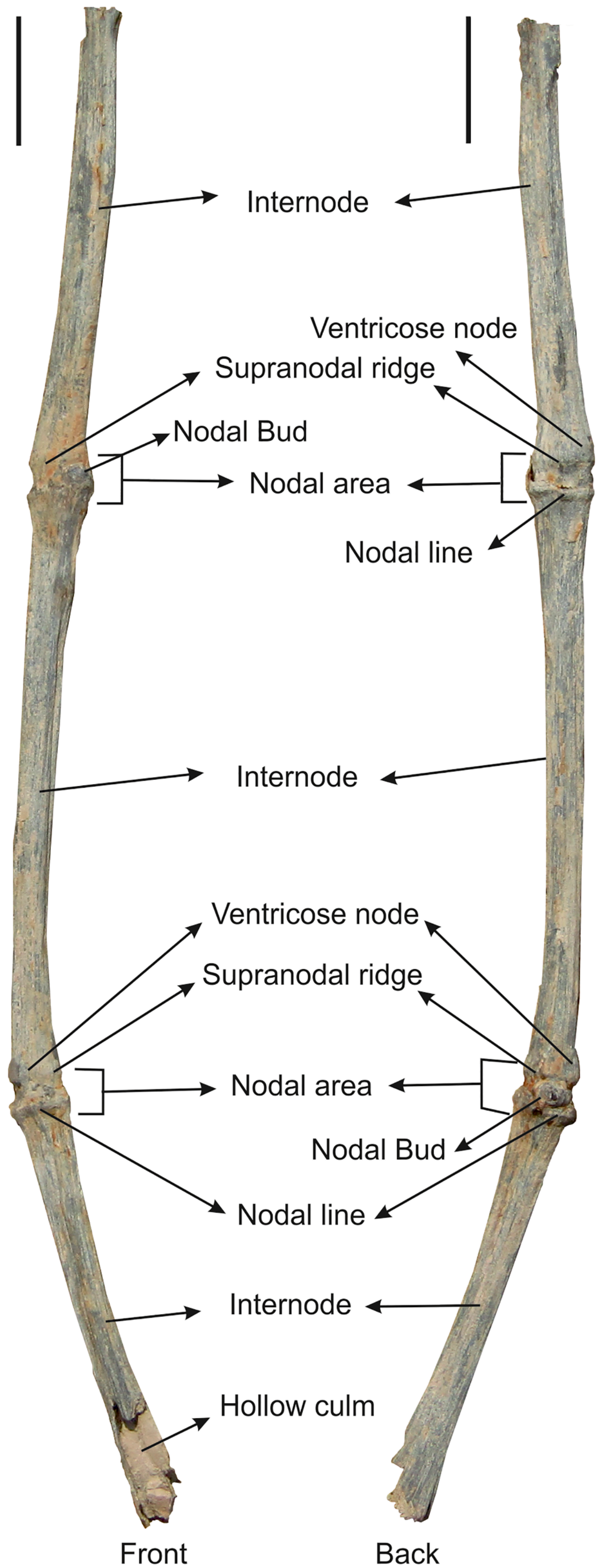

Figure 4. Front and back view of the fossil culm of the *Ventriculmus neyveliensis* Bhatia et Srivastava gen. et sp. nov. showing all the characteristics features preserved
(Scale bar: 1 cm).

Lower Siwalik (middle–late Miocene) sediments of Himachal Pradesh, India,[19] *Guadua zuloagae* from the Pliocene sediments of Argentina,[20] and a *Guadua* fossil from the upper Pliocene–upper Pleistocene sediments of Peru.[21] Li et al.[22] reported a bamboo culm from the Pliocene sediments of Yunnan, but it lacked detailed morphological features. These fossils differ from the present specimen in the absence of nodal buds and swollen nodes. Given the distinct characteristics of the present fossil specimen compared to previously published fossil bamboo culms, we have placed it under the newly formed organ genus *Ventriculmus* H. Bhatia et G. Srivastava gen. nov. and describe a new species, *Ventriculmus neyveliensis* H. Bhatia et G. Srivastava gen. et sp. nov.

Evolutionary ecology and biogeography

Bamboos are categorized into three monophyletic tribes: Arundinarieae, Bambuseae, and Olyreae.[23] Species in Arundinarieae are found in Africa, Asia, and North America. Species in Bambuseae, which are mostly woody, thrive in tropical regions, while Olyreae species, which are herbaceous, are found in the Americas. Modern woody bamboos are present in all the continents except Europe and Antarctica. The fossil record of bamboos generally mirrors their current distribution, though some fossils, found in Europe, occur at higher latitudes than their modern counterparts[12,24,25,26] (Figure 9).

The biogeography, diversification, and origin of the Bambusoideae remain areas of significant scientific interest. Fossil evidence can provide new insights into the ecology of Bambusoideae, but reliable fossil records of Bambusoideae are rare.[18] Reliable bamboo macrofossils globally date back to the Oligocene.[12–14] Peola[12] described a bamboo leaf fragment, *Bambusa alexandrina*, from the Oligocene of Monferrato, Italy, while Srivastava et al.[13] reported bamboo culms from the late Oligocene of Assam, India. Although *Chusquea oxyphylla* was once considered the oldest bamboo macrofossil, current evidence suggests that the South American bamboo fossil record dates to no earlier than the Pliocene.[14,20,21,27] In southeastern North America, Pleistocene fossils of *Arundinaria* have been discovered.[28,29] European bamboo fossils range from the Oligocene to the Pleistocene.[12,24,25] Probable fossil bamboos are also reported from eastern Australia and New Zealand,[30,31] where no native modern bamboos exist. Modern native Australian bamboos are confined to the northern coast.[32] Despite the presence of modern woody bamboo in Africa, there are no fossil bamboo records from the continent.

The ecological history of bamboo in Asia remains poorly understood due to the scarcity of fossil records. Bamboo fossils in Asia range from the late Oligocene to the Pliocene. In China, they span from the middle Miocene to the Pliocene.[11,18,22] In India, fossils date from the late Oligocene to the Pliocene.[13,19,33,34] Nepal has bamboo fossils dating to the late Miocene,[35] while they have been reported from the Miocene sediments of Japan.[36] The aforesaid fossil records

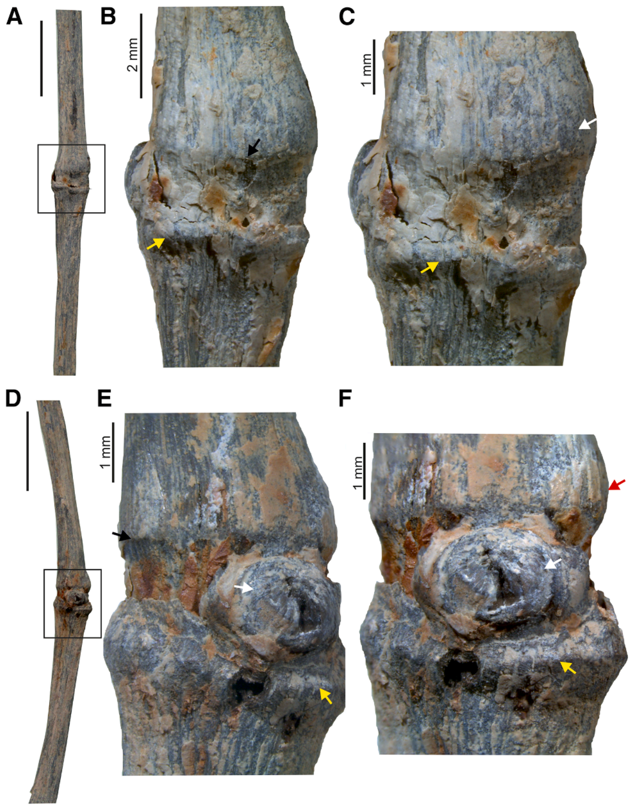

Figure 5. Fossil specimen showing the back part of the bamboo culm

(A) Enlarged portion showing the node and internode.

(B and C) Microscopic enlarged portion of the inset of (A) showing the nodal area with supranodal ridge (black arrow), nodal line (yellow arrow), and ventricose nodes (white arrow).

(D) Enlarged portion showing the node, nodal bud, ventricose node, and internodes.

(E and F) Microscopic enlarged portion of the inset of (D) showing the nodal area with supranodal ridge (black arrow), nodal line (yellow arrows), ventricose node (red arrow), and nodal bud (white arrows) probably preserved with prophylls. (Scale bar: 1 cm unless specified).

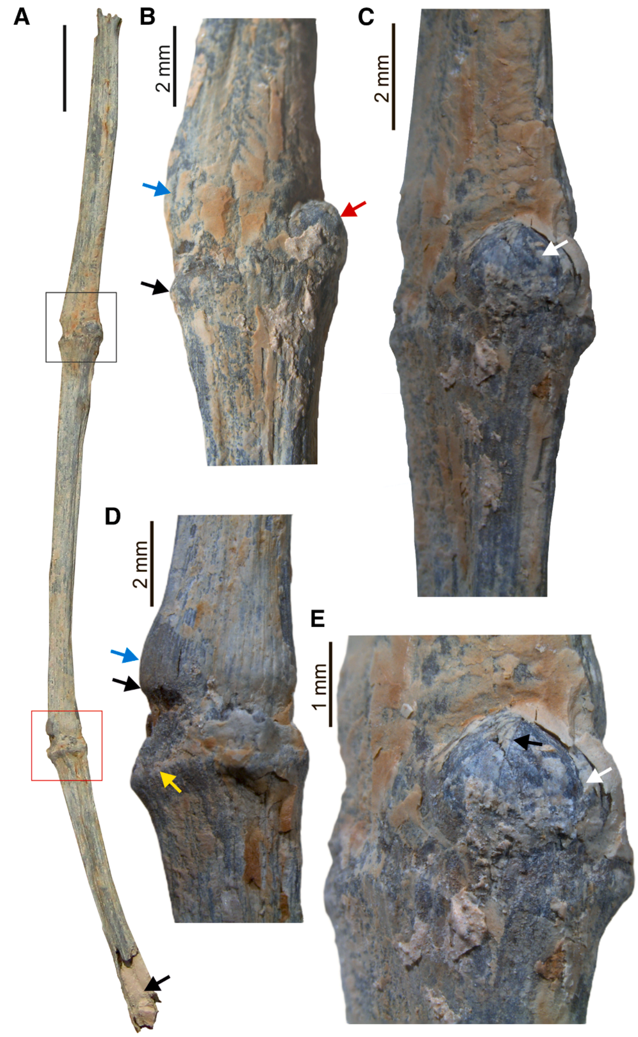

Figure 6. Fossil specimen showing the front part of the bamboo culm

(A) A completely preserved fossil culm.

(B) Microscopic enlarged portion of the black color inset of (A) showing the side view of the nodal bud (red arrow) with nodal line (black arrow) and ventricose nodes (sky blue arrow).

(C) Microscopic enlarged portion of the black color inset of (A) showing the front view of the nodal bud (white arrow).

(D) Microscopic enlarged portion of the red color inset of (A) showing the nodal area with supranodal ridge (black arrow), nodal line (yellow arrow), and ventricose node (sky blue arrow).

(E) Microscopic enlarged portion of the (C) showing the nodal bud (white arrow) with transverse lines present on the bud (black arrow), probably representative of the prophylls covering the bud. (Scale bar: 1 cm unless specified).

suggest that the ancestors of Asian extant bamboo have Gondwanan lineage[13] and they most likely evolved in India. As the Indian plate drifted from the southern to the northern Hemisphere and collided with the Eurasian plate, these bamboos might have migrated from India to China and Southeast Asia following the joining of the Indian and Eurasian plates in the Neogene. The newly discovered fossil specimen from the early Miocene of South India further supports the hypothesis of a Gondwanan origin for Asian bamboos. Molecular phylogenetic data also suggest that the crown node of Bambusoideae might have originated around 54 million years ago in the Indo-malayan region of Gondwanaland.[37] The megafossils record (Figure 9) also suggests that bamboos were already widespread across Asia during the Miocene, with evidence from India, China, Japan, and Nepal. The present fossil shows some morphological similarity to species of *Chimonobambusa*, *Sinobambusa*, and *Brachystachyum*. *Chimonobambusa* is distributed across the eastern Himalaya, China, Indo-China, Taiwan, and Japan; *Sinobambusa* is native to China (Fujian, Guangdong, Guangxi) and Vietnam; and *Brachystachyum* species are native to southern China. The distribution of these species, along with the fossils, suggests that bamboos were widespread across Asia during the Miocene and likely migrated from India to China and Southeast Asia following the Neogene connection of the Indian and Eurasian plates.

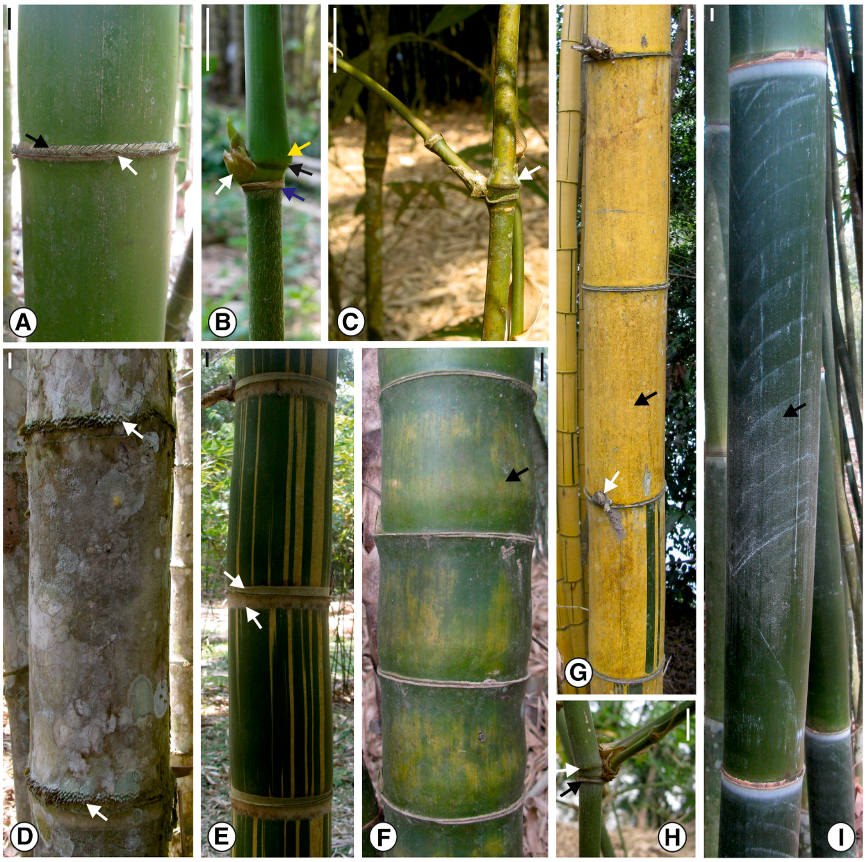

Figure 7. Morphological features of different extant bamboo culms and branches showing nodes, length of the internodes, buds and other features preserved

(A) Culm of *Bambusa spinosa* Roxb. (Tribe Bambuseae) showing nodal line (white arrow) and remnant of leaf sheaths surrounding the node (black arrow).

(B) Individual branch of *Bambusa bambos* (L.) Voss (Tribe Bambuseae) showing the ventricose node (yellow arrow), supranodal ridge (black arrow), nodal line (blue arrow) and nodal buds (white arrow).

(C) Branch and culm of *Chimonobambusa tumidissinoda* Ohrnb. (Tribe Arundinarieae) showing the ventricose node (white arrow).

(D) Culm of *Dendrocalamus* Nees (Tribe Bambuseae) showing the rootlet hairs present at the nodes (white arrows).

(E) *Guadua chacoensis* (Rojas Acosta) Londoño & P.M.Peterson (Tribe Bambuseae) culm showing nodes surrounded with white band of thick hairs above and below the nodes (white arrows).

(F) *Bambusa ventricosa* McClure (Tribe Bambuseae) culm showing the swollen internode (black arrow).

(G) *Bambusa balcooa* Roxb. (Tribe Bambuseae) culm showing internode (black arrow) and nodal bud (white arrow).

(H) Culm and branch of *Bambusa spinosa* (Tribe Bambuseae) showing supranodal ridge (white arrow) and nodal line (black arrow).

(I) *Schizostachyum funghomii* McClure (Tribe Bambuseae) culm with a very long internode (black arrow). (Images courtesy: Xishuangbanna Tropical Botanical Garden, CAS, Mengla 666303, China) (Scale bar: 1 cm).

Morphological diversity in bamboo fossils is often limited to culms and leaves, with preserved features typically restricted to internodes and nodes. However, the *Guadua* fossil from Pliocene–Pleistocene sediments in Peru, South America, adds notable diversity by representing thorny bamboo species. Notably, no previously reported bamboo fossils have preserved nodal buds, making the present fossil significant for its depiction of morphological diversity of the nodal area, including swollen nodes and nodal buds. The present bamboo fossil, characterized by its distinct ventricose nodes and nodal buds, might indicate that bamboo diversity gradually increased during the Miocene in Asia, with further diversification potentially occurring during or after the late Neogene. Moreover, this is the earliest record of bamboo from southern India, which extends the distributional range of bamboo from northern India to southern India during the Miocene, and it potentially sheds light on the environmental conditions and ecological niches that ancient bamboo occupied in the region. It has been suggested that ancient Asian bamboo evolved in a tropical seasonal climate with warm and humid conditions.[13,37] Consequently, the present fossil implies that a tropical warm and humid climate most likely existed in the fossil locality during the early Miocene. The distinctive features such as ventricose nodes and presence of nodal buds, rarely observed in fossil records, suggest advanced structural adaptations, contributing to the broader narrative of ecology and evolutionary history of bamboo. This specimen stands out as the only known fossil bamboo exhibiting such detailed morphological characteristics, underscoring its importance in the study of bamboo diversity and evolution.

Conclusions

The discovery of an early Miocene bamboo fossil from the Neyveli lignite mine in southern India, featuring rare nodal buds and ventricose nodes, significantly enhances our understanding of bamboo ecology and morphological evolution. This unique specimen, currently the earliest known bamboo fossil from southern India, provides crucial insights into the morphological diversity of ancient bamboo. The detailed characteristics observed in this fossil are seldom found in the fossil record, making it an invaluable addition to the study of bamboo diversity. Additionally, this fossil suggests that the diversity of bamboos might have gradually increased during the Miocene in Asia, where ancient bamboos thrived in tropical, warm, and humid climates.

Limitations of the study

The present study is based on a single small fossilized portion of the branch/culm. Therefore, to further strengthen our study, future discoveries of other parts of the bamboo fossils, such as

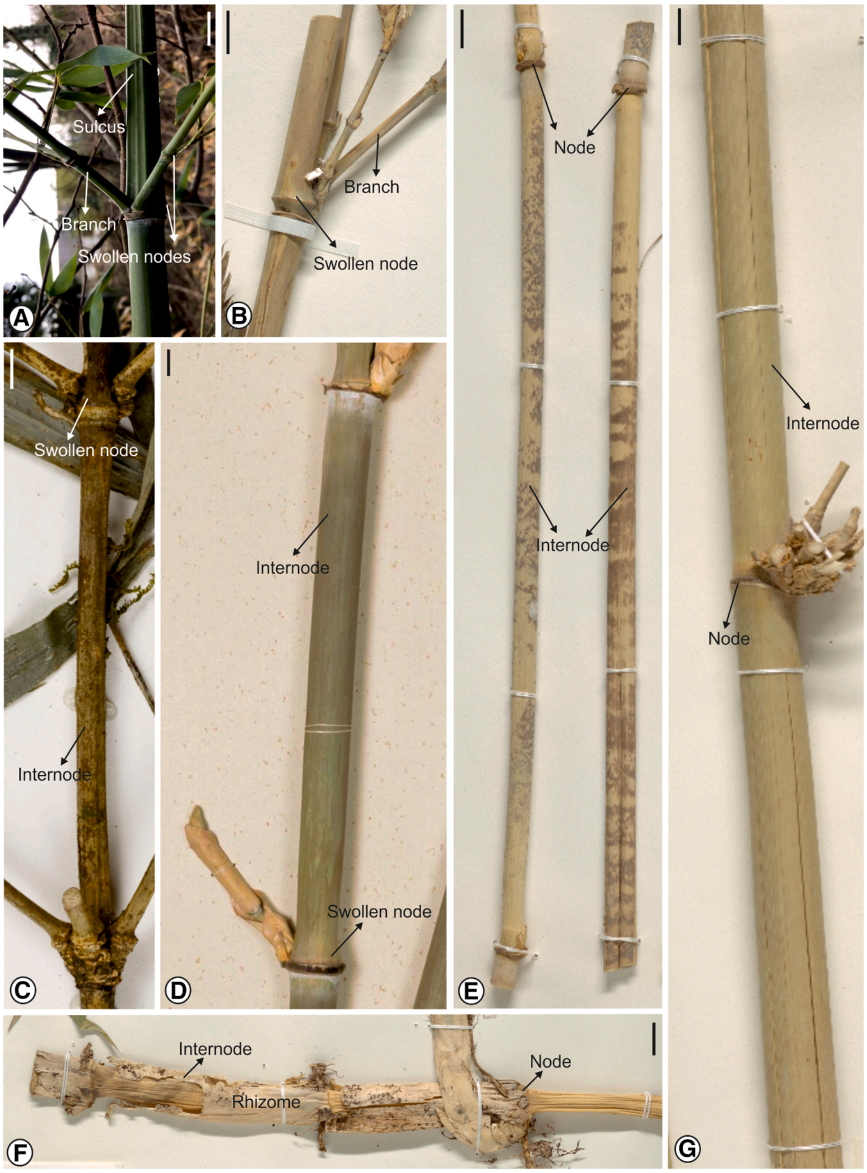

Figure 8. Morphological characteristics of various extant bamboo species, highlighting features of culms, branches, and rhizomes

(A) Culm and branch of *Phyllostachys* Siebold & Zucc. (Tribe Arundinarieae) showing swollen nodes and sulcus. (GBIF: https://www.gbif.org/occurrence/4887858531).

(B) Culm and branch of *Semiarundinaria* Makino ex Nakai (Tribe Arundinarieae), showing swollen node. (GBIF: https://www.gbif.org/occurrence/1320234587).

(C) Culm of *Chimonobambusa armata* (Gamble) Hsueh f. & T.P. Yi (Tribe Arundinarieae) showing swollen node and length and diameter of the internode. (GBIF: https://www.gbif.org/occurrence/2569345166).

(D) Culm of *Sinobambusa tootsik* (Makino) Makino ex Nakai (Tribe Arundinarieae) showing swollen node and the internode. (GBIF: https://www.gbif.org/occurrence/4608038157).

(E) *Ochlandra stridula* Thwaites (Tribe Bambuseae) culm showing features of node and length and diameter of the internode. (GBIF: https://www.gbif.org/occurrence/1318885058).

(F) Rhizome of *Sinobambusa tootsik* (Makino) Makino depicting features of nodal area and the internode. (GBIF: https://www.gbif.org/occurrence/1317830717).

(G) Culm of *Melocanna baccifera* (Roxb.) Kurz (Tribe Bambuseae) showing node and the internode. (GBIF: https://www.gbif.org/occurrence/1321626012).

leaves or rhizomes, from the same locality, could provide a more complete understanding of the bamboo diversity in the region.

RESOURCE AVAILABILITY

Lead contact

Further questions should be directed to the lead contact, Gaurav Srivastava (gaurav_jan10@yahoo.co.in).

Materials availability

Specimen BSIP 42329 is deposited in the Museum of Birbal Sahni Institute of Palaeosciences, India.

Data and code availability

- All data reported in this article are included in the article. Additional information will be shared by the lead contact upon request.
- No novel code was used in this study.
- Any additional information required to reanalyze the data reported in this article is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Harshita Bhatia: conceptualization, methodology, formal analysis, data curation, writing–original draft, writing–review and editing. Purushottam Adhikari: data collection and writing–review and editing. Poonam Verma: data collection, writing–original draft, and writing–review and editing. Yogesh P.

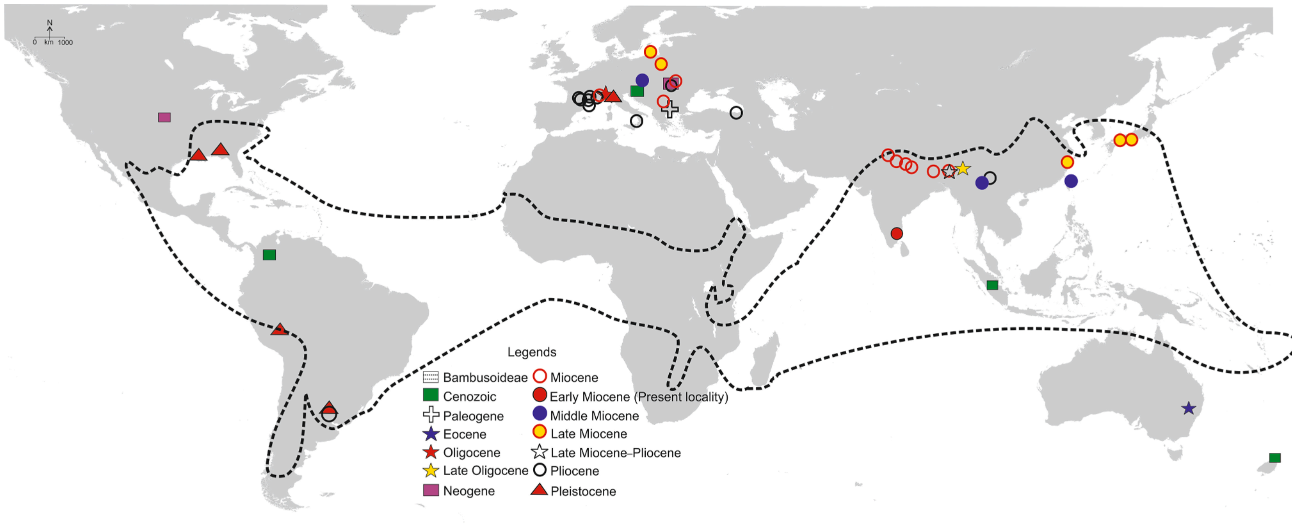

Figure 9. Showing macrofossil records of bamboo and modern distribution of Bambusoideae

Singh: writing–review and editing. Tao Su: writing–review and editing. Gaurav Srivastava: conceptualization, supervision, data collection, data curation, writing–original draft, and writing–review and editing.

DECLARATION OF INTERESTS

The authors declare that they have no conflicts of interest.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Fossil specimen	Birbal Sahni Institute of Palaeosciences, India.	BSIP 42329

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Plants

All specimens used here are listed in the key resources table.

METHOD DETAILS

Specimen preparation

The fossil material described here was recovered from the Mine I (11.57° N; 79.49° E) of the Neyveli lignite mine, Tamil Nadu (Figure 1). South Arcot basin or Ariyalur–Pondicherry sub-basin of the Cauvery basin on the east coast at Neyveli area, Tamil Nadu (Figure 1). One complete fossil bamboo culm is reported. The fossil was carefully cleaned using a soft brush and fine chisel to remove any adhering sediment or debris without causing damage to the delicate structures. Photographs of the fossil were taken under low-angle natural light using a digital camera (Canon SX430) to capture its macroscopic features. Details of the fossil were further examined under a Leica S8APO stereomicroscope, enabling a closer inspection of diagnostic features such as nodes, internodes, and other structural adaptations. The morphological description of the fossil culm is based on the terminology provided by Soderstrom and Young,[38] Brea and Zucol,[20] and Wang et al.[18]

Geological setting

The Neyveli lignite deposits embrace the vastest exploitable lignite of India, to date, which reserves more than 3300 million tons spreading over around 480 sq. km. The lignite resources in this region belong to the South Arcot basin or Ariyalur–Pondicherry sub-basin of the Cauvery basin on the east coast at Neyveli area, Tamil Nadu (Figure 2). The Cauvery Basin is a pericratonic basin situated in the eastern continental margin of the South Indian peninsular shield that came into existence due to Gondwana break up during the Late Jurassic–Early Cretaceous by NE-SW aligned rift process of the Precambrian basement.[39] The Cauvery Basin is known for its tectonically controlled huge sedimentation, with a few considerable breaks, from the Late Jurassic to the Recent age.[40] In the Ariyalur–Pondicherry sub-basin of the Cauvery Basin, a complete Upper Cretaceous–Neogene succession is known.[41] As per the lithostratigraphic classification,[41] the Upper Cretaceous successions belonging to Valudavur and Mettuveli Formations unconformably overlie the Archean basement, subsequently followed by the Paleocene–Eocene Karasur and Manaveli formations, followed by unconformably overlain by the Miocene–Pliocene Cuddalore Formation.[42–45] Another lithostratigraphic scheme suggests a subsurface Neyveli Formation that comprises black clays, shales, and sandstones with lignite seams present unconformably below the Cuddalore Formation in the Ariyalur–Pondicherry sub-basin.[46–48] However, this lithostratigraphic scheme was contested by Singh et al.,[44] who presented various counter-evidences in their paper.

Despite the lapse of nearly five decades of geological research on the Neyveli deposits, there are still controversies related to the age and depositional environment of these lignites. Singh et al.[44] conducted a comprehensive study on the Neyveli lignite deposits in the Cauvery Basin, classifying the entire Tertiary lithostratigraphic sequence into the Miocene Cuddalore Formation and the underlying Eocene deposits (unnamed Formation). The Cuddalore Formation comprises alternate beds of sandstone, clayey sandstone, sandy clay, clay and carbonaceous clay, in addition to the lignite seam and unconformably overlies the Eocene sediments in the area.[44,46] Eocene sediments comprise of black clays, shales, grey coloured sandstones, calcareous sandstones and siliceous limestones.[44,46] In initial studies, the deposit including the lignite-bearing Cuddalore Formation were considered Miocene–Pliocene in age.[43,46,49,50] Later, the Eocene age was inferred for the lignite seam through palynological and geological evidence.[51,52] Later on, Siddhanta,[47] Saxena[53] and Mandaokar and Mukherjee,[54] based on stratigraphic and palynological analyses, suggested Paleocene–Eocene age for the Neyveli lignite seam.

Venkatachala[55] suggested that lignite occurrences in the Cauvery Basin are time-transgressive, ranging from the Eocene to the Pliocene. Eocene lignite is found in the southern part (Karaikal area), while further north in Mayavaram, the lignite is of Oligocene age. In the extreme north, north of Cuddalore and south of Pondicherry at Bahur, the lignite deposit is Pliocene. The northward younging trend of these deposits suggests a probable Miocene age for the Neyveli lignite. Additionally, the evolutionary history based on plant megafossil records further supports the Miocene age for the Neyveli lignite.[56–60] Consequently, Ramanujam,[61] Reddy et al.,[62] Ramanujam and Reddy,[63] and Singh[64] reaffirmed an early to middle Miocene age for the lignite seam and the underlying clay bed based on palynological evidences.

Singh et al.[44] analyzed samples from the main lignite seam and the underlying lignitic clay bed and clay from the Neyveli lignite mine. Based on the palynoassemblages of the lignite seam and underlying lignitic clay bed they reveal that palynologically, these are more or less similar. Their analysis further revealed similarities in the pollen assemblage between these deposits and the better time-constrained Miocene Warkalli lignites of Kerala, while also highlighting differences from the well-studied Eocene lignites of Gujarat and Rajasthan, western India. Additionally, they have also noted the presence of numerous typical Neogene pollen genera such as *Cauveripollis*, *Tiliaepollenites* (synonymous with *Intratriporopollenites*), *Maculoporites*, *Tricollaraeporites*, *Crassoretitriletes*, *Pteridacidites*, *Polynonacidites*, and *Quilonipollenites* from Neyveli lignite mine.[52] Further, they highlighted the significant taxonomic diversity of *Trilatiporites* (synonymous with *Retitrilatiporites*), *Ctenolophonidites*, *Margocolporites*, and *Meliapollis*, which is characteristic of Miocene records in southern India. Therefore, synthesizing both existing and new geological, geophysical, biopetrological, megafloral, and palynological evidence, Singh et al.[44] concluded that the main lignite seam in the Neyveli dates to the Miocene epoch. Consequently, the present fossil was excavated from the clay just above the lignite seam exposed in the area (Figure 3). Since the main lignite seam is considered to be Miocene in age, therefore, the fossil horizon here is considered, most likely, to be of early Miocene, based on the lithostratigraphy of the exposed fossil section (Figure 3).

The Neyveli lignite mine I consists of ∼139 m thick succession of clay, sand, lignite, sandy clay and sandstone with topsoil[65] (Figures 3A–3E). Geological map of the fossil locality (Figure 2, modified after Anandan[65]) shows the geological details of the Neyveli lignite mine I. In the composite litholog of the Neyveli lignite mine I, the lower part (∼25 m) of the exposed section consisted mainly of sand and clay, followed by two seams of lignite intercalated with a thick (∼9.1 m) sand layer with marcasite (Figure 3D). The lower lignite seam was ∼2 m thick, whereas the upper main seam was ∼12.9 m thick. Further, the upper part of the section was found mainly consisting of successive beds of carbonaceous clay (0.4 m), white sandy clay (13 m), mottled clayey sandstone (51 m), and lateritic sandstone (4 m) and topsoil (2 m). During the fieldwork, we have observed ∼13 m thick succession near upper lignite beds. The upper lignite seam was overlain by a carbonaceous clay (∼0.2 m) and followed by granulated sand layer of ∼1.2 m that graded into a thin (∼0.3 m) coarse sand band. The sand band was successively found overlain by buff clay (∼2.7 m) with 1–2 mm sand partings that yield the plant fossil and followed by sandy clay (∼0.4 to 0.7) and coarse sand (∼0.3 m) (Figure 3E).

QUANTIFICATION AND STATISTICAL ANALYSIS

No statistical analysis is included in this study.