First record of Podocarpoid fossil wood in South China

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A new species of fossil conifer wood, Podocarpoxylon donghuaiense sp. nov., is described from the late Eocene of Nadu Formation in Baise Basin of the Guangxi Province, South China. This fossil wood is characterized by distinct growth rings, circular to oval tracheids in cross section, 1–2-seriate opposite pits on radial tracheid walls, uniseriate (rarely biseriate) rays, smooth end walls of ray parenchyma cells, and the absence of resin ducts, suggesting its affinity to Podocarpaceae. The new species is distinctive from other Cenozoic woods ascribed to this family by the combination of distinctive growth rings, the absence of axial parenchyma, the occurrence of bordered pits on tangential tracheid walls, and the occurrence of 3–4 cupressoid or taxodioid pits on cross-fields. This represents the first record of podocarpoid fossil wood in South China and provides fossil evidence for the early dispersal and diversification of Podocarpaceae in eastern Asia as well as for mild temperate seasonal climate in this region during the late Eocene.

As the second largest family within the conifers, the modern Podocarpaceae largely comprises evergreen trees and shrubs belonging to 194 species within 19 genera1. This family is mainly distributed in tropical and subtropical regions from central to South America, Africa (include Madagascar), Indochina through Malesia to Australia and Oceania1,2, extending as far north as China and Japan as well as to Mexico and the Caribbean3–5. Podocarpaceae are most abundant in montane tropical rainforests, but occasionally occur in lowland forests6. In comparison with extensive investigations on extant phylogenetics and geography of the family, its early evolution and migration in deep time are still poorly known, mainly due to the lack of megafossils, especially of Cenozoic age.

Fossil records of podocarps from the Mesozoic were well documented in both the Northern and Southern hemispheres. Molecular and fossil evidence suggests that the podocarps originated during Triassic-Jurassic time in Gondwana and apparently spread to the Northern Hemisphere during the Jurassic7. Although the family appears to be of ancient origin, molecular dating analysis suggests that the majority of extant genera have arisen relatively recently in the Upper Cretaceous to Cenozoic8.

Although modern Podocarpaceae are widespread mostly in the Southern Hemisphere, there are numerous reports of Cenozoic megafossils and palynomorphs attributable to this family from the Northern Hemisphere. Podocarpus shoots were found in Eocene deposits of Tennessee9, whereas pollen seemingly belonging to this genus is known from the Miocene of Oregon and Idaho10 and late Eocene of Colorado11. In Europe, leaves of Prumnopitys have been reported from the Eocene of England12, while leaf fossils assigned to Podocarpus have been found in Eocene to Oligocene deposits of Ukraine13,14 and of the southeastern regions of European Russia15. A phylloclade of Phyllocladus has also been described by Krasnov13 from Eocene deposits of the Kharkov region (Ukraine). The assignment of these fossils to Podocarpus and Phyllocladus need special examination, however. In particular, several records of Podocarpus-like leaves from Eocene to Miocene localities of central and eastern Europe ascribed to the species Podocarpus eocenica Ung. have been reconsidered by Ferguson et al.16 as members of Amentotaxus, a genus of the Taxaceae. In addition, podocarpoid fossil wood has been reported from the Oligocene-Miocene of southern Ural17. Podocarpaceae palynomorphs occur widely in Europe from the Paleocene to the Miocene18–20, whereas the records of Podocarpus pollen from the Pliocene of Iceland21 and Pleistocene of Belgium22,23 possibly result from redeposition from older beds19.

In Asia, several fossil woods attributed to Podocarpoxylon are known from the early Tertiary to Pliocene of India24. Podocarpus leaves have been reported from the Oligocene of Assam24, while Nageia leaves have also been
described from Eocene deposits of Hainan Island and Guangdong Province, South China\textsuperscript{25,26}. Podocarpaceae fossil wood of Cenozoic age has not been recorded in China before but several apparent podocarpaceous woods, including \textit{Podocarpus (Nageia) nagi} Pilger\textsuperscript{27} have been reported from Lower Cretaceous deposits\textsuperscript{28,29}. As for microfossils, Paleocene palynological records of Podocarpaceae locally occur in India, but they are very poorly represented in Southeast Asia where the pollen of \textit{Podocarpus sensu lato} appears in the late Eocene\textsuperscript{7}. In northern Kazakhstan, Podocarpaceae pollen grains have also been reported from the Eocene, but they disappear there in the late Oligocene\textsuperscript{30}.

Here we describe a new fossil wood of \textit{Podocarpoxylon} from the late Eocene Nadu Formation of Baise Basin, Guangxi Province of South China, and review the phytogeographic and ecological implications of our finding. This is the first occurrence of fossil Cenozoic Podocarpaceae wood from South China.

Results

Systematics. Order: Araucariales Gorozh.
Family: Podocarpaceae Endl.
Genus: \textit{Podocarpoxylon} Gothan, 1908.
Species: \textit{Podocarpoxylon donghuaiense} Li, Jin, Quan et Oskolski, sp. nov.

Etymology. The specific name “Donghuai” is the locality name where the fossils were collected.

Holotype. DHW006.
Paratypes. DHW001 to DHW005, DHW007 to DHW0013.

Repository. Fossil wood samples and microscopic slides are deposited in the Museum of Biology, Sun Yat-sen University, Guangzhou, China.

Type locality and horizon. Nadu Fm., late Eocene. Specimens were collected in Donghuai coal-mine, Baise City, Guangxi Province (Fig. 1).

Diagnosis. Growth rings with prominent latewood, transition from earlywood to latewood gradual; circular pits on radial tracheid walls uniseriate, sometimes biseriate opposite, circular pits rarely occur in tangential walls of tracheids; cross-field pits cupressoid and taxodioid, circular to oval, 1–4 pits (mean 2) in opposite 1–2 rows per cross-field; axial parenchyma absent; rays predominately uniseriate, rarely partially biseriate; ray cells with smooth horizontal and tangential walls; ray tracheids absent; resin ducts absent.

Description. Growth rings distinct, 5.2–7.9 mm wide, with prominent latewood, transition from earlywood to latewood gradual (Fig. 2A). Earlywood tracheids thin-walled, circular to oval in cross-sectional outline, 23–40 $\mu$m (mean 32 $\mu$m) in tangential diameter and 23–56 $\mu$m (mean 37 $\mu$m) in radial size (Fig. 2B). Latewood tracheids moderately thick-walled, circular to oblong in cross-sectional outline, 7–23 $\mu$m (mean 13 $\mu$m) in tangential diameter and 11–21 $\mu$m (mean 15 $\mu$m) in radial size.

Pits in radial tracheid walls uniseriate, occasionally also biseriate opposite (Fig. 2E). Pits bordered, circular (11–17 $\mu$m in diameter with the average of 15.7 $\mu$m) to oval (14–20 $\mu$m in size) in outline. Crassulae absent. Bordered pits of 8.2–15.0 $\mu$m in diameter rarely occur also on the tangential walls of latewood tracheids. Well-developed tightly spaced spiral and branched thickenings present on radial and tangential walls of latewood tracheids (Fig. 2D,F), with angles to the tracheid axes ranging from $4^\circ$ to $6^\circ$.

Axial parenchyma absent.

Rays 42–331 $\mu$m (mean 100 $\mu$m) in height, predominately 1-seriate (Fig. 2C,D) and rarely partially 2-seriate (Fig. 2G), completely composed of parenchyma cells, 1–16 cells (mean 5 cells). Ray cells oval or elliptical in...
Figure 2. Wood structure of Podocarposylon donghuaiense sp. nov. (DHW006). (A) Transverse section showing distinct growth rings (arrow). Scale bar = 400μm. (B) Transverse section of early wood showing circular to oval tracheids. Scale bar = 100μm. (C) Tangential section showing the predominately uniseriate rays. Scale bar = 100μm. (D) Tangential section of late wood showing spiral thickenings in tracheids (arrow). Scale bar = 100μm. (E) Radial section showing 1–2 seriate opposite pits in radial tracheid walls (arrow). Scale bar = 20μm. (F) Radial section showing spiral and branched thickenings on tracheid walls. Scale bar = 20μm. (G) Tangential section showing partially 2-seriate rays (arrow). Scale bar = 50μm. (H) Radial section showing cupressoid and taxodioid pits on cross-fields. Scale bar = 20μm. (I) Radial section showing cupressoid pits on cross-fields. Scale bar = 10μm. (J) Radial section showing taxodioid pits on cross-fields. Scale bar = 10μm.
tangential section, both vertical and horizontal walls of ray parenchyma cells smooth, indentures absent. Cross-field pits possibly cupressoid or taxodioid type, circular to oval of 6–12 μm in size, with 1–4 pits (mean 2) per cross-field (Fig. 2H–J). Crystals not found. Resin ducts absent.

**Discussion**

**Comparison with modern materials.** Within the conifer families, the fossil wood from Donghuai may not be placed into Pinaceae, Cupressaceae or Cephalotaxaceae, as it has no resin ducts, axial parenchyma and ray tracheids. This late Eocene wood is also distinctive both from Araucariaceae by the absence of two or more seriate alternate intertracheary pitting and by the lacking crowded araucarioid cross-field pits, and from Sciadopityaceae by the absence of window-like cross-field pits. Therefore, it remains for us to consider the relationships of this fossil wood to Taxaceae or Podocarpaceae.

The presence of spiral and branched thickenings on the walls of latewood tracheids in combination with smooth horizontal and tangential walls of ray cells suggests the fossil wood from Donghuai may be considered as a member of Taxaceae. After careful examination of the thickenings on tracheid walls in this sample we suggest, however, that these structures are not of the same nature as the spiral tertiary thickenings that occur in all modern genera of this family, with the exception of Austrotaxus R.H. Compton. Extant Taxaceae show finer spiral thickenings, more widely spaced and tilted at lower angles (usually not exceeding 45°) in respect to the tracheid axes than the thickenings observed in the late Eocene wood from Donghuai. Such features of the fossil wood as tracheids bearing spiral thickenings confined only to the latewood and their absence in the earlywood has also not been reported in any modern Taxaceae. Therefore, the spiral and branched structures occurring in tracheids of the Donghuai wood are more likely artifacts (probably, effects of wood compression) than true tertiary thickenings. The occurrences of similar artifacts in fossil woods seemingly belonging to Taxaceae have been surveyed by Afonin & Philippe. In fossil woods assigned to Podocarpaceae these structures have been reported by Chudajberdyev in tracheids of Podocarpxylon uralense Chudajb.

As far the thickenings on tracheids are recognized as artifacts rather than diagnostic traits, the suite of other characters (smooth horizontal and tangential walls of ray cells without indentures, cupressoid and taxodioid pits on cross fields) indicates that the fossil wood reported here has greatest affinity to the Podocarpaceae. This family, however, shows considerable diversity of wood structure that does not allow distinction between its genera using wood anatomical traits. The late Eocene wood from Donghuai is different from most modern Podocarpaceae in growth rings with conspicuous latewood, lacking axial parenchyma and the occurrence of 1–4 pits on the cross-field. However, the presence of prominent latewood portion has been reported in growth rings of Podocarpxylon acutifolius Kirk, Podocarpxylon macrophyllus (Thunb.). D. Don., Lagarostrobos (Dacrydium) franklinii (Hook. f.) Quinn, Halocarpus (Dacrydium) bidwillii (Hook. f. ex. T. Kirk) Quinn, Phylocladius glaucus Carr. and P. trichomanoides D. Don. Axial parenchyma is also lacking in Dacrydium elatum (Roxb.) Wall. ex. Hook., D. colensoi Hook., D. biforme (Hook.) Pilg., D. kirkii F. Muell. ex. Parl., D. intermedium Kirk, D. taxifolium Banks & Sol. ex. D. Don, Halocarpus bidwillii Lepidothamnus intermedius (Kirk) Quinn., Manoao colensoi (Hook.) Molloy, Microcachrys tetragona (Hook.) Hook., Phylocladius alpinus Hook., P. glaucus, P. trichomanoides, Podocarpus elongatus (Aiton) L’Hér. ex Pers., Prumnopitys harmsiana (Pilg.) de Laub., and P. taxifolia (Sol. ex. D. Don) de Laub. and other characters in combination with the absence of axial parenchyma and the occurrence of cross-fields with up to 1–4 cupressoid or taxodioid pits has been reported for Dacrydium pittieri, D. intermedium, Podocarpus hallii, Microcachrys tetragona and Retrophyllum minor (Carrière) C. N. Page. Therefore, the fossil wood from Donghuai shows most resemblance to some species of Prumnopitys (especially P. taxifolia) as well as to some members of Podocarpus, Dacrydium and Microcachrys, but it cannot be convincingly placed in any extant genus of Podocarpaceae on the basis of its anatomical traits.

**Comparison with fossil materials.** The fossil wood described here is characterized by an absence of axial parenchyma and by the cross-fields with cupressoid and/or taxodioid pits. Within fossil woods ascribed to Podocarpxylon, these traits are found in some species of the genus Podocarpxylon Gothan, as well as in the monospecific genus Prumnopitysxyylon Franco & Brea that was recently described from the Upper Cenozoic of Argentina. Moreover, this combination of wood traits has also been reported for Phylocladloydos xyylon annulatus Patton from the Oligocene of Australia. The fossil sample from Donghuai exhibits similarities to Cenozoic species of Podocarpxylon as well as with Prumnopitysxyylon gnaedingerae Franco & Brea and Phylocladloydos xyylon annulatus Patton (Table 1).

Within seven species that have no axial parenchyma (Prumnopitysxyylon gnaedingerae Franco & Brea, Podocarpxylon aparenchymatosum Gothan, P. dusenii Kräusel, P. latrobenis Greenwood, P. sahnii (Ramanujam) Trivedi & Srivastava, P. tigrivakkaraiamum (Ramanujam) Trivedi & Srivastava, and Phylocladloydos xyylon annulatus Patton), cross-fields with more than two pits occur only in P. aparenchymatosum and P. gnaedingerae. Podocarpxylon aparenchymatosum from the Eocene deposits of Antarctica differs, however, from the Donghuai wood in possessing 3-seriate pitting on radial tracheid walls. Unlike Prumnopitysxyylon gnaedingerae, the Donghuai wood sample shows distinct growth rings, and by higher rays height with the occasional occurrence of bi-seriate portions.

It follows from its unique character combinations that the late Eocene wood from Donghuai can be recognized as a new species named here as Podocarpxylon donghuaiense. Although this fossil wood shows certain similarity to Prumnopitysxyylon, Franco & Brea’s diagnosis of this genus lacks sufficient detail to separate it from Podocarpxylon. Any of the wood traits, that have been considered by these authors as diagnostic for Prumnopitysxyylon (i.e. “slightly distinct or indistinct growth rings; absence of axial parenchyma; uniseriate and homocellular rays; uniseriate or biseriate, opposite or sub-opposite, separate or contiguous tracheid pitting; taxodioid or cupressoid cross-field pitting, with 1–5 bordered pits per field”) can be also found elsewhere in Podocarpxylon, and their occurrences are consistent with Gothan’s diagnosis of this genus. For this reason, we ascribe the new species to Podocarpxylon rather than to Prumnopitysxyylon.
| Species | Age | Locality | Growth rings | Axial parenchyma | Pitting on radial walls, diameter of pits | Pitting on tangential walls | Ray width (cells) | Ray height (cells) | Number and diameter of pits on cross-field | Reference |
|---------|-----|----------|--------------|-----------------|----------------------------------------|---------------------------|----------------|----------------|-----------------------------------------------|-----------|
| Wood from Donghui | Eocene | China | distinct | absent | 1(2)-seriate 11–20 μm | − | 1(2) | 1–16 | 1–46–12 μm | Patton |
| Phyllocadoxylon annulatus Patton | Oligocene | Australia | distinct | absent | 1(2)-seriate 12–18 μm | − | 1 | 1–7 | 1–28–13 μm | Patton |
| Podocarpoxylon neypticum Kräusel | Oligocene | Egypt | distinct | abundant | 1-2-seriate | ? | 1 | 3–6 | 1-few | Kräusel |
| P. aparenchymatosum Goethan | Eocene | Germany | distinct | sparse | 1-2-seriate <18 μm | − | 1 | ? | 1–2(4)–9–12 μm | Schönfeld |
| P. aperiporosum aegyptiacum | Eocene | Antarctica | distinct | absent | 1(2)-seriate | 11–19 μm | − | 1 | 1–20 | 1–2(3) | Goethan |
| P. articulatum Süss & Velitzelos | Lower Miocene | Greece | distinct | sparse | 1(2)-seriate | 20–25 μm | ? | 1–2(3) | 1–20 (100) | 1–3 μm | Süss & Velitzelos |
| P. australe Kräusel | Tertiary | Australia | indistinct to absent | sparse | 1(2)-seriate | 12–18 μm | − | 1(2) | 1–12 | 1–3–15–12 μm | Kräusel; Patton |
| P. bruxellense Stockmans | Eocene | Belgium | distinct | abundant | 1(2)-seriate | ? | 1(2) | 2–26 | 1 | Stockmans |
| P. dacyrioides Zalewski | Tertiary | Poland | indistinct | abundant | 1–2(3)-seriate | 13 μm | − | 1(2) | 1–31 | 1(2) 8 μm | Zalewska |
| P. durseni Kräusel | Tertiary | Argentina | distinct | absent | 1-seriate | − | 1(2) | 1–20 (40) | 1–2 | Kräusel |
| P. graciliradiatum Süss & Velitzelos | Lower Miocene | Greece | distinct | relatively abundant | 1(2)-seriate | 18–20 μm | ? | 1 | 1–30 (70) | 1–3 | 10–12 μm | Süss & Velitzelos |
| P. juri Blokhina | Eocene-Oligocene | Russia (Kuril islands) | distinct | sparse | 1(2)-seriate | ? | 1(2) | 1–21 | 1–5 | Blokhina |
| P. aff. javanicus Merrill. | Pliocene | Georgia | distinct | sparse | 1-seriate | − | 1 | 1–12 | 1 | Shilkina |
| P. kubarti Rössler | Pliocene | Austria | indistinct | sparse | 1-seriate | ? | 1(2) | <23 | 1–4 | Rössler |
| P. kurilese Blokhina | Eocene-Oligocene | Russia (Kuril islands) | distinct | sparse | 1-seriate | ? | 1 | 1–17 | 1–2 | Blokhina |
| P. kutchensis Lakhanpal, Guleria & Awasthi | Pliocene | India | indistinct | sparse | 1(2)-seriate | ? | 1(2) | 1–41 | 1–2 | Lakhanpal, Guleria & Awasthi |
| P. latrobeensis Greenwood | Miocene | Australia | indistinct | scanty to absent | 1-2-seriate | 15 μm | − | 1 | 2–18 | 1 (2) | Greenwood |
| P. mababalei (Agashe) Trivedi & Srivastava | Miocene-Pliocene | India | distinct | abundant | 1-seriate | ? | 1 | 1–30 | 1 | Trivedi & Srivastava |
| P. mazzoni (Petriella) Müller-Stoll & Schultze-Motel | Paleocene | Argentina | indistinct | sparse | 1-2-seriate | + | 1(2) | 1–38 | 1–2 | Müller-Stoll & Schultze-Motel |
| P. minor Patton | Oligocene | Australia | indistinct | sparse | 1-seriate | 8–13 μm | + | 1 | 1–7 | 1–3 | 2.5–7.5 μm | Patton |
| P. nainsi (Ramanujam) Trivedi & Srivastava | Miocene-Pliocene | India | distinct | absent | 1-seriate | ? | 1(3) | 1–20 | 1–2 | Trivedi & Srivastava |
| P. schmidianum Sahni | Tertiary | India | indistinct | sparse | 1-2-seriate ca. 20 μm | ? | 1(2) | 2–36 (100) | 1–2 | Sahni |
| P. speciosum (Ramanujam) Trivedi & Srivastava | Miocene-Pliocene | India | distinct | abundant | 1-2-seriate | ? | 1(2) | 1–18 | 2–4 | Trivedi & Srivastava |
| P. tiruvakkaranam (Ramanujam) Trivedi & Srivastava | Miocene-Pliocene | India | indistinct | absent | 1-2-seriate | ? | 1 | 3–50 | 1 | Trivedi & Srivastava |
| P. turniense Zalewski | Tertiary | Poland | distinct | abundant | 1-2-seriate | 15–17 μm | + | 1(2) | 1–45 | 1–2 | Zalewska |
| P. utulense Chudaib. | Oligocene-Miocene | Russia (south Urals) | distinct | 1-seriate | 13–14 μm | − | 1 | 1–12 | 2–3 (5) | Chudaibergy |
| P. vibramii Bande & Prakash | Tertiary | India | indistinct | sparse | 1(2)-seriate | 15–20 μm | ? | 1 | 1–42 | 1–2 | 10–15 μm | Bande & Prakash |
| P. welkitti Lemogne & Beauchamp | Tertiary | Ethiopia | distinct | sparse | (1) –seriate | ca. 15 μm | ? | 1 | 1–18 | 1–3 | Lemogne & Beauchamp |
| P. yallournensis Patton | Oligocene | Australia | indistinct | relatively abundant | 1(2)-seriate | 12–18 μm | + | 1 | 1–6 | 1–3(5) | 3–10 μm | Patton |
| Podocarpus falcatus R. Br. ex Mirb. | Cenozoic | South Africa | indistinct | sparse | 1(2)-seriate | ? | 1 | 1–3–12 | 1 | Adamson & Currin |

Continued
### Table 1. Comparison of the fossil wood from Baise Basin with Cenozoic species of *Podocarpoxylon* and other selected taxa

| Species                        | Age      | Locality         | Growth rings | Axial parenchyma | Pitting on radial walls, diameter of pits | Pitting on tangential walls | Ray width (cells) | Ray height (cells) | Number and diameter of pits on cross-field | Reference |
|-------------------------------|----------|------------------|--------------|------------------|------------------------------------------|-----------------------------|------------------|-------------------|---------------------------------------------|-----------|
| *Podocarpus* sp.              | Pliocene | Columbia         | indistinct to absent | abundant | 1-seriate 8–17μm | ? | 1 | 1–7 | 19–13 μm | Wijninga72 |
| *Prumnopityoxylon gaedingerae* Franco & Brea | Pliocene-Pleistocene | Argentina | indistinct | absent | 1(2)-seriate 13–17μm | + | 1 | 2–8 | 1–5 3–9 μm | Franco & Brea82 |

**Biogeographic implications.** *Podocarpoxylon donghuaiense* sp. nov. is the first record of podocarpoid fossil wood in China. Coeval macrofossils assigned to Podocarpaceae have already been reported from the South China: well-preserved leaves of *Nageia* have recently been described from the Eocene Changchang Formation of Hainan Island, and the Eocene Youganwo and Huangniuling formations of Guangdong Province25,26. *Podocarpoxylon donghuaiense* is distinct, however, from the wood of extant *Nageia* species by the absence of axial parenchyma32–34. Thus it is very unlikely that the fossil wood from Guangxi belonged to the same plant taxon as the fossil leaves from Hainan and Guangdong, despite the geographical proximity and nearly the same age of these three findings.

Jin et al.25 and Liu et al.56, as well as our data confirm that the common occurrence of the Podocarpaceae species in the late Eocene vegetation of South China, that is consistent with the age of initial appearance of this family in Southeast Asia estimated by palynological records5. As the results of molecular dating suggest4, diversification of Podocarpaceae during Eocene gave rise to such modern genera distributed now in this region, as *Dacrydium*, *Podocarpus* and *Nageia*. Although *Podocarpoxylon donghuaiense* shares some wood traits with some extant species of *Podocarpus* and *Dacrydium*, this fossil wood can be convincingly ascribed to neither of them, probably because these taxa had not yet been emerged as distinct entities in the late Eocene.

Most modern species of Podocarpaceae have growth rings with indistinct to very narrow latewood, or growth rings lacking. Contrastingly, the growth rings of *Podocarpoxylon donghuaiense* show relatively high proportion of latewood with gradual transition from earlywood to latewood. These traits are indicative for plants with long growing period without rapid shift to seasonal dormancy that are encountered mainly in the middle latitudes of both hemispheres46–48. Within modern Podocarpaceae, this type of growth rings has been reported only in six species (*Podocarpus macrophyllus* ranged from Myanmar through mainland China and Taiwan to Japan, *Podocarpus acutifolius*, *Halocarpus bidwillii*, *Phyllocladus glaucus* and *P. trichomanoides* from New Zealand, and *Lagarostrobus franklinii* from Tasmania49) which are restricted to the temperate regions without dry season, with hot or warm summer (*Cfa* and *Cfb* climate types of Köppen’s classification)50. The occurrence of Podocarpaceae wood with prominent latewood in distinctive growth rings may therefore be an indicator that South China had mild temperate seasonal climate during the late Eocene.

**Conclusion**

A new species of fossil conifer wood, *Podocarpoxylon donghuaiense* sp. nov., is described from the late Eocene of Baise Basin of Southern China. This is the first Cenozoic record of podocarpoid fossil wood in Southern China. The new species is distinguished from other Cenozoic woods ascribed to Podocarpaceae by the unique combination of distinctive growth rings, the absence of axial parenchyma, the lack of bordered pits on tangential tracheid walls, and the occurrence of 3–4 cupressoid or taxodioid pits on cross-fields. The tightly spaced thickenings on latewood tracheid walls of the fossil wood are recognized as artifacts (probably, effects of wood compression) rather than true tertiary thickenings. Therefore, *Podocarpoxylon donghuaiense* sp. nov. provides the first robust physical evidence for the early steps of dispersal and diversification of Podocarpaceae in eastern Asia, as well as for warm and wet climate in this region, and the presence of clear growth rings also suggest this was a seasonal climate during the late Eocene.

**Methods**

The fossil woods described here were collected from the Nadu Formation outcropping at Donghuai Coal-mine in the west part of the Baise Basin (transliterated also as the Bose Basin by some authors), Guangxi, South China (23°52′14.84″N, 106°34′49.22″E, Fig. 1). The geological age of the formation is believed to be late Eocene based on the well-studied Nadu Mammalian Fauna51.

The well-preserved wood specimens examined represent portions of a main trunk (DHW001-013). The holotype DHW006 is about 10 cm diameter by 15 cm in length. Thin-sections were prepared according to standard methods of cutting, grinding, and polishing using different grades of carborundum powder52. Wood slides were examined using a Carl Zeiss Axio Scope A 1 light microscope. Microphotographs were taken using a Cool Snap digital camera fitted with QCapture Pro 6.0 photographic software. Wood anatomical characters were measured and described according to the IAWA list of microscopic features for softwood identification53. The systematic position of the fossil wood was determined by consulting the key to morphogenera of fossil conifer woods54 and by carefully comparing with similar modern and fossil woods. Fossil wood generic nomenclature and circumscripton followed the criteria of Philippe & Bamford55. Fossil wood specimens and thin sections are housed in the Museum of Biology, Sun Yat-sen University, Guangzhou, China.
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L.L. and A.A.O. wrote the manuscript and formatted the text. All authors read and approved the final manuscript.

Author Contributions
C.Q., J.-H.J. and L.L. collected the fossil wood from Donghuai. J.-H.J., C.Q. and L.L. participated in the design of the study. L.L. and A.A.O. photographed specimens and arranged figures. L.L. and A.A.O. conducted taxonomic treatments, phytogeographic and ecological interpretation. L.L. and A.A.O. collected the fossil wood from Donghuai. J.-H.J., C.Q. and L.L. participated in the design of the study. L.L. and A.A.O. photographed specimens and arranged figures. L.L. and A.A.O. conducted taxonomic treatments, phytogeographic and ecological interpretation.

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