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How to cite:

Wang, Bo; Shi, Gongle; Xu, Chunpeng; Spicer, Robert A.; Perrichot, Vincent; Schmidt, Alexander R.; Feldberg, Kathrin; Heinrichs, Jochen; Chény, Cédric; Pang, Hong; Liu, Xingyue; Gao, Taiping; Wang, Zixi; Ślipiński, Adam; Solórzano-Kraemer, Mónica M.; Heads, Sam W.; Thomas, M. Jared; Sadowski, Eva-Maria; Szwedo, Jacek; Azar, Dany; Nel, André; Liu, Ye; Chen, Jun; Zhang, Qi; Zhang, Qingqing; Luo, Cihang; Yu, Tingting; Zheng, Daran; Zhang, Haichun and Engel, Michael S. (2021). The mid-Miocene Zhangpu biota reveals an outstandingly rich rainforest biome in East Asia. Science Advances, 7(18), article no. eabg0625.

Link(s) to article on publisher's website:
http://dx.doi.org/doi:10.1126/sciadv.abg0625

ENVIRONMENTAL STUDIES

The mid-Miocene Zhangpu biota reveals an outstandingly rich rainforest biome in East Asia

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During the Mid-Miocene Climatic Optimum [MMCO, ~14 to 17 million years (Ma) ago], global temperatures were similar to predicted temperatures for the coming century. Limited megathermal paleoclimatic and fossil data are known from this period, despite its potential as an analog for future climate conditions. Here, we report a rich middle Miocene rainforest biome, the Zhangpu biota (~14.7 Ma ago), based on material preserved in amber and associated sedimentary rocks from southeastern China. The record shows that the mid-Miocene rainforest reached at least 24.2°N and was more widespread than previously estimated. Our results not only highlight the role of tropical rainforests acting as evolutionary museums for biodiversity at the generic level but also suggest that the MMCO probably strongly shaped the East Asian biota via the northern expansion of the megathermal rainforest biome. The Zhangpu biota provides an ideal snapshot for biodiversity redistribution during global warming.

INTRODUCTION

The Mid-Miocene Climatic Optimum (MMCO), characterized by global warmth with a low latitudinal temperature gradient and high CO_2 levels, was a key period for the origin and evolution of modern terrestrial biomes (*1*, *2*). It is also widely considered to be an analog for our current era of anthropogenic global warming and its projected consequences (*3*–*5*). Meteorological observations suggest a recent poleward expansion of megathermal conditions, where every month has a mean temperature of 18°C or above, probably in response to anthropogenic climatic changes (*6*). However, the long-term responses of terrestrial biodiversity and ecosystems to the poleward expansion of today's tropical climate remain unclear (*7*, *8*). Paleobiological records from the middle Miocene can provide critical information for resolving these questions, but data documenting megathermal climates and terrestrial ecosystems from this period are quite limited.

Here, we report an exceptionally rich middle Miocene biota preserved in amber and associated sedimentary rocks from the Fotan Group [~14.7 million years (Ma) ago] (*9*) in southeastern China (Fig. 1 and fig. S1). Biomarker analysis and fossil winged fruits of Dipterocarpaceae (fig. S2) that occur in the same bed indicate that the amber was produced by ancient dipterocarp trees (*10*), which are dominant elements of most southeastern Asian tropical rainforests today. Zhangpu amber is preserved in blue-gray sandy mudstone and is yellow-brown to brownish-red in color. The fossil layer yields not only amber but also abundant plant fossils, gastropods, and vertebrates (figs. S1 and S2).

RESULTS

The plant fossils from the amber-bearing sedimentary rocks include leaves of two ferns, three monocots, 78 dicots, and ~20 types of fruits and seeds (table S1). Among the recognizable fossils, the most diverse and abundant are those of the Dipterocarpaceae (fig. S2), Leguminosae (fig. S3), Lauraceae, and Clusiaceae. Other megathermal pantropical plant families identified from the sedimentary rocks include Annonaceae, Anacardiaceae, Burseraceae, Euphorbiaceae, Melastomataceae, Moraceae, Myristicaceae, and Myrtaceae (fig. S3).

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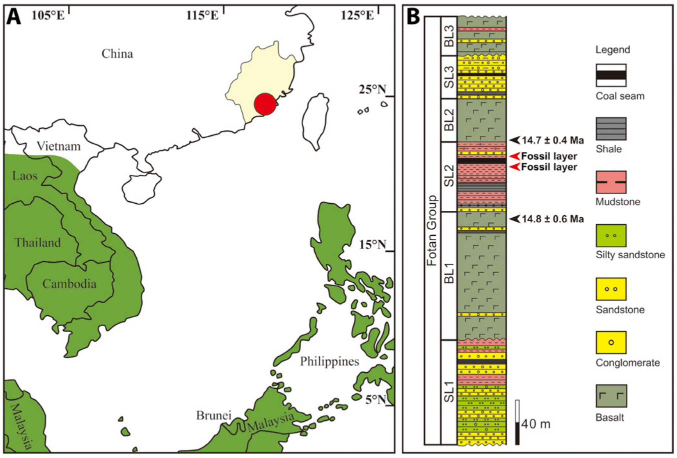

Fig. 1. Locality map and stratigraphy of the study area. (**A**) Distribution map of modern wild *Dipterocarpus* trees forest (green color) (*39*), Fujian Province in southeastern China (yellow color) and fossil site (red circle). (**B**) The Fotan Group stratigraphic section showing biostratigraphy and geochronologic ages. BL, basaltic layers; SL, sedimentary layers. Two fossil layers indicated by red arrowheads both yield abundant amber and compression/impression fossils.

All these families are dominant or abundant in today's southeastern Asia tropical rainforests (*11*). Leaf physiognomy also suggests that this middle Miocene flora represents a megathermal seasonal rainforest, with its leaf trait spectrum most similar to that of modern vegetation from central Thailand, central India, and the Ganges Delta (Fig. 2). Paleoclimate estimates (table S2) derived from leaf form reveal a marginally megathermal climate in Zhangpu during the middle Miocene, with a mean annual temperature of 22.5° ± 2.4°C, a warm month mean temperature (WMMT) of 27.1° ± 2.9°C, a cold month mean temperature (CMMT) of 17.2° ± 3.6°C, ~12-month growing seasons, growing season precipitation of 1929 ± 643 mm, and spring was the driest season as suggested by the highest mean vapor pressure deficit. Leaf traits also indicate a relatively equitable temperature throughout the year, with a difference of ~10°C between the WMMT and CMMT, which is less than the present-day difference of ~15°C in Zhangpu. Precipitation seasonality during the middle Miocene was, however, comparable with present-day conditions (table S2), with a precipitation ratio for the three consecutive wettest months to that in the three consecutive driest months of ~6.

The Zhangpu amber biota substantiates this climatic prediction as it contains a rich and exquisitely preserved fossil arthropod fauna and abundant inclusions of plants, fungi, snails, and even feathers (Figs. 3 and 4). The preservation of inclusions is usually excellent, displaying colors and three-dimensional (3D) details that can be reconstructed clearly using x-ray micro–computed tomography (micro-CT) (movies S1 to S3). Botanical inclusions include bryophytes (liverworts and mosses) and angiosperms (Fig. 3 and fig. S4). In particular, bryophytes (nonvascular land plants) are rich, including at least seven extant genera of liverworts and five extant genera of mosses. One amber specimen shows evidence of an epiphyte community composed of minute liverwort representatives of the living genera *Leptolejeunea* and *Cololejeunea* growing on a much larger specimen of Plagiochilaceae (fig. S4B). The closest extant relatives of Zhangpu amber bryophytes occur today in wet tropical forests, supporting the paleoclimatic reconstruction.

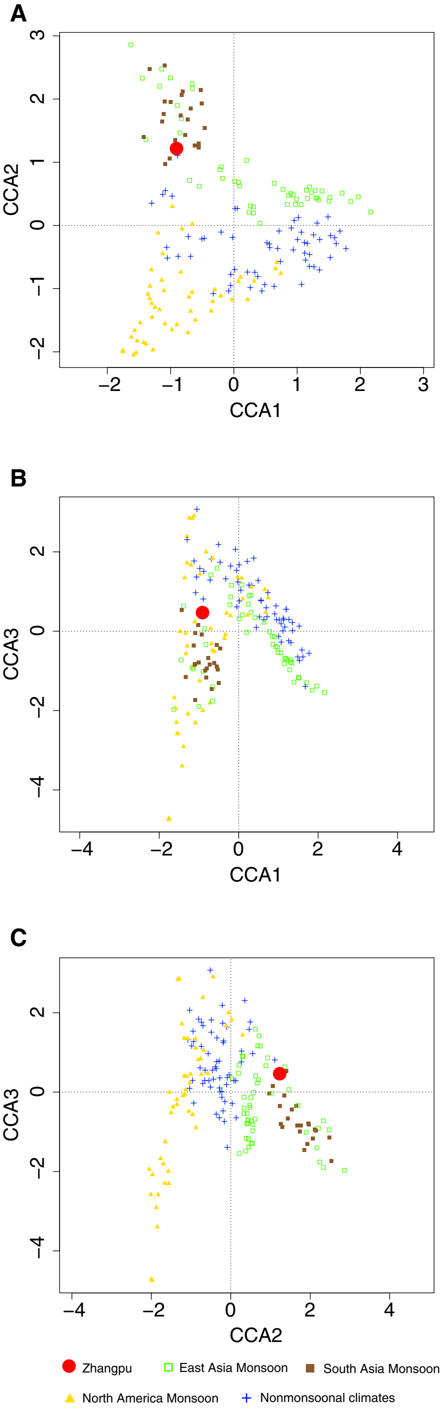

Fig. 2. CLAMP plots showing the position of the middle Miocene Zhangpu flora in PhysgAsia2 calibration space. (**A**) Canonical correspondence analysis (CCA) plot of axes 1 versus 2. (**B**) CCA plot of axes 1 versus 3. (**C**) CCA plot showing axes 2 versus 3. CCA plots showing the relationship between the Zhangpu flora (red filled circle) and modern vegetation in different climate regimes. Modern climate regimes include East Asia Monsoon (green open squares), South Asia Monsoon (brown filled squares), nonmonsoonal climates (blue crosses), and the North American Monsoon (yellow triangles). The Zhangpu flora lies within the East Asia monsoonal vegetation but very close to the South Asia monsoonal vegetation in all three dimensions, with the closest modern sites from Khorat (central Thailand), Madhya Pradesh (central India), and the Ganges Delta.

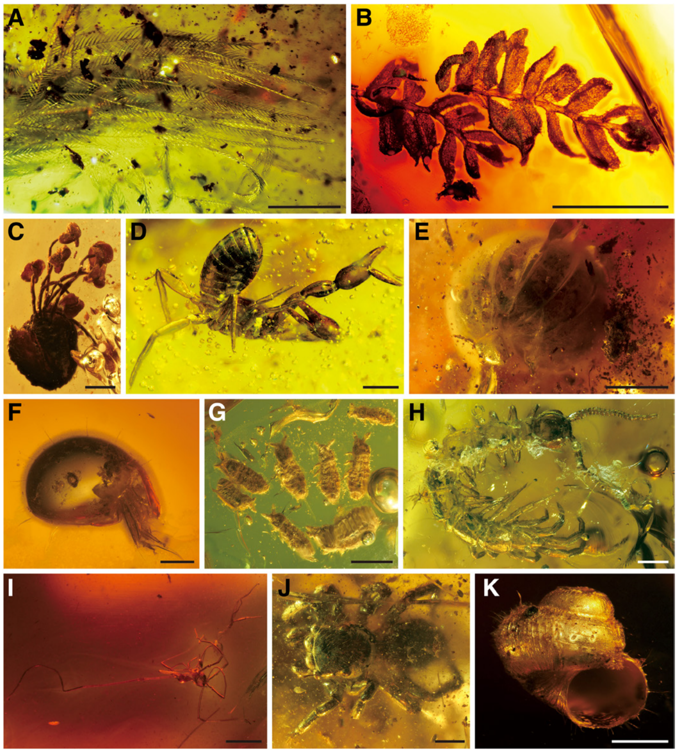

Fig. 3. Representative inclusions in Zhangpu amber. (**A**) Feather. (**B**) Moss (Bryophyta: Anomodontaceae: *Haplohymenium*). (**C**) Flower (Fagales: Fagaceae). (**D**) Pseudoscorpion (Pseudoscorpiones). (**E**) Pill woodlouse (Isopoda). (**F**) Water mite (Acari: Hydrachnidia). (**G**) Springtail swarm (Collembola: Hypogastruridae: *Ceratophysella*). (**H**) Centipede (Chilopoda). (**I**) Harvestman (Opiliones). (**J**) Jumping spider (Araneae: Salticidae). (**K**) Snail (Gastropoda: Cyclophoridae). Scale bars, 1 mm (A, B, and E), 0.5 mm (C, D, G, H, J, and K), 0.2 mm (F), and 2 mm (I).

Arthropod inclusions cover an impressive array of more than 250 families (Figs. 3 and 4). They currently comprise the Isopoda, Diplopoda, Chilopoda, Collembola, arachnid orders Acariformes, Parasitiformes, Araneae, Opiliones, Pseudoscorpiones, and at least 200 families of Insecta in 20 orders (figs. S5 to S8 and table S3). This extremely high arthropod variety ranks Zhangpu amber one of the world's four richest amber biotas, along with the widely known Cretaceous Burmese amber (>568 families), Eocene Baltic amber (>550 families), and Miocene Dominican amber (205 families) (*12*, *13*). However, the Zhangpu amber biota is unique because it is noncommercially extracted and consequently lacks any anthropogenic selective bias. Moreover, its precise age and climate are well-constrained by radioisotopic dating (*9*) and associated plant compression/impression fossils, respectively.

As in other amber deposits, large arthropods are rare in Zhangpu amber, and more than 99% of the inclusions are less than 10 mm in length. Spiders and mites are frequent (Fig. 3, F and J) and mostly appear to be juveniles. Theridiidae (cobweb spiders) and Salticidae (jumping spiders), dominant in extant dipterocarp lowland rainforests (*14*), are also the most abundant spiders in Zhangpu amber (Fig. 3J). A notable character of the biota is the high abundance and diversity of springtails, including more than 19 extant genera within 10 families. The insect fauna is dominated by Diptera (55% of all 12,661 insects in 8350 pieces), Hymenoptera (24%), Coleoptera (8%), and Hemiptera (7%). Diptera are mainly composed of Cecidomyiidae (gall midges) (Fig. 4H), Phoridae (humpbacked flies) (fig. S5E), Sciaridae (dark-winged fungus gnats), and Psychodidae (moth flies), which are quite abundant in modern tropical rainforests. Chironomidae (nonbiting midges) are less common in Zhangpu amber, a contrast to their extreme high abundance in other Cenozoic ambers (*14*). Hymenoptera are largely represented by ants, stingless bees, and various parasitoid wasps and Coleoptera by Staphylinidae (rove beetles) and Platypodinae (ambrosia beetles). Hemiptera are mainly composed of Cicadellidae (leafhopper nymphs).

DISCUSSION

The insect fauna in Zhangpu amber is consistent with the reconstructed borderline megathermal monsoon climate, supported by the presence of many typical elements such as certain genera of ants (Fig. 4B), bees (Fig. 4C), lacewings (Fig. 4E), stick insects (Fig. 4F), termites (Fig. 4, G and L), and grasshoppers (fig. S6A) that are today restricted to tropical Southeast Asia and/or New Guinea. The composition of the Zhangpu amber insect fauna is similar to that of early Eocene Cambay amber of India (fig. S9), probably because of their similar environments and ecologies stemming from their similar floras (*15*). Perhaps the most unexpected find in our biota is that the high diversity of ants and springtails all belong to living genera. In addition, the vast majority of hitherto identified insects in Zhangpu amber, such as bark lice, grasshoppers, beetles, and bees, can also be attributed to living genera. These results suggest that there has been stasis of Asian rainforest insect communities since at least the middle Miocene, and thereby highlights the notion of tropical rainforests acting as museums of biological diversity at the generic level (*16*, *17*). The relative ecological stability of megathermal environments from the middle Miocene may favor the maintenance of comparatively ancient lineages and facilitate the continued accumulation of species diversity (*16*–*18*).

During the middle Miocene, most of South China was thought to be in a warm-temperate forest zone (*19*). However, our results based on the amber biota and plant compression/impression fossils demonstrate that megathermal seasonal rainforests in the middle Miocene reached at least 24.2°N (modern-day latitude), which is north to the Tropic of Cancer (23.5°N), and thus more widespread than previously estimated (*19*). Throughout this hyperthermal event, the Zhangpu area had a relatively equitable temperature and intensified monsoon rainfall, similar to those in the current climatic change predictions for South China, due to the continuing strengthening of the East Asian monsoon (*20*). However, there are differences and large uncertainties (including local temperature and precipitation) among different climate models regarding change within South China (*20*, *21*); our results may provide constraints on these projections of South China including precipitation and mean annual temperatures for the coming century.

During the middle Miocene, there was a strong homogenizing effect on the composition and distribution of plant and animal communities, notably, biotic exchange between the Indian subcontinent, mainland Asia, the Malay Archipelago, Australia, New Guinea, and many Pacific Islands (*22*, *23*). Our findings confirm that a megathermal biota existed in the middle Miocene Zhangpu area and extend the biological and physical homogenization of Asian tropical forests to most areas of South China. The middle Miocene expansion of Asian tropical rainforests, with potential alterations of local food webs, biogeochemical cycles, and climatic conditions

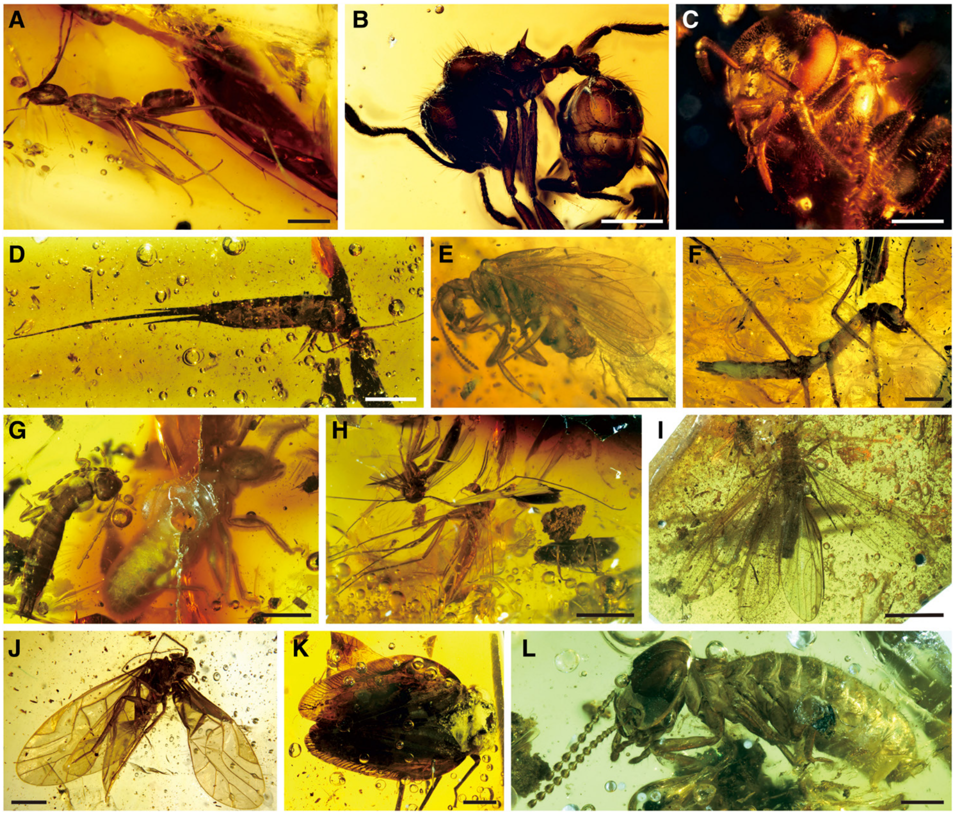

Fig. 4. Representative insects in Zhangpu amber of biogeographic and ecological significance. (**A**) Ant (Hymenoptera: Formicidae: *Leptomyrmex*). (**B**) Ant (Hymenoptera: Formicidae: *Lophomyrmex*). (**C**) Bee (Hymenoptera: Apidae: *Tetragonula*). (**D**) Bristletail (Archaeognatha: Machilidae). (**E**) Dustywing (Neuroptera: Coniopterygidae: *Heteroconis*). (**F**) Stick insect (Phasmida: Lonchodidae: *Orxines*). (**G**) Earwig (Dermaptera: Labiduridae) and termite (Isoptera: Rhinotermitidae: *Coptotermes*). (**H**) Two flies (Diptera: Mycetophilidae) and one leafhopper (Hemiptera: Cicadellidae). (**I**) Stonefly (Plecoptera: Nemouridae: *Podmosta*) and scale insect (Hemiptera: Coccoidea). (**J**) Bark lice (Psocodea: Psocidae). (**K**) Planthopper (Hemiptera: Issidae). (**L**) Termite (Isoptera: Rhinotermitidae: *Coptotermes*). Scale bars, 1 mm (A, C, and G), 0.5 mm (B, E, J, and L), and 2 mm (D, F, H, I, and K).

(*24*), is consistent with the concurrent diversification of various plants and animals (*25*–*27*) and probably laid the foundation for today's East Asian terrestrial biota. In conclusion, the MMCO probably strongly shaped the East Asian biota via the northern expansion of the megathermal rainforest biome, which favored both increasing diversity and had a homogenizing effect on the composition and distribution of plant and animal communities.

Compared to the modern climate in Zhangpu, the most notable difference is that the middle Miocene Zhangpu climate had a warmer winter, leading to a relatively equitable temperature throughout the year. In scenarios of global warming, winter warming is commonly more pronounced than summer warming and has larger and more widespread effects on terrestrial and marine ecosystems (*28*). It reduces "winterkills" and is beneficial for reproduction and growth of tropical animals and plants (*29*). Therefore, winter warming is likely to have been a major driver of the northern expansion of the megathermal biota in South China during the MMCO.

The Zhangpu amber biota together with co-occurring fossils from associated sedimentary rocks—collectively called the Zhangpu biota—is the richest Cenozoic megathermal seasonal rainforest paleobiota found so far, and on the basis of the preserved biodiversity, this new amber deposit ranks among the top four worldwide. This glimpse into such a biota provides a new insight into how modern tropical ecosystems evolve, and helps predict how they will respond to future environmental perturbation.

MATERIALS AND METHODS

Materials

The Fotan Group hosts abundant amber and plant fossils and occurs widely throughout eastern and western Fujian. It consists primarily of three basaltic layers and three sedimentary layers (*30*). A typical stratigraphic section includes basalts, arenaceous conglomerates, sandstone, and mudstone interbedded with lignite (fig. S1). Both plant compression/impression fossils and amber are preserved in two mudstone unites, and some amber pieces and fossil woods also occur within coal seams. We did not find any compression fossil insects within these fossil layers. The ages of basalt samples underlying and overlying the fossil layers are 14.8 ± 0.6 and 14.7 ± 0.4 Ma, respectively (Fig. 1) (*9*, *31*).

Single pieces of Zhangpu amber can be very large (fig. S1D), but they are usually fragile and thus not suitable for making jewelry. The Zhangpu amber is characterized by amyrin and amyrone-based triterpenoids and cadalene-based sesquiterpenoids (*10*). It is considered derived from the tropical angiosperm family Dipterocarpaceae, based on these compounds and the co-occurring fossil winged fruits typical of the family also in the Zhangpu deposits (*32*).

From 2010 to 2019, we collected approximately 25,000 amber samples with inclusions in Zhangpu County, Fujian Province, southeastern China. So far, 8350 specimens have been polished carefully and identified. To reconstruct the paleoclimate, we also collected approximately 5000 plant fossils from the amber-bearing sedimentary rocks of the Fotan Group in Zhangpu. All these specimens are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS).

Optical photomicrography

Specimens were photographed using a Zeiss Stereo Discovery V16 microscope system at the NIGPAS. All images were taken by using digitally stacked photomicrographic composites of approximately 40 individual focal planes using the image-editing software Helicon Focus 6 (www.heliconsoft.com).

X-ray micro–computed tomography

To three-dimensionally reconstruct amber inclusions, we scanned the fossils at the micro-CT laboratory of NIGPAS, using a 3D x-ray microscope (3D-XRM), Zeiss Xradia 520 versa. Unlike conventional micro-CT, which relies on maximum geometric magnification and a flat panel detector to achieve high resolution, 3D-XRM uses charge-coupled device (CCD)–based objectives to achieve higher spatial resolution. On the basis of the size of the fossil specimen, a CCD-based 0.4× objective was used, providing isotropic voxel sizes of 13.36 μm with the help of geometric magnification. During the scan, the acceleration voltage for the x-ray source was 40 to 90 kV, and a thin filter (LE3) was used to avoid beam hardening artifacts. To improve the signal-to-noise ratio, 2001 projections over 360° were collected, and the exposure time for each projection was 1.5 to 3.5 s. Volume data processing was performed using software VGStudio Max (version 3.0, Volume Graphics, Heidelberg, Germany).

Paleoclimatic reconstruction

The paleoclimate of the middle Miocene Zhangpu flora was reconstructed quantitatively using the Climate-Leaf Analysis Multivariate Program (CLAMP), a taxonomy-independent, multivariate statistic technique based on canonical correspondence analysis (CCA) (*33*, *34*). CLAMP correlates the leaf physiognomy of woody dicots in modern vegetation with corresponding climate data and uses these correlations to estimate the climatic conditions prevailing during growth of the fossil plants. The database used in CLAMP scores 31 leaf characters averaged over a minimum of 20 woody dicot leaf morphotypes for each site.

Seventy-eight morphotypes of woody dicot leaves were recognized among ~5000 plant compression/impression fossils (tables S1 and S2). The leaf traits of the Zhangpu morphotypes were scored following the standard protocols as defined on the CLAMP website (http://clamp.ibcas.ac.cn) (data file S1). For analysis, we used the PhysgAsia2 calibration dataset, which contains vegetation sites from both temperate and tropical regions of the Northern Hemisphere. The analysis is also accompanied by a recently developed climate calibration based on high spatial resolution (~1 km^2) WorldClim2 climate data to obtain a broader range of the climatic variables than in the traditional CLAMP calibrations (*35*).

Amber insect assemblage comparisons

We compared the insect assemblages at order level of unbiased collections of Fushun (2780 insects) (*36*), Baltic (including Bitterfeld amber; 19,461 insects) (*37*), Rovno (868 insects) (*37*), Cambay (987 insects in Bonn collection) (*15*), and Zhangpu amber archives (12,661 insects in Nanjing collection). The Fushun, Baltic (including Bitterfeld amber), and Rovno ambers occur almost across a similar paleolatitude, and all were formed by conifers under a warm temperate or subtropical climate (*36*–*38*). Consequently, it is not unexpected that the composition of the Fushun insect fauna is more similar to those of the Baltic and Rovno ambers (fig. S9), probably because of their more comparable environments and ecologies stemming from their similar floras. Similarly, the composition of the Zhangpu amber insect fauna is more similar to that of early Eocene Cambay amber (fig. S9), probably because of their more comparable environments and ecologies again stemming from their closely similar floras (*15*).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/7/18/eabg0625/DC1

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Acknowledgments: We thank F. Stebner, A. P. Rasnitsyn, F. Zhang, J. Dunlop, P. Selden, P. Vršanský, H. Jiang, H. Wang, and Y. Fang for helpful discussions; L. Zhu, H. Shen, S. Yin, and F. M. B. Jacques for assistance and help during scientific fieldwork; and S. Wu for helping with micro–computed tomography reconstructions. We are grateful to the editor and three anonymous reviewers for careful comments that improved this manuscript. **Funding:** This research was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB26000000), the National Natural Science Foundation of China (41688103 and 41772014), Youth Innovation Promotion Association, CAS (2017359), and the German Research Foundation (DFG; grant numbers FE 1240/2-1 and 423862824). R.A.S. was supported by Natural Environment Research Council (UK)/National Natural Science Foundation of China Project NE/P013805/1. M.M.S.-K. was supported by the German VolkswagenStiftung (project no. 90946). J.S. and D.A. thank the Chinese Academy of Sciences for the financial support under the President's International Fellowship Initiative (PIFI). **Author contributions:** B.W. and G.S. discovered the type fossil locality and designed the project. B.W., G.S., V.P., C.C., Z.W., J.S., Y.L., J.C., Qi Zhang, Qingqing Zhang, T.Y., D.Z., and H.Z. carried out fieldwork and collected the specimens. B.W., C.X., V.P., C.C., H.P., X.L., T.G., A.Ś., M.M.S.-K., S.W.H., M.J.T., J.S., D.A., Y.L., A.N., J.C., Qi Zhang, Qingqing Zhang, C.L., T.Y., and M.S.E. identified the amber inclusions except plants. G.S., A.R.S., K.F., J.H., Z.W., and E.-M.S. identified the amber plants. G.S., R.A.S., and Z.W. identified the plant fossils and performed the paleoclimatic analysis. B.W., G.S., R.A.S., V.P., A.R.S., and M.S.E. performed paleoecological and paleoenvironmental research. B.W., G.S., C.X., V.P., A.R.S., and M.S.E. drafted the paper. B.W., G.S., C.X., V.P., and C.C. made the plates. All co-authors commented on the manuscript and provided input to its final version. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 8 December 2020
Accepted 11 March 2021
Published 30 April 2021
10.1126/sciadv.abg0625

Citation: B. Wang, G. Shi, C. Xu, R. A. Spicer, V. Perrichot, A. R. Schmidt, K. Feldberg, J. Heinrichs, C. Chény, H. Pang, X. Liu, T. Gao, Z. Wang, A. Ślipiński, M. M. Solórzano-Kraemer, S. W. Heads, M. J. Thomas, E.-M. Sadowski, J. Szwedo, D. Azar, A. Nel, Y. Liu, J. Chen, Q. Zhang, Q. Zhang, C. Luo, T. Yu, D. Zheng, H. Zhang, M. S. Engel, The mid-Miocene Zhangpu biota reveals an outstandingly rich rainforest biome in East Asia. *Sci. Adv.* **7**, eabg0625 (2021).

Science Advances

The mid-Miocene Zhangpu biota reveals an outstandingly rich rainforest biome in East Asia

Bo Wang, Gongle Shi, Chunpeng Xu, Robert A. Spicer, Vincent Perrichot, Alexander R. Schmidt, Kathrin Feldberg, Jochen Heinrichs, Cédric Chény, Hong Pang, Xingyue Liu, Taiping Gao, Zixi Wang, Adam Slipinski, Mónica M. Solórzano-Kraemer, Sam W. Heads, M. Jared Thomas, Eva-Maria Sadowski, Jacek Szwedo, Dany Azar, André Nel, Ye Liu, Jun Chen, Qi Zhang, Qingqing Zhang, Cihang Luo, Tingting Yu, Daran Zheng, Haichun Zhang and Michael S. Engel

Sci Adv **7** (18), eabg0625.
DOI: 10.1126/sciadv.abg0625

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