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Understanding the Evolution of Biodiversity in Asia

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A revolution is required in our understanding of the history of the Earth's most important biodiversity hotspots. In regard to Asia, biodiversity hotspots across south and east Asia, i.e., the Indo-Burma, the Western Ghats and the South-Central China hotspots, are among the most important centres of diversity on our planet (Myers et al., 2000), and their conservation is vital to sustain ecosystem services for the world's most dense human populations. Despite numerous investigations spanning modern taxon inventories, molecular phylogenetics and so far somewhat limited well-dated fossil data, our understanding of the evolutionary history of biodiversity in Asia is still far from enough to fully understand how this biodiversity came about, and what is required to sustain it under rapidly changing environmental conditions driven by regional economic development and global climate change.

It is becoming clear that Asia experienced dramatic Cenozoic tectonism, with the collision between the Indian and Eurasian plates, initiated around ~55±10 Ma, being the most important event (Royden et al., 2008; Wu et al., 2013). This collision contributed to the creation of the present Qinghai-Tibetan Plateau, the highest and largest plateau around the world, and had a profound influence on the modern topography in adjacent regions such as southwestern China and Southeast Asia (Li et al., 2017, Linnemann et al. 2018, Su et al. 2019a, 2019b). Significantly the collision leads directly to the uplift of the Himalaya (Ding et al., 2017; Gebelin et al., 2013). These tectonic upheavals also influenced the intensity and spatial chracateristics of the Asian monsoonal systems, which are mainly characterized by wet summers and dry winters and springs (Spicer, 2017). Inevitably, the coupled complexity of both geodiversity and palaeoclimate in Asia largely shaped regional biodiversity patterns.

Cenozoic fossil floras in Asia are exceptionally rich, and document plant diversity as the topography and monsoon systems evolved. They provide the only unequivocal evidence for specific taxa existing at specific locations through time, allowing the direct investigation of the evolutionary history of these Asian biodiversity hotspots. However, palaeobotanical studies in large parts of Asia are still far from adequate to reveal detailed evolutionary patterns, and far less explored than coeval Northern Hemisphere floras, especially those from North America and Europe. Associated with infrastructural development across Asia this situation is changing rapidly and now is the time to take a wide overview of what the fossil record does tell us about Cenozoic biodiversity in Asia in order to target better future exploration.

In East Asia, particularly in China, many new fossil floras have been found and reported, including those from the core area of the Qinghai-Tibetan Plateau (Jia et al., 2019; Jiang et al., 2019; Liu et al., 2019; Su et al., 2019b). In South China extremely rich fossil deposits record numerous first occurrences of plants (e.g., Aleksandrova et al., 2015; Quan et al., 2016, Huang et al., 2017) and across South Asia generally new finds open the door to a better understanding of plant exchange between India and Asia (e.g., Srivastava et al., 2018a).

In addition to new finds, new techniques are being applied in palaeobotanical studies, such as Micro-CT scanning, which can reveal more detailed characters for the systematic assignment of fossil specimens (Su et al., 2015). Different methods have been utilized for paleoclimatic reconstructions for many Cenozoic assemblages in Asia, e.g., the Climate-Leaf Analysis Multivariate Program and the Coexistence Approach, the results of which indicate a general trend of Asian monsoon intensification in the Miocene (Jacques et al., 2011; Srivastava et al., 2018b; Xia et al., 2009; Xing et al., 2012), and that a monsoon climate existed across large parts of Asia in the Eocene (Spicer et al., 2016). Linked to monsoon characteristics and other palaeoenvironmental parameters such as temperature, rainfall and thus biodiversity patterns are palaeoelevation and palaeo-CO_2, both of which have been reconstructed by using Asian Cenozoic floras (Jacques et al., 2014; Hu et al., 2015; Su et al., 2019a, 2019b). Papers documenting and comparing the rich modern plant diversity of Asia, Taxonomy of palaeobotany from Asia are badly needed. One new genus and eight new species are described in this special issue. Meanwhile, we integrate different aspects of palaeobotany, palaeoclimatology, palaeoecology, geology and other disciplines to better understand the biodiversity history and its palaeoenvironmental background in South and East Asia.

Cunninghamia shangcunica Kodrul, Grodenko et Kokolva, based on helically arranged and radially spread polymorphic leaves, is a new taxon reported from the lower Oligocene rocks of Guangdong Province, South China. This species is similar to the extant species *C. konishii* in shoot and leaf morphology, and to *C. lanceolata* in the characters of the epidermis. The new Oligocene species increases the known diversity of the genus

Cunninghamia in its refugial region and contributes to a greater understanding of the specific variability and ecology of this conifer (Kodrul et al., 2018).

The fig genus, *Ficus*, is adundant in tropical regions, with some species extending to subtropical or temperate regions. Various habits and life-forms can be found within the genus due to their extensive distribution and adaptations to a variety of climate regimes. Huang and colleagues report a new species, *Ficus microtrivia* J. Huang et Z. K. Zhou, from middle Miocene lacustrine sediments in the Wenshan Basin, Yunnan, southwestern China. Its leaf architectural characters and its nearest living relative, *Ficus trivia*, is restricted to the karst shrub habitat in southern China and northern Vietnam, indicating that open shrubby karst vegetation may have already existed in the early to middle Miocene (Huang et al., 2018).

Ulmus (Ulmaceae) has a rich Cenozoic fossil record from the Northern Hemisphere. Compared to its abundant leaf fossils, fruit fossils of *Ulmus*, which allow accurate dentification, are still scarce. Zhang and colleagues report two new species *Ulmus prelanceaefolia* Q.Y. Zhang et Y.W. Xing and *U. maguanensis* Q.Y. Zhang et Y.W. Xing, both represented by well-preserved fossil samaras, from the middle Miocene Wenshan and Maguan basins, southeastern Yunnan, southwestern China. Zhang et al. deduce that the narrow-winged fruit may be primitive and the two narrow-winged sections, sect. *Chaetoptelea* and *Trichoptelea* are the earliest evolved lineages in *Ulmus* and have diversified since the Eocene. The Oligocene was an important epoch for the rapid diversification of broad-winged lineages of *Ulmus*, which was likely due to dispersal advantage in the more open forests originating as the global climate began to cool. Zhang et al. also found exchanges/dispersals and extinction events between and within North America, Asia, and Europe since the Eocene, and that the North Atlantic and Bering Land bridges served as important dispersal corridors for *Ulmus* during the Cenozoic (Zhang et al., 2018).

Paliurus (Rhamnaceae) has only five extant species, but *Paliurus* records are abundant and have a broad geographic distribution across the Northern Hemisphere during the

Cenozoic. It is an important taxon for biogeographic studies (Hauenschild et al., 2018). However, *Paliurus* fossils in China are rare. Ding et al. add a new fossil record of *Paliurus*, namely *P. hirsuta* J.L. Dong et B.N. Sun, from the middle Miocene of Zhangpu County, South Fujian Province. East China (Ding et al., 2018).

Fissistigma (Annonaceae) is a genus of tropical subtropical climbing lianas and is distributed in eastern India, low-latitude East Asia, and to northeastern Australia. The fossil record of *Fissistigma* is scarce with only one occurrence from the Miocene of India and another from the Pleistocene of Guangxi, but Li et al. report a new one, *F. nanningense* Li from the Oligocene Yongning Formation of Nanning, Guangxi, southern China, based on well-preserved mummified leaves. The climbing habit of this genus suggests that a multilayered structure likely existed in the Oligocene forests of Guangxi (Li et al., 2018).

Wood fossils are important paleobotanical resources for palaeobiodiversity studies, although to date comparative wood fossil studies in China are woefully rare compared to those in many other parts of the world. Such fossils do exist but tend to be overlooked in favour of other plant parts. Excellent material does exist in China and Huang et al. demonstrate this by establishing a new genus and species, *Litseoxylon nanningensis* (Luaraceae) based on well-preserved mummified fossil wood from the upper Oligocene Yongning Formation of the Nanning Basin, Guangxi, South China (Huang et al., 2018).

Podocarpium (Fabaceae) is one of the most common legumes in the Cenozoic of Eurasia. Two new fossil records of *Podocarpium* are reported in this special issue. Yan et al. (2018) describe fossil *Podocarpium Podocarpum* (A. Braun) Herendeen from the Oligocene of the western Qaidam Basin, northern Tibetan Plateau, China, while Li et al. (2018) re-examined fossils of *Podocarpium* from the Oligocene Ningming Formation of Guangxi, in South China, the early Miocene Guide Group of Qinghai in Northwest China and the middle–late Miocene Shengxian Formation of Zhejiang in Southeast China. They confirm the occurrences of *Podocarpium podocarpum* (A. Braun) Herendeen from these localities. Furthermore, both Yan et al. (2018) and Li et al. (2018) discuss dispersal routes and the paleoecological significance of *Podocarpium* in these areas.

Srivastava et al. (2019) report two new fossil species of bamboo culms, namely *Bambusiculmus tirapensis* and *Bambusiculmus makumensis* from the late Oligocene, and two new impressions of bamboo leaves, namely *Bambusium deomarense* and *Bambusium arunachalense* from the late Miocene to Pliocene sediments of northeastern India. These bamboo fossils from India are the earliest records of bamboos from South Asia so far, thereby indicating that bamboos may have dispersed to Asia from India after the collision of the Indian Plate with the Eurasian Plate (Srivastava et al., 2019).

Pollen fossil assemblages can reflect continuous variation of vegetation in a region over geological time and play important role in paleobotany and paleoecology. Two such papers form part of this special issue. Zhang et al. (2018) study pollen fossil assemblages from Pliocene of Changbaishan Mountains, which shows that vegetation changed from a warm temperate mixed conifer and broad-leaved forest to a montane cold temperate coniferous forest. The modification of wet air masses from the Sea of Japan would bring about this change. Yang et al. (2018) studied a Miocene palynoflora from Shengxian Formation, Zhejiang Province, East China in which two fossil assemblages were recognized: *Quercus* E.–*Liquidambar*–*Carya* assemblage and *Quercus* E.–*Fagus*–*Artemisia* assemblage. By compiling published sporopollen data, Yang et al. establish a Miocene palynological succession, and in combination with megafossil plant records, it shows zonal vegetation during the depositional period was similar to its modern counterpart, but with more distinct altitudinal zonality. This is because the occurrence of *Larix* and thermophilous trees dominated the vegetation during the late Early to early Middle Miocene, and conifers increased and aquatic plants such as *Trapa* thrived during the late Middle–early Late Miocene. The Miocene palynological succession in this paper corresponds well to global climate changes during this period (Yang et al., 2018).

Three papers in the special issue focus on palaeoecological studies. Metasequoia glyptostroboides Hu et W.C.Cheng (Cupressaceae) is a relic plant with a narrow natural distribution in central China. In the Cenozoic *Metasequoia* was much more widely distributed with fossils reported from more than five hundred localities. Wang et al. (2018) report the southernmost *Metasequoia* fossil from the middle Miocene of Zhengyuan, Yunnan, Southwest China and discuss the possible reasons of the disappearance of *Metasequoia* there. They conclude that the disappearance might be related to the evolutionary stasis of *Metasequoia*, most likely preventing necessary adaptations of the plants to increasing winter and spring aridity induced by changes in the Asian monsoon in this region during the Miocene (Wang et al., 2018).

In order to understand the interactions between climate and biota in South Asia, Shukla and Mehrotra (2018) reconstruct the early Eocene vegetation of western India. Based on nearest living relatives (NLRs), they conclude that a highly diversified tropical evergreen forest was present in most of the basins of western India, and this is consistant with the equatorial position of the Indian subcontinent during the early Eocene. Fossil records of Rhamnaceae, Combretaceae and Lythraceae known since the Late Cretaceous in India indicate their possible Gondwanan origin.

CO_2 is a well-known greenhouse gas and investigation of historic CO_2 levels can help to understand climate and biodiversity change in the deep past. The stomatal frequency preserved in fossil leaves has been recurrently used for palaeo-CO_2 reconstruction, but simultaneous investigation of both palaeo-temperature and palaeo-CO_2 using the same fossil assemblage has been rarely performed. This is important because stomata control not only CO_2 uptake but also transpirational water loss, which is temperature related. Wang et al. (2018) conducted such analyses of *Quercus gilva* from a leaf bed in the Sayama Formation (1.66–1.55 Ma) in central Japan. They estimate the palaeo-CO_2 values in an interglacial stage (MIS 57 or 55) at 36.41 ± 2.58 pa, which is generally higher than the previously reported data from the early Pleistocene. To understand the climate under this high CO_2 level, Wang et al. (2018) calculated the mean annual temperature (MAT) by using the leaf margin analysis (LMA) approach. The calculated MAT was 11.0 °C, suggesting a relatively warm climate during the interglacial stage. This result revealed a warm environment under high CO_2 level during the early Pleistocene, which suggests the vital role of CO_2 in controlling the early Pleistocene interglacial temperature (Wang et al., 2018).

We thank our colleagues who submitted their work to this special issue. Collectively it is illustrative of the breadth of taxonomic and palaeoenvironmental work being conducted in Asia at the present time, and hopefully will encourage similar multifaceted research. Without a detailed historical perspective it will be impossible to manage responsibly the unique Asian biodiversity resource bequeathed to us from the past.

References

Aleksandrova, G.N., Kodrul, T.M., Jin, J.H., 2015. Palynological and paleobotanical investigations of Paleogene sections in the Maoming basin, South China. Stratigr. Geol. Correlat. 23, 300-325.

Ding, L., Spicer, R.A., Yang, J., Xu, Q., Cai, F., Li, S., Lai, Q., Wang, H., Spicer, T.E.V., Yue, Y., Shukla, A., Srivastava, G., Khan, M.A., Bera, S., Mehrotra, R., 2017. Quantifying the rise of the Himalaya orogen and implications for the South Asian monsoon. Geology 45, 215-222.

Dong, J.-L., Sun, B.-N., Mao, T., Jin, P.-H., Wang, Z.-X., 2018. Two samaras of Rhamnaceae from the middle Miocene of southeast China. Rev. Palaeobot. Palynol. 259, 112-122.

Gebelin, A., Mulch, A., Teyssier, C., Jessup, M.J., Law, R.D., Brunel, M., 2013. The Miocene elevation of Mount Everest. Geology 41, 799-802.

Hauenschild, F., Favre, A., Michalak, I., Muellner-Riehl, A.N., 2018. The influence of the Gondwanan breakup on the biogeographic history of the ziziphoids (Rhamnaceae). Journal of Biogeography 45, 2669-2677.

Hu, J.-J., Xing, Y.-W., Turkington, R., Jacques, F.M.B., Su, T., Huang, Y.-J., Zhou, Z.-K., 2015. A new positive relationship between pCO2 and stomatal frequency in *Quercus guyavifolia* (Fagaceae): a potential proxy for palaeo-CO2 levels. Ann. Bot. 115, 777-788.

Huang, J., Su, T., Jia, L.-B., Spicer, T., Zhou, Z.-K., 2018. A fossil fig from the Miocene of southwestern China: Indication of persistent deep time karst vegetation. Rev. Palaeobot. Palynol. 258, 133-145.

Huang, L-L., Jin J.-H. , Quan C., Oskolski, A. A., 2017. Camellia nanningensis sp. nov.: the earliest fossil wood record of the genus Camellia (Theaceae) from East Asia. J Plant Res. 129:823-831

Huang, L.-L., Sun, J., Jin, J.-H., Quan, C., Oskolski, A.A., 2018. *Litseoxylon* gen. nov. (Lauraceae): The most ancient fossil angiosperm wood with helical thickenings from southeastern Asia. Rev. Palaeobot. Palynol. 258, 223-233.

Jacques, F.M.B., Guo, S.-X., Su, T., Xing, Y.-W., Huang, Y.-J., Liu, Y.-S., Ferguson, D.K., Zhou, Z.-K., 2011. Quantitative reconstruction of the Late Miocene monsoon climates of southwest China: A case study of the Lincang flora from Yunnan Province. Palaeogeography, Palaeoclimatology, PalaeoecologyPalaeogeogr. Palaeoclimatol. Palaeoecol. 304, 318-327.

Jacques, F.M.B., Su, T., Spicer, R.A., Xing, Y.-W., Huang, Y.-J., Zhou, Z.-K., 2014. Late Miocene southwestern Chinese floristic diversity shaped by the southeastern uplift of the Tibetan Plateau. Palaeogeogr. Palaeoclimatol. Palaeoecol. 411, 208-215.

Jia, L.-B., Su, T., Huang, Y.-J., Wu, F.-X., Deng, T., Zhou, Z.-K., 2019. First fossil record of *Cedrelospermum* (Ulmaceae) from the Qinghai–Tibetan Plateau: Implications for morphological evolution and biogeography. J. Syst.Evol. 57, 94-104.

Jiang, H., Su, T., Wong, W.O., Wu, F., Huang, J., Shi, G., 2019. Oligocene *Koelreuteria* (Sapindaceae) from the Lunpola Basin in central Tibet and its implication for early diversification of the genus. J. Asian Earth Sci. 175, 99-108.

Kodrul, T., Gordenko, N., Sokolova, A., Maslova, N., Wu, X., Jin, J., 2018. A new Oligocene species of *Cunninghamia* R. Brown ex Richard et A. Richard (Cupressaceae) from the Maoming Basin, South China. Rev. Palaeobot. Palynol. 258, 234-247.

Li, Q., Liu, Y., Jin, J., Quan, C., 2018. Late Oligocene *Fissistigma* (Annonaceae) leaves from Guangxi, low-latitude China and its paleoecological implications. Rev. Palaeobot. Palynol. 259, 39-47.

Li, S., Advokaat, E.L., van Hinsbergen, D.J.J., Koymans, M., Deng, C., Zhu, R., 2017. Paleomagnetic constraints on the Mesozoic-Cenozoic paleolatitudinal and rotational history of Indochina and South China: Review and updated kinematic reconstruction. Earth-Sci. Rev. 171, 58-77.

Li, X., Ma, F., Xiao, L., He, W., Sun, B., Quan, C., Yao, Y., Ren, D., Wang, X., Wang, Q., Xie, S., 2019. New records of *Podocarpium* A. Braun ex Stizenberger (Fabaceae) from the Oligocene to Miocene of China: Reappraisal of the phylogeographical history of the genus. Rev. Palaeobot. Palynol. 260, 38-50.

Liu, J., Su, T., Spicer, R.A., Tang, H., Deng, W.-Y.-D., Wu, F.-X., Srivastava, G., Spicer, T., Van Do, T., Deng, T., Zhou, Z.-K., 2019. Biotic interchange through lowlands of Tibetan Plateau suture zones during Paleogene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 524, 33-40.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853-858.

Quan, C., Fu, Q., Shi, G., Liu, Y., Li, L., Liu, X., Jin, J., 2016. First Oligocene mummified plant Lagerstätte at the low latitudes of East Asia. Sci. China Earth Sci. 59, 445-448.

Royden, L.H., Burchfiel, B.C., van der Hilst, R.D., 2008. The Geological Evolution of the Tibetan Plateau. Science 321, 1054-1058.

Shukla, A., Mehrotra, R.C., 2018. Early Eocene plant megafossil assemblage of western India: Paleoclimatic and paleobiogeographic implications. Rev. Palaeobot. Palynol. 258, 123-132.

Spicer, R.A., 2017. Tibet, the Himalaya, Asian monsoons and biodiversity-In what ways are they related? Plant Divers. 39, 233-244.

Spicer, R.A., Yang, J., Herman, A.B., Kodrul, T., Maslova, N., Spicer, T.E.V., Aleksandrova, G., Jin, J., 2016. Asian Eocene monsoons as revealed by leaf architectural signatures. Earth Planet. Sci. Lett. 449, 61-68.

Srivastava, G., Mehrotra, R.C., Dilcher, D.L., 2018a. *Paleocene Ipomoea* (Convolvulaceae) from India with implications for an East Gondwana origin of Convolvulaceae. PNAS 115, 6028-6033.

Srivastava, G., Paudayal, K.N., Utescher, T., Mehrotra, R.C., 2018b. Miocene vegetation shift and climate change: Evidence from the Siwalik of Nepal. Glob. Planet. Change 161, 108-120.

Srivastava, G., Su, T., Mehrotra, R.C., Kumari, P., Shankar, U., 2019. Bamboo fossils from Oligo–Pliocene sediments of northeast India with implications on their evolutionary ecology and biogeography in Asia. Rev. Palaeobot. Palynol. 262, 17-27.

Su, T., Farnsworth, A., Spicer, R.A., Huang, J., Wu, F.-X., Liu, J., Li, S.-F., Xing, Y.-W., Huang, Y.-J., Deng, W.-Y.-D., Tang, H., Xu, C.-L., Zhao, F., Srivastava, G., Valdes, P.J., Deng, T., Zhou, Z.-K., 2019a. No high Tibetan Plateau until the Neogene. Sci. Adv. 5, eaav2189.

Su, T., Spicer, R.A., Li, S.-H., Xu, H., Huang, J., Sherlock, S., Huang, Y.-J., Li, S.-F., Wang, L., Jia, L.-B., Deng, W.-Y.-D., Liu, J., Deng, C.-L., Zhang, S.-T., Valdes, P.J., Zhou, Z.-K., 2019b. Uplift, climate and biotic changes at the Eocene-Oligocene transition in south-eastern Tibet. Natl Sci. Rev. 6, 495-504.

Su, T., Wilf, P., Huang, Y.-J., Zhang, S.-T., Zhou, Z.-K., 2015. Peaches preceded humans: Fossil evidence from SW China. Sci. Rep. 5, 16794.

Wang, L., Kunzmann, L., Su, T., Xing, Y.-W., Zhang, S.-T., Wang, Y.-Q., Zhou, Z.-K., 2019. The disappearance of *Metasequoia* (Cupressaceae) after the middle Miocene in Yunnan, Southwest China: Evidences for evolutionary stasis and intensification of the Asian monsoon. Rev. Palaeobot. Palynol. 264, 64-74.

Wang, Y., Momohara, A., Ito, A., Fukushima, T., Huang, Y.-J., 2018. Warm climate under high CO_2 level in the early Pleistocene based on a leaf fossil assemblage in central Japan. Rev. Palaeobot. Palynol. 258, 146-153.

Wu, Z.-H., Hu, D.-G., Ye, P.-S., Wu, Z.-H., 2013. Early Cenozoic Tectonics of the Tibetan Plateau. Acta Geol. Sin. - Engl. Ed. 87, 289-303.

Xia, K., Su, T., Liu, Y.-S., Xing, Y.-W., Jacques, F.M.B., Zhou, Z.-K., 2009. Quantitative climate reconstructions of the late Miocene Xiaolongtan megaflora from Yunnan, southwest China. Palaeogeogr. Palaeoclimatol. Palaeoecol. 276, 80-86.

Xing, Y.-W., Utescher, T., Jacques, F.M.B., Su, T., Liu, Y.-S., Huang, Y.-J., Zhou, Z.-K., 2012. Paleoclimatic estimation reveals a weak winter monsoon in southwestern China during the late Miocene: Evidence from plant macrofossils. Palaeogeogr. Palaeoclimatol. Palaeoecol. 358-360, 19-26.

Yan, D.-F., Zhang, L., Han, L., Yang, T., Chen, Y.-Q., 2018. *Podocarpium* from the Oligocene of NW Qaidam Basin, China and its implications. Rev. Palaeobot. Palynol. 259, 1-9.

Yang, Y., Wang, W.-M., Shu, J.-W., Chen, W., 2018. Miocene palynoflora from Shengxian Formation, Zhejiang Province, southeast China and its palaeovegetational and palaeoenvironmental implications. Rev. Palaeobot. Palynol. 259, 185-197.

Zhang, Q.-Y., Huang, J., Jia, L.-B., Su, T., Zhou, Z.-K., Xing, Y.-W., 2018. Miocene *Ulmus* fossil fruits from Southwest China and their evolutionary and biogeographic implications. Rev. Palaeobot. Palynol. 259, 198-206.

Zhang, S.-H., Chen, T.-Y., Zeng, X., Yu, Y., Zhang, Y., Xie, S.-P., 2018. Plant–insect associations from the upper Miocene of Lincang, Yunnan, China. Rev. Palaeobot. Palynol. 259, 55-62.

Zhang, S.-Q., Wang, W.-M., Sun, G., Wang, P.-J., Gao, Y.-F., Yang, T., Chen, C.-Y., Wang, Y.-Q., 2019. Late Cenozoic palynofloras revealing significant environment and climate changes in Changbai Mountain area, NE China. Rev. Palaeobot. Palynol. 261, 1-10.