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A late Eocene palynological record of climate change and Tibetan Plateau uplift (Xining Basin, China)

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A B S T R A C T

Climate models suggest that Asian paleoenvironments, monsoons and continental aridification were primarily governed by tectonic uplift and sea retreat since the Eocene with potential contribution of global climate changes. However, the cause and timing of these paleoenvironmental changes remain poorly constrained. The recently well-dated continental mudflat to ephemeral saline lake sedimentary succession, situated in the Xining Basin at the northeastern margin of the Tibetan Plateau (NW China), provides a unique opportunity to develop additional proxy successions in this area that are placed accurately in time. Here, a palynological record from this succession is reported. High abundances of desert and steppe–desert taxa such as Ephedripites and Nitrariadites/Nitrariopolis are found, which can be differentiated by the presence of broad leaved deciduous forest taxa in the lower part of the section (particularly up to 36.4 Ma; magnetostratigraphic C16r), and a sudden increase of Pinaceae (Pinuspollenites, Piceaepollenites and Abiespollenites) which is dated at 36.1 Ma (C16n.2n). Coexistence Approach (CoA) indicates that from 39.9 to 36.4 Ma (C17n.1n) regional climate was warm and wet, while from 36.4 to 33.5 Ma (C16n.2n–C13r) climate tends to be cooler and drier. The data indicate that paleoenvironmental and palynological changes on the NE part of the Tibetan Plateau resulted from a combination of long-term tectonic uplift forcing and long- and short-term climate changes. The increase of taxa such as Piceaepollenites and Abiespollenites indicates not only a cooling and drying trend prior to the Eocene/Oligocene (E/O) boundary, but also the existence of high altitude mountain habitats in the periphery of the Xining Basin. The sudden Pinaceae event correlates closely in time with a marked aridification step as viewed from the lithology of the Xining Basin that was linked to the sea retreat out of the Tarim Basin.

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1. Introduction

The Eocene is a key period for Asian paleoenvironmental changes. This period is marked by the Indo–Asia collision with associated regional mountain uplift and sea retreat probably responsible for monsoon intensification and continental aridification (Bosboom et al., 2011). In addition, it is a period of global climate changes from greenhouse to icehouse conditions in the so-called “doubthouse” times marked by climatic cooling, rapid growth of the Antarctic ice sheet, and a supposed drop in atmospheric carbon dioxide levels leading to the Eocene Oligocene Transition (EOT) (Eldrett et al., 2009; Pearson et al., 2009).

Deciphering between potential forcing mechanisms of Asian paleoenvironments remains a challenge but, in principle, the combination of high-resolution age control and the analysis of fossil pollen assemblages enable to reconstruct the vegetation changes over time and indirectly detect paleoenvironmental conditions associated with tectonic and/or climatic change. In NW China, palynological analysis has been extensively applied in the petroleum basins as biostatigraphic tool (e.g. Wang et al., 1990; Zhang and Zhan, 1991; Gao et al., 2000). However, the age dating resolution on the studied sedimentary successions is usually insufficient to enable precise correlation to the global climate records. Previous studies indicate that the continental lacustrine stratigraphy from the Xining Basin in NE Tibet...
(Fig. 1) holds an Eocene to Oligocene sedimentary record of both Tibetan Plateau uplift (Dupont-Nivet et al., 2008) and global climate changes leading the EOT (Dupont-Nivet et al., 2007; G.Q. Xiao et al., 2010; Abels et al., 2011). These successions have recently been constrained by detailed magnetostratigraphic, cyclostratigraphic, and sedimentologic analyses providing an improved chronostratigraphy, and a record of stepwise aridification preceding and coinciding with the EOT (Abels et al., 2011).

Here the existing palynological records from these successions is extended with a detailed analysis of previous and new palynological samples providing higher sampling resolution based on an existing improved age control on these successions (Abels et al., 2011). Characteristic pollen taxa are illustrated by light- and scanning electron microscope photography with emphasis on typical aridity indicators such as the xerophytic Nitrariadites/Nitraripollis and Ephedripites groups. Nearest Living Relatives (NLR) and Coexistence Approach (CoA) methods were performed to estimate mean annual temperature (MAT) and precipitation (MAP) rates. The data set provides a precisely dated reference for other Asian Eocene basins within the wider Eocene context of a broad arid belt extending across China from northwest to southeast. Finally, a detailed palynological study of this key period leading to the EOT in combination with well-established paleomagnetic and cyclostratigraphic studies permit to explore the interplay between regional aridification, global cooling, sea retreat, and uplift of the Tibetan Plateau.

2. Regional setting

2.1. General geology

The most spectacular continent–continent collision belt on Earth is the Himalayan–Tibetan orogen created by the Indo–Asian collision. However, timing of the initiation of uplift and deformation across the Tibetan Plateau remains controversial and is still poorly constrained, especially for the Paleogene period (Yin and Harrison, 2000). The onset of the Indo–Asia collision is generally assumed to have occurred during Eocene times with a large range of ages (Tapponnier et al., 1986; Qinghai et al., 2012) including recent paleomagnetic estimates at 49 ± 6 Ma (Dupont-Nivet et al., 2010; van Hinsbergen et al., 2012). After the onset of the collision, there is growing evidence for accelerated intracontinental convergence, deformation and uplift during the Early Cenozoic (Horton et al., 2002; Spurlin et al., 2005; Rowley and Currie, 2006; DeCelles et al., 2007; C. Wang et al., 2008; Q. Wang et al., 2008; van der Beek et al., 2009; Song et al., 2010). In the northern Tibetan Plateau, evidence for high elevation is provided by the occurrence of pollen taxa related to high altitude vegetation in the Xining Basin by ca. 38 Ma (Dupont-Nivet et al., 2008; now dated at 36.1 Ma (C16n.2n), see Abels et al., 2011). Additionally, there is evidence for tectonism and exhumation starting at 45–50 Ma in the West Qinling range at the southern edge of the Xining basin (Dupont-Nivet et al., 2004; Horton et al., 2004; Clark et al., 2010).

The interaction between the lithospheric deformation and the atmosphere makes the Himalayan–Tibetan orogen of even greater interest. Climate models show that uplift of the Tibetan Plateau and the redistribution of land and sea, associated with the continent–continent collision of India and Asia, caused continental aridification and intensification of the monsoons (Ramstein et al., 1997; Boos and Kuang, 2010). As a result, paleoenvironmental records have invariably associated Tibetan and Himalayan uplift with evidence for aridification north of the Tibetan Plateau and monsoon intensification to the south (e.g. Sun and Wang, 2005). The oldest loess deposits have now been dated to be 22 Ma (Guo et al., 2002) and possible even slightly older (Qiang et al., 2011). Recently it has been demonstrated, from the stratigraphy in the Xining Basin, that Asian palaeoenvironment is also governed by global climate changes. Using high-resolution chronostratigraphy, aridification recorded in the studied stratigraphy is closely correlated to the Eocene–Oligocene transition; an abrupt cooling event at 34 Ma associated with the glaciation of Antarctica (Dupont-Nivet et al., 2007; G.Q. Xiao et al., 2010). Also, an older aridification event around 36.6 Ma has been tentatively related to a combination of incipient ice sheet development, retreat of the Tarim sea and reduced moisture transport to the Xining Basin, indicating global climate impact on this region (Abels et al., 2011; Bosboom et al., 2011).
2.2. The Xining Basin: genesis, stratigraphy and lithofacies

Tectonic deformation during the late Mesozoic and Cenozoic growth of the Tibetan Plateau resulted in active rift basins in the east of China and compressional depression basins in the west (Bally et al., 1986). In total, more than 200 sedimentary basins with Cenozoic clastic infill have been identified. A few of these include non-marine sediments of Paleogene age, among which the Xining Basin is located at the northeastern margin of the Tibetan Plateau (Fig. 1). This basin probably initiated during the Late Jurassic–Early Cretaceous as a fault-controlled high subsidence basin (Horton et al., 2004), while subsequent slow subsidence yielded slow accumulation of Paleogene lacustrine sediments that may be associated with 45–50 Ma exhumation of the West Qinling Range reported to the south of the Xining Basin (Clark et al., 2010). During the Miocene, slow subsidence was disrupted by shortening related to the Indo–Asian collision, resulting in localized range uplift and enhanced fluvial subsidence and basin compartmentalization (Lease et al., 2011). Consequently the Longzhong Basin was subdivided into sub-basins: the Xining Basin to the west, the Lanzhou and Longxi basins to the east, and the Linxia Basin to the southwest (Lease et al., 2007; Hough et al., 2011).

Deposition started in the Xining Basin around 55 Ma (Dai et al., 2006). The accurate age control from magnetostratigraphy makes the long, continuous sedimentary succession in the Xining Basin (Fig. 1) perfect for studying the tectonic and climatic processes during the Eocene and Oligocene (Dupont-Nivet et al., 2007; Abels et al., 2011). The Cenozoic successions in the Xining Basin lay disconformably on the Mesozoic alluvial sediments of the Hezhou and Minhe Groups (possibly lower and upper Cretaceous respectively) or unconformably on older basement rocks. This Cenozoic saline lake to fluvo-lacustrine succession is divided into Xining and Guide Groups. The Xining Group is subdivided into Qijiachuan Formation (Paleocene to possibly lower Eocene), the Honggou Formation (Eocene), and the Mahalagou Formation (Eocene–Oligocene). On top of the Xining Group lies the Guide Group which is unconformably overlain by the late Miocene to Pliocene Linxia Group (Dai et al., 2006). The direct objective of this study was focused on the Honggou and Mahalagou Formations.

The Honggou Formation consists of red-orange sandstones and green-white muddy gypsum beds (Horton et al., 2004; Dai et al., 2006). The gypsum layers in the lower part of the succession are laterally continuous and formed by decimeter- to meter-thick tabular, nodular or laminar beds of alabastrine massive gypsum. These beds grade into green mudstone with lacustrine laminations (Dupont-Nivet et al., 2007). In the Mahalagou Formation green-white muddy gypsum alternate with red gypsiferous mudstone at meter scale. These alterations are interpreted as alternating saline lake environments with dry mudflat environments (Abels et al., 2011). Cyclostratigraphic analysis has shown that orbital forcing of climate was the most likely causal mechanism behind the gypsum–mudstone cycles in the Shuiwan section (G.Q. Xiao et al., 2010; Abels et al., 2011). In the upper part of the Paleogene succession, the gypsum layers disappear and red beds remain. This shift is indicative of a change from saline-lake environments to predominant dry mudflat environments and has been interpreted as regional aridification (Dupont-Nivet et al., 2007). In time, the disappearance of the gypsiferous saline lake deposits has been precisely correlated to the first step of the Eocene–Oligocene greenhouse to icehouse transition (G.Q. Xiao et al., 2010).

2.3. Present climate and vegetation in Xining

The Xining Basin is currently situated at an elevation of ~2000 m, and characterized by a cold semi-arid climate. In the city of Xining the monthly daily averages range from −7.4 °C in January to 17.3 °C in July, and the annual mean is 6.1 °C. Rainfall occurs mainly between May and September and on average precipitation rates are 374 mm per year (source: http://en.wikipedia.org/wiki/Xining). Grassland vegetation predominates and is primarily composed of Poaceae (Stipa bungeana and S. breviflora), Asteraceae and shrubs (Reaumuria soongorica and Peganum harmala), whereas in the valley slopes Nitraria can be found. The estimated C4 plants abundance is less than 10% of the total biomass of living plants at Xining (Sun and Wang, 2005; Liu et al., 2007).

3. Palynological methods and analysis

The palynological content and biostratigraphic position of the Eocene–Oligocene gypsum–mud succession in the Qinghai and Xinjiang region were previously documented by Chinese researchers such as Wang et al. (1990) and Zhang and Zhan (1991). In light of their results and the new magnetostratigraphic framework (Dai et al., 2006; Dupont-Nivet et al., 2007; Abels et al., 2011), an exploratory palynological study permits a better understanding of environmental and climatic developments in the late Eocene of China (Dupont-Nivet et al., 2008, 2009). The palynological approach in this study is explained below.

3.1. Sample and data processing

The 54 palynological samples, each of about ca. 500 g, complement and supersede previous palynological sampling from the Shuiwan section reported in Dupont-Nivet et al. (2008, 2009). Sampling has been intensified in critical parts of the record showing indications of environmental changes and sampling has been extended downwards (Fig. 2). Pollen were almost exclusively preserved in the greenish, muddy, gypsum beds and pollen recovery was achieved in more than 50% of the samples collected in these lithologies. Red beds were also sampled but only yielded rare oxidized pollen. Palynological preservation, as expected, can be of high-quality within the gypsum beds. This is because in ephemeral saline-lake environments brine insulates pollen from oxidation (Horowitz, 1992). The relatively high pollen concentrations in these lithologies are due to the low sedimentation rates in these environments. However, weathering of the exposed beds deteriorates the organic matter content. This is obvious when comparing material recovered from an active quarry (lower section; 23.6 m to 57.5 m), where percentages of corroded pollen are low, and material collected outside the quarry (upper section) where the proportion of corroded pollen is higher (see Fig. 2, last graph in diagram).

Processing was carried out at the Sediment Laboratory of the Vrije Universiteit, Amsterdam using a method modified after A. Horowitz (1992), which is described in the data repository of Dupont-Nivet et al. (2008). Here the main steps are summarized: 1) 50 to 100 g of sediment for each sample was washed, dried and crushed. 2) The sample was submerged in diluted hydrochloric acid (10%), heated to boiling, topped up with demineralised water, and left to rest for circa 12 h. 3) This process was repeated twice until the suspension became completely transparent and pH neutral. 4) The samples were then submerged in sodium pyrophosphate (1%), heated to boiling point and then left to cool down. 5) The samples were brought in suspension and sieved in small portions over an 8 µm screen. 6) The residue was split over 4 centrifuge tubes (15 ml each), followed by heavy liquid separation by sodium polywolframate of density 2.0. This separation was repeated once and the 4 floating parts were added together resulting in one pollen residue for each sample. 7) The residues were washed several times with demineralized water until the liquid was clear, this is to wash out the last clay particles. To remove the very last silica present 10 µl of HF was added. 8) The residue was placed in glycerine and dried in the oven. 9) Finally, the residues were mounted in ‘Kaisers’ glycerine–gelatine and sealed with paraffin.

A wide selection of fossil pollen types and some of their modern relatives was photographed using Nomarski Differential Interference
Fig. 2. Total pollen diagram based on palynological samples from the Shuiwan section (Xining, NW China). The corroded and indeterminate pollen are excluded from the pollen sum but calculated in relation to this sum. To the left, the magnetostratigraphy and correlation to the geologic time scale are given (Abels et al., 2011).
Plate 1. Characteristic pollen types of the late Eocene fossil record in the Xining Basin (China); code of reference sample follows species name or type.

1 a–b. Ephedripites (D) sp., type 1 (PSW03)
2. Ephedripites (D) sp., type 2 (PSW32)
3. Ephedripites (D) sp., type 3 (P387)
4. Ephedripites (E) sp., type 4 (P387)
5. Ephedripites (E) sp., type 5 (P387)
6. Ephedripites (E) sp., type 6 (PSW40)
7. Ephedripites (E) sp., type 8 (PSW43a)
8. Piceapollenites sp. (PSW02)
9. Ruguvesiculites sp. (PSW27)
10. Spinos全新世colpites sp. (PSW 20)
11 a–b. Retitricolpites sp. (PSW20c)
12. Caryapollenites sp. (PSW31)
13. Mornipites sp. (P387)
14. Engelhardtioipollenites sp. (PSW31b)
15. Tripoporopollenites sp. (PSW30a)
16. Zonaropollis sp. (P11)
17. Jugfanspollenites rotundus (P387)
18. Jugfanspollenites verus (PSW29)
19. Ulimipollenites sp. (PSW387)
20. Carophyllidites sp. (PSW29)
21. Carophyllidites sp. (PSW31)
22. Chemopodipollis sp. (PSW31b)
23. Abutilonacidites sp. (PSW28)
24. Chlonovaia sp. (PSW24)
25. Scabiosapollis haianensis (sp.1, long spines)(P387a)
26. Scabiosapollis haianensis (sp.1, long spines)(PSW31b)
27 a–b. Scabiosapollis minutus (PSW02)
28. Fraxinoipollenites sp. (P12)
29 a–b. Fraxinoipollenites sp. (P12)
30. Retitricolpites sp., type 2 (P387)
31 a–b. Retitricolpites sp., type 1c (PSW29a)
32. Retitricolpites sp., type 1a (PSW 02)
33 a–b. Retitricolpites sp., type 1b aff. Tamarix (PSW02)
34 a–b. Retitricolpites sp., type 1b aff. Tamarix (PSW34)
35 a–b. Retitricolpites sp.
36. Retitricolpites maturaensis (PSW44)
37. Retitricolpites magnus (P11)
38. Retitricolpites magnus (PSW25)
39 a–b. Placipollis sp. (PSW29)
40 a–b. Cupuliferoidaepollenites sp. (3c) (PSW30a)
41 a–b. Striaticolpites sp., aff. Acer (P384)
42. Sapindaceidites cf. triangularus, type 1 (P387)
43. Sapindaceidites sp., type 2 (P387)
44. Sapindaceidites terriorus (P12)
45 a–b. Retibrevitricolpites sp. (P387)
46. Echitricolpites sp. (PSW02).

Plate 2. Characteristic pollen types of the late Eocene fossil record in the Xining Basin (China); code of reference sample follows species name or type. (see on page 22)

1a–b. Labitricolpites minor (PSW03)
2. Labitricolpites major (PSW27)
3. Labitricolpites minor (P379)
4 a–b. Nitrariadites sp., type 3 (PSW02)
5 a–b. Nitrariadites sp., type 2 (PSW31); cf. Nitrariadites rotundiporus (aff. N. tangutorum)
6 a–b. Nitrariadites sp., type 5 (PSW32); cf. Nitrariadites pachypolarus
7 a–c. Nitrariadites sp., type 1 (P385); cf. Nitrariadites commis or Nitrariadites tunganxensis (aff. N. sphaerocarpa)
8 a–c. Nitrariadites sp., type 5 (PSW02); cf. Nitrariadites pachypolarus
9 a–b. Nitrariadites sp., type 5 (PSW27b); cf. Nitrariadites pachypolarus
10. Nitrariadites sp., type 5 (PSW 26); cf. Nitrariadites pachypolarus
11. Nitrariadites sp. corroded (PSW30a)
12 a–c. Nitrariadites sp., type 4 (PSW27b)
13. Nitrariadites sp., type 9 (PSW27b)
14 a–b. Nitrariadites sp. (PSW28)
15 a–b. Nitrariadites sp., type 7 (PSW26)
16 a–b. Nitrariadites sp., type 2 (PSW30); cf. Nitrariadites rotundiporus
17 a–c. Nitrariadites sp., type 8 (P387); cf. Nitrariadites ellipticus
18 a–b. Nitrariadites sp., type 8 (PSW27b); cf. Nitrariadites ellipticus
19 a–c. Euphorbiacites cf. reticulatus (P12)
20. Euphorbiacites cf. reticulatus (PSW45b)
21 a–b. Euphorbiacites cf. reticulatus (P387)
22 a–c. Euphorbiacites cf. reticulatus (PSW27b)
23 a–b. Retitricolpites sp., type 1 (was type 33) (PSW 29a)
24 a–b. Cupuliferoidaepollenites sp. (3c)(PSW26)
25 a–b. Quercoidites sp. (evergreen type) (PSW31b).
Contrast (DIC) microscopy (Plates 1–4) (Bercovici et al., 2009). While making the photos, the varying z-axis was recorded and images were later combined through manual z-stacking in photoshop. This stacking technique combines different layers to provide a sense of depth to the images with a comparable result to 3D photography. In addition, some of the most characteristic pollen types were photographed using a Zeiss DSM 960 Digital Scanning Electron Microscope at the Department of Paleontology, University of Vienna, Vienna, Austria (Plates 5 and 6). The protocol for this procedure is further described in Ferguson et al. (2007).

Out of 54 samples, 31 samples were proven to be productive for pollen and the remaining 23 samples were very poor or barren. In the productive samples, 84 pollen types were identified which are listed in Appendix 1. For each sample, a minimum pollen sum of 100 was used, but where possible 300 grains were counted; for pollen sums see Fig. 2 and Supplement 1.
Pollen grains were identified using the Genera File of Fossil Pollen and Spores (Jansonius and Hills, 1976 and recent updates), Xi and Sun (1987), Xi and Zhang (1991), Wang et al. (1990), and Zhang and Zhan (1991). The palynological data are represented in diagrams (Figs. 2, 3a–b, and 4a–b) constructed with the programs C2 (Juggins, 2005), Tilia version 5, and Tilia TGView (Grimm, 1987). For a better visualization, the pollen diagram (Fig. 2) only includes taxa that have a frequency of more than 1% in a minimum of three samples. To formally estimate variations in the record, the diagram was divided into zones using CONISS (Constrained Incremental Sums of Squares).
cluster analysis), an application that is part of the Tilia program. This method selects the two most similar, stratigraphically adjacent samples, and combines them. The combination is then treated as a single sample, and the search is repeated (Grimm, 1987).

3.2. Nearest Living Relatives (NLR) and Coexistence Approach (CoA)

To reconstruct past climates and environmental and altitudinal conditions of the Shuiwan area, the fossil pollen are compared with the NLR in modern pollen assemblages of well-defined ecosystems. Ecological groups or Plant Functional Types (PFTs) relate to ecosystems or biomes, which can be used to infer the palaeoclimate of a region (Prentice et al., 1996). Yu et al. (1998) tested the applicability of this procedure, originally developed for Europe, to assign modern surface samples from China to biomes and successfully indicated the major vegetation types of China. These authors showed a good agreement between modern vegetation and surface pollen distribution across the Tibetan Plateau, which strongly suggests that specific suites of fossil pollen taxa can be used to reconstruct past vegetation patterns.

NLRs were assigned based on Song et al. (2004) and the taxa were grouped according to biome types listed in Yu et al. (2000) and Ni et al. (2010) (see Table 1), and filtered for pollen taxa found in the Eocene record of Xining. Subsequently 6 biome types were assigned based on more general versions of the PFTs and biomes described by Yu et al. (2000): 1) xerophytic vegetation (desert and steppe), 2) conifer forest, 3) temperate broad leaved forest, 4) warm broad leaved forest, 5) tropical forest, and 6) pteridophytes. Taxa that did not fit these groups were placed in a group labeled ‘other taxa’.

Based on the NLR, the CoA is applied, a method for quantitative palaeoclimate reconstruction (Mosbrugger and Utescher, 1997). The CoA employs climatic requirements of all NLR known for a fossil flora in order to identify for a given climate variable a range in which a maximum number of NLR can coexist. The resulting “coexistence interval” is considered to represent the conditions under which the fossil flora existed and the methodology proved its robustness in numerous applications throughout the Cenozoic. As in other NLR techniques, the quality of the NLR concept and closeness of fossils and related extant plants play an important role, and hence it is clear that uncertainties in general increase with the age of the studied flora, but still were successful when accepting restrictions in the

Plate 4. Modern species of *Nitraria* from Iran and China (courtesy Morteza Djamali and Frank Schlütz).

1 a–b. *Nitraria tangutorum* (slides from F. Schlütz)
2 a–b. *N. tangutorum*
3 a–b. *N. tangutorum* (polar view)
5 a–b. *N. sphaerocarpa* (polar view)
6 a–c. *N. sphaerocarpa*
7 a–b. *N. sphaerocarpa*
8 a–c. *Nitraria sibirica* (from F. Schlütz, west Mongolia, HAL 40706)
9 a–c. *N. sibirica*
10 a–b. *N. sibirica* (polar view)
11 a–b. *N. sibirica*
12 a–b. *N. sibirica* (polar view)
13 a–c. *Nitraria raborowskii* (from F. Schlütz)
14 a–c. *N. raborowskii*
15 a–b. *Nitraria schoberi* (from Iran, courtesy of Morteza Djamali)
16 a–d. *N. schoberi* (from Iran, courtesy of Morteza Djamali).

Plate 5. Scanning Electron Microscope (SEM) photographs of selected fossil taxa in the Eocene Shuiwan succession (sample PSW387). See bar for scale in microns. (see on page 26)

1. *Ephedrinites* (E) sp., type 7
2. *Ephedrinites* (E) sp., type 9
3. *Ephedrinites* (E) sp., type 8
4. *Ephedrinites* (E) sp., type 5
5. *Ephedrinites* (D) sp., type 3
7. *Retrithocolpites magnus*
8. *Ulmipollenites* sp.
9. *Betidiporites* sp.
10. *Scabiosapollis haianensis* (long spines)
11. *Scabiosapollis haianensis* (corroded specimen)
12. *Quercoidites* sp. (3cp evergreen type).

Plate 6. Scanning Electron Microscope (SEM) photographs of selected fossil taxa in the Eocene Shuiwan succession (sample PSW387). (see on page 27)

1. *Sapindaceidites* cf. *triangulus*, type 1
2. *Sapindaceidites* sp., type 3
3. *Sapindaceidites* tetricus
4–6. *Euphorbiacites* cf. *retilatus*
7. *Retrithocolpites* sp. type 3
8. *Erichipites* sp.
9. *Nitrariopollis/Nitrariadites* sp., type 47
10. *Nitrariopollis/Nitrariadites* sp., type 57
11. *Nitrariopollis/Nitrariadites* sp., type 47
12. *Nitrariopollis/Nitrariadites* sp., type 17
13. *Brochotriletes bellus*
climatic resolution (e.g., Roth-Nebelsick et al., 2004; Poole et al., 2005; Grein et al., 2011). The CoA was effectively tested with modern vegetation (Mosbrugger and Utescher, 1997; Pross et al., 2000), the application on Cenozoic macrofloras of Central Europe provided a continuous climate record showing the evolution from almost tropical conditions in the Lutetian to a temperate climate in the Gelasian, with temperatures near to present, and testify the close correlation of inferred continental and marine temperature (Mosbrugger et al.,
Plate 6 (caption on page 24).
2005; Bruch et al., 2007; Utescher et al., 2009a,b). In various cases, it is shown that CoA estimates overlap with results obtained from different approaches (e.g. leaf margin analysis, European Palaeogene: Roth-Nebelsick et al., 2004; Grein et al., 2011; CLAMP, European Cenozoic: Uhl et al., 2003; leaf margin analysis, CLAMP, Asian Neogene: Xia et al., 2009; Jacques et al., 2011), and with data obtained from other proxies, respectively (e.g. crocodilians, cf. Mörs, 2002). Applied on various palynomorph records from Cenozoic sections with independent dating, the CoA proved its potential for resolving detailed trends and orbital-scale variability of climate (e.g., Utescher et al., 2000; Ivanov et al., 2002; Utescher et al., 2009b, 2012).

At least 8 taxa contributing with climate data in the analysis are required in order to obtain reliable results (Mosbrugger and Utescher, 1997). Presently, CoA is applied on all 31 microfloras and calculates mean annual temperature (MAT) and mean annual precipitation (MAP) (Fig. 4c–d). To reconstruct regional climate evolution along the section, the CoA is applied on a “forest group” comprising a total of 33 woody plants identified as Nearest Living Relatives of the palynomorphs at the generic or family level. Local elements, namely components of the xerophytic vegetation as well as pteridophytes, are not included here. To reduce white noise in this time series, only taxa present with > 1% of the total palynomorph sum are considered.

In the analysis, the number of taxa for which climate data exist ranges from 2 to 23 (mean: 10 taxa; std 5.6). In 11 out of 31 samples less than 8 taxa are available for calculations, hence the significance of the results is diminished. Data based on diverse palynomorph spectra are indicated in Fig. 4(c and d), and Supplement 2 giving the complete set of palaeoclimatic data. To assess local rainfall rates, coexistence intervals for MAP from the xerophytic vegetation are determined. Here, 3 different taxa (Artemisia, Nitraria, Ephedra) can be discerned providing more specific climatic information. Although the CoA can work with few taxa, or even with a single one, results obtained from less than 10 taxa usually are treated with care because outliers and inconsistencies might not be detected in the analysis (Mosbrugger and Utescher, 1997). For all that, these data may provide important clues on thresholds of precipitation rates within the basin.

In a recent study, the CoA was applied to various modern floras and referred to as “useless” for climate reconstructions (Grimm and Denk, 2012). However, the results presented there and the conclusions drawn may be challenged. Though being useful to unfold erroneous entries regarding climatic ranges of extant plant taxa cited in the Palaeoflora data base (Utescher and Mosbrugger, 2012), the study is not qualified to assess reliability and potential of the CoA for the reason of various methodological flaws. These include the partly very low number of taxa contributing with climate data in the analysis (according to the method, a maximum number should be used), the use of unspecific climatic data (e.g. climate data for plant families when the more specific data for a lower taxonomic level were not contained in the data base) to reconstruct very specific climatic conditions (e.g. the climate of the Alpine zone in Georgia), and extensions of the climatic ranges derived from extreme stands in high altitudinal areas thus introducing an additional bias (insufficiently known lapse rates, microclimate, snow depth in the cold season, etc.). The Palaeoflora database is checked and updated in regular intervals (Utescher and Mosbrugger, 2012) and new tests of the CoA on additional modern floras from various continental areas that follow the published standard of the procedure (Mosbrugger and Utescher, 1997) are on the way in order to provide further evidence for the reliability of the method.

4. Results

4.1. Stratigraphic zonation based on pollen

The palynological diagram is subdivided into three zones (A, B and C) which are described from base to top (see Fig. 2). The zone boundaries are positioned at the upper limit of the samples that mark each boundary and ages based on Abels et al. (2011).

4.1.1. Zone A (7 samples, 19.4–36 m, ~38.8–37.7 Ma)

The zone is dominated by Ephedripites and Nitrariadites/Nitraripollis; each of these taxa fluctuates between 20% and 80% but together always makes up close to 80% of the pollen sum. At the base Nitrariadites/ Nitraripollis dominates, whereas in the top half Ephedripites prevails. Other xerophytic taxa, such as the Chenopodiaceae, Amaranthaceae, Caryophyllaceae (CAC group) are less common, with amounts not larger than 5%. Conifer pollen (e.g. Pinuspollenites, Piceaepollenites, Abiespollenites) are rare, while broad leaved (temperate and warm) taxa occur in low percentages. Among these Fraxinoipollenites and Quercoidites (tricolporate type) are the most prominent. Other taxa such as Labritricipolites and Retritricipolites (’small variety’) occur in low percentages (<5%). Pteridophytes have scattered occurrences.

4.1.2. Zone B (12 samples, >36.0–66.4 m, ~37.7–36.4 Ma)

Ephedripites (10–50%) is characterized by relatively high percentages at the base, while Nitrariadites/Nitraripollis (25–85%) dominates in the top half of the zone. Other xerophytic taxa are less common, although the CAC group can reach around 10%. This zone is distinguished from zone A by new appearances, and higher percentages, of broad leaved, tropical and 'other taxa': Ulmipollenites is relatively abundant, together with Momipites, Fraxinoipollenites, Salixipollenites, Juglanspollenites, Rutaepollenites and Ephorbiacidia. Broad leaved forest taxa such as Ostryoipollenites, Tiliaepollenites, aff. Rosaceae, Cupuliferopollenites, and Engelhardthiopollenites appear in this zone for the first time. Beyond this zone Euphorbiacidia cf. reticulatus virtually disappears until zone C3. Also the tropical taxon Monosulcites, and cf. Abutilonacoides and echinate pollen (tricolpate type) appear and are restricted to this zone. Conifer pollen have single occurrences in this zone; pteridophytes have scattered occurrences.

4.1.3. Zone C (12 samples, >66.4–165.4 m, ~36.4–33.9 Ma)

This zone differs from zones A and B by a substantial drop of the broad leaved forest taxa relative to the previous zones, and later on by the rise of Pinaceae at stratigraphic level 74.8. Although sample densities are relatively low in this 100 m interval, this part of the section is tentatively divided into 4 subzones (C1, C2, C3 and C4).

4.1.3.1. Subzone C1, (4 samples, >66.4 m–111.2 m, ~36.4–35.0 Ma)

The base of the zone is marked by the decline of in broad leaved and tropical forest taxa. Nitrariadites/Nitraripollis is the most dominant group (45–65%) while Ephedripites is less abundant (10–30%), but together they make up for 70–90% of the total pollen count. Other xerophytic taxa remain low and Scabiosapollis haiianensis (sp. 1, ‘with long spines’) disappears in this zone. Most noticeable is the increase of conifer pollen, which is first observed at stratigraphic level 74.8 m (36.1 Ma) in the section. However, the transition from broad leaved to conifer forest is marked by a gap since stratigraphic level 66.4 m (36.4 Ma) shows neither prevalence of broad leaved forest taxa nor conifers. This could point at a temporary decline of all forest types in the region. In the zone Pinuspollenites has values reaching up to 20% and Piceaepollenites up to 10%. However, conifer pollen slightly decrease again at the top of the zone. Some broad leaved forest taxa, such as Caryapollenites, Triropollenites, Cupuliferopollenites, Quercoidites (tricolpate and tricolporate), and ‘other taxa’ such as Labritricipolites minor, Labritricipolites major and Retritricipolites (small type) continue throughout the zone. Besides Lycopodiumsporites, pteridophytes are absent in this part of the succession.

4.1.3.2. Subzone C2 (2 samples, >111.2–128.7 m, ~35.0–34.5 Ma)

This subzone is characterized by peaks in conifer pollen with values of Pinuspollenites and Piceaepollenites each up to almost 20%. Other taxa such as Abiespollenites and Cedripites are low in abundance.
Towards the top of the zone the values of the conifer pollen decrease again. *Ephedripites* also is abundant, with highest values around 40% and lowest values around 15%. *Nitrariadites*/Nitraripollis shows a large decline, down to percentages of 20%, but increasing towards the top again. *Artemisiaepollenites* modestly peaks in this part of the succession as well. Most broad leaved trees, 'other taxa' and pteridophytes do not – or only sporadically – occur in this interval.

4.1.3.3. Subzone C3 (3 samples, >128.7–160 m, 34.5–34.0 Ma). This zone differs from the previous one because of a further decline of
As is argued below, changes observed in the dry xerophytic group taxa (at 66.4 and 74.8 m, respectively 36.4 and 36.1 Ma) (Figs. 2 and 3a). The N/E ratio of these taxa may be used as a measure of relative humidity in desert environments suggesting that the ratio of these taxa may be used as a measure of relative humidity in this dry environment. It should be noted though that sampling was restricted to the gypsum beds and thus the palaeoenvironmental reconstruction based on pollen are only valid for the periods in which the construction based on pollen are only valid for the periods in which the

4.1.3.4. Subzone C4 (3 samples, >160–165.4 m, ~34.0–33.9 Ma). This zone is characterized by the increase of conifer taxa such as Pinus pollenites (15%), Piceaepollenites (20%), and the presence of Podocarpidites, Abiespollenites, Tsugapollenites and Cedripites. There is a slight increase in the hygrophilic pteridophytes and the broad leaved (temperate and warm) forest taxa, but also Compositoipollenites and Retitricolpites (aff. Tamarix) and 'other taxa' such as Euphorbiacidae cf. reticulata rise in value. Ephedripites and Nitrariadites/Nitrariipollis values drop.

In summary, two main results are immediately apparent from the palynostratigraphic zonation (Fig. 2). Firstly, the predominance of xerophytic, halophytic shrubs such as Ephedripites and Nitrariadites/Nitrariipollis throughout the section with averages of around 80%, but occasionally with peaks up to 90%. The second, and most important, result is expressed by a sharp change in the mainly non-xerophytic taxa (at 66.4 and 74.8 m, respectively 36.4 and 36.1 Ma) (Figs. 2 and 3a). As is argued below, changes observed in the dry xerophytic group (mostly Ephedripites and Nitrariadites/Nitrariipollis) are independent from changes in the non-xerophytic taxa (mostly forest taxa) suggesting that these taxa respond differently to palaeoenvironmental variations.

4.2. Xerophytic vs. non-xerophytic taxa

4.2.1. The Xerophytic taxa: Nitraria/Ephedra (N/E) ratio

Past occurrences of Ephedripites and Nitrariadites/Nitrariipollis in the Tibetan region date as far back as early Paleogene, coinciding with the time when an arid belt extended over most of China (Wang et al., 1990; Horton et al., 2004; Sun and Wang, 2005). The abundance of xerophytes such as Ephedripites and Nitrariadites/Nitrariipollis in the Xining Basin (Figs. 2, 3a, and 4a) fits well in this context. The modern equivalents of Ephedripites and Nitrariadites/Nitrariipollis are Ephedra and Nitraria respectively, and together with the Chenopodiaceae they are typical for the alluvial gravelly plains and the treeless alpine desert landscape such as the Alashan Plateau in northwest China (Herzschuh et al., 2003, 2006). In the modern deserts of northwestern China, where these taxa presently occur, annual rainfalls of less than 100 mm are measured which makes these among the most arid regions in the world (Sun and Wang, 2005).

Ephedra and Nitraria have slightly different ecological ranges; Ephedra prefers aridity (semi-desert) while Nitraria is a relatively more humid steppe/desert taxon (Xi and Sun, 1987; Cour et al., 1999; Sun and Wang, 2005; Jiang and Ding, 2008; Ma et al., 2008; Li et al., 2009; Zhao and Herzschuh, 2009). According to Li et al. (2005) the Nitraria/Ephedra (N/E) ratio is below 1 in typical desert communities and above 1 in steppe/desert environments suggesting that the ratio of these taxa may be used as a measure of relative humidity in this dry environment. It should be noted though that sampling was restricted to the gypsum beds and thus the palaeoenvironmental reconstruction based on pollen are only valid for the periods in which the saline lakes existed, i.e. the wetter part of the cyclicity, and do not apply for the drier climatic conditions during which red-bed
The nearest living relatives and the fossil taxa grouped according to the information from the biome studies. Nearest living relatives (NLR) and biomes based on fossil pollen assemblage. The list below follows from grouping taxa based on modern vegetation and pollen data in C. Yu et al., 2000 and J. Ni et al., 2010. For each group fossil taxa and their likely NLR are indicated. Biome names are based on J. Ni et al., 2010.

<table>
<thead>
<tr>
<th>1 Steppe–desert (Ephedro-Nitraria)</th>
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<tbody>
<tr>
<td>Ephedripites subgen. Spirapolites</td>
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<tr>
<td>Ephedripites subgen. Dystachyopites</td>
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<tr>
<td>Ephedripites subgen. Ephedripites</td>
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<tr>
<td>Nitrariadites/Nitraripollis sp. (9 different types)</td>
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<tr>
<td>cf. Qinghuiipollis sp. and Povrovskya sp.</td>
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<tr>
<td>2 Steppe–desert (others)</td>
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<tr>
<td>CAC group</td>
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<tr>
<td>cf. Artemisiaepollenites sp. (Artemisia)</td>
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<tr>
<td>Chenopodipollis sp. (Chenopodiaceae/Amaranthaceae)</td>
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<tr>
<td>Caryophyllidites (Caryophyllaceae)</td>
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<tr>
<td>Compositoipollenites sp. (Asteraceae)</td>
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<tr>
<td>Graminidites sp.</td>
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<tr>
<td>Liliacidites sp.</td>
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<td>Retitriceps sp. type 4b (Tamarix)</td>
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<tr>
<td>Scabiosisopollis sp. 2 (Scabiosa)</td>
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<td>Scabiosisopollis sp. 1 (Scabiosa)</td>
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<tr>
<td>sp. (Asteraceae)</td>
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<tr>
<td>Chenopodipollis sp. (Caryophyllaceae)</td>
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<tr>
<td>3 Conifer forest</td>
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<td>Abiespollenites sp. (Abies)</td>
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<td>Cedripites sp. (Cedrus)</td>
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<td>Pinuspollenites sp. (Pinus)</td>
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<tr>
<td>Picearipollis sp. (Picea)</td>
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<tr>
<td>cf. Podocarpidites sp. (Cathaya)</td>
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<td>Tsugapollis sp. (Tsuga)</td>
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<tr>
<td>4 Temperate broad leaved forest</td>
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<td>Abiespollenites sp. (Abies)</td>
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<td>Betulaepoipollenites sp. (Betula)</td>
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<tr>
<td>Caryapollenites sp. (Caryaceae)</td>
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<tr>
<td>Carpinipites sp. (Carpinus)</td>
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<tr>
<td>cf. Carpinipollis sp. (Viburnum)</td>
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<tr>
<td>Cupuliferoipollenites sp. (3c) (Cupuliferae)</td>
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<tr>
<td>Cupuliferoipollenites sp. (3cp) (Castanea, Cupuliferae) (also subtropical)</td>
</tr>
<tr>
<td>Ericrepis sp. (Ericaceae)</td>
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<tr>
<td>Echitricolpites sp. (Rosaceae)</td>
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<tr>
<td>Euphorbiaceae (Croton type)</td>
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<tr>
<td>Elaeangnacites sp. (Elaeagnaceae)</td>
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<td>Fraxinoipollenites sp. (Fraxinus)</td>
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<td>Hexpollenites sp. (Hexas)</td>
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<td>Juglanpollenites rotundus (Juglandaceae)</td>
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<td>Juglanpollenites verus (Juglandaceae)</td>
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<td>Lonicericus sp. (Lonicera)</td>
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<td>Ostryoipollenites sp. (Ostrya)</td>
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<td>Psilatricolpites sp. (Fagaceae)</td>
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<tr>
<td>Quercoidites sp. (3c) (Quercus, deciduous)</td>
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<tr>
<td>Sapindaceites tetrostris (Elaeagnaceae?) (also subtropical)</td>
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<tr>
<td>Sapiindicrites sp. (Sapindaceae)</td>
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<tr>
<td>Salixipollenites sp. (Salix) (also subtropical)</td>
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<tr>
<td>Straticolpites sp. (Acer)</td>
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<tr>
<td>Triporoipollenites sp. (Corylus)</td>
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<td>Ulipollenites sp. (Tiliaeae)</td>
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<tr>
<td>Umlipollenites sp. (Ulmaceae)</td>
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<tr>
<td>5 Warm broad leaved forest</td>
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<tr>
<td>Engelhardtipollenites sp. (Engelhardtia) (also subtropical)</td>
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<tr>
<td>Momipites sp. (Engelhardtia) (also subtropical)</td>
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<tr>
<td>Quercoidites cf. microcarinisp. (3cp)/Quercus, evergreen)</td>
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<tr>
<td>Rutaceipollenites sp. (Rutaceae) (also subtropical)</td>
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<tr>
<td>6 Tropical forest</td>
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<td>cf. Arecipites sp.</td>
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<td>Monosulcites sp.</td>
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<tr>
<td>Spinicotipollis sp.</td>
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<tr>
<td>Sapindaceipollenites sp.</td>
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<tr>
<td>7 Others/affinity unknown</td>
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<tr>
<td>cf. Abutlonicadas (Abutlonia)</td>
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<tr>
<td>Chlonovaia sp.</td>
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<tr>
<td>Echitricolpites sp. (2 types)</td>
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<td>Echitricolpites sp.</td>
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<tr>
<td>Echitricolpites sp.</td>
</tr>
<tr>
<td>Ephorbiacites cf. reticulatus (3cp) (Tiliaeae?)</td>
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<tr>
<td>Ephorbiacites cf. reticulatus (3cp) (Tiliaeae?)</td>
</tr>
<tr>
<td>cf. Ephorbiacites minor</td>
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<tr>
<td>cf. Ephorbiacites sp.</td>
</tr>
<tr>
<td>Labitricolpites major</td>
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<tr>
<td>Labitricolpites minor</td>
</tr>
</tbody>
</table>

deposition took place. C. Xiao et al. (2010) reported on limited pollen recovery from these red-beds and it is likely that these intervals may contain additional clues on the climatic evolution in the region. However, differential pollen preservation in red-beds compared to gypsum would hamper such analysis.

The observed subtle fluctuations between the percentages of Ephedripites and Nitrariadites/Nitraripollis (Fig. 4b) suggest that the xerophytic vegetation was not uniform over time and may have varied following climatic variability (arid/humid phases) prior to the EOT. Herbs such as Poaceae and Asteraceae and other xerophytic taxa, such as from the CAC group and Artemisiaepollenites, nevertheless, seem impervious to such variability as they remain rather constant throughout the EOT and do not rise above 10%. Variations in the dry Ephedripites and Nitrariadites/Nitraripollis group are independent from changes in the non-xerophytic pollen and other groups. This suggests that the Ephedripites and Nitrariadites/Nitraripollis group have a different source than the non-xerophytic taxa and other groups. The Ephedripites and Nitrariadites/Nitraripollis group most likely reflect varying conditions in the surrounding desertic areas while the forest taxa indicate variations from regional mountainous regions.

These results concur with Eocene records from the Juqian Basin (Miao et al., 2008) located several hundreds of kilometers north in the Hexi corridor also showing short-term climatic fluctuations, which in the Xining Basin are registered as fluctuations of Ephedripites and Nitrariadites/Nitraripollis. However, there are some important differences in the non-xerophytic pollen content that may result from (1) the northern location of the Juqian section away from the uplifting Eocene ranges, (2) the age control on the Juqian section and (3) the depositional environment of the Juqian basin dominated by alluvial, fluvial and lacustrine (water) transport, whereas the saline lake environment in Xining is more prone to trapping wind-transported pollen. In a larger time scale, Zone A (in this record) is dominated by Ephedripites, suggestive of drier (desert) conditions; and zone B and C1 by Nitrariadites/Nitraripollis suggestive of wetter (steppe–desert) conditions. In zone C2 Ephedripites again dominates the xerophytic vegetation suggesting more desert-like conditions. These large-scale
fluctuations occur throughout the succession and are in line with the lithofacies analysis (Abels et al., 2011) showing aridification at the transition between Zone B and Zone C. Moreover, in zones A and B the dominance of dry taxa pollen influx is somewhat higher whereas in the upper part of the section, in zone C, it decreases at the expense of non-xerophytic taxa becoming more important suggesting some important change is occurring at this time.

4.2.2. The non-xerophytic (mainly forest) taxa
When the dominant signal of the dry xerophytic taxa is excluded (Fig. 3b), it is clearly shown that broad leaved forest taxa (both temperate and warm), ‘other’ angiosperm taxa and pteridophytes dominate in the lower part of the section (zones A and B). Typical taxa of the deciduous forests are Quercoidites, Caryapollenites, Celtipollenites, Ulmipollenites, Cupuliferoipollenites, Juglanapollenites, Tiliaepollenites, Betulaeipollenites and pollen types with affinity Fagaceae. These taxa mostly occur in the lower part of the section (zones A and B) and are indicative of temperate and warm, humid climates, which at present form the lower vegetation belts in temperate to subtropical mountainous regions (Wang et al., 1990; Horton et al., 2004; Sun and Wang, 2005; Fauquette et al., 2006; Miao et al., 2008). Subtropical pollen taxa are rare in the succession except for e.g. Engelhardtioipollenites, Sapindaceidites, Cupuliferoipollenites, Monosulcites and Rutaceoipollenites, which also mostly occur in zones A and B. These taxa are indicative of a climate with relatively higher average temperature and humidity (Li and Zhang, 2000; Sun and Wang, 2005).

In the upper part of the succession (zone C), however, Pinaceae dominate the non-xerophytic pollen assemblage. In detail, this transition sets in at ~36.4 Ma (magnetochron C16n.2n). At this point, broad leaved forest taxa drop while subsequently, at ~36.1 Ma, the Pinaceae increase with an average of 30% and peak up to 40% of the pollen sum. Associated with this change is a decline of Euphorbiacites and Rettescolpites. The humidity dependent pteridophytes diminish just below the onset of the Pinaceae while herbs such as Chenopodiaceae, Amaranthaceae, Caryophyllaceae (the CAC group), Poaceae, and Asteraceae remain scarce throughout the section. Just below the EOT, the broad leaved taxa and the pteridophytes show a very modest increase, but unfortunately the gypsum layers stop at the EOT.

4.3. Climatic estimates for the Xining Basin through Coexistence Approach (CoA)
Mean Annual Precipitation (MAP) records are depicted for the forest group, potentially representing the vegetation of neighboring uplands, and for the dominant xerophytic group considered to reflect conditions within the sedimentary basin (Fig. 4c). For the dominant xerophytic group, CoA derived MAP estimates range from ca. 30 to 700 mm with the lower limit defined by the requirements of Ephedra and the upper one by the demands of Nitraria. Both components of the dominant xerophytic group occur in all studied samples, and since only presence/absence is considered in the CoA, uniform results are obtained for the whole profile. On the one hand, CoA data are in agreement with the very dry conditions (desert; steppe–desert) concluded from other proxies (e.g., sedimentary facies). On the other hand, precipitation requirements of the 3 dominant xerophytic components regarded (Artemisia, Ephedra, Nitraria) are too unspecific at the generic level to resolve any variability or trend in the section.

When calculating MAP for the forest group, humid conditions result for the levels with diverse spectra. MAP of at least 820 mm results for 13 samples (CoA ranges commonly from 823 to ca. 1700 mm), namely for depth levels 31.4 m, 38.3–47.4 m, 57.5 m, 63.6–66.4 m, 74.8 m, 106.2 m, 111.2 m, as well as for 162.6 m in the topmost part of the section. In 8 cases, drier conditions are not excluded (CoA ranges from 373 to ca. 1700 mm). Even drier limits of CoA ranges are obtained for poor assemblages. This might be referred to drier climate conditions in the upland areas or to a reduced preservation potential of palynomorphs within the basin. With regard to the wetter CoA intervals, lower limits are set by Engelhardtia (823 mm), which indicates warm and humid conditions (see above). For drier MAP ranges the limit is set by various arboreal forest taxa, and thus is comparatively well constrained but already below the threshold that can be assumed for a close forest cover (~370 mm; e.g., Abies, Carya, Tilia).

Mean annual temperature (MAT) data obtained for the forest group reveal a comparable pattern (Fig. 4d). Warm temperate conditions with MAT > ~15 °C result for the depth levels were Engelhardtia is present in the spectra, with the upper limits of CoA ranges being around 24 °C, especially in the lower part of the profile, and ranging to ca. 22 °C when Picea is present. From depth level 23.6 m to 35.7 m, and at 49.1 m, cooler MAT ranges of at least ca. 8 °C are obtained, with Liriodendron and Sapindaceae being the delimiting taxa, pointing to a climate that was at least temperate. For poor assemblages, even cool temperate climate conditions are not excluded (samples at 53.7 m, 142.9 m, 160 m), but, as stated above, these data cannot be regarded as significant in the sense of the method.

Based on these observations it can be concluded that, in the studied time interval, the uplands sourcing pollen into the basin were repeatedly under warm and humid conditions. The most distinct warm and humid phase is located at depth range 38.3 to 47.4 m and coincides with a maximum in the broad leaved forest taxa. That part might represent the warmest and wettest phase in the section. In the profile part from 80.5 to 160 m, an all over declining trend of CoA interval means combined with a decrease of the upper CoA interval limits by ca. 2 °C (presence of Picea) and the spreading of conifer forest, might conceal a longer-term cooling trend. In this part, however, only few results are based on diverse spectra. It is important to note that in all cases where Engelhardtia is present there is no overlapping of MAP intervals determined for the dominant desert vegetation and the forest group respectively. This further suggests different source areas for these groups. The appearance and presence of conifer pollen, in particular Picea and Abies, therefore are indicative for relatively cooler and dryer, high altitude, conditions. Indeed, in modern equivalents, such as the warm-temperate broad leaved deciduous forests in China, the annual mean temperature is 9 to 14 °C and the annual precipitation is 500 to 900 mm (Sun and Wang, 2005). Instead in a present cold-temperate conifer forest, consisting mainly of Abies, Picea and Pinus, the annual average temperature is 2.2 to 5.5 °C, and the annual precipitation is 350 to 550 mm (Sun and Wang, 2005). This implies that after ~36.4 Ma (C16r), somewhere in the periphery of the Xining Basin a cold-temperate conifer forest developed, under comparatively colder and dryer conditions than prior to this time. This, together with the CoA results, suggests that the zones A and B were warmer and wetter than zone C, which is in general agreement with the lithofacies and depositional environmental changes reported from this section (Abels et al., 2011).
have now also been found several millions of years prior to the actual E/O boundary. At ~36.6 Ma (top chron C17n.1n) a first drop in the gypsum production is interpreted as regional aridification; later at ~34.7 Ma (base chron C13r), an increase in clastic sedimentation rates is observed (Abels et al., 2011). Dupont-Nivet et al. (2008) previously reported on the main palynological features associated with the interval preceding the EOT, however, these results did not yet incorporate improved ages based on new magnetostratigraphic and cyclostratigraphic results from Abels et al. (2011). The palynological signal is in agreement with the lithofacies change following ~36.6 Ma (top chron C17n.1n), and suggests that the sedimentary succession was formed proximal to the mountains and that climatic cooling and aridification changed the forest composition, shifting from a broad leaved to a conifer forest. Prior to 36.4 Ma (C16r) the forested vegetation was characterized by a broad leaved forest (warm and temperate) that thrived in humid conditions on the mountain slopes. From 36.1 Ma onwards, this vegetation changed into a conifer-dominated forest that preferred drier and cooler conditions. The palynological evidence indicating cooling and drying in combination with Coexistence Approach is therefore in agreement with the stepwise late Eocene aridification indicated by the lithofacies changes. However, no notable palynological change is associated with the 34.7 Ma shift in accumulation rates suggesting it does not also relate to cooling and drying.

5. Discussion

The combined palynological data carry an intriguing message on the interplay of climatic cooling, aridification, and the principle existence—or ongoing formation—of mountain habitats in the periphery of the sedimentary basin. The general increase of Pinaceae, or ‘Pinaceae pollen phase’, throughout the Paleogene palynological records has previously been related to global cooling and increased tectonism (Gao et al., 2000). Although Pinus can be transported over long distances (>1000 km) other conifers such as Picea are much less prone to transport (Lu et al., 2008; Zhou and Li, 2011) and are therefore a good proxy for regional palaeoaltitudes especially when found in such high percentages. Pinus pollen can have occurrences of up to 10–50% in the palynological assemblages of deserts and steppe-deserts, where pine trees are absent, as the result of long-distance transport by wind (Ma et al., 2008). However, the abundance of Picea is more significant as Picea pollen distribution in present environments strongly dwindles at any distance from the spruce forests (Lu et al., 2008; Zhou and Li, 2011). The Piceaepollenites percentages (ca. 20% at some levels) in the Xining Basin therefore suggest that a relatively proximal conifer forest is responsible for the raised conifer percentages.

Present-day analogs of Piceaepollenites and Abiespollenites (Picea and Abies) are found at minimum 1500 m.a.s.l and optimally occur at elevations from 2500 to 4000 m.a.s.l. (Lu et al., 2008) together with other high-altitude elements such as Tsuga and Cedrus (Fauquette et al., 2008). Dupont-Nivet et al. (2008) therefore suggested that mountain habitat formation was the most likely causes for the Pinaceae increase in the late Eocene record and estimated the minimum palaeoaltitude of 1500 m.a.s.l. in the periphery of the basin, considering higher Eocene global temperatures and the absence of drastic climate cooling that could explain the change in the considered time interval. However, the location of the elevated source terrain remained elusive. The present day elevation of the Xining basin ~2300 m (m.a.s.l.) is barely sufficient to explain the pollen signature and this elevation likely results from tectonism younger than the Eocene pollen itself (Xiao et al., 2012). Based on pollen transport properties, the most likely candidate as source area for the palaeo-Pinaceae forest is the nearby tectonic exhumation of the West Qinling Shan recently reported to have started at 45–50 Ma (Clark et al., 2010). This exhumation, located 30 to 70 km south of the sampling area, probably formed the southern margin of the Xining Basin at this time. Subsequent exhumation near the Xining Basin only arises at 25–20 Ma in the Laji Shan situated a few kilometers to the south of the sampling area (Lease et al., 2011; Xiao et al., 2012). As argued in Clark et al. (2010), the total vertical offset associated with the exhumation is ~5.5 km with higher age/depth gradient between ~45 and 35 Ma followed by slower erosion rates after ~35 Ma within a factor of two, and again faster between 17 and 18 Ma. Together with the 36.1 Ma high-altitude pollen appearance in the Xining basin, this suggests that the West Qinling Shan reached threshold elevation for Pinaceae forest development (at least 1500 m.a.s.l) 10 to 15 Myr after the onset of exhumation. We therefore propose the ~35 Ma decrease in erosion rate to be related to the late Eocene aridification as indicated by the stepwise lithofacies changes from 36.6 to 34.0 Ma (E/O Boundary) in the Xining Basin (Abels et al., 2011), although decreasing fault offset may have also contributed (Clark et al., 2010).

Regionally, lines of evidence for high Tibetan altitudes early on in the collision have been previously reported. The Qiangtang Block bears evidence that the central Tibetan Plateau already was at considerable elevation as early as 45–38 Ma ago (C. Wang et al., 2008; Q. Wang et al., 2008). Further south, oxygen-isotope-based estimates of palaeoaltitude from late Eocene–Oligocene formations in the Lunpola Basin in central Tibet indicate that the central Tibetan Plateau has been characterized by elevations in excess of 4 km since 35 ± 5 Ma (Rowley and Currie, 2006). Also, Song et al. (2010) recently suggested, based on pollen, that altitudes for Eocene central–southern Tibet were a minimum of 3285–3495 m. Altogether this indicates that elevated topography extended away from the collision zone very early after initial collision such that an early plateau formation may have already contributed to monsoon intensification together with Paratethys sea retreat (Ramstein et al., 1997; Zhang et al., 2007).

In addition to the rising topography, the data here presented suggest that the Picea appearance is also associated with a relatively rapid climate change between 37 and 36 Ma. This is supported by the short time interval of palynological change (36.4–36.1 Ma) characteristic of climate fluctuations as previously suggested in Dupont-Nivet et al. (2008). Sudden climate cooling is further indicated by the CoA results in this interval and regional aridification is evidenced by the nearly coeval lithofacies change at ~36.6 Ma (Abels et al., 2011). This regional aridification has previously been linked to the coeval retreat of the Tarim Sea to the West (Abels et al., 2011; Bosboom et al., 2011) which may have further enhanced monsoons with increasing aridification in the basins. Increased drought in the basin versus humidity on the slopes is expected with monsoonal intensification such that local topography might have played an important role in mediating regional climate changes, as induced by uplifting air in the surrounding mountains and subsidence of air masses in a basin (Zhao et al., 2010).

The ultimate cause for the sea retreat remains equivocal with potential forcing from tectonism or global sea level (Bosboom et al., 2011). The time interval prior to the EOT is referred to as the climate ‘doubthouse’ characterized by temporary ice caps in the Antarctic and in the Northern Hemisphere possibly causing several periods of longer and shorter cooling events recorded in the oceanic realm (Tripati et al., 2005; Eldrett et al., 2009). Eocene glacial sediments in East Antarctica (Ehrmann, 1998) and ice-rafterd dropstones in middle Eocene sediments from Lomonosov ridge in the Arctic support early glacial onset (Tripati et al., 2005) but their timing and duration remain disputed. Potentially, build up of these ice caps, lowered sea level, and decreased oceanic evaporation made less atmospheric water vapor available for precipitation in continental interiors. High-latitude climate influence on the study area is suggested by strong obliquity domination of sedimentary cyclicity in the whole late Eocene interval (G.Q. Xiao et al., 2010; Abels et al., 2011). This has been related to strong fluctuations of incipient ice sheets at high latitudes. Northern high-latitude pollen and spore assemblages
recorded in the Eocene and Oligocene interval (Eldrett et al., 2009) indicate a loss, or reduction, of warm and temperate broad leaved forest taxa and a rise of conifer forest taxa at the end of the Eocene that are similar to the results here presented. Eldrett et al. (2009) relate their findings to ice buildup in the Northern Hemisphere. While taking into account the lower latitudinal position of Tibet, this all reinforces the scenario in which the rise of the Pinaceae in Tibet was controlled by both tectonics and global climatic change.

In recent years, an abrupt atmospheric CO2 decline and has been reported for the E/O transition (Pearson et al., 2009). Enriched CO2 levels in the atmosphere greatly enhance growth and water use efficiency in almost all vegetation types. Arid and semi-arid systems where Nitraria and Ephedra thrive are thought to be among the most responsive to changes in atmospheric CO2 (Smith et al., 2000). Productivity of arid land plants is predicted to increase substantially with rising atmospheric carbon dioxide concentrations due to enhancement in plant water-use efficiency (Housman et al., 2006). Trees at high altitudes are also particularly sensitive to CO2 enrichment, because they live in an atmosphere of lower partial pressure of CO2 (Hattenschwiler et al., 2002). The current literature indicates a significantly larger average long-term biomass increment under elevated carbon dioxide for Pinaceae than for deciduous trees in studies not involving stress components (Saxe et al., 1998). New data on the effects of changing CO2 on the evolution of the vegetation in Tibet are needed to evaluate the impact of decreasing atmospheric CO2 levels on the studied flora.

6. Conclusions

Palynological evidence from the NE Tibetan region coupled with magnetostratigraphic dating and high-resolution lithofacies analysis indicates that during the latest Eocene mountain habitats already existed, and perhaps were still evolving. Tectonic exhumation of the nearby West Qinling Shan, at the southern margin of the Xining Basin, could easily have harbored the broad leaved forest, and subsequently the Picea and Abies forests that characterize the fossil pollen record at Shuiwan. In view of this it is concluded that the palynological signal in the E/O transition records a climatic stepwise variation that overprints the tectonic signal.

When comparing the palynological data with the 2-step variation in sedimentation rates in the succession it is noted that:

a) the first step, a drop in gypsum production at 36.6 Ma, virtually coincides with the palynological transition marked by the disappearance of broad leaved forests (36.4 Ma, top magnetochnor C16r) and the appearance of conifer forests (36.1 Ma, C16n2n). This change is considered to be a product of vegetation change following regional aridification initiated at ~36.6 Ma (C16r) and is coeval with the retreat of the Tarim sea (Abels et al., 2011; Bosboom et al., 2011);

b) a second step, an increase in clastic sedimentation rate at ~34.7 Ma, however, is not mirrored by palynological change.

Palynological studies on the Chinese terrestrial sections of Eocene and Oligocene age may in future elucidate further the evolution of the palaeoflora under climatic and tectonic changes, including the transition from the Ephedra and Nitraria dominated steppe of the Paleogene to the typical Artemisia and CAC dominated steppe of the Neogene to Present (i.e. Miao et al., 2011).

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Appendix 1. Taxonomic information on all pollen and spores and the references

Palynological references

Further details on genera can be found in Jansonius’ Genera File of Fossil Spores (see also “A key to the genera of fossil angiosperm pollen” by Jan Jansonius in Review of Palaeobotany and Palynology, volume 26, issues 1–4, 1978, pages 143–172).

Gymnospermae

Ephedripites group aff. Ephedraceae
Ephedripites subgen. Spiralisites Krutzsch 1970
Ephedripites subgen. Dystachyapites Krutzsch 1961
Ephedripites subgen. Ephedripites Krutzsch 1961
Ephedrinites (D) sp., type 1; Plate 1.1
Ephedrinites (D) sp., type 2; Plate 1.2
Ephedrinites (D) sp., type 3; Plate 1.3; 5.5
Ephedrinites (E) sp., type 4; Plate 1.4
Ephedrinites (E) sp., type 5; Plate 1.5; 5.4
Ephedrinites (S) sp., type 6; Plate 1.6
Ephedrinites (E) sp., type 7; Plate 5.1
Ephedrinites (E) sp., type 8; Plate 1.7; 5.3
Ephedrinites (E) sp., type 9; Plate 5.2
Abiespollenites Thiergart in Raatz (1937) 1938
Abiespollenites sp. aff. Abies
Cedripites Wodehouse 1933
Cedripites sp. aff. Cedrus
Pinuspollenites Raatz 1938 ex Potonié 1958
Pinuspollenites sp. aff. Pinus
Piceapollenites Potonié 1931
Piceapollenites sp. aff. Picea; Plate 1.8
Podocarpidites Cooke ex Couper 1953
Podocarpidites sp. aff. Cathaya
Rugubivesiculites Pierce 1961
Rugubivesiculites sp.; Plate 1.9
Tsugapollenites Raatz 1937, 1938
Tsugapollenites sp. aff. Tsuga

Angiospermae

Monocolpate
Areceipites Wodehouse 1933
Areceipites sp. aff. Palmae
Liliacidites Couper 1953
Liliacidites sp.
Monosulcites Cooke ex Couper 1953
Monosulcites sp. aff. Palmae (was Sabalpollenites sp. in Dupont-Nivet et al., 2008)
Spinizonocolpites Muller 1968
Spinizonocolpites sp. aff. Nypa (Palmae); Plate 1.10
Monoporate
Graminidites Cookson ex Potonié 1960
Graminidites sp. aff. Poaceae

Diporate
Retidiporites Varma & Rawat 1963
Retidiporites sp.; Plate 1.11; 5.9

Triporate
Abutilonacidites Guan Xue-ting & Zheng Ya-hui 1989
Abutilonacidites than
sp. aff. Quercus

Retitricolpites (van der Hammen 1956a) van der Hammen & Wijmstra 1964
Retitricolpites cf. matauraensis (type 6) (Couper) Song et Zheng, 1981; Plate 1.36
Retitricolpites sp. type 1b, aff. Tamarix; Plate 1.33–34
Retitricolpites sp. type 1a (small); Plate 1.32
Retitricolpites sp. type 1c (small); Plate 1.31
Retitricolpites sp. type 2 (large); Plate 1.30

Scabiosapolis Sung Tzechen & Zheng Yahui in Li Manying, Sung Tzechen & Li Zaiping 1978
Scabiosapolis haianensis (sp.1, long spines) Song et Zheng; aff. Scabiosa; Plate 1.25–26; 5.10–11
Scabiosapolis sp. (short spines)
Scabiosapolis minutus; Plate 1.27

Triporate
Abutilonacidites (Zaklinskaja 1956) ex Li, Sung & Li 1978, Sung & Li
Cupuliferoipollenites Potonié 1951 ex Potonié 1960
Cupuliferoipollenites sp. aff. Poaceae; Plate 1.27

Verrucitricolpites Pierce 1961
Verrucitricolpites sp.

Tricolporate
Euphorbiacites (Zaklinskaja 1956) ex Li, Sung & Li 1978, Sung & Li
Euphorbiacites cf. reticulatus (3cp) aff. Tiliaeaceae Li, Sung & Li; Plate 2.19 & 21–22; 6.4–6
Euphorbiacites cf. reticulatus (3c) aff. Tiliaeaceae; Plate 2.20
cf. Euphorbiacites minor in Zhang et Zhan 1991
cf. Euphorbiacites sp.

Ilexpollenites Raatz (1937) 1938 ex Potonié 1960
Ilexpollenites sp. (short spines)

Verrucitricolpites van der Hammen ex Germeraad, Hopping & Muller 1968

Echitrichitricolpites van der Hammen ex Germeraad, Hopping & Muller 1968
Echitrichitricolpites sp. aff. Rosaceae; Plate 3.1

Echitricolporites sp. aff. Rosaceae; Plate 3.1

Artemisiiaeipollenites Nagy 1969
Cupuliferoipollenites Wodehouse 1933
cf. Cupuliferoipollenites sp. aff. Viburnum; Plate 3.12

Compositoipollenites Potonié 1951 ex Potonié 1960
Compositoipollenites sp. aff. Asteraceae

Cupuliferoipollenites Potonié 1951 ex Potonié 1960
Cupuliferoipollenites sp. (3cp) aff. Castanea; Plate 2.24

Echitrichitricolpites van der Hammen ex Germeraad, Hopping & Muller 1968

Echitrichitricolpites sp. aff. Rosaceae; Plate 3.1

Euphorbiacites (Zaklinskaja 1956) ex Li, Sung & Li 1978, Sung & Li
Euphorbiacites cf. reticulatus (3cp) aff. Tiliaeaceae Li, Sung & Li; Plate 2.19 & 21–22; 6.4–6
Euphorbiacites cf. reticulatus (3c) aff. Tiliaeaceae; Plate 2.20
cf. Euphorbiacites minor in Zhang et Zhan 1991
cf. Euphorbiacites sp.

Ilexpollenites Raatz (1937) 1938 ex Potonié 1960
Ilexpollenites sp. aff. Ilex; Plate 3.10

Lonicerapolipites Krutzsch 1962

Lonicerapolipites sp. aff. Loniceraceae; Plate 3.14–15

Tricolporopollenites Pflug & Thomson in Thomson & Pflug 1953
Tricolporopollenites sp.

Nitrariadites/Nitraripollis group, aff. Nitrariaceae
Nitrariadites Zhu & Xi Ping in Zhu Zunghao et al. 1985
Nitraripollis Xi Yizhen & Sun Mengrong 1987

Nitraripollis sp., type 2; cf. Nitraripollis rotundiporus

Zhu & Xi Ping in Zhu Zunghao et al. 1985

Nitraripollis sp., type 2; cf. Nitraripollis rotundiporus

Xi Yizhen & Sun Mengrong 1987; Plate 2.5

Nitraripollis sp.; Plate 3.14

Loniceralpollis Krutzsch 1962

Loniceralpollis sp. aff. Lonicera; Plate 3.14–15

Tricoloporopollenites Pflug & Thomson in Thomson & Pflug 1953
Tricolporopollenites sp.

Nitrariadites/Nitraripollis group, aff. Nitrariaceae
Nitrariadites Zhu & Xi Ping in Zhu Zunghao et al. 1985
Nitraripollis Xi Yizhen & Sun Mengrong 1987

Nitraripollis sp., type 2; cf. Nitraripollis rotundiporus

Xi Yizhen & Sun Mengrong 1987; Plate 2.5

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Nitraripollis sp., type 3; Plate 2.4

Nitraripollis/Nitrariadites sp., type 1; cf. Nitrariadites communis
Zhang et Zhan 1991

or Nitraripollis tungxiensis (was Melacoeidites rhomboiporus)
(aff. N. sphaerocarpa) Xi Yizhen & Sun Mengrong 1987; Plate 2.7; 6.12

Nitraripollis sp., type 2; cf. Nitraripollis rotundiporus

Xi Yizhen & Sun Mengrong 1987; Plate 2.5

Nitraripollis/Nitrariadites sp., type 3; Plate 2.4

Nitraripollis/Nitrariadites sp., type 1; cf. Nitrariadites communis
Zhang et Zhan 1991

or Nitraripollis tungxiensis (was Melacoeidites rhomboiporus)
(aff. N. sphaerocarpa) Xi Yizhen & Sun Mengrong 1987; Plate 2.7; 6.12

Nitraripollis sp., type 2; cf. Nitraripollis rotundiporus

Xi Yizhen & Sun Mengrong 1987; Plate 2.5

Nitraripollis/Nitrariadites sp., type 3; Plate 2.4
Nitrariopollis/Nitrariadites sp., type 4; Plate 2.12; 6.9 & 11
Nitrariopollis/Nitrariadites sp., type 5; cf. Nitrariadites pachypolarus
Zhang et Zhan 1991; Plate 2.6 & 8–10; 6.10
Nitrariopollis/Nitrariadites sp., type 7; Plate 2.15
Nitrariopollis/Nitrariadites sp., type 8; cf. Nitrariadites ellipticus
Zhang et Zhan 1991; Plate 2.17–18
Nitrariopollis/Nitrariadites sp., type 9; Plate 2.13

Oleoidearumpollenites Nagy 1969
Oleoidearumpollenites sp.; Plate 3.6–8

Psilaticrolporites (van der Hammen 1956a) van der Hammen & Wijmstra 1964
Psilaticrolporites sp. aff. FAGACEAE

Quercoidites Potonié, Thomson & Thiergart 1950 ex Potonié 1960
Quercoidites cf. microhenrici Potonio 1931 (3cp/evergreen type) aff. Quercus; Plate 2.25; 5.12

Rhoipites Wodehouse 1933
Rhoipites sp.

Retitricolporites (van der Hammen 1956) van der Hammen & Wijmstra 1964
Retitricolporites sp., type 1 (was type 33); Plate 2.23
Retitricolporites sp., type 2; Plate 3.2–3
Retitricolporites sp., type 3 Plate 6.7

Rutaceoipollens He Yue-ming & Sun Xiang-jun 1977
Rutaceoipollens sp.; aff. Rutaceae; Plate 1.17

Srivastava 1967 (Jan.)

Nagy 1969

Sun & Zhang 1979 in Sun, Zhang & Hou 1981
Zonorapollis
Zonorapollis sp. aff. Alnus

Rhoipites Wodehouse 1933
Rhoipites sp.

Retitricolporites (van der Hammen 1956) van der Hammen & Wijmstra 1964
Retitricolporites sp., type 1 (was type 33); Plate 2.23
Retitricolporites sp., type 2; Plate 3.2–3
Retitricolporites sp., type 3 Plate 6.7

Rutaceoipollenites He Yue-ming & Sun Xiang-jun 1977
Rutaceoipollenites sp. aff. Rutaceae; Plate 3.11

Salixipollenites Srivastava 1967 (Jan.)
Salixipollenites sp. aff. Salix; Plate 3.9

Sapindaceites Sun & Zhang 1979 in Sun, Zhang & Hou 1981
Sapindaceites cf. triangulus (type 1) in Zhang et Zhan 1991, aff. Elaeagnaceae? Plate 1.42; 6.1
Sapindaceites sp. (type 2) aff. Elaeagnaceae? Plate 1.43
Sapindaceites sp. (type 3) Plate 6.2
Sapindaceites tetrornis in Zhang et Zhan 1991, aff. Elaeagnaceae? Plate 1.44; 6.3
(was “Elaeagnacitides” & “Myrtaceites” in Dupont-Nivet et al., 2008)

Sapotaceidaepollenites Thomson & Thiergart 1950 ex Potonié 1960
Sapotaceidaepollenites sp. aff. Sapotaceae

Striaticrolporites Van der Hammen ex Leidelmeyer 1966
Striaticrolporites sp. (= Type 28); Plate 3.4

Trudopolis Pflug 1953b
Trudopolis sp.

Tiliaeollenites Potonié 1931
Tiliaeollenites sp. aff. Tilia; Plate 3.5

Verrucocolporites van der Hammen & Wijmstra 1964
Verrucocolporites sp.

Zonaropolis Sung & Li in Sung, Li & Li 1976
Zonaropolis sp. (was Santalocites) aff. Santalum; Plate 1.16
aff. Euphorbiaceae (Croton type)

Stephanoporate

Ulmipollenites Wolff 1935
Ulmipollenites sp. aff. Ulmaceae; Plate 1.19; 5.8

Stephanocolporate

Alnipollenites Potonié 1931a
Alnipollenites sp. aff Alnus

Periporate

Chenopodiaceae–Amaranthaceae–Caryophyllaceae Group
Chenopodiopollis Krutzsch 1966
Chenopodiopollis sp. aff. Chenopodiaceae/Amaranthaceae; Plate 1.22

Carophyllidites Couper 1960 (September)
Carophyllidites sp. aff. Caryophyllaceae; Plate 1.20–21

Juglanspollenites Raatz 1939
Juglanspollenites rotundus Ke & Shi aff. Juglans; Plate 1.17
Juglanspollenites verus Raatz aff. Juglans; Plate 1.18

Persicariopollis Krutzsch 1962a
Persicariopollis sp. aff. Persicaria

Tetrade

Eriicipites Wodehouse 1933
Eriicipites sp. aff. Eriaceae; Plate 3.16; 6.8

Pteridophyta

Monolete

Echinopsoris Krutzsch, 1967
Echinopsoris sp.

Verrucatosporites (Pflug, 1952) ex Potonié 1956
Verrucatosporites sp.

Diverse indeterminate psilate, monolete spores

Trilete

Brochotritelles Naumova 1939 ex Ischenko 1952
Brochotritelles bellus Wang; Plate 3.21; 6.13

Crassotritelles Germeraad, Hopping & Muller 1968
Crassotritelles nanhaensis Zhang et Li 1981; Plate 3.19

Echitritelles Potonié 1956
Echitritelles sp. aff. Selaginella; Plate 3.18; 6.14

Lycopodiumsporites Thiergart 1938
Lycopodiumsporites sp.

Undulatisporites Pflug in Thomson & Pflug 1953
Undulatisporites sp.; Plate 3.17

Verrucotritelles van Hoeven-Klinkenberg 1966
Verrucotritelles sp.; Plate 3.20

Diverse indeterminate psilate, trilete spores

References