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The intensification of the East Asian winter monsoon contributed to the disappearance of *Cedrus* (Pinaceae) in southwestern China

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ABSTRACT

Climate change during the Quaternary played an important role in the distribution of extant plants. Herein, cone scales of *Cedrus* (Pinaceae) were uncovered from the Upper Pliocene Sanying Formation, Longmen Village, Yongping County of Yunnan Province in southwestern China. Detailed comparisons show that these fossils all belong to the genus *Cedrus* (Pinaceae), and a new species is proposed, *Cedrus angusta* sp. nov. This find expands the known distribution of *Cedrus* during the Late Pliocene to Yunnan, where the genus no longer exists in natural forests. Based on the analysis of reconstructed Neogene climate data, we suggest that the intensification of the East Asian winter monsoon during the Quaternary may have dramatically increased seasonality and given rise to a much drier winter in Yunnan. Combined with information on *Cedrus* fossil records and its seed physiology, we conclude that the intensification of a drier climate after the Late Pliocene may have prevented the survival of *Cedrus* seedlings, leading to the eventual disappearance of *Cedrus* in western Yunnan. This study indicates that the topography in southwestern China acted as a vital refuge for many plants during the Quaternary, but that other species gradually disappeared due to the intensification of the monsoonal climate.

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Introduction

Both the change in climate and the diversification of angiosperms in the Cenozoic have greatly shaped the modern distribution of gymnosperms (Crisp and Cook, 2011). Climate during the Late Cenozoic in China changed dramatically due to the uplift of the Himalayas and the thinning of the Arctic ice cap (Han et al., 2012). This was characterized by the intensification of the Asian monsoon in southwestern China and aridification in western China (Sun and Wang, 2005). Owing to the scanty regional records of fossils, little is known of how gymnosperms responded during this transitional period.

The genus *Cedrus* (the true cedar) (Pinaceae) is well known for its horticultural use. There are now only four living species in *Cedrus* (Fig. 1). *Cedrus deodara* (Roxb.) Loud. is found in the western Himalayas. The other three species are all present in the Mediterranean region, viz. *Cedrus atlantica* (Loud.) Manetti in the Atlas Mountains of Morocco and Algeria, *Cedrus brevifolia* (Hook. f.) Henry in Cyprus, and *Cedrus libani* Loud. in Lebanon, Syria and Anatolia (Maheshwari and Biswas, 1970) (Fig. 1). Fossil pollen records indicate that *Cedrus* was once widely distributed in the Northern Hemisphere during the Cenozoic (Ferguson, 1967; Magri and Parra, 2002). Evidence from both fossil records and phylogenetic analyses suggests that *Cedrus* might have originated in the higher latitudes of Eurasia (Qiao et al., 2007) (Fig. 1). The earliest known *Cedrus*-like pollen was reported from the Jurassic of the Central Urals in Russia (Papulov and Bronnikova, 1963). Megafossils of *Cedrus* are scarce and are mainly represented by cone scales and wood remains (Fig. 1). *Cedrus lopatinii* Heer, the earliest record in the form of seed cones, seeds and cone scales, was uncovered from the Upper Cretaceous in Siberia (Samylina, 1988). The earliest record of wood, *Cedrus penzhinaensis* Blokhina & M. Afonin, was reported from the Lower Cretaceous in Kamchatka, Russia (Blokhina and Afonin, 2007).

Previous works mainly focused on the impact of Quaternary paleoenvironmental change in the distribution pattern of *Cedrus* around the Mediterranean (Cheddadi et al., 2009; Hajar et al., 2010). In northern Africa, *C. atlantica* from Algeria and Tunisia expanded during the last glacial period and the early Holocene, and then retreated in some areas thereafter about 8000 ^{14}C yr BP (Cheddadi et al., 2009). The distribution of *C. libani* in Lebanon and Syria declined as a result not only of the change in climate during the Quaternary (Hajar et al., 2010) but also of human activities in the Holocene (Loffet, 2004).

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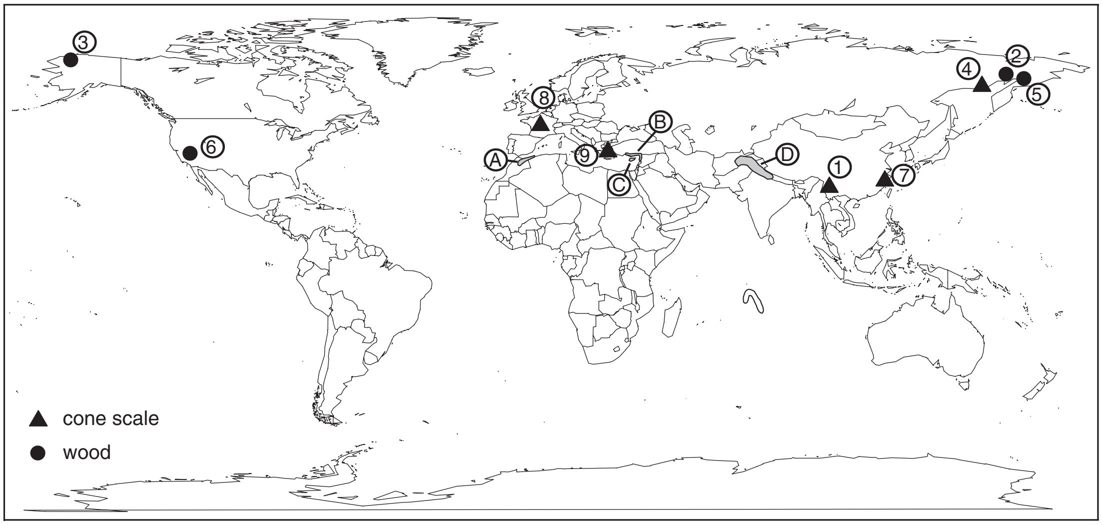

Figure 1. World map showing the modern distribution and megafossil records of *Cedrus*. Modern distribution: A. *Cedrus atlantica* (Loud.) Manetti; B. *C. libani* Loud; C. *C. brevifolia* (Hook. f.) Henry; D. *C. deodara* (Roxb.) Loud. Megafossil records: 1. *C. angusta* sp. nov., this study; 2. *C. penzhinaensis* Blokhina & M. Afonin from the Lower Cretaceous of Kamchatka, Russia (Blokhina and Afonin, 2007); 3. *C. alaskensis* Arnold from the upper Albian–Cenomanian of Alaska, USA (Arnold, 1952); 4. *C. lopatinii* Heer from the Upper Cretaceous of Siberia, Russia (Samylina, 1988); 5. *C. kamtschatkaensis* Blokh. from the Lower Eocene of Kamchatka, Russia (Blokhina, 1998); 6. *C. penhallowii* (Jeffrey) Bailey from the Miocene of California, USA (Barghoorn and Bailey, 1938); 7. *C. zhejiangensis* Li from the Pliocene of Zhengjiang, China (Nanjing Institute of Geology and Ministry of Geology and Mineral Resources of PR China (NIGMGMRPRC), 1982); 8, 9. *C. vivariensis* N. Boulay from the Pliocene of France and Greece, respectively (Boulay, 1887, 1892; Mai and Velitzelos, 1992).

Even though extant *Cedrus* survives in China, it has a much narrower distribution range than in the past. A single species, *C. deodara*, grows naturally in China where it is restricted to a small area in extreme southwestern Tibet (Fu et al., 1999; Fig. 1), but *Cedrus* pollen grains are quite common in Cenozoic sediments from China (Liu, 1990; Li, 1995; Lin et al., 2000; Xu et al., 2003; Xiao et al., 2009; Zhang and Jiang, 2010; Zhang et al., 2010). As far as the megafossil is concerned, only one record with cone scales is known until now: *Cedrus zhejiangensis* Li., reported from the Pliocene Qingtinggang Formation in Zhejiang Province, southeastern China (Nanjing Institute of Geology and Ministry of Geology and Mineral Resources of PR China (NIGMGMRPRC), 1982). Here we describe a new species of *Cedrus* based on cone scales from the Upper Pliocene Sanying Formation of Yunnan Province in southwestern China, where it is outside the present distribution range of living *Cedrus*. The shrinking distribution of *Cedrus* in response to the late Cenozoic change in climate is discussed.

Materials and methods

Geological setting

Fossil specimens were uncovered from Longmen village, Yongping County, western Yunnan Province, southwestern China (25°30′48″ N, 99°31′11″ E; Fig. 2). The fossil locality is situated at the southeastern boundary of the Qinghai-Tibet Plateau. At present, western Yunnan is under the influence of both the East Asian monsoon and the South Asian monsoon, with a warm, wet summer and a dry, cool winter (Wang, 2006). The fossil-bearing sediment belongs to the Sanying Formation, a widely distributed Upper Pliocene horizon in western and northwestern Yunnan Province (Compiling Group of the Regional Stratigraphic Table of Yunnan (CGRSTY), 1978; Ge and Li, 1999). Floras from the Sanying Formation are characterized by the dominance of evergreen sclerophyllous oaks (*Quercus* sect. *Heterobalanus*) (Tao and Kong, 1973), which are similar to the flora from the Upper Pliocene Yebokangjiale Formation in Xixiabangma Mountain in Tibet (Hsü et al., 1973). They are quite different from the Miocene floras in this region, such as the Miocene Shuanghe Formation from Jianchuan County, northwestern Yunnan, which is dominated by both Fagaceae and Lauraceae (Tao, 2000). In the Longmen flora, evergreen sclerophyllous oaks are the most abundant (Su, 2010), resembling other floras in western and northwestern Yunnan from the same formation (Tao and Kong, 1973; Ge and Li, 1999). Besides, both paleomagnetic studies (Li et al., 2013) and the mammal fossil record (Su et al., 2011) further support the geological assignment of the Longmen flora to the Upper Pliocene. Materials studied here were collected from the fine clay of the top layer in the sediment. The stratigraphy was extensively described by Su et al. (2011).

Materials

Approximately 2000 plant fossil specimens have been collected from the fossil-bearing layer of the Sanying Formation in Longmen village. Among them, 21 specimens bear coniferous cone scales. All the fossil specimens were collected over six fieldwork excursions between 2008 and 2010, and are deposited in the Paleobotany Laboratory, Xishuangbanna Tropical Botanical Garden, the Chinese Academy of Sciences. All the specimens illustrated here were photographed with a digital camera (Canon SX100). Detailed morphology of the fossils was observed under a dissecting microscope (Leica S8APO).

Specimens of the living species of *Cedrus* were checked in the Herbaria of Kunming Institute of Botany, the Chinese Academy of Sciences (KUN); Southwest Forestry University (SWFC), and Institute of Botany, the Chinese Academy of Sciences (PE). Fossil pollen records of *Cedrus* from Yunnan were compiled from previous literature (Fig. 2; Table 1).

Methods

The size of the cone scales in *Cedrus* varies, mainly depending on where the cone scales are located on a cone. We observed the cone scales only from the middle part of a cone to make these measurements comparable. Also, being the largest in size, these scales should be the most developed and therefore have morphological stability. Quantitative morphometric measurements of the scales were obtained by using the software ImageJ 1.45 s on digital images of the fossils (Wayne Rasband, National Institutes of Health, USA).

Late Cenozoic climate in Yunnan

The paleoclimates of Yunnan since the Late Miocene have been reconstructed quantitatively in recent years (Kou et al., 2006; Xia et al., 2009; Xie et al., 2012; Xing et al., 2012). These results indicate a

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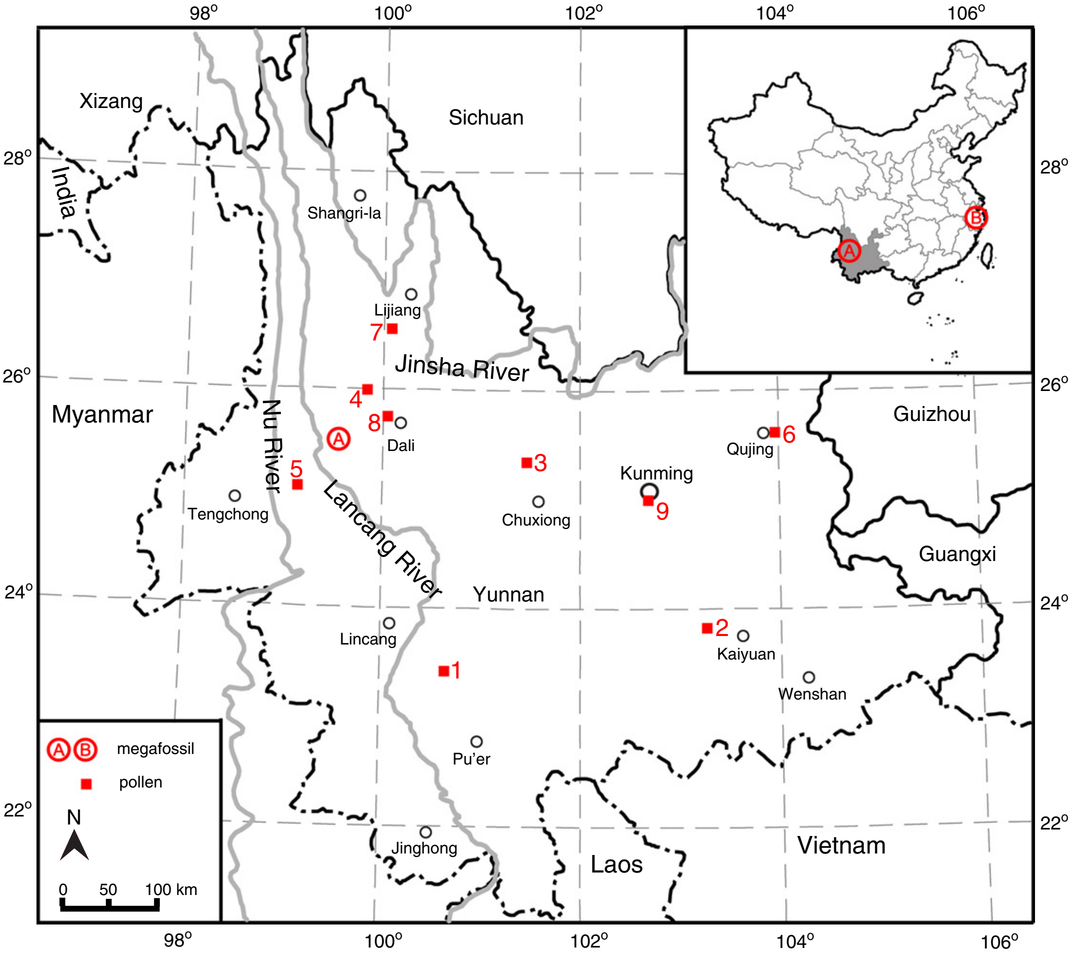

Figure 2. Map showing megafossil localities of *Cedrus* in China and fossil pollen sample localities of *Cedrus* in Yunnan Province. A. *C. angusta* with cone scales (this study); B. *C. zhejiangensis* Li. with cone scales (NIGMGMRPRC, 1982). 1–9, pollen records of *Cedrus* in Yunnan Province: 1. Jinggu Basin (Lin et al., 2000); 2. Xiaolongtan, Kaiyuan (Wang, 1996); 3. Lühe, Nanhua (Xu et al., 2000); 4. Sanying, Eryuan (Tao and Kong, 1973); 5. Yangyi, Baoshan (Xu et al., 2003); 6. Zhujie, Qujing (Wang and Shu, 2004); 7. Heqing Basin (Xiao et al., 2009); 8. Diancang Mountain, Dali (Kuang et al., 2002); 9. Dian Lake, Kunming (Tong et al., 1990).

warmer and wetter climate during the Neogene than the present day, which could be closely associated with the intensification of the Asian monsoon (Sun and Wang, 2005; Su et al., 2013). The monsoon intensity was quantified in a recent study by:

$$\mathrm{MSI} = (3\mathrm{WET} - 3\mathrm{DY}) * 100/\mathrm{GSP}$$ (Xing et al., 2012).

MSI is the monsoon intensity index, a high MSI indicates a higher precipitation difference in seasonality and a higher monsoon intensity (Xing et al., 2012); Precipitation during the three wettest months (3WET) and precipitation during the three driest months (3DRY); GSP is the precipitation with mean month temperature being no less than 10°C.

Table 1
Fossil pollen records of *Cedrus* in Yunnan Province. Site numbers correspond to those used in Fig. 2. Fossil sites indicated by asterisk have been investigated quantitatively, providing relative pollen percentages.

No.	Site	Age	Location	Reference
1	Jinggu Basin	Early Miocene	23°31′N, 100°43′E	Lin et al. (2000)
2	Xiaolongtan, Kaiyuan	Late Miocene	23°48′N, 103°11′E	Wang (1996)
3	Lü he, Nanhua	Middle Late Miocene to Early Pliocene	25°07′N,101°18′E	Xu et al. (2000)
4	Sanying, Eryuan	Late Pliocene	26°00′N, 099°49′E	Tao and Kong (1973)
5	Yangyi, Baoshan	Late Pliocene	24°57′N, 099°15′E	Xu et al. (2003)
6	Zhujie, Qujing*	Late Pliocene to Holocene	25°31′N, 103°53′E	Wang and Shu (2004)
7	Heqing Basin*	Late Pliocene to Holocene	26°34′N, 100°10′E	Xiao et al. (2009)
8	Diancang Mountain, Dali	Late Pleistocene	25°42′N, 100°08′E	Kuang et al. (2002)
9	Dian Lake, Kunming*	Quaternary	24°56′N, 102°42′E	Tong et al. (1990)

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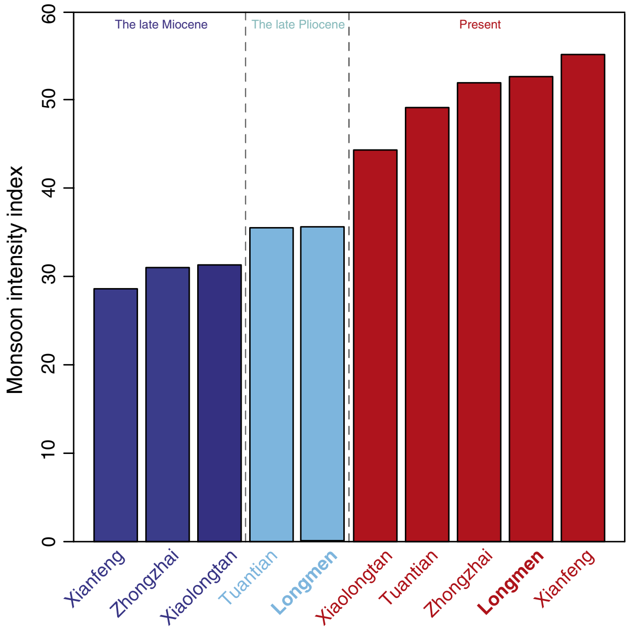

Figure 3. The evolution of the Asian monsoon since the Late Miocene in Yunnan, southwestern China (modified from Su et al., 2013). Climate data are from (1) Xianfeng (Xing et al., 2012); (2) Zhongzhai (Jacques et al., 2011a); (3) Xiaolongtang (Xia et al., 2009); (4) Tuantian (Su et al. (2013), recalculated paleoclimate data based on leaf physiognomic data from Xie et al. (2012)); (5) Longmen (Su et al., 2013). Climate data of the present day are from Yunnan Provincial Meteorological Bureau (1983).

MSIs of five Neogene floras in Yunnan are discussed here based on data from previous studies. Among them, three Late Miocene floras are included: the Xiaolongtan flora (Xia et al., 2009), the Zhongzhai flora (Jacques et al., 2011a) and the Xianfeng flora (Xing et al., 2012); and there are two Late Pliocene floras: the Tuantian (Xie et al., 2012) and the Longmen floras (Su et al., 2013). Paleoclimate data to calculate MSIs of all the five floras were obtained using Climate Leaf Analysis Multivariate Program (CLAMP) with a dataset calibrated by samples from Chinese living forests (PhysgAsia1 (Jacques et al., 2011b), available online: http://clamp.ibcas.ac.cn). CLAMP is a method for quantitative paleoclimate reconstruction based on Canonical Correspondence Analysis (CCA). Thirty-one leaf character states and 11 climate parameters derived from more than 200 samples from modern forests worldwide are available in the CLAMP datasets. Eleven paleoclimate parameters of a flora such as GSP, 3WET, 3DRY and mean annual temperature (MAT) can be quantitatively calculated if the leaf physiognomic data of this flora are known.

MSIs of these floras indicate a slight reinforcement of the Asian monsoon from the Late Miocene to the Late Pliocene, and a significant reinforcement since the Late Pliocene in Yunnan (Fig. 3). Meanwhile, a much drier winter is observed in the present day (Su et al., 2013), due to a drier airflow from the Siberian High since the Late Pliocene and the development of an ice cap at high latitudes in the Northern Hemisphere (Meyers and Hinnov, 2010). These results show an intensification of the Asian winter monsoon in southwestern China during the Quaternary.

Systematics

Order — Pinales Dumort, 1829.

Family — Pinaceae Lindley, 1836.

Genus — *Cedrus* Trew, 1757.

Species — *Cedrus angusta* sp. nov. T. Su, Z. K. Zhou et Y. S. Liu (Fig. 4).

Holotype: YP741A (Fig. 4A).

Paratypes: YP741B, YP734 (Fig. 4B), YP728 (Fig. 4C), YP735 (Fig. 4D), YP732 (Fig. 4E), YP737 (Fig. 4F).

Repository: Xishuangbanna Tropical Botanical Garden, the Chinese Academy of Sciences.

Type locality: Yangjie coalmine, Longmen village, Yongping County, western Yunnan Province, southwestern China (Fig. 2).

Stratigraphy: The Upper Pliocene Sanying Formation.

Etymology: The specific epithet *angusta*, narrow in Latin, refers to the narrow notch on the lateral margin relative to the wider notches in extant species.

Diagnosis: Cone scales flabellate or widely cuneate, wider than long. Upper margin round, smooth or slightly convex in the middle. The two lateral margins smooth or slightly wavy; symmetric and lobed; gradually narrowing towards the base. Radiate striae on cone scales. The middle part of the lateral margin with a notch. The basal part of cone scales wedged. A depressed groove extending from the base towards the middle of the ventral side of cone scale.

Description: Cone scales are flabellate or widely cuneate in shape (Fig. 4). The scales are wider (20–42 mm) than long (16–30 mm). The upper margin is round and smooth. Some cone scales present a convex middle part in the upper margin, 1 mm wide and 3–4 mm long (Figs. 4A and F). The two symmetric and lobed lateral margins are smooth (Fig. 4A) or slightly wavy (Fig. 4F). The lateral margin gradually narrows towards the base, at a 100°–160° angle. Dense radiate striae distributed equally on cone scales (Figs. 4A–F). Two parallel and narrow notches are present on both sides of lateral margins, 3–8 mm long and 0–1 mm wide (Fig. 4F). The wedged basal part is 8–14 mm wide and 6–10 mm long, with two seed impressions presenting on the dorsal side (Fig. 4F). A depressed groove runs through the middle of the base of the cone scale on the ventral side; it is 1–2 mm wide and 9–12 mm long, and extends throughout the basal part (Figs. 4A–E).

Remarks: Dispersed *Cedrus*-like winged seeds were uncovered from the same layer. These seeds are round on one margin and flat on the distal margin, 3–4 mm wide and 8–10 mm long (Figs. 4G and H). The wing is large and membranous, the distal half is the widest part of the wing (Figs. 4G and H). Two flat margins of the wing roughly form a right angle on the distal part (Figs. 4G and H), with the proximal margin 10–12 mm long and the distal margin ~13 mm long. Another proximal margin is round and ~12 mm long. These morphological characters are quite similar to seeds of *Cedrus*, but we did not find seeds attached to cone scales; therefore, it is too early to assign these seeds to *Cedrus* based on these limited morphological characters.

Discussion

Comparisons with living and fossil species

Within Pinaceae, cone scales of *Cedrus* closely resemble those of *Abies* (Liu, 1971). For example, the flabellate cone scales in *C. angusta* are similar to species such as *Abies concolor* (Gord. et Glend.) Lindl., *Abies grandis* (Dougl.) Lindl. and *Abies magnifica* A. Murr, and the size of the cone scales in *C. angusta* is similar to *Abies umbellata* Mayr. Cone scales of *Cedrus* mainly differ from those of *Abies* in three characters (Table 2). Firstly, the base of the cone scales in *Cedrus* is much wider than in most *Abies* species. Cone scales in *Cedrus* have a wedged base, whereas the cone scale of *Abies* has a narrow pedicel (Fig. 5A). An exception is *Abies cephalonica* Loud. var. *graeca* (Fraas) Liu, which has a broad cuneate base. Secondly, seeds in *Cedrus* are fully attached to the scale, but seeds in most *Abies* species hang in the air, such as in *Abies koreana* Wils., *Abies fargesii* Franchet (Fig. 5A) and *Abies nephrolepis* (Trautv.) Maxim. Thirdly, and most importantly, there is a notch in the middle part of the lateral margin of cone scales in *Cedrus*, whereas the notch is absent from *Abies*.

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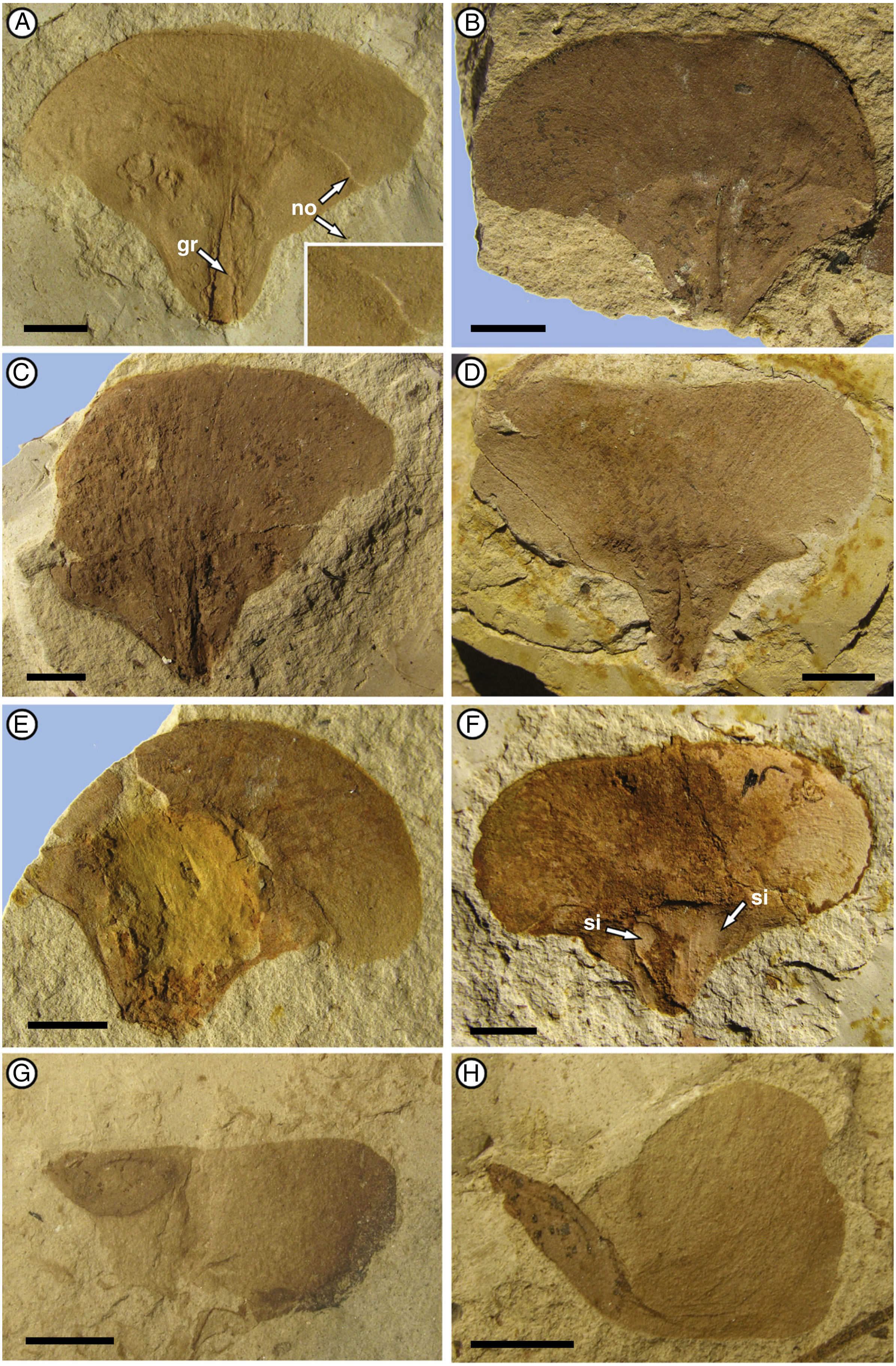

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Table 2
Morphological comparisons of cone scales in *Cedrus angusta* sp. nov. and selected species in Pinaceae.

Species	Length and width (mm)[a]	Shape	Middle part of the lateral margin	Width and length of the notch (mm)[a]	Pedicel
Cedrus angusta	30; 42	Flabellate or widely cuneate	Narrow notch	~0; 6	Wedged
C. atlantica	30; 40	Flabellate or widely cuneate	Wide notch	2; 8	Wedged
C. deodara	33; 45	Flabellate or widely cuneate	Wide notch	2; 9	Wedged
C. libani	37; 60	Flabellate or widely cuneate	Wide notch	3; 11	Wedged
C. zhejiangensis	27; 36	Flabellate	Wide notch	2; 5	Wedged
Abies cephalonica var. *graeca*	20; 30	Cyathiform or flabellate	Flat	–	Broad cuneate
A. concolor	30; 35	Flabellate	Suddenly constricted	–	Narrow pedicel
A. fargesii	14; 17	Flabellate	Auricled	–	Pedicel
A. grandis	25; 30	Flabellate	Suddenly constricted	–	Narrow pedicel
A. koreana	09; 20	Wing	Suddenly constricted	–	Narrow pedicel
A. mariesii	22; 25	Flabellate	Auricled	–	Pedicel
A. nephrolepis	12; 16	Reniform	Suddenly constricted	–	Pedicel

[a] Because of the large variation of size in cone scales of one cone, the biggest morphological values of cone scales in one species were listed here. In living species, the biggest cone scales are in the middle part of a cone. Measurements of *Cedrus* cone scales were made in this study; information on *Abies* is from Liu (1971).

Furthermore, in many *Abies* species, cone scales are more or less auricled at the middle part of two lateral margins, and cone scales in most *Abies* species are much smaller than in *C. angusta*.

C. angusta and the living *Cedrus* species share characters such as flabellate or widely cuneate-shaped cone scales and a notch in the middle of the lateral margin (Figs. 5B–D; Table 2). Cone scales of living *Cedrus* species have a raised ridge in the middle of the base on the ventral side (Fig. 5B) that separates the two winged seeds; there are two distinctive seed impressions on the dorsal side. These characters are also present in *C. angusta*. A depressed groove resembling an impression of the ridge was observed on the ventral side of cone scales in some specimens of *C. angusta* (Figs. 4A–D). Seed impressions were observed on the dorsal side of cone scales in *Cedrus* (Fig. 5C), and are present in *C. angusta* (Fig. 4F). Based on the shapes and sizes of the cone scales, *C. angusta* is similar to *C. atlantica* and *C. deodara*, but is significantly smaller than *C. libani* (Table 2).

The notch in the middle of the lateral margin in *C. angusta* is much narrower than in any living species of *Cedrus* (Table 2). Taphonomic constraints should be taken into account when comparing morphologies between fossil species and living species. We have noticed that some cone scales in living *Cedrus* bend when soaked in water, thus making a narrow notch. However, most cone scales of *C. angusta* are flat, and it is hard to say if this morphology is the same as before the preservation procedure, or has resulted from sediment pressure. Here, we assign these fossil materials to a new species based upon the morphological difference.

Some fossil records of cone scales have been reported from the Northern Hemisphere. For example, *C. lopatinii* Heer, the earliest fossil record of cone scales was reported from the Upper Cretaceous of western and eastern Siberia, since then some seeds and cones of *C. lopatinii* were discovered (e.g., Papulov and Bronnikova, 1963; Terekhova and Filippova, 1983). The shape of the cone scales resembles those of *C. angusta*, but because no cones are known from the Longmen flora, the shape of the seed cones cannot be compared. Another *Cedrus* with cone scales, *Cedrus vivariensis* N. Boulay, was reported from the Pliocene in Europe, e.g., Ardèche and Puy-de-Dôme of France (Boulay, 1887, 1892), and Vegora and Floria of Greece (Mai and Velitzelos, 1992). The lobed lateral margin of *C. vivariensis* is much wavier than that of *C. angusta*. In China, only one fossil species of *Cedrus* with cone scales has been reported. This species, *C. zhejiangensis* Li, from the Pliocene Qingtinggang Formation, Yuyao County, Zhejiang Province in eastern China (NIGMGMRPRC, 1982) is different from *C. angusta* in having a rapid contraction at the middle part of the lateral margin and a much wider notch in the middle of the lateral margin (Table 2).

Ecological implications

There are two ecological implications of this new find based on the preservation condition of the fossil materials and the fossil assemblage.

Firstly, the adaptation of seed dispersal in *Cedrus* by wind might have formed as early as the Late Cretaceous and has been maintaining ever since. It is interesting to notice that most of the confirmed records of cone scales in *Cedrus* appear to be dispersed and detached from their cones (Papulov and Bronnikova, 1963; NIGMGMRPRC, 1982; Mai and Velitzelos, 1992). They can be dated back to the Late Cretaceous record from both western and eastern Siberia (Papulov and Bronnikova, 1963). During our six field trips, we did not find any *Cedrus* fossil cones; only separated cone scales and *Cedrus*-like seeds were discovered. In the living species of *Cedrus*, cone scales and winged seeds usually detach from the central axis of the ripe cone, as is also the case in *Abies* and *Pseudolarix* (Fu et al., 1999). *Cedrus* seeds are characterized by a large membrane wing that might be associated with wind dispersal. The detachment of cone scales and seeds from the ripe cone would further facilitate wind dispersal.

Secondly, it is likely that *Cedrus* maintained a montane habitat in western Yunnan in the Pliocene. During the Pliocene, a series of mountains in western Yunnan Province were built as a consequence of the uplift of the Himalayas (Kou et al., 2006), which in turn inevitably created an opportunity for altitudinal differentiation of vegetation zones. About three-quarters of the total 2000 specimens collected in the Longmen flora appear to be evergreen sclerophyllous oaks (*Quercus* sect. *Heterobalanus*) (Su, 2010), strongly indicating that a dense oak forest must have been present in this region during the Pliocene. In modern environments, without human disturbance, evergreen sclerophyllous oaks tend to form a monodominant forest with a thick canopy, excluding all other woody species. Therefore, it is likely that *C. angusta* coexisted with other woody species found in the Longmen flora, such as *Populus*, *Rhododendron* and *Salix*, and would have lived at a higher altitude than the evergreen sclerophyllous oak forests (Su, 2010).

The disappearance of Cedrus in southwestern China is closely associated with the monsoon intensification

Widespread pollen fossil records suggest that *Cedrus* occurred widely in the Paleogene throughout northern China (e.g., Liu, 1990; Zhang and Jiang, 2010; Zhang et al., 2010). However, Paleogene pollen records of *Cedrus* appear to be quite rare in southern China. This supports the hypothesis of the high latitude origination of *Cedrus*

Figure 4. *Cedrus angusta* sp. nov. and *Cedrus*-like seeds, scale bar = 5 mm. A–F. Cone scales. A–D. ventral side; F: dorsal side. A. Holotype YP741A. no = the notch on the lateral margin; gr = the depressed groove in the middle of the basal part of cone scale. B. Paratype YP734. C. Paratype YP728. D. Paratype YP735. E. Paratype YP732. F. Paratype YP737. si = seed impression. G, H. *Cedrus*-like seeds. G. Paratype YP1695. H. Paratype YP739.

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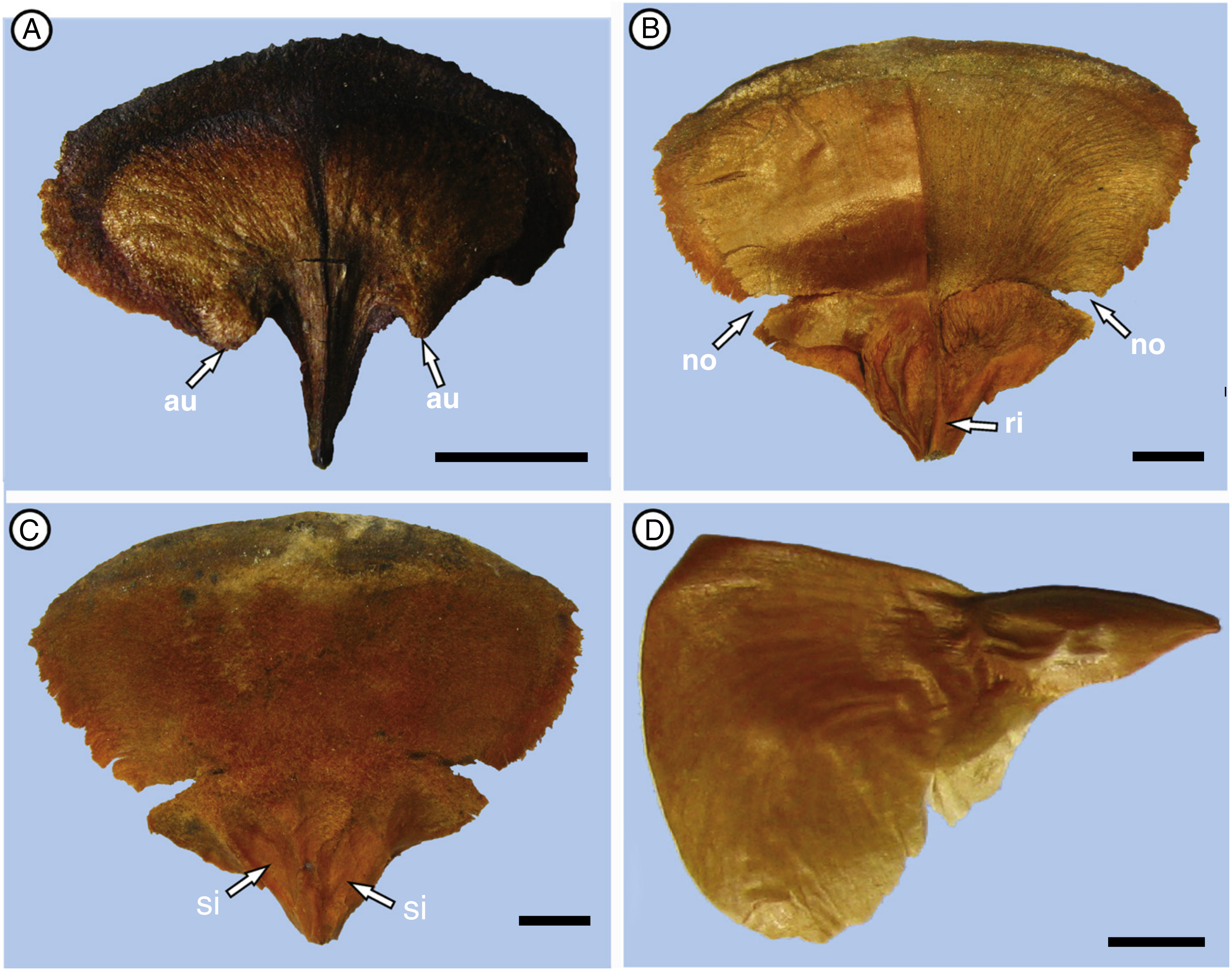

Figure 5. Morphology of cone scales and seeds in *Cedrus* and *Abies*. Scale bar = 5 mm. A. *Abies fargesii* Franchet, ventral view. au = auricle. B, C. *Cedrus atlantica* (Loud.) Manetti. B. Ventral view; C. Dorsal view. si = seed impression. D. Winged seed of *C. atlantica*.

concluded by molecular work (Qiao et al., 2007). The presence of *C. zhejiangensis* confirms the existence of *Cedrus* in eastern China during the Pliocene (NIGMGMRPRC, 1982). But most of the Neogene *Cedrus* pollen fossils are reported from southwestern China (Table 1). Using pollen records in Yunnan as an example, *Cedrus* pollen was reported from the Upper Miocene in Jinggu County (Lin et al., 2000; Fig. 2). There are also some Late Miocene *Cedrus* pollen records from Yunnan, e.g., in Kaiyuan (Wang, 1996; Fig. 2) and Nanhua (Xu et al., 2000; Fig. 2). An investigation of a coring sample in Heqing, western Yunnan, revealed that *Cedrus* pollen occurred from the Late Pliocene to the middle Holocene (Xiao et al., 2009; Fig. 6). However, the percentage of *Cedrus* pollen was low with evidence of decreasing abundance through geological time (Fig. 6). This might suggest that *Cedrus* populations were declining during the Quaternary in Yunnan. It would be expected that detailed work on high-resolution sampling is needed to evidence when *Cedrus* disappeared there.

The discovery of *C. angusta* in the Longmen flora provides megafossil evidence confirming the existence of *Cedrus* in southwestern China during the Late Pliocene. As mentioned above, *Cedrus* might have survived in this region at a higher altitude than evergreen sclerophyllous oak forests along the mountains in the Late Pliocene, but then it disappeared there. The disappearance of *Cedrus* in southwestern China was not likely due to the human activity, because *Cedrus* was not used in Chinese traditional culture. The distribution pattern of plants is closely associated with climate (Quirk et al., 2013); temperature and precipitation are the most important climate factors for plant distribution (Woodward, 1987). It is probable that lower temperatures during the Quaternary glaciations affected the distribution of *Cedrus* in western Yunnan, but these cold periods would have only had a minor impact on the survival of *Cedrus*: Cheddadi et al. (2009) mentioned that the last glaciation contributed to *Cedrus* expanding. We hypothesize that the disappearance of *Cedrus* in southwestern China during the Quaternary may be linked to the intensification of the Asian winter monsoon as discussed below.

During the Neogene, the uplift of the Himalayas gradually increased the intensification of the Asian monsoon (Xia et al., 2009; Jacques et al., 2011a; Xing et al., 2012), which formed seasonal variation in precipitation in southwestern China and aridification in northern and western China (Sun and Wang, 2005). Paleoclimate reconstructions based on plant fossils show that the seasonality of precipitation during the Neogene was not as strong as at present in southwestern China (Kou et al., 2006; Xie et al., 2012; Xing et al., 2012). After the Late Pliocene, the Asian winter monsoon became significantly stronger, because the development of ice at high latitudes in the Northern Hemisphere leads to the strengthening of a drier airflow from the Siberian High (Meyers and Hinnov, 2010). The

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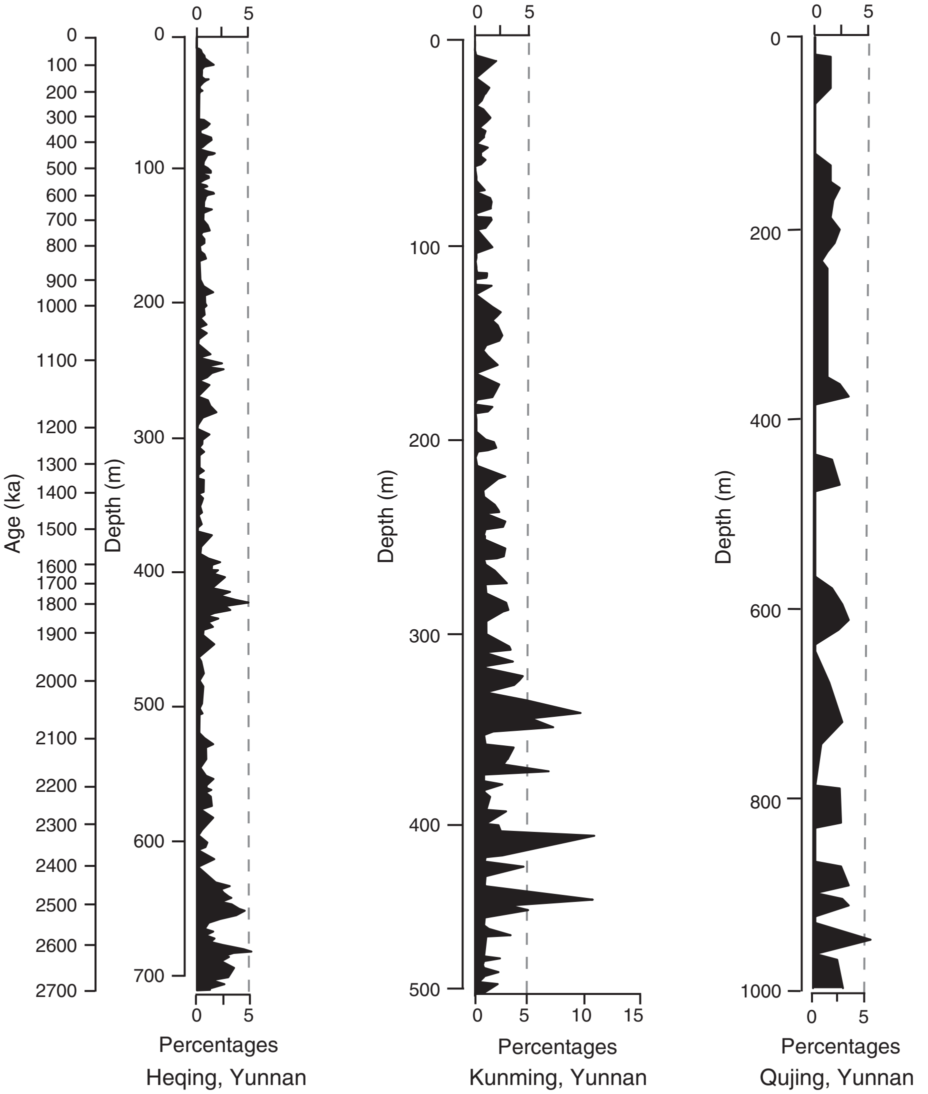

Figure 6. Fossil pollen diagrams of *Cedrus* in three sediments of Yunnan Province. Site numbers correspond to Fig. 2 and Table 1. Heqing, southwestern Yunnan (after Fig. 2 in Xiao et al., 2010); Kunming, central Yunnan (after Fig. 1 in Tong et al., 1990); Qujing, northeastern Yunnan (after Fig. 1 in Wang and Shu, 2004).

enhancement of the Asian winter monsoon during the Quaternary has been revealed by Chinese loess records (Han et al., 2012). Neogene climate reconstructions in Yunnan further support this enhancement (Su et al., 2013). Paleoclimate reconstructions indicate that the monsoon intensity increased slightly from the Late Miocene to the Late Pliocene, but increased significantly after the Late Pliocene (Fig. 3). Nowadays, the Asian winter monsoon has greatly decreased the winter precipitation in southwestern China (Wang, 2006). For example, the precipitation in winter during the Late Pliocene was 800 mm in Longmen (Su et al., 2013), whereas the precipitation in winter has now dramatically dropped to 43 mm (Fig. 7H; YPMB, 1983).

Seeds of *Cedrus* are recalcitrant and germinate immediately when they mature (Kumar et al., 2011). These seeds usually detach from the central axis of cones when cones ripen in autumn (Maheshwari and Biswas, 1970). Seeds of *Cedrus* germinate soon after they fall to the ground in autumn, and the young seedlings benefit from the wet winter for survival. In regions where living *Cedrus* occur naturally, the winter is relatively wet (Figs. 7A–G). The Mediterranean climate is characterized by a wet winter and a dry summer. For example, in Hadeth el Jebbe, Lebanon where *C. libani* lives, the precipitation during the winter is 654 mm, whereas the precipitation during the summer is only 6 mm (Fig. 7C). Even if the winter precipitation in the western Himalaya is much lower than in the Mediterranean, the driest season in the western Himalaya usually occurs in autumn, and precipitation in winter is higher than in the eastern Himalaya (Figs. 7E and F).

Therefore, the wetter winter during the Neogene could have allowed *Cedrus* to survive in the mountains of southwestern China. Under the current climate; however, new seedlings of *Cedrus* would suffer a dry period from late autumn to late spring when the wet season comes (Fig. 7H). Consequently, *Cedrus* may encounter trouble in seedling establishment for seasonal lack of water. Ward et al. (2005) point out that the extinction of one species might take place over a long period in deep time; thus *C. angusta* gradually disappeared under the climate change of southwestern China during the Quaternary.

Conclusions

A new fossil species, namely *C. angusta*, is proposed with cone scales discovered from the Upper Pliocene of Yongping in southwestern China, which is outside the present geological distribution range of living *Cedrus* species. We conclude that *Cedrus* disappeared from southwestern China because of the strength of the Asian winter monsoon during the Quaternary, which formed a much drier winter than the winter during the Neogene in southwestern China, and also drier than the winter in the distribution regions where living *Cedrus* exist.

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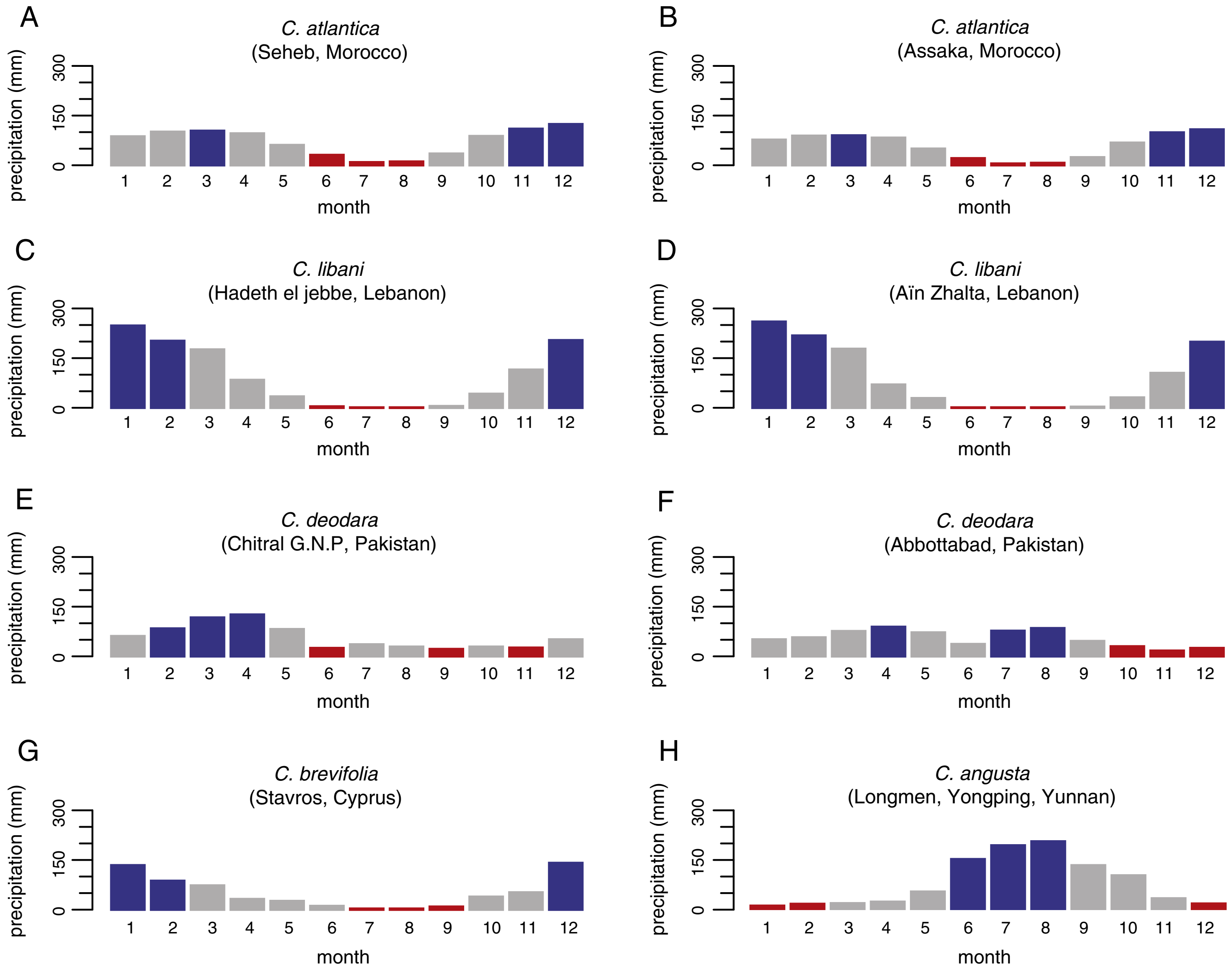

Figure 7. Mean monthly precipitation of selected sites where natural *Cedrus* forests exist and mean monthly precipitation of Yongping County at present. Location information: A, B: Cheddadi et al. (2009); C, D, G: Ducrey et al. (2008); E, F: Ahmed et al. (2011); H: this study. Precipitation data of Yongping today (H) are from Yunnan Provincial Meteorological Bureau (YPMB), 1983. Precipitation data of sites A–G are from Worldclim (http://www.worldclim.org). Blue = precipitation in the three wettest months; Red = precipitation in the three driest months.

Because the seeds of *Cedrus* tend to germinate immediately when they mature in the autumn, the young seedlings of *Cedrus* would be unable to survive under such a prolonged dry period. Consequently, *Cedrus* disappeared in southwestern China.

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