A new *Tsuga* species from the upper Miocene of Yunnan, southwestern China and its palaeogeographic significance

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Abstract

A new fossil species, *Tsuga xianfengensis* Xing et Zhou, n. sp., is reported based on two compressed seed cones. The fossil cones were discovered from the upper Miocene Xiaolongtan Formation at the Xianfeng Basin of Yunnan, southwestern China. The discovery of the *Tsuga* cones confirms the presence of *Tsuga* in the Miocene of central Yunnan and represents the earliest *Tsuga* macrofossils in the southwestern China. The new species reveals a close affinity with East Asian *Tsuga* species, *T. chinensis* and *T. dumosa*. It provides fossil evidence to support the molecular data that the Asian clade might be differentiated in the Miocene.

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Keywords: *Tsuga xianfengensis* n. sp.; Upper Miocene; Palaeobiogeography; Yunnan; China

1. Introduction

The hemlock (genus *Tsuga*), belonging to the family Pinaceae, is an important component of the subalpine and lowland humid coniferous and broad-leaved forests (Horikawa, 1972; Farjon, 1990; Fu et al., 1999). As *Tsuga* species are shade tolerant and cannot tolerate long periods of drought, they are usually considered as good indicators of the past environment (LePage, 2003; Yang et al., 2009). Up to twenty five extant species of *Tsuga* have been described in the past, with eight to thirteen species currently accepted by different authors (Flois, 1936; Gaussen, 1966; Zheng, 1983; Silba, 1986; Farjon, 1990; Fu et al., 1999; Eckenwalder, 2009; Farjon, 2010). Currently, the most accepted system is Farjon’s classification, which contains nine species and two of them occur in western North America, two in eastern North America, two in Japan, and three in China and Himalayas (Farjon, 1990, 2010).

It is difficult to explain the biogeography of *Tsuga* according to phylogenetic analyses based solely on extant species (Havill et al., 2008). For instance, the latest phylogeny showed that one eastern North American species, *T. canadensis*, is sister to the Asian clade whereas the other eastern North American species, *T. caroliniana*, is nested with Asian species (Havill et al., 2008). They accounted for this current disjunct distribution pattern as a result of an initial widespread circumpolar distribution with subsequent vicariance and extinction events.

Fossil evidence provides another source to understand the biogeography of *Tsuga*. The fossil record of *Tsuga* was well represented in North America and Eurasia from the Late Cretaceous to Plio-Pleistocene including wood, leaves, seeds, pollen, and seed cones (see review in LePage, 2003). The earliest fossil record of *Tsuga* was represented by pollen from the Late Cretaceous (ca. 90 Ma) in Poland (Macko). During the Paleocene, fossil pollen of *Tsuga* was found from the Spitsbergen and Scotland (Manum, 1962; Boulter and Manum, 1989). From the Eocene to the Pliocene, *Tsuga* pollen spread into the whole Eurasia and North America (see review in LePage, 2003). During the Pleistocene, *Tsuga* pollen is found in middle latitudinal regions of Eurasia and eastern North America but disappeared in high latitudinal regions of Eurasia and western North America (see review in LePage, 2003). The earliest known *Tsuga* macrofossils were discovered from the middle Eocene deposits (ca. 48.7 Ma) in North America (Currah et al., 1998). By examining the distribution patterns of *Tsuga* fossils, LePage (2003)
concluded that the exchange of representatives between North America and Europe occurred across the North Atlantic land bridges prior to their demise at the end of the Eocene, whereas the exchange between North America and Asia occurred throughout the Cenozoic across the Beringian Corridor.

Fossil pollen records indicate that *Tsuga* has been widely distributed in North and Northeast China during the Cenozoic (Li, 1998; Wang, 1999; Sun and Wang, 2005; Yang et al., 2009). During the Paleogene, *Tsuga* species were widely distributed in North and Northeast China at least to 48°N (Xia and Wang, 1987; Li, 1998). Since the Miocene, *Tsuga* fossil pollen records were abundant from northwestern to eastern China (Wang, 1999; Sun and Wang, 2005). However, the fossil record of *Tsuga* is sparse in the southwestern China where one-third of extant *Tsuga* occur. Up to the present, the oldest macrofossil *Tsuga* preserved as fossil wood in this region was discovered from the

![Fig. 1. Location and sampled outcrop of fossil locality (black triangle) of *Tsuga xianfengensis* n. sp.](image)
Pliocene deposits from Yunnan Province in southwestern China, which was assigned to the extant *T. dumosa* (*Yi* et al., 2005). A few fossil cones have been reported from the late Pliocene Mula Formation, Sichuan Province (*Chen* et al., 1986). However, molecular phylogeny suggested that the differentiation of Asian species happened during the Miocene (*Havill* et al., 2008). The controversy between fossil and molecular data limited our understanding on the evolution of *Tsuga*.

In the present study, we report a new *Tsuga* fossil species based on two compressed cones from the late Miocene Xianfeng flora of Yunnan. This new species is compared with all extant and selected fossil *Tsuga* species. The discovery of the new species confirms the presence of *Tsuga* in southwestern China since the late Miocene and agrees with the molecular data that the Asian lineage might be differentiated in the Miocene.

### 2. Geological setting

Two fossil cones were collected from Xianfeng coal mine (*Fig. 1*; 25°25′N, 102°51′E, 2200 m AMSL), located about 60 km north of Kunming, Yunnan Province, southwestern China. The geology of this coal mine was discussed in several studies and the fossiliferous layers were assigned to the Xiaolongtan Formation (*Fig. 2; Xing et al., 1999; Wu et al., 2006*). The lithological sequence of this formation comprises four members, named as N1 1–x–N1 4x. The present fossils were collected in the layer of N1 3x, which also yielded abundant plant macrofossils, shells, and insect fragments (*Xing* et al., 1999; *Wu* et al., 2006; *Xing* et al., 2010, 2012, 2013). Based on mammal fossils (*e.g.*, *Potamochoerus parvulus* and *Listriodon* sp.) (*Dong, 2001*), plant macrofossils (*Zhou, 1985, 2000,*), and pollen (*Wang, 1996*), the geological age of the Xiaolongtan Formation was determined as the late Miocene.

### 3. Materials and methods

The fossil and extant cones for comparison were photographed using Canon PowerShot SX100 IS. The paratype was demineralized in cold 5% HCl for 24 h to remove all carbonates, rinsed with distilled water and immersed in 48% HF for 3–5 days. The HF was changed at least twice to ensure removal of silicates. The specimen was then rinsed with distilled water and dried in air. The internal structure of the paratype was examined using X-ray CT scanner (Comscan Techno Co. Ltd., ScanXmate-A130S145) at Chuo University, Japan. All the specimens of fossil and living comparatives are housed in the Herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences. Description of morphology follows terminology of Flora of China (*Fu* et al., 1999). To better determine its systematic position, we compared the morphology of the current fossils with both extant and fossil gymnosperm species. The morphological data of extant species are based on the Flora of China (*Fu* et al., 1999), Flora of North America (*Taylor, 1993*), and the Gymnosperm database (*Earle, 1997*).

### 4. Results

#### 4.1. Systematics

Family Pinaeae Lindley  
Genus *Tsuga* (Endl.) Carrière

*Tsuga xianfengensis* Xing et Zhou, n. sp.  
(*Figs. 3A–G, 4A, D*)

### Etymology: The specific epithet refers to the name of fossil locality.

**Types:** Holotype: HLT 1300 (*Figs. 3A, 4A, D*). We choose a fragmentary seed cone as the holotype, because the complete one (HLT 1301) may represent an immature cone. Paratype: HLT 1301 (*Fig. 3B–G*).

**Diagnosis:** Seed cone narrowly ovate, symmetric. Scales ovate-elliptic to broadly ovate-elliptic, with rounded to acute apices, entire and slightly recurved margins. Bracts nearly cuneate, margin smooth. Cone axis thin. Narrow pith constructed of parenchyma cells. Seeds ovoid to oblong.

**Collecting locality:** The Xianfeng Basin (25°25′N, 102°51′E), about 60 km north of Kunming, Yunnan Province, China (*Fig. 1*).  
**Occurrence:** The upper sub-member (N1 3x) of the third member of the Xiaolongtan Formation, upper Miocene.  
**Repository:** Herbarium of the Kunming Institute of Botany, Chinese Academy of Sciences (KUN).

#### 4.2. Description

4.2.1. **External morphology**

The fossil cones are narrowly ovate, closed, symmetric, 20–30 mm long, 10–15 mm wide (*Fig. 3A, B,*). There are 16–20 woody ovuliferous scales helically arranged around the central axis. The scales are obovate, 6–10 mm long, 5–8 mm wide. The exposed part of the scale is striate. The cone scales near the apex and base of the cone are slightly smaller than those located near the middle (*Fig. 3A, B,*). The apices of the scales are rounded to acute, entire and slightly recurved margins (*Fig. 3A, B,*). The scales of the paratype are slightly thin, which might represent a younger cone (*Fig. 3B,*).

4.2.2. **Internal morphology**

The internal characters of the paratype were examined under the X-ray CT scanning (*Fig. 3C–G*). The cone axis is roughly 10 mm long, 1.2 mm in diameter. The pith is ca. 0.5 mm in diameter, constructed of parenchyma cells (*Fig. 3C, G,*). Resin canals and sclerenchyma are absent from the pith (*Fig. 3C, F, G,*). The bracts are minute, ca. 3–4 mm long, cuneate in shape (*Fig. 3D, E,*). The seed bodies were not seen. However, there are several seed positions can be seen under the CT scanning (*Fig. 3D,*). It shows that two seeds are borne on the adaxial surface of each ovuliferous scale (*Fig. 3D,*). The seeds are ovoid-oblong, 2–3 mm long, and 1.5–2 mm wide (*Fig. 3D,*). The seed wing cannot be seen.
Fig. 2. Stratigraphy and lithology of the Xianfeng coal mine (after Xing et al., 2010). The member where the fossils were collected is marked as pentagram.

5. Discussion

The fossils possess helically arranged cone-scale complex. In all gymnosperm families, only Pinaceae and Araucariaceae have such cone-scale complex. However, Araucariaceae scales are one-seeded and without distinct bracts, which are different from the current fossils (Silba, 1986). Thus, these two fossils can be clearly assigned to the family Pinaceae. The current fossils can be distinguished from the genera Pinus (4–50 cm long, Frankis, 2002), Cedrus (5–10 cm long, Vidakovic, 1991), Abies (6–30 cm long, Farjon, 1990), Picea (5–18 cm long, Fu et al., 1999) and Keteleeria (6–25 cm long, Fu et al., 1999) in the Pinaceae, which have much larger cone (Fu et al., 1999). The present fossils are differentiated from Cathaya by having thinner scales than Cathaya (Fu et al., 1999). Pseudotsuga could be easily distinguished from the current fossils in having distinctly
exserted bracts and *Pseudolarix* differs from our fossils in having ovate-lanceolate (pointed triangular) scales (Fu et al., 1999). Our fossils share similar cone size, shapes and scale characters with the genera *Larix* and *Tsuga*. However, *Larix* has ovate or lanceolate bracts (Fu et al., 1999) whereas our fossils have cuneate bracts. Thus, the features of current fossils leave no doubt that the cones belong to the genus *Tsuga*. In order to better determine the taxonomy of current fossils, we compared them with both extant and fossil species based on the characters of the cones (Table 1).

5.1. **Comparison with living species of Tsuga**

The cone-scale complex characters of the genus *Tsuga* are very important features and can provide reliable identification and separation of living and fossil species (LePage, 2003). Seed cones of *T. xianfengensis* are narrowly ovate, the scales are obovate, scale apex is nearly rounded and margins are slightly recurved, and the bracts are cuneate. The western North American species, *T. mertensiana*, differs from *T. xianfengensis* in several characters such as having oblong cylindric cone shape, larger cone size and ligulate to cuspidate bract shape (Table 1; Taylor, 1993; LePage, 2003). *T. diversifolia* differs from *T. xianfengensis* in possessing a smooth, not striate, exposed part of the scales (Table 1; Earle, 1997). The fossils could not be distinguished from other extant species by cone shape, size, and other external features. However, bract morphology is a useful, but commonly overlooked, feature for species level segregation in the family Pinaceae (Liu, 1971; LePage and Basinger, 1991, 1995; LePage, 2001). After examining the bract morphology
Table 1
Comparison of *Tsuga xianfengensis* n. sp. to living and fossil *Tsuga* species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
<th>Cone shape</th>
<th>Cone size (length × width, cm)</th>
<th>Scale shape</th>
<th>Scale size (length × width, cm)</th>
<th>Scale apex</th>
<th>Exposed part of scale</th>
<th>Bract shape</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Tsuga xianfengensis</em> n. sp.</td>
<td>Yunnan, southwestern China</td>
<td>Narrowly ovate</td>
<td>2–3 × 1–1.5</td>
<td>Obovate to narrowly ovate</td>
<td>0.6–0.8 × 0.5–0.8</td>
<td>Nearly rounded to acute, entire, margins slightly recurved</td>
<td>Striate, margin not thickened</td>
<td>Cuneate</td>
</tr>
<tr>
<td><em>T. dumosa</em></td>
<td>Himalayan region</td>
<td>Ovate or narrowly ovate</td>
<td>1.5–3 × 1–2</td>
<td>Obovate-orbicular</td>
<td>1–1.4 × 0.7–1.2</td>
<td>Nearly round to acute, entire, margins slightly recurved</td>
<td>Striate, margin not thickened</td>
<td>Cuneate-rhombic, margin denticulate, apex 2-lobed</td>
</tr>
<tr>
<td><em>T. chinensis</em></td>
<td>South China</td>
<td>Ovate</td>
<td>1.5–2.5 × 1.2–1.6</td>
<td>Pentagonal-ovate, subsquare, or suborbicular</td>
<td>0.9–1.2 × 0.8–1.1</td>
<td>Rounded or nearly truncate</td>
<td>Striate, glabrous</td>
<td>Cuneate-obovate or obtriangular, apex erose, sometimes 2-lobed</td>
</tr>
<tr>
<td><em>T. forrestii</em></td>
<td>Southwestern China</td>
<td>Narrowly ovoid or ovoid-cylindric</td>
<td>(2)2.5–4 × 1.5–3</td>
<td>Narrowly ovate or oblong</td>
<td>1.3–1.5 × 1–1.3</td>
<td>Rounded or nearly truncate</td>
<td>Striate, margin thickened</td>
<td>Cuneate-obovate or obtriangular, apex erose, sometimes 2-lobed</td>
</tr>
<tr>
<td><em>T. sieboldii</em></td>
<td>South Japan</td>
<td>Ovoid-conic</td>
<td>(1.6)2–2.5 × 1.4–2</td>
<td>Nearly round</td>
<td>0.8–1.2 × 0.8–1.2</td>
<td>Rounded</td>
<td>Striate</td>
<td></td>
</tr>
<tr>
<td><em>T. diversifolia</em></td>
<td>North Japan</td>
<td>Ovate to elliptic</td>
<td>1.5–2.5 × 1.5–2</td>
<td>Orbicular to ovate</td>
<td>0.5–1.2 × 0.4–1</td>
<td>Rounded and entire</td>
<td>Not striate</td>
<td>Truncate and bi-apiculate</td>
</tr>
<tr>
<td><em>T. heterophylla</em></td>
<td>West North America</td>
<td>Ovoid</td>
<td>1.5–2.5 × 1.5–2.5</td>
<td>Suborbicular to ovate to ovoid-oblong to oblong</td>
<td>0.5–1.6 × 0.4–1</td>
<td>Rounded to obtuse</td>
<td>Striate</td>
<td>Triangular</td>
</tr>
<tr>
<td><em>T. caroliniana</em></td>
<td>East North America</td>
<td>Ovate to elliptic</td>
<td>2.5–4 × 1.5–2.5</td>
<td>Ovate to cuneate</td>
<td>0.6–2 × 0.5–1.2</td>
<td>Rounded and entire</td>
<td>Striate</td>
<td>Weakly trilobite</td>
</tr>
<tr>
<td><em>T. canadensis</em></td>
<td>East North America</td>
<td>Ovoid</td>
<td>1.5–2.5 × 1–1.5</td>
<td>Ovate to cuneate</td>
<td>0.5–1.2 × 0.4–1</td>
<td>Rounded and often projected outward</td>
<td>Striate</td>
<td>Flabellate to truncate and denticulate</td>
</tr>
<tr>
<td><em>T. mertensiana</em></td>
<td>West North America</td>
<td>Oblong to cylindric</td>
<td>3–8 × 1.1–3</td>
<td>Obovate to cuneate</td>
<td>0.5–1.5 × 0.5–0.7</td>
<td>Rounded to acute</td>
<td>Not striate</td>
<td>Ligulate to cuspidate</td>
</tr>
<tr>
<td><em>T. swedaea</em> (fossil)</td>
<td>West North America</td>
<td>Elliptic to narrow elliptic</td>
<td>2–3.2 × 1–1.5</td>
<td>Obovulate to wide elliptic</td>
<td>0.5–1 × 0.5–0.7</td>
<td>Rounded and entire</td>
<td>Not striate</td>
<td>Ligulate to cuspidate</td>
</tr>
</tbody>
</table>
Fig. 4. Comparison of the fossil cones and bract with the extant East Asian Tsuga species. (A, D) HLT 1300; (B, E) T. chinensis, KUN 0012413; (C, F) T. chinensis, KUN 0142646; (G, J, H, K) T. dumosa, KUN 0012727; (I, L) T. forrestii, KUN 0143088. Scale bar = 5 mm.

of the extant species, LePage (2003) stated that the bract shape is distinct within all extant species (Table 1). As T. xianfengensis has cuneate bracts, it could be distinguished from T. sieboldii, T. diversifolia, T. heterophylla, T. caroliniana, and T. candensis, which all have different bract shapes (Table 1). Though LePage (2003) stated that all extant species possess distinct bracts, our examination showed that bract shape is not a stable character at least in three species from the southwestern China and each species in this region usually possesses different types of bracts (Fig. 4E, F, J–L). However, the cuneate bract could only be found in the three East Asian species. In these three extant species, T. forrestii usually has thickened scale margins, which is different from the current fossils (Fu et al., 1999). Thus, according to the above discussions, T. xianfengensis...
5.3. Ecological and palaeogeographical implications of *Tsuga* xianfengensis

Modern *Tsuga* species are shade tolerant and cannot tolerate long periods of drought, and they require at least 720 mm mean annual precipitation and 634 mm precipitation during growing season in the Asian monsoon region (Yang et al., 2009). In southwestern China, *Tsuga* species usually occur in the broad-leaved evergreen forests (Fu et al., 1999). The closely related extant species of *T. xianfengensis*, *T. chinensis* and *T. dumosa*, all require a warm and humid climate. *T. chinensis* requires an MAT of 10.9–18.6 °C and an MAP of 635–1489 mm (Yang et al., 2009) and *T. dumosa* requires an MAT of 15.7–21.7 °C and an MAP of 1096–1864 mm (Utescher and Mosbrugger, 1997–2012). Thus, the discovery of the new *Tsuga* cones indicates a relatively humid climate in the late Miocene of the central Yunnan, which is also consistent with the palaeoecological reconstructions of the Xianfeng flora. The recent palaeoclimatic reconstruction shows that the Xianfeng flora had a warmer (MAT from Coexistence approach: 17.2–21.7 °C) and much more humid (MAP from Coexistence approach: 1206.0–1613.0 mm) climate than the present (MAT: 14.9 °C; MAP: 1003.2 mm) during the late Miocene (Xing et al., 2012).

As mentioned above, molecular data suggested that the differentiation of the Asian *Tsuga* species happened in the Miocene (Havill et al., 2008). However, the previous fossil records of *Tsuga* in southwestern China, such as the *Tsuga* wood fossil from the Yangyi Formation (Yi et al., 2005) and fossil cones from the Mula Formation (Chen et al., 1986), are of the Pliocene age. The discovery of the new fossil cones confirms the existence of hemlock in Yunnan since the late Miocene. It suggests that the differentiation of *Tsuga* species can be traced back at least to the late Miocene in southwestern China, which is consistent with the molecular data.

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