Acta Palaeobotanica 47(1): 281–289, 2007

Epidermal structures of *Cryptomeria japonica* and implications to the fossil record

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Received 2 August 2006; accepted for publication 12 December 2006

ABSTRACT. Epidermal structures of leaves from two varieties of *Cryptomeria japonica* D. Don, *var. japonica* occurring in Japan and *var. sinensis* distributed within south China, were investigated. The results suggest that the two varieties cannot be discriminated based on epidermal structures, but the epidermal structures can be used to distinguish *Cryptomeria* from other genera of the former Taxodiaceae (now included in the Cupressaceae). The leaves are amphistomatic, the stomatal bands on the adaxial leaf surface are more strongly developed than those on the abaxial surface in *Cryptomeria*, and they are generally the same as or less than those on the abaxial leaf surface in *Sequoia*, *Metasequoia*, *Taxodium,* and *Glyptostrobus*, or sometimes there are no stomata on the adaxial leaf surface in these genera. The oblique stomata of *Cryptomeria* are one of the particular features among the genera of the Taxodiaceae, for the long axes of stomata are mostly parallel to that of leaves in other genera except for *Taxodium* and *Glyptostrobus* (scale leaves). The subsidiary cells of *Cryptomeria* are apparently distinguishable from those of the *Athrotaxis*-type. The subsidiary cells of *Metasequoia*, *Taxodium,* and *Cunninghamia* are more similar to those of the *Athrotaxis*-type than of other taxodiaceous genera. Fossil records of *Cryptomeria* were traced back to the Lower Cretaceous and mainly found from the Upper Cretaceous to the Tertiary. The presence of *Cryptomeria* commonly reflects a warm climate with a permanently high degree of humidity.

KEY WORDS**:** *Cryptomeria*, leaf, cuticle, stomata, habitat

INTRODUCTION

Cryptomeria D. Don is a monotypic genus of the former conifer family Taxodiaceae. It is commonly suggested that the family Taxodiaceae should be merged with the family Cupressaceae based on the homology of the reproductive organs and molecular data (Eckenwalder 1976, Brunsfeld et al. 1994, Fu et al. 1999a). The two families are commonly distinguished by leaf forms and phyllotaxis. Many fossil specimens are usually preserved as foliage shoots. Therefore, for pragmatic reasons, the traditional family Taxodiaceae is maintained here and we refer only to the representatives of the former Taxodiaceae. The genus *Cryptomeria* is monospecific today and the only living species is *C. japonica* D. Don with two varieties. The trees of *C. japonica* var. *japonica* occurring in Japan and *C. japonica* var. *sinensis* are endemic to southern China (Yu 1994, Fu et al. 1999b). As a relic species, the fossil records of *Cryptomeria* were traced back to the Lower Cretaceous in China and are common from the Upper Cretaceous through the Tertiary in East Asia, North America, and Europe (Yu 1995). It is difficult to identify these specimens, for the shape and arrangement of the leaves and branchlets are similar in most genera of the Taxodiaceae. The taxonomic assignments are further complicated, when similar remains of two or more genera

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are present in one fossil assemblage (Ma & Gu 2000, Ma et al. 2005a).

Epidermal characters reflected in the leaf cuticles are the standard source of valuable cellular information in foliage-compression fossils. They would offer additional and decisive parameters in classifying the fossil specimens in the family Taxodiaceae (Boulter 1970, Vickulin et al. 2003, Ma et al. 2005a). The detailed leaf epidermal structures of living species in the genera *Sequoia* Endlicher, *Metasequoia* Miki. Hu & Cheng, *Glyptostrobus* Endlicher, *Taxodium* Richard, *Athrotaxis* D. Don, and *Sequoiadendron* Buchholz were described by the present authors (Ma & Li 2002a, b, Ma & Zhang 2003, Ma et al. 2004, 2005b, 2006a, b). Only few works have simply described epidermal structures of *Cryptomeria* so far (Florin 1931, Sveshnikova 1963, Boulter 1970, Yao & Hu 1982, Van der Ham et al. 2001). The present work examined the foliage of two varieties of *Cryptomeria japonica* using both Scanning Electron Microscopy (SEM) and Light Microscopy (LM), and provided a more detailed picture about the epidermal characters of *Cryptomeria*. The habitats of the trees of *Cryptomeria* are also discussed. The new data obtained from this study will provide reference in classifying the species of the Taxodiaceae and in reconstructing palaeoclimate.

MATERIAL AND METHODS

The specimens were collected from the arboretum of Nanjing, China. The reliability of epidermal structures obtained from cuticle is affected by the process of maceration (Alvin & Boulter 1974, Ma & Li 2002b, Ma et al. 2005c). Two maceration methods were used in the present study. The leaves to be examined by LM were macerated in > 30 percent hydrogen peroxide (H_2O_2) and 99 percent glacial acetic acid (CH_3COOH) at 1:1, and the leaves by SEM were macerated in chromium trioxide (CrO_3). The maceration time is more important than different reagents in the factors of influencing the reliability of demonstrating epidermal structures. The thickened walls of guard cells and the polar lamellae in some genera of the Taxodiaceae are partly dissolved after prolonged processing in the maceration solution, so these features are not always found on the overly processed cuticles.

The photos of epidermis were taken under the SEM (FEI Quanta 200) and the LM (Olympus BX50). The sizes of epidermal cells and stomata were measured on each variety ($N = 50$). The values of epidermal cells and stomata size are represented by means ± standard deviation. The numbers of subsidiary cells of a stoma were determined on each variety ($N = 100$).

DESCRIPTION

The trees of *Cryptomeria japonica* are evergreen and monoecious. The inflorescences develop from February to April, and the seeds maturate from October to November. The leaves are spirally arranged, comprised of 5 ranks, crowded on the axis of branchlets. They are soft and coriaceous in texture, subulate in shape. The leaves are quadrangular in cross section, both the adaxial and abaxial surfaces are convex. The base of the leaves is decurrent (Fig. 1: 1, 2).

The leaf epidermal structures of both varieties are very similar. The leaves are amphistomatic (Fig. 2: 1–4, Fig. 3: 1, 3). The epidermal cells are rectangular within the non-stomatal areas. The long axis of epidermal cells is parallel to that of the leaves (Fig. 3: 3). The epidermal cells of non-stomatal areas are 59.1 ± 16.8 µm (58.7 ± 13.3 µm in var. *japonica*, 59.4 ± 19.9 µm in var. *sinensis*) long and 16.4 ± 1.9 µm (16.9 ± 1.5 µm in var. *japonica*, 15.9 ± 2.0 µm in var. *sinensis*) wide, with the length/width ratio (L/W) 3.67 ± 1.23 (3.53 ± 0.96 µm in var. *japonica*, 3.81 ± 1.45 µm in var. *sinensis*). The shape and size of epidermal cells on the stomatal areas are irregular in comparison with those of non-stomatal areas. They have no apparent long axis and are rectangular, triangular or polygonal on the intrastomatal zones (Fig. 2: 5, Fig. 3: 2–4). Pits can be clearly seen in the walls of epidermal cells both on non-stomatal areas and on intrastomatal zones. The shape and size of epidermal cells on an area of high stomatal density are more irregular than those on an area of lower stomatal density.

Stomata are located on each side of the midvein and distributed on both the abaxial and adaxial leaf surfaces. The two stomatal bands on the same (adaxial or abaxial) surface of one leaf are almost similar. Most stomatal bands on the adaxial surfaces comprise 6–9 lines of stomata. The widest part of the stomatal band is located on the middle part of the leaves (Fig. 2: 1, 3). The length of stomatal band is nearly the same as that of the leaves. Commonly and obviously, the numbers of stomatal lines decrease near the base and tip of leaves.

The numbers of stomatal lines and the length of stomatal bands on the abaxial surface are commonly different among different leaves. Mostly, the length of each stomatal band on the abaxial surface is nearly the same

Fig. 1. **1**– foliage shoot of *Cryptomeria japonica* var. *japonica*, scale bar = 17 mm; **2** – foliage shoot of *Cryptomeria japonica* var. *sinensis*; scale bar – 17 mm.

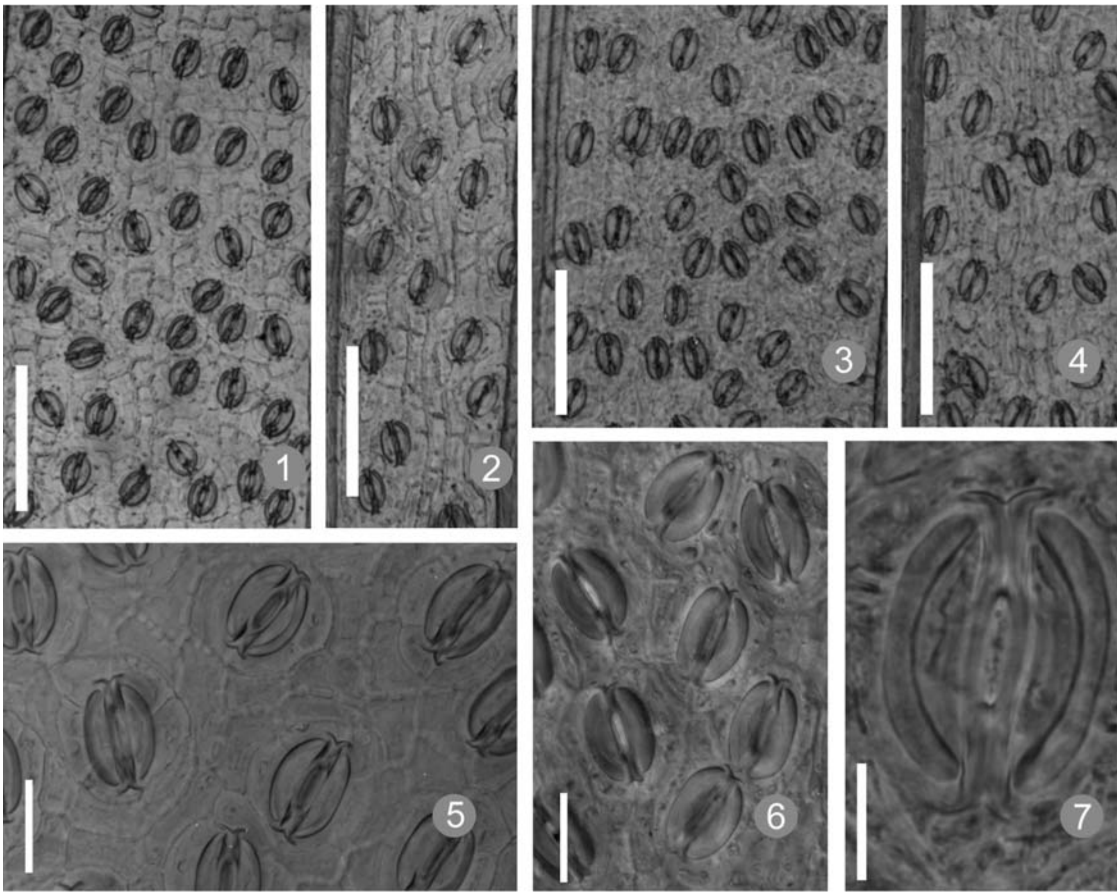

Fig. 2. **1, 2, 5** – LMs of *Cryptomeria japonica* D.Don var *japonica*; **3, 4, 6, 7** –, LMs of *Cryptomeria japonica* D.Don var *sinensis*. **1** – cuticle of the adaxial leaf surface; **2** – cuticle of the abaxial leaf surface; **3** – cuticle of the adaxial leaf surface; **4** – cuticle of the abaxial leaf surface; **5** – guard cells of the adaxial surface of leaf; **6** – guard cells of the adaxial leaf surface; **7** – guard cells of the adaxial leaf surface. Scale bars: 165 µm for 1–4, 60 µm for 5–6, 17 µm for 7

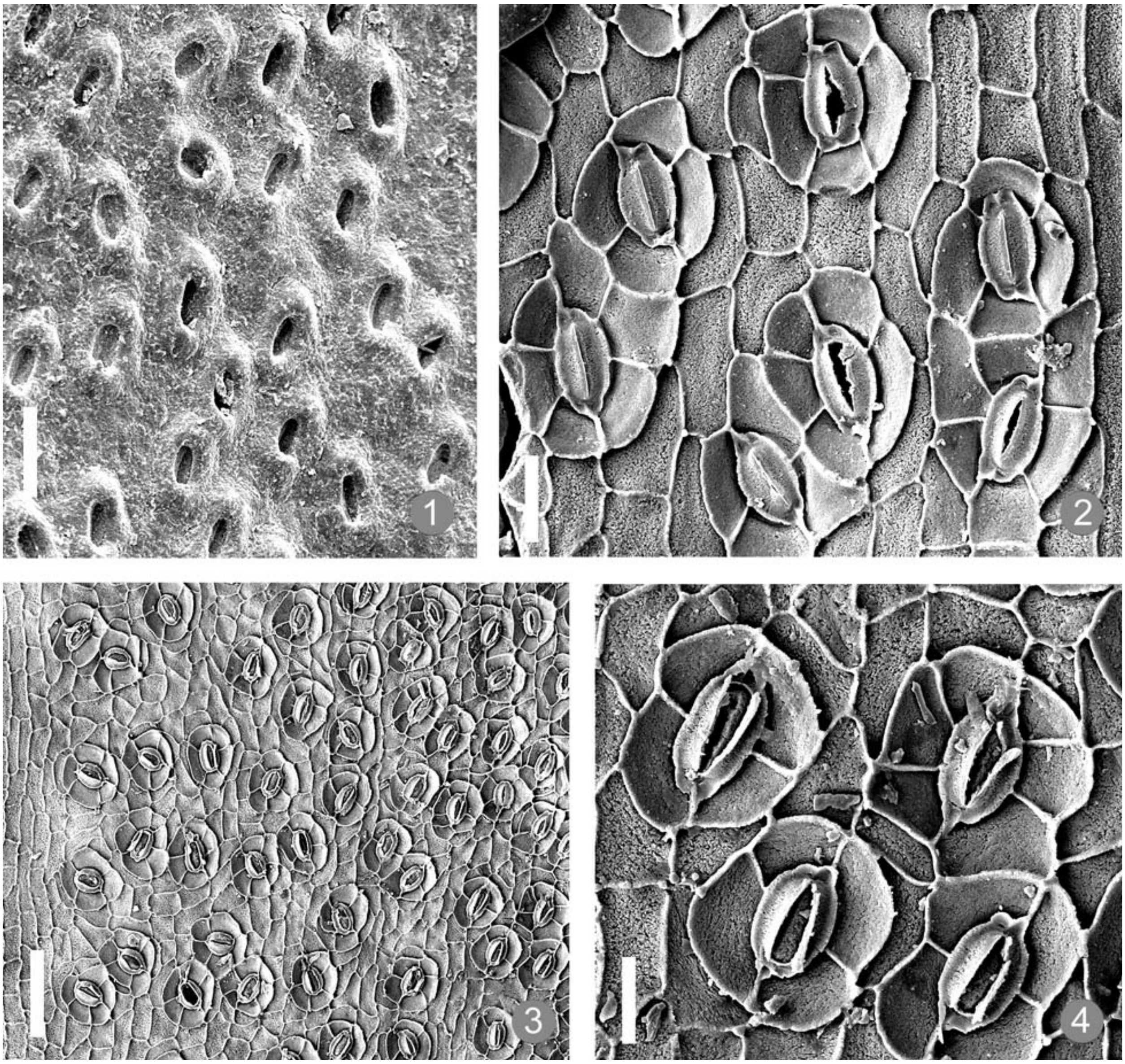

Fig. 3. **1,2** – SEMs of *Cryptomeria japonica* D.Don var. *japonica*; 3, 4 – SEMs of *Cryptomeria japonica* D.Don var. *sinensis*; **1** – outer surface of the abaxial cuticle; **2** – inner surface of the abaxial cuticle; **3** – inner surface of the adaxial cuticle; **4** – details of stomata (part of 12 enlarged). Scale bars: 50 µm for 1, 25 µm for 2, 4, 100 µm for 3

as that of the leaf. The stomatal band comprises 3–7 lines of stomata. The widest part of stomatal band is located on the leaf base (Fig. 2: 2, 4). The numbers of stomata are the least on the middle part of the leaves, and the numbers of stomatal lines decrease to 1–5 on this part. Sometimes, the majority of stomatal lines are gathered at the leaf base. There are no stomata on the median portion of the leaves, and fewer lines of stomata are discontinuously distributed on the distal parts. Rarely, the stomatal bands comprise 3–7 lines of stomata on the leaf base, and no stomata were found from the middle to apical leaf parts.

The number of stomata on the adaxial leaf surface is higher than that on the abaxial surface. The length of the stomatal band on the adaxial surface is also longer than that on the abaxial leaf surface. Near the leaf base, the space among the stomatal lines on the abaxial surface is larger than that on the adaxial surface. Accordingly, the width of a stomatal band on the abaxial surface is larger than that on the adaxial surface. Abaxially, the number of stomatal lines in the median and apical parts of the leaves is fewer than that near the leaf base. Accordingly, the width of a stomatal band on the abaxial surface is smaller than that of the adaxial surface in the median and apical leaf parts (Fig. 2: 1–4).

Stomata of the two varieties are very similar in structure. Stomata and pores are elliptic. The long axes of the stomata are oblique to that of leaves (Fig. 2: 1–7, Fig. 3: 2–4). Guard cells have thickened periclinal walls, especially on outer margins. The thickened outer margins of the cell walls are banana-like in shape. The thickened walls of guard cells form polar lamellae that produce protrudings and curved ends at the poles of the stomata (Fig. 2: 5–7). The stomata may have 4–6 subsidiary cells, occasionally have 7. Forty-three percent (47% in var. *japonica*, 39% in var. *sinensis*) of the stomata have 4 subsidiary cells, 41% (42% in var. *japonica*, 40% in var. *sinensis*) have 5, 15% (11% in var. *japonica*, 19% in var. *sinensis*) have 6, and 1% (none in var. *japonica*, 2% in var. *sinensis*) have 7 subsidiary cells.

The subsidiary cells are slightly raised compared to the general level of the epidermal cells in the view of the outer surface of the cuticle (Fig. 3: 1). So, the subsidiary cells are sunken below the general level of the epidermal cells in the view of the inner surface of the cuticle (Fig. 3: 2–4). The shape of the subsidiary cells is different from that of the epidermal cells. The epidermal cells are commonly rectangular, triangular or polygonal on intrastomatal zones. The subsidiary cells are quadrilateral, and the exterior and interior side of the subsidiary cells are incurved. The subsidiary cells have a different level of insertion to those of the epidermal cells. The group of subsidiary cells of each stoma exhibits a very distinctive oval or round appearance on the inner surface of the cuticle (Fig. 3: 2–4).

Stomata are 48.5 ± 3.0 µm (47.9 ± 3.3 µm in var. *japonica*, 49.1 ± 2.6 µm in var. *sinensis*) long and 30.7 ± 2.1 µm (31.2 ± 1.9 µm in var. *japonica*, 30.1 ± 2.3 µm in var. *sinensis*) wide, with the L/W ratio 1.59 ± 0.19 (1.55 ± 0.18 µm in var. *japonica*, 1.64 ± 0.19 µm in var. *sinensis*). The value of stomatal sizes between the two varieties is small, so the differences would not be a standard characteristic in distinguishing the two varieties.

INTRASPECIFIC COMPARISON

Cryptomeria japonica D. Don. is a genetically variable taxon (Farjon 1999). The number of archegonia in the archegonial complex of var. *sinensis* is less than that of var. *japonica*. The var. *sinensis* does not form an archegonial chamber with chalazal and lateral archegonia, while var. *japonica* does (Liu & Wu 1986). Most pollen cones are higher than their subtending leaves in var. *japonica*, while they are shorter than those in var. *sinensis*. The seed cones of var. *japonica* are larger than those of *var. sinensis*, and the number of scales of var. *japonica* (20–30) is also higher than that of var. *sinensis* (20). Each cone scale has 2–5 seeds in *var. japonica*, 2 seeds in var. *sinensis*. The toothlike projections on the distal margin of the bract and cone scales are 2–3.5 mm in var. *japonica*, and 1–2 mm in var. *sinensis* (Zheng & Fu 1978, Yu 1994, Fu et al. 1999b).

The angle of the leaf divergence is 35–55° in var. *japonica*, and it is 15–40° in var. *sinensis* (Fu et al. 1999b). Leaves are straight or incurved near the apices in var. *japonica*, but they are usually strongly incurved throughout in var. *sinensis* (Zheng & Fu 1978, Yu 1994, Fu et al. 1999b). These features overlap in the two varieties. *Cryptomeria japonica* was described with amphistomatic leaves, oblique stomata, and 4–7 subsidiary cells of each stoma (Sveshnikova 1963, Zheng & Fu 1978, Yao & Hu 1982, Fu et al. 1999b, Van der Ham et al. 2001). The thickened walls of guard cells in var. *japonica* were described, and they were also well preserved in some fossil specimens of *Cryptomeria* (Boulter 1970). The differences in sizes of the epidermal cells and the stomata between the two varieties are small, so they would not be a standard characteristic in distinguishing the two varieties.

The fossil record of *Cryptomeria* is not well studied and is poorly understood. Some fossil specimens attributed to this genus were based on the superficial impressions of foliage remains which may be confused with those of other genera (Aulenback & LePage 1998). Epidermal structures of some fossil specimens are almost similar to those of the living *Cryptomeria* (Sveshnikova 1963, Boulter 1970). The genus *Cryptomeria* has some unique epidermal structures, which may be used to differentiate *Cryptomeria* from other genera of the Taxodiaceae.

COMPARISON WITH SOME GENERA OF TAXODIACEAE

The leaves are linear, subulate, lanceolate or scale-like in the Taxodiaceae. Some genera and even species may possess two or three leaf shapes. Thus the stoma orientation was described as random on leaves of *Taxodium*, *Glyptostrobus,* and *Cryptomeria* (Florin 1931, Aulenback & LePage 1998, Vickulin et al. 2003). Ma et al. (2005b) described the long axes of stomata as mostly perpendicular or oblique (>45°) in *Taxodium*. Epidermal structures, such as stomata orientation and distribution, may be variable in the same shape of leaves in one species, such as *Metasequoia glyptostroboides* Hu & Cheng or *Sequoia sempervirens* Endl. (Ma & Li 2002a, b, Ma & Zhang 2003). They may also differ in leaves of different shape within a living species *Glyptostrobus pensilis* K. Koch, or within a fossil species *Glyptostrobus europaeus* (Brongn.) Ung. (Kovar-Eder 1996, Vickulin et al. 2003, Ma et al. 2004). They are also variable in the different species within one genus as in *Taxodium* or *Athrotaxis* (Ma et al. 2005b, 2006b). The long axes of stomata mostly are parallel to that of the leaf in other genera of the Taxodiaceae (Tab. 1).

The subulate leaves of *Cryptomeria* are amphistomatic, and the number of stomata on the adaxial surface is higher than that on the abaxial leaf surface (Tab. 1). In *Cryptomeria* the stomatal distribution is similar to that of *Taiwania*. Contrary, in *Sequoia*, *Metasequoia*, *Taxodium*, and *Glyptostrobus*, the number of stomata is generally the same as or less than that on the abaxial surface of linear leaves, or sometimes there are no stomata adaxially on the leaves in these genera (Ma & Li 2002a, b, Ma & Zhang 2003, Ma et al. 2004, 2005a, b). In *Athrotaxis*, the number of stomata is higher adaxially than abaxially in *A. selaginoides* D. Don and *A. laxifolia* Hook, while they are less numerous adaxially in *A. cupressoides* D. Don (Tab. 1). The oblique stomata (mostly <45°) are one of the key characteristics in the epidermal structures of the leaves in *Cryptomeria*.

In *Cryptomeria,* the subsidiary cells differ in shape from the epidermal cells, and they are sunken below the general level of the epidermal cells in the view of the inner surface of the cuticle. Therefore, the group of subsidiary cells of each stoma exhibits a very distinctive oval or round appearance. The stomata in *Athrotaxis* are called *Athrotaxis*-type (Hill et al. 1993). There, the subsidiary cells are arranged at the same surface level. Their shapes are almost similar to those of the epidermal cells and the subsidiary cells of one stoma are not distinctive as they are in *Cryptomeria* (Hill et al. 1993, Ma et al. 2006b). The subsidiary cells in *Metasequoia*, *Taxodium*, and *Cunninghamia* are more similar to those of the *Athrotaxis*-type than in other taxodiaceous genera (Tab. 1).

Boulter (1970) reported that the polar lamellae of *Cryptomeria* have pointed tips which facilitate the distinction from those of *Sequoia* and *Sequoiadendron*. The polar lamellae of *Sequoia* and *Sequoiadendron* have rounded ends which protrude very little from the polar extremity of the guard cells, and the polar lamellae of *Sequoia* are less prominent than those of *Sequoiadendron*. According to the present authors the polar lamellae have a wide range of variation within the genera *Sequoia* and *Sequoiadendron*. *Sequoia* and *Sequoiadendron* also have polar lamellae which are like those of *Cryptomeria* (Boulter 1970, Ma & Li 2002a, b, Ma et al. 2006a).

Table 1. Comparative features of stomata in Taxodiaceae (after Van der Ham et al. 2001, Ma & Li 2002a, 2002b, Ma & Zhang 2003, Ma et al. 2004, 2005a, b, 2006a, b). **ADM** – amphistomatic and the stomatal bands on the adaxial surface are more strongly developed than those on the abaxial surface of leaves; **ABM** – amphistomatic and the stomatal bands on the abaxial surface are more strongly developed than those on the adaxial surface of leaves; **AS** – Amphistomatic; **HS** – hypostomatic; **PE** – perpendicular; **OB** – oblique; **PA** – parallel; **S** – similar to *Arthrotaxis*-type

Genus	Distribution of the stomatal bands	Orientation of the stomatal bands	*Athrotaxis*-type
Cryptomeria	ADM	OB (<45°)	No
Taxodium	ABM or HS	PE or OB (>45°)	S
Metasequoia	Mostly HS	PA	S
Glyptostrobus	ABM (linear leaves) or AS (linear-subulate and scale leaves)	PA (linear and linear-subulate leaves) or OB or PE (scale leaves)	No
Sequoia	AS or HS	PA	No
Sequoiadendron	AS	PA	No
Athrotaxis	ADM (*A. selaginoides* and *A. laxifolia*) or ABM (*A. cupressoides*)	PA	Yes
Cunninghamia	HS or ABM	PA	S
Taiwania	ADM	PA	No

Therefore, these features are not very useful in separating the genera *Cryptomeria*, *Sequoia*, and *Sequoiadendron*.

ECOLOGY OF *CRYPTOMERIA*

Genera of the Taxodiaceae family, are largely confined to warm-temperate regions of Asia, North America, and Australia where precipitation is high and climate is warm, humid, and generally frost free (Page 1990). *Glyptostrobus* and *Taxodium* live almost exclusively in marshy environments. *Sequoia* and *Sequoiadendron* are less sensitive to frost. *Cryptomeria* lives under more severe thermal conditions, i.e. it withstands three to six months of cold weather. Though some species in the family Taxodiaceae can withstand seasonal cold, all require a permanent and high degree of humidity. The two climatic components, rainfall and temperature, along with geographical heterogeneity, have been illustrated as leading to the extinction of species in the Taxodiaceae (Michaux et al. 1979).

Fossil records indicate that *Cryptomeria* has a long range in the geologic past. One of the methods for reconstructing Tertiary terrestrial climates is to identify the Nearest Living Relatives Species (NLR-species) of the elements in a given fossil flora, and then applies the range of climate parameters of the NLR-species to the fossil site (Li et al. 2001, Royer et al. 2002). Now the only living species of *Cryptomeria* occurs in Japan and southern China. In the regions of the living *Cryptomeria*, the mean temperature of January is –8.2°C for the northern limit of its distribution, and is about +10°C in the southern limit. In these regions, the mean July temperature is 20 to 30°C and the mean annual temperature varies from 5.0 to 19°C (Hayashi 1960, Tsukada 1982, Zheng 1983, Takahara & Kitagawa 2000). The temperature is not the most significant environmental factor influencing the natural distribution of *Cryptomeria*. The natural distribution of *Cryptomeria* is closely related to the amount of annual precipitation (Tsukada 1982). On average, the mean annual precipitation for the living species of *Cryptomeria* is normally above 1000 mm. In areas where *Cryptomeria* is densely distributed at the present time, annual precipitation is above 2000 mm while a minimum annual precipitation is 1600 mm (Hayashi 1960). The species of *Cryptomeria* commonly reflects a warm climate with a permanently high degree of humidity.

CONCLUSIONS

The relic species of *Cryptomeria* is endemic to Japan and south China, and the fossil records of *Cryptomeria* have been traced from the Lower Cretaceous to the Neogene in East Asia, North America and Europe. The parameters of epidermal structures are quite similar between the two varieties of *C. japonica* D.Don, and epidermal structures of the fossil specimens of *Cryptomeria* are nearly similar to those of living species. The genus *Cryptomeria* has some unique epidermal structures, which could offer additional and decisive parameters in differentiating *Cryptomeria* from other genera in the Taxodiaceae. The stomata numbers and length of stomatal bands on the adaxial leaf surface in *Cryptomeria* are more developed than those on the abaxial surface. These characteristics are different from those in the genera *Sequoia*, *Metasequoia*, *Taxodium*, and *Glyptostrobus*. The long axes of the stomata are mostly parallel to the median axis of the leaf in most genera of the Taxodiaceae. Therefore, the oblique stomata in *Cryptomeria*, *Taxodium,* and *Glyptostrobus*, are particular features compared to other genera in the Taxodiaceae. In *Cryptomeria*, the group of subsidiary cells of each stoma exhibits a very distinctive oval or round appearance on the inner surface of the cuticle, which is distinguishable from those of the *Athrotaxis*-type. The stomata of *Metasequoia*, *Taxodium,* and *Cunninghamia* are more similar to those of the *Athrotaxis*-type than are other taxodiaceous genera. Today, *Cryptomeria* can withstand three to six months of cold weather, but the appearance of *Cryptomeria* commonly reflects a warm climate with a permanent and high degree of humidity.

ACKNOWLEDGEMENTS

Special thanks are given to Francis M. Hueber for scientific consultation and modifying the manuscript.This project was supported by the Foundation for Excellent Talents of Beijing (No. 20061D1100500398), Natural Science Foundation of Beijing (No. 8073026), China Postdoctoral Science Foundation (No. 20060390400), and the National Natural Science Foundation of China (Nos 30500034 and 40599423)

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