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Cuticular anatomy of *Sphenobaiera huangii* (Ginkgoales) from the Lower Jurassic of Hubei, China[1]

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Sphenobaiera huangii (Sze) Hsü is typical Early Mesozoic fossil foliage of Ginkgoales in China. It has been recorded from the Upper Triassic to the Lower Jurassic. The cuticular anatomy is investigated based on material from the type locality, Lower Jurassic Hsiangchi Formation, Zigui County, Hubei Province. The specimens are similar to *S. huangii*, but contain new information about leaf morphology and cuticular anatomy. Lower and upper cuticle is investigated using light and electron microscopy (LM, SEM, and TEM). Many features are described for the first time, including general structures of lower and upper cuticle, stomata, papillae, and cuticular ultrastructure. At the ultrastructural level, two layers have been distinguished in both lower and upper cuticle, including a homogeneous outer layer with granules and a heterogeneous inner layer with fibrils. Based on a literature comparison between *S. huangii* and other relevant species of *Sphenobaiera*, *S. huangii* may represent the best-known taxon in the genus *Sphenobaiera* in both leaf morphology and cuticular structures. This study provides the first detailed ultrastructural data on the leaf cuticle of *Sphenobaiera*, one of the oldest foliage taxa of Ginkgoales, and offers further evidence for potential discussion on the taxonomic relationships of *S. huangii* with other ginkgoalean taxa.

Key words: China; fossil; Ginkgoales; Jurassic; leaf cuticle; *Sphenobaiera huangii*; ultrastructure.

The origin and evolution of the ''living fossil'' *Ginkgo* have received increased attention and interest from botanists and palaeobotanists. In particular, the discovery and investigation on the reproductive organs (pollen and ovules) of fossil Ginkgoales have provided valuable evidence for understanding its long evolutionary history (Zhou and Zhang, 1988, 1989, 1992; Schweitzer and Kirchner, 1995; Poort et al., 1996; Zhou et al., 2002; Zhou and Zheng, 2003; Zheng and Zhou, 2004). However, a number of fossil specimens assigned to Ginkgoales are preserved as compression and/or impression foliage. Therefore, the cuticular structure and anatomy undoubtedly play a significant role for exploring the systematics of foliage taxa of Ginkgoales.

Sphenobaiera is one of the oldest fossil foliage types of Ginkgoales and has a global distribution, mainly in the Northern Hemisphere. It can be traced from the Lower Permian well into the Cretaceous (Taylor and Taylor, 1993). Florin (1936) established this genus for leaves originally included in *Baiera* Braun that are distinguished from those of the type species *Baiera muensteriana* (Presl in Sternberg) Heer, mainly by having wedge-shaped leaves that lack a distinct petiole. Later, Harris and Millington (1974) made an important refinement, transferring the wedge-shaped leaves borne in a bundle of dwarf shoots, to the Czekanowskiales (*Sphenarion* Harris and Miller, 1974). Since then, *Sphenobaiera* is generally defined for wedge-shaped leaves that are distinguishable from *Ginkgo*, *Ginkgoites*, and *Baiera* by the absence of a distinct petiole (see also Lydon et al., 2003). So far, over 50 species have been described worldwide for *Sphenobaiera*, and for some of them cuticle details are known. However, only a few specimens have been reported as closely associated with the reproductive organs. For example, several *Sphenobaiera*-type leaves were reported associated with the ovule-organ *Karkenia* from the Lower Cretaceous of Argentina, the Upper Jurassic of Siberia, the Liassic of Germany, Rhaetic to Jurassic of Iran and Afghanistan, and the Jurassic of Henan, China (Archangelsky, 1965; Krassilov, 1972; Schweitzer and Kirchner, 1995; Zhou et al., 2002). According to a recent systematic review by Zhou (1997, 2003), it is quite possible for some species of *Sphenobaiera*, which are characterized by having less divided wedge-shaped leaves and broad segments, to be referred to the family Karkeniaceae of Ginkgoales. The systematic status of most other species of this form-genus is still unknown at the family level.

About 25 species of *Sphenobaiera* have been described

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from Mesozoic deposits in China. Among them, *Sphenobaiera huangii* (Sze) Hsü is the most typical and widespread leaf found in these deposits. It was initially described as *Baiera huangii* by Sze (1949), based on impression specimens from the Lower Jurassic Hsiangchi flora in western Hubei. Subsequently, Hsü (in Sze and Hsü, 1954) transferred it to the genus *Sphenobaiera*. Since then, this species has been described from a number of Mesozoic localities in China. Available data show that specimens of *S. huangii* are also recorded from the Upper Triassic to Middle Jurassic in Jinmen, Hubei (Feng et al., 1977; Chen, 1984), western and eastern parts of Sichuan (Yang, 1978; Duan and Chen, 1982; Chen et al., 1987), Fengxian and Yan'an of Shaanxi (Liu, 1982; Zhang et al., 1998); Jiangning of Jiangsu (Wang et al., 1982), Yima of Henan (Zeng et al., 1995), Beipiao of western Liaoning (Mi et al., 1996), Datong of Shanxi (Li and Hu, 1984), and eastern Hunan (Zhang, 1986) in China. However, most specimens referred to as *S. huangii* are poorly preserved so yield little information about cuticular anatomy and foliar morphology.

Recently, numerous compressed specimens of *Sphenobaiera huangii* were collected from the Lower Jurassic Hsiangchi Formation in western Hubei, China. Other plants associated with *S. huangii* in this formation include nilssonialeans (*Nilsonnia*), bennettitaleans (*Pterophyllum*, *Ptilophyllum*, *Tyrmia*, *Otozamites*, *Anomozamites*, *Weltrichia*, *Zamites*, and *Ctenis*), ferns (*Todites*, *Marattia*, *Phlebopteris*, *Dictyophyllum*, *Clathropteris*, *Hausmannia*, *Coniopteris*, and *Cladophlebis*), other ginkgoaleans (*Ginkgoites*, *Baiera*), Czekanowskialeans (*Czekanowskia*, *Phenicopsis*, *Ixostrobus*, and *Stenorachis*), conifers (*Podozamites*, *Ferganiella*, *Swedenborgia*, and *Elatocladus*), and a pteridosperm (*Ctenozamites*) (see Wang, 1999, 2002). Some of the ferns have been investigated describing fertile organs, in situ spores, and ultrastructure (Wang, 1999, 2002; Wang and Mei, 1999; Wang et al., 2001). In this paper, we reinvestigate typical ginkgoalean foliage *S. huangii*, with emphasis on cuticular anatomy, by using scanning and transmission electron microscopy (SEM, TEM), and light microscopic (LM) observations. This study presents the first information of cuticle ultrastructure for the genus *Sphenobaiera* based on well-preserved Chinese material.

MATERIALS AND METHODS

More than 70 specimens of *Sphenobaiera huangii* containing cuticle have been collected since 1998 from the type locality in Xiangxi Town of Zigui County, Hubei Province (30°50′20″ N, 110°40′15″ E), where the Jurassic is well exposed. It consists of an extensive succession of red clastic sediments of Middle to Upper Jurassic and a coal-bearing sequence of Lower Jurassic, which is known as the Hsiangchi Formation. This formation is generally regarded as Early Jurassic based on various palaeontological evidence, such as plant megafossils, spores, pollen, bivalves, and megaspores (Li and Shang, 1980; Wu et al., 1980; Meng, 1987; Meng and Zhang, 1987; Yang and Sun, 1987; Zhang and Zhang, 1987). The Hsiangchi Formation is up to 205 m thick and composed of grey to greyish black sandstones, siltstones, mudstones, and carbonaceous shales, intercalated by thin coal seams. This formation unconformably overlies the Upper Triassic Shazhenxi Formation and is conformably overlain by the Xietan Formation of Middle Jurassic age (for detailed information on the stratigraphy, refer to Wang, 1999, 2002). All specimens are well preserved as compressions with evident venation and cuticle. In addition, three original specimens from the same locality figured by Sze (1949) as *Baiera huangii* were reexamined. They are in the palaeobotanical collection of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), Nanjing, with catalog numbers PB 931, PB 933, and PB 934.

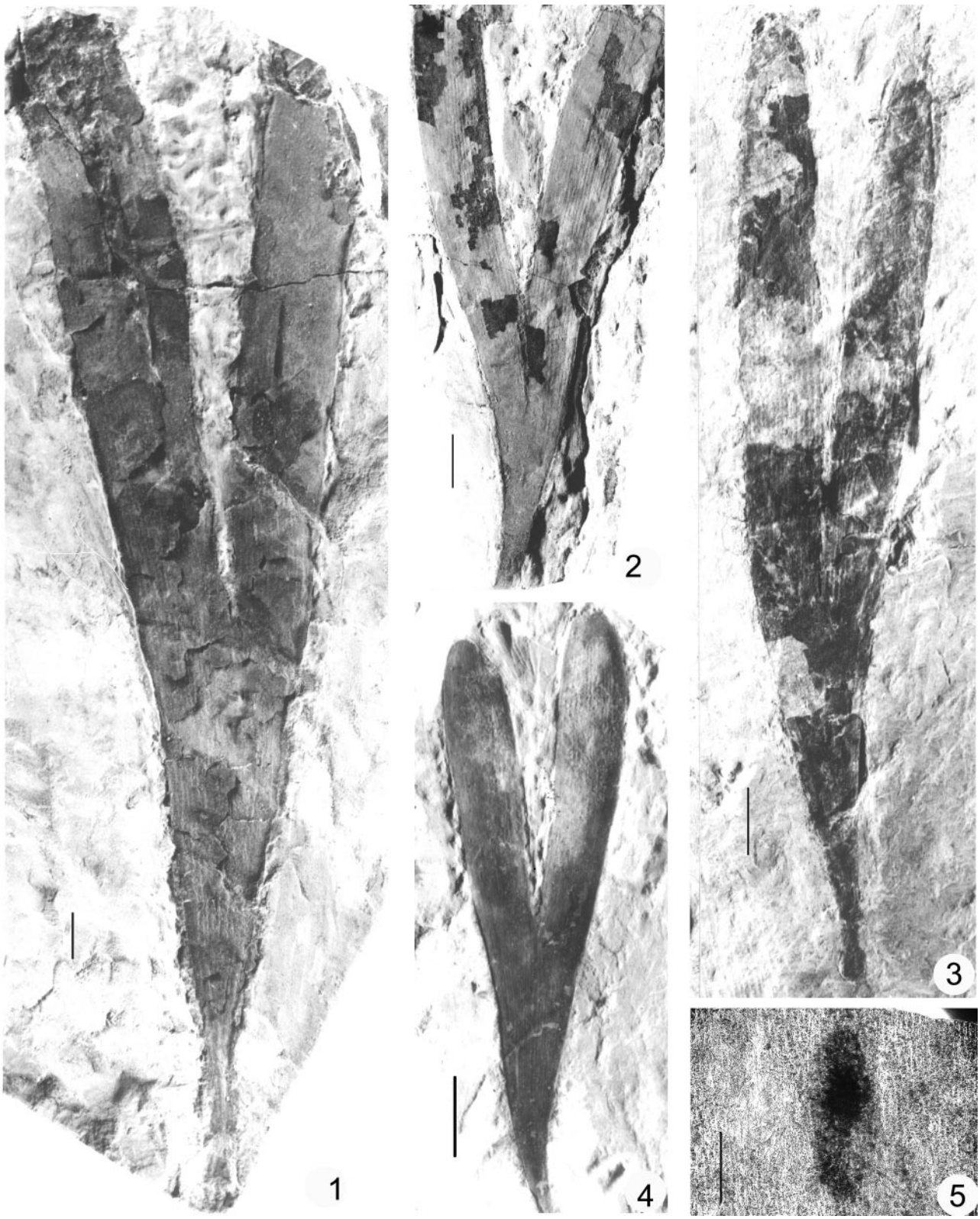
Selected cuticles were cleaned with hydrofluoric acid and hydrochloric acid, followed by a maceration in Schulze's solution and a short treatment with 5% ammonia. The lower and upper cuticle were separated and then divided into three fractions for different microscopic observations. A part of the cuticle was mounted on permanent slides for observation and photography under LM. For SEM, the samples were prepared on standard stubs and viewed using a JSM 6300 scanning electron microscope (JEOL, Tokyo, Japan) at an acceleration voltage of 15kV.

For TEM, samples were prepared as for fossil cuticle described in Zhou and Guignard (1998) and Guignard et al. (1998, 2001). The cuticle was prestained with osmium tetroxide before embedding in epoxy resin (epon) and stained with uranyl acetate and lead citrate after cutting with a Reichert Ultracut S ultramicrotome (Reichert-Leica, Vienna, Austria). Transverse and longitudinal sections were cut in the lower and upper cuticle. Twelve resin blocks, belonging to four specimens, and more than 90 grids were made for observation under a Philips CM120 transmission electron microscope (Philips, Eidhoven, Netherlands). The maceration and SEM observations were undertaken in NIGPAS, Nanjing, China, while TEM work was done at the Electron Microscope Center of Biology and Geology (CMEABG) of University Claude Bernard Lyon 1, Villeurbanne, France. All specimens examined in this study (including slides and SEM stubs) are deposited in the palaeobotanical collection of NIGPAS, Nanjing, China with registration numbers PB 931 to PB934 and PB20041 to PB20075. The TEM blocks and sections are retained in the Guignard collection of the University of Lyon 1, France.

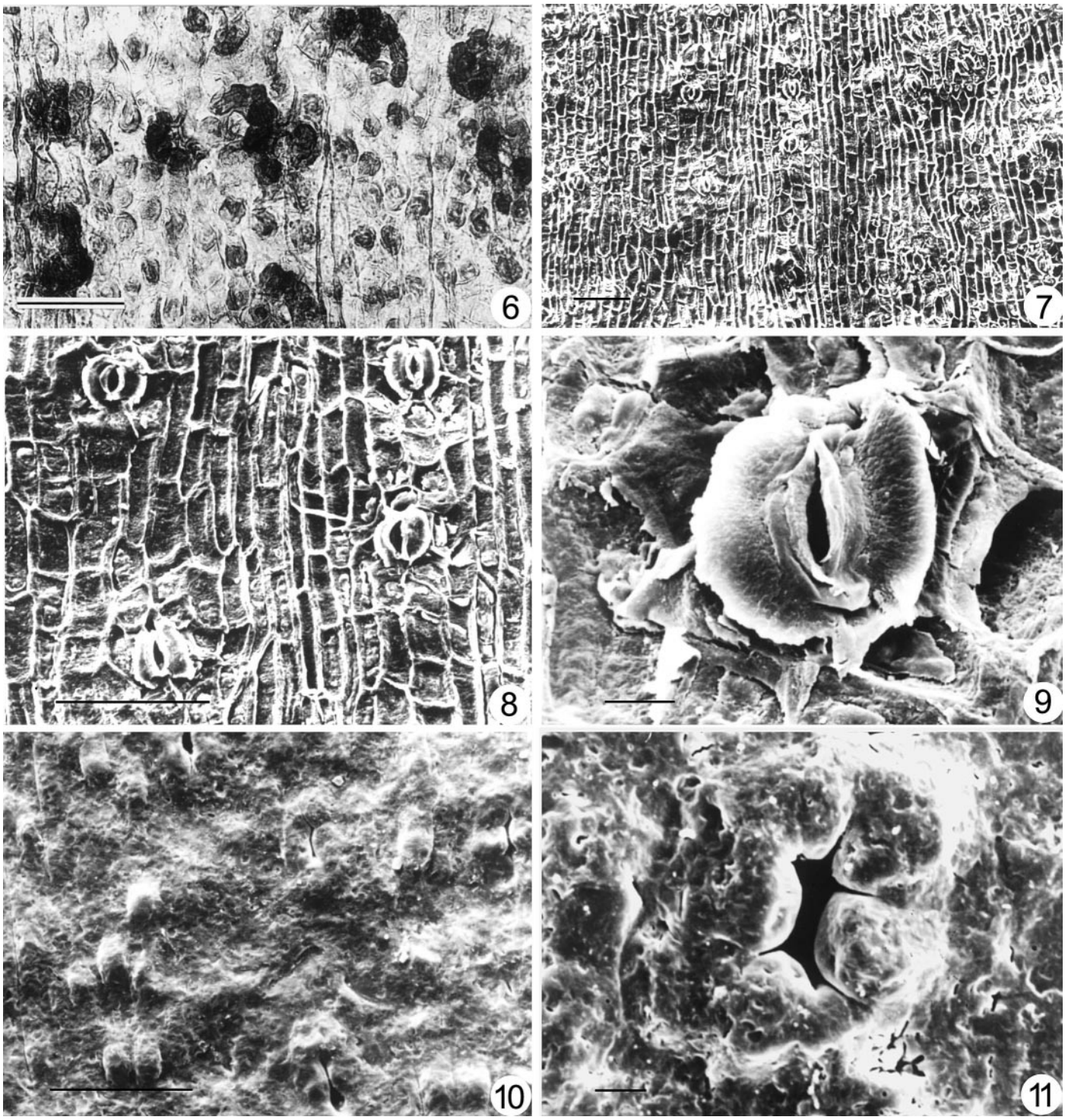
RESULTS

Leaf morphology—More than 70 specimens of *Sphenobaiera huangii* have been investigated in our collection. The material referred to as *S. huangii* exhibits a wide range in leaf size, varying from 7.5 to 25 cm long (Figs. 1–4). The leaf is narrowly wedge-shaped, becoming gradually narrower toward the base, but without a distinct petiole. In some well-preserved specimens, a swollen base is attached (Figs. 1, 3). The leaves are divided into two nearly equal lobes. The basal undivided portion is 3–12 cm long or about half the leaf length. The width of the leaf base is 2–5 mm (average 4 mm). The two lobes form a basal acute angle that varies from 10° to 25°. The lobes vary from 6.5 to 12 cm long and 8 to 21 mm wide (average 14 mm wide). The apices of the lobes are blunt or rounded (Figs. 1–4). The venation is parallel in the lobes and converges slightly towards the apex (Figs. 2–4). The number of veins are 12–20 per lobe (average 15–16 per lobe), 10–11 veins/cm. Fusiform resin bodies occur on the leaf cuticle and are 200–250 × 700–850 μm in size (Fig. 5).

General cuticular structure—The cuticular structure on leaves of different sizes is identical in all essential aspects. Leaves are amphistomatic. The lower cuticle is 3–5 μm thick, and strips of stomatal and non-stomatal zones are well defined (Figs. 7, 8). The stomatal zone is 70–190 μm wide, consisting of 4–6 rows of isodiametric, polygonal to rectangular epidermal cells (Figs. 7, 8). The non-stomatal zone is marked by vein courses of 100–180 μm wide, consisting of 6–10 rows of longitudinally elongated, rectangular cells (Figs. 7, 8). The anticlinal wall is straight and thicker (up to 4 μm thick) than those in the upper cuticle. The periclinal wall of the cuticle is smooth and bears distinct papillae in each epidermal cell (Figs. 6, 10). Papillae are more developed than those in the upper cuticle, and are rounded or oval in shape, varying in size from 18 to 31 μm (average 24 μm based on 18 measurements) (Fig. 11). Stomata are regularly distributed between vein courses and are longitudinally oriented (Figs. 7, 8). Stomata density in the lower cuticle is higher, up to 20–48 stomata/ mm^2 (average



Figs. 1–5. *Sphenobaiera huangii* (Sze) Hsü from the Lower Jurassic Hsiangchi Formation in Hubei, China. **1.** The largest specimen found in the type locality in Hubei, China (the specimen is 25 cm long). Specimen no. PB20041. **2.** Leaf showing two lobes and the basal undivided part. Specimen no. PB20043. **3.** A complete leaf showing two lobes and the basal undivided portion. Note the round-shaped apices in lobes and the swollen leaf base. Specimen no. PB20045. **4.** One of the impression specimens originally figured as *Baiera huangii* by Sze (1949) from the Lower Jurassic Hsiangchi Formation in Zigui, Hubei, China. It is the smallest specimen of *S. huangii* found so far. Specimen no. PB931. **5.** A fusiform resin body from the cuticle of specimen no. PB20044. Scale bars = 1 cm except in Fig. 5 where scale bar = 300 μm.



Figs. 6–11. *Sphenobaiera huangii* (Sze) Hsü from the Lower Jurassic Hsiangchi Formation in Hubei, China. Light and scanning electron microscopy (LM, SEM) photos of the lower cuticle. **6.** Lower cuticle showing well-developed papillae in ordinary epidermal cells and around the stomata (LM). Negative no. 35. Specimen no. PB20065. 7–9. Inner view of the lower cuticle from specimen PB20064. **7.** Lower magnification showing well-defined vein courses and stomata bands. Negative no. 980671. **8.** Detail of Fig. 7 showing four stomata longitudinally orientated and ordinary epidermal cells. Negative no. 980672. **9.** A stomata complex showing exposed guard cells, subsidiary cells, and the elliptical to fusiform stomatal pit mouth. Note the fine radial striations in guard cells. Negative no. 980673. Scale bar = 10 μm. **10.** Outer view of the lower cuticle showing developed papillae in ordinary epidermal cells. Negative no. 98048, specimen no. PB20044. **11.** Outer view of lower cuticle showing a stomatal complex. Negative no. 98035, specimen no. PB20041. Scale bars = 100 μm except where noted.

32 stomata/mm^2 based on 15 measurements) than those in the upper cuticle.

The upper cuticle is thicker (4–6.5 μm) than the lower one and is composed of ill-defined, alternating bands of elongated and isodiametric or polygonal cells, up to 50 μm wide and 120 μm long (Figs. 12, 13). The periclinal wall of ordinary epidermal cells is smooth and bears papillae (Figs. 16, 17). The anticlinal wall is straight to scarcely undulate and up to 1.5–2.0 μm thick. Stomata (Figs. 13, 14) are scattered among epidermal cells and are similar in structure to those of the lower cuticle. The stomata density for the upper cuticle is 13–25 stomata/mm^2 (average 18 stomata/mm^2 based on 20 measurements).

The stomata complex in both lower and upper cuticle is separated from one another and is oval to rounded in shape (Figs. 8, 9, 14, 15), up to 48–67 μm wide and 48–80 μm long (average 56 × 66 μm based on 20 measurements). Guard cells are sunken, 28–42 × 33–44 μm in size (average 32 × 38 μm). Guard cell poles are usually exposed and beneath the subsidiary cells, and surface walls are thickened next to the stomatal aperture (Figs. 9, 15). Guard cell inner surfaces usually have fine striations radiating from the aperture region (Figs. 9, 15). Apertures are mostly slitlike and are longer or as long as the length of the pit mouth. There are 5–8 lateral subsidiary cells per stomata with regular shape and size; two of them are polar and the others lateral. Most subsidiary cells are thickened at the proximal margin and many bear distinct and solid papillae overhanging the pit mouth (Figs. 6, 11, 17). The thickened margins of subsidiary cells are connected to one another, forming a complete thickened rim surrounding the stomatal pit (Figs. 11, 17).

Cuticular ultrastructure—The lower and upper cuticle were observed under TEM, both in transverse (Figs. 18–29) and longitudinal sections (Figs. 30–34). These cuticular constructions are generally similar and are composed of two layers: outer layer A and inner layer B (Figs. 18, 30). Layer A is homogeneous and composed of granules about 5 nm in diameter (Figs. 19, 20, 23, 27, 32). Layer B is heterogeneous and composed mainly of fibrils, variable in density and thickness (5–10 nm) (Figs. 21, 24, 25, 29, 33), as well as a mixture of granules that are similar in diameter as observed in layer A. Fibrils are usually short and wavy (Figs. 21, 25, 29, 33), though sometimes they are straight and longer (Fig. 24). The thickness of layers A and B is variable depending on the position of the cuticle. In ordinary epidermal cells, cuticle layer A (about 5 μm thick, 76% of the total cuticle thickness) is thicker than layer B (about 1.5 μm thick, 24% of the total cuticle thickness) (Fig. 18) in transverse sections. No lamellae or polylamellae have been found in the outermost part of the present material.

In the stomatal complex, the subsidiary cell cuticle is thicker than the guard cell cuticle. The outer part of the subsidiary cell cuticle is composed of layer A near the stomatal aperture (Fig. 23). This layer is mixed with wavy fibrils that are characteristic of the middle to inner part of layer B (Figs. 24, 25). The guard cell cuticle is similar to the ordinary cell cuticle and consists of layer A with granules, as well as layer B with fibrils (Figs. 26–29).

In general, the two-layered ultrastructure is consistent among different parts of lower and upper cuticle, both in transverse and longitudinal sections. Minor differences lie in varying thickness of the two layers in different cuticular parts (i.e., layer A is thicker in ordinary epidermal cells and anticlinal cell walls, whereas it becomes thinner in subsidiary cells near stomata pits and also in papillae cuticle cells). To summarize all anatomical characters and ultrastructural patterns, a three-dimensional reconstruction of *S. huangii* cuticle is proposed in Fig. 35.

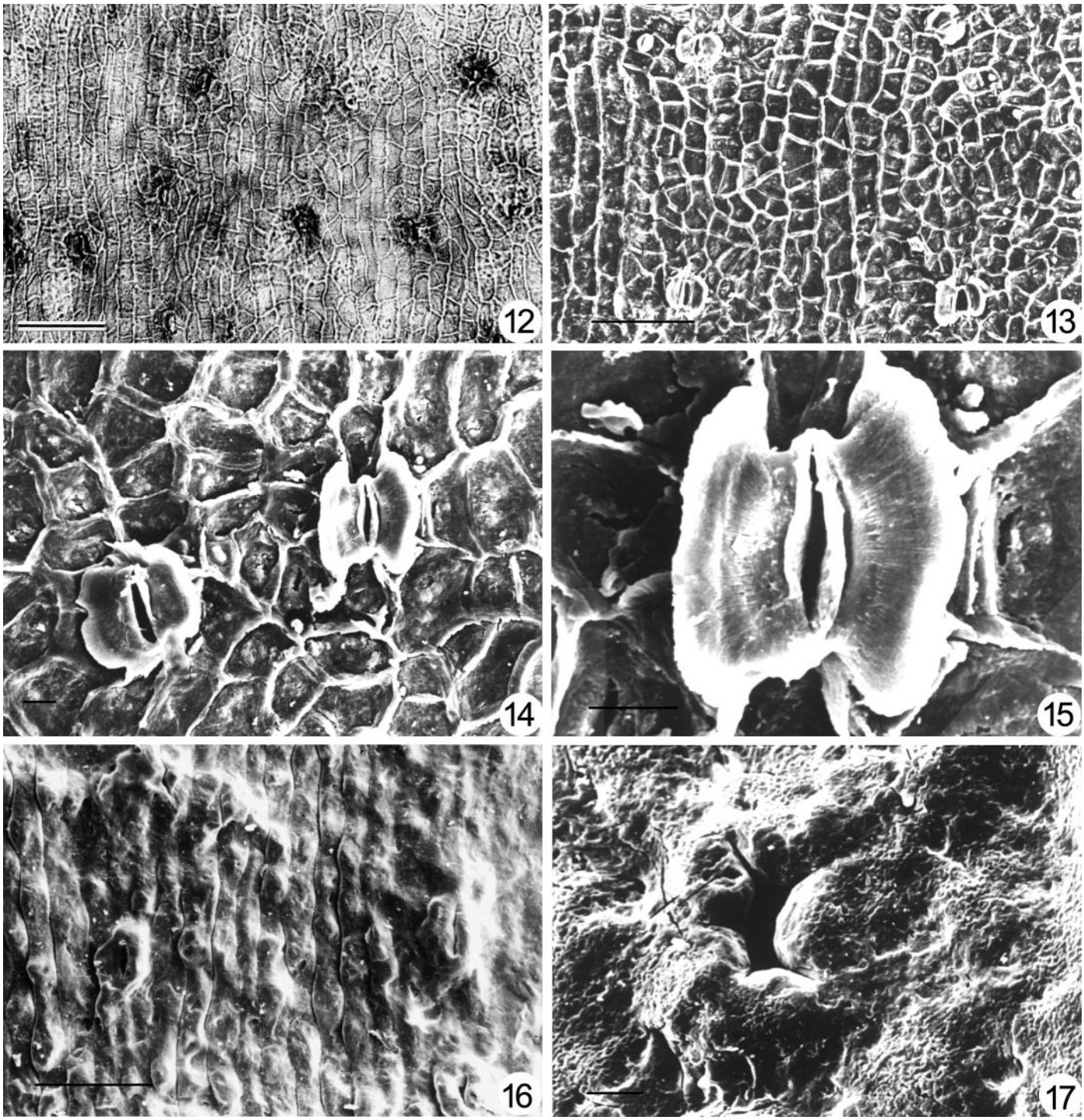
DISCUSSION

Wu et al. (1980) first described *S. huangii* cuticle based on two fragmentary specimens from the same locality in Hubei. Some cuticular features of their specimens are generally similar to those described in the present paper according to the light microscopic illustrations. However, in Wu et al.'s specimens, the papillae are absent in the cuticle; they are well developed in our material. In addition, Huang and Zhou (1980) described several fragmentary specimens as *S. huangii* from the Lower Jurassic Fuxian Formation in Fugu County of Shaanxi Province, northern China. According to their LM micrographs, the cuticle of *S. huangii* from Shaanxi has some similarities to our material from Hubei. However, many features such as papillae, resin bodies, and the stomatal density are not recorded in the material from Shaanxi. Detailed comparison is difficult due to poor preservation of specimens from not only Shaanxi, but also other localities in China, even though a few cuticle fragments were based on LM observations (Zeng et al., 1995; Mi et al., 1996). In some of the literature, such as Zhang (1986) and Zhang et al. (1998), *S. huangii* was only cited, descriptions and photographs were lacking.

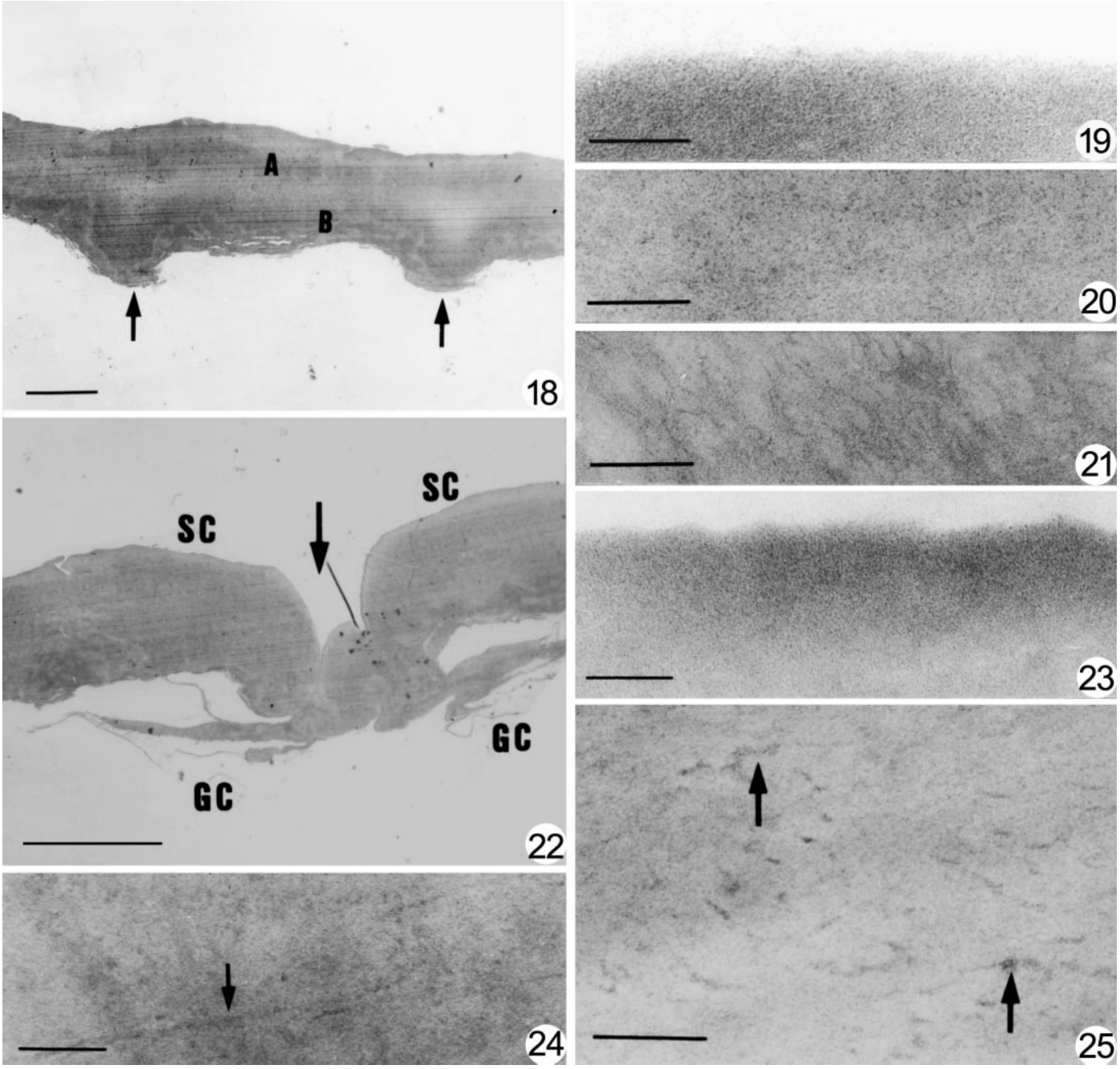
Sphenobaiera huangii is comparable to several other species with bilobed leaves or less divided leaves and broader lobes or segments, both in leaf morphology and cuticular structure, e.g., *S. biloba* Prynada (Prynada, 1938; Samylina, 1967; Chen et al., 1988; Deng, 1995; Deng et al., 1997), *S. jugata* Zhou (Zhou, 1989), *S. ikorfatensis* (Seward) Florin (Lydon et al., 2003; Sun et al., 2003), and *S. pulchella* (Heer) Florin (Heer, 1876, 1878; Samylina, 1963). Their main differences and similarities in terms of leaf morphology and cuticular structure are summarized in Table 1. It is evident that *S. huangii* from the Lower Jurassic of Hubei, China, may represent the best-known species so far of the genus *Sphenobaiera*.

The cuticular ultrastructure of *Sphenobaiera* has not been investigated using electron microscope techniques until now, although other related ginkgoalean or czekanowskialean members (such as *Ginkgo*, *Ginkgoites*, *Phoenicopsis*, and *Arctobaiera*), have been studied using SEM and TEM (Taylor et al., 1989; Villar de Seoane, 1997a; Zhou and Guignard, 1998; Guignard and Zhou, in press). At the ultrastructural level, *S. huangii* has two distinct layers—an outer granular layer (A) and an inner fibrillar layer (B)—in ordinary epidermal cells, stomata complex (subsidiary and guard cells), anticlinal walls, and in papillate cell cuticle, both in transverse and longitudinal sections. No polylamellate layer was found in the cuticle.

Compared with epidermal cells, the stomatal complex cuticle of *S. huangii* has a thicker layer B; that is, the cuticle in both guard cells and subsidiary cells is more fibrillous. This minor structural difference between stomatal complex cells and ordinary epidermal cells was also recorded in other taxa, e.g., *Hirmeriella muensterii* (Schenk) Jung, belonging to Cheirolepidiaceae of the conifers (Guignard et al., 1998). This cuticular anatomy of the stomatal complex is known, in extant plants, to be directly related to the exchange of water and other



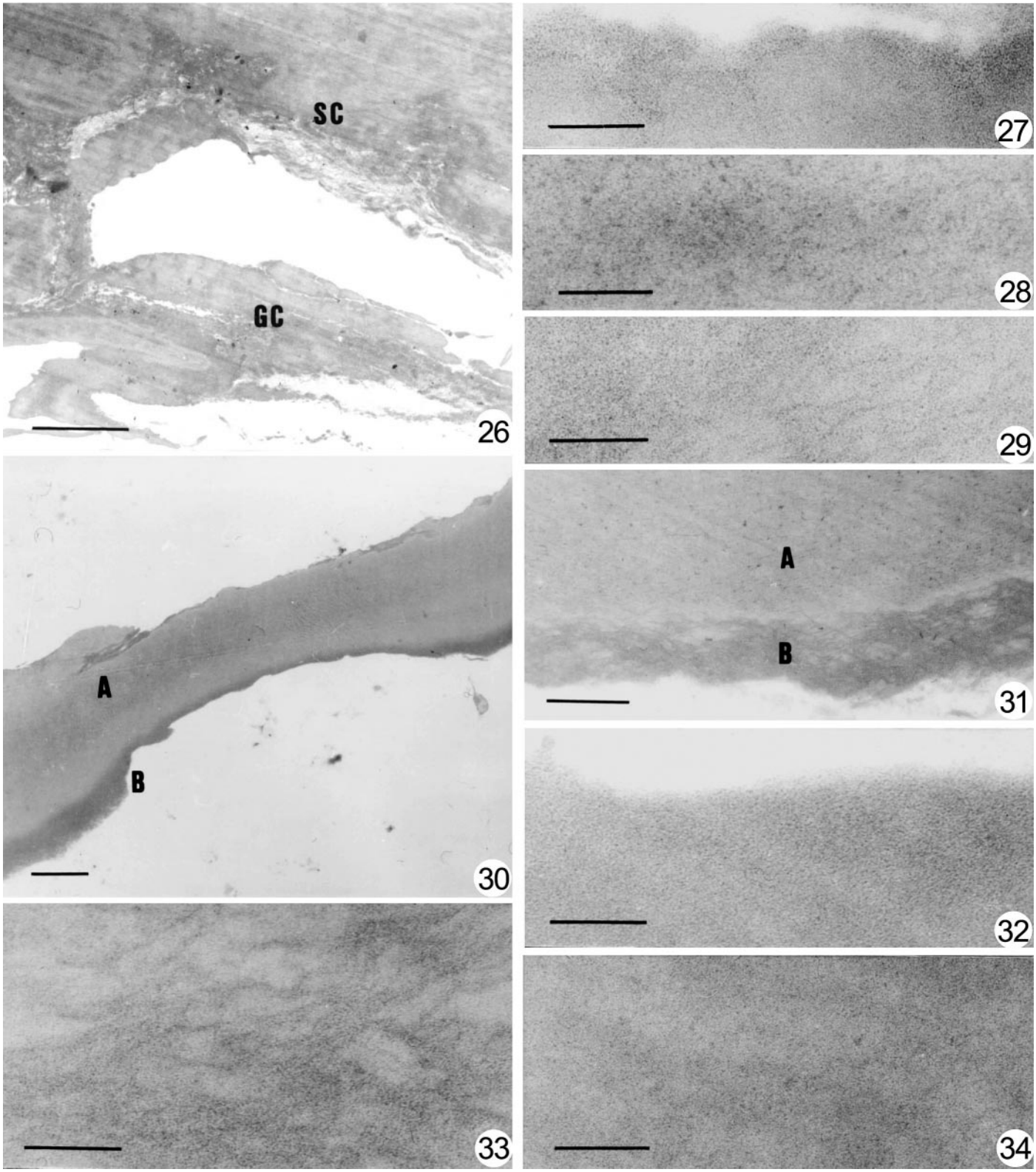
Figs. 12–17. *Sphenobaiera huangii* (Sze) Hsü from the Lower Jurassic Hsiangchi Formation in Hubei, China. Light and scanning electron microscopy (LM, SEM) photos of the upper cuticle. **12.** Lower magnification showing epidermal cells and the distribution of stomata (LM). Negative no. 980671, specimen no. PB20060. Scale bar = 100 μm. **13.** Four stomata, isodiametric and polygonal ordinary cells. Negative no. 98031, specimen no. PB20061. Scale bar = 100 μm. **14.** Two stomata and the outline of epidermal cells. Negative no. 98032, specimen no. PB20041. Scale bar = 10 μm. **15.** Detail of a stoma in Fig. 14 showing exposed guard and subsidiary cells and elliptical to fusiform stomatal pit mouth. Note the fine radial striations in guard cells. Negative no. 98032. Scale bar = 10 μm. **16.** Outer view of the upper cuticle showing papillae and stomata. Negative no. 99052. Specimen no. PB20045. Scale bar = 100 μm. **17.** Outer view of a stoma showing thickened subsidiary cells and papillae overhanging the stomata pit. Negative no. 980670, specimen no. PB20064. Scale bar = 10 μm.



Figs. 18–25. *Sphenobaiera huangii* (Sze) Hsü from the Lower Jurassic Hsiangchi Formation in Hubei, China. Transmission electron microscopy (TEM) photos of the lower cuticle. All transverse sections. Specimen no. PB20041. **18.** General view of a part of the cuticle composed of two anticlinal walls (arrows). The cuticle is composed of a homogeneous outer layer A with granules and a heterogeneous inner layer B mainly with fibrils. Negative no. gtx379. Scale bar = 5 μm. **19.** Detail of Fig. 18 showing the outermost part of the cuticle with layer A with a high density of fine granules. Negative no. gtx364. Scale bar = 100 nm. **20.** Detail of Fig. 18 showing the middle part of the cuticle with layer A with a low density of fine granules. Negative no. gtx358. Scale bar = 100 nm. **21.** Detail of Fig. 18 showing the innermost part of the cuticle of layer B consisting of fine fibrils. Negative no. gtx365. Scale bar = 200 nm. **22.** A wide-opened stoma showing stomata pit (arrow), subsidiary cell (SC), and guard cell (GC) cuticle. Negative no. gtx367, specimen no. PB20045. Scale bar = 10 μm. **23.** Detail of outer part of the subsidiary cell cuticle near the stomatal pit, showing layer A. Negative no. gtx371. Scale bar = 100 nm. **24.** Detail of middle part of the subsidiary cell cuticle near the stomatal pit with layer B showing fibrils (arrow). Negative no. ggw5143. Scale bar = 100 nm. **25.** Detail of inner part of the subsidiary cell cuticle, showing fibrils (arrows). Negative no. gtx372. Scale bar = 100 nm.

molecules (Larcher, 1995). In *S. huangii*, the guard cell cuticle is thinner than subsidiary cell cuticle. From a structure–function view, considering that guard cells are responsible for the opening and closing of stomata, a thinner cuticle is certainly more efficient than a thicker one.

To date, the leaf cuticular ultrastructure of Ginkgoales has been reported only for a few fossil and living taxa in the families Karkeniaceae and Ginkgoaceae, including *Ginkgoites tigrensis* Archangelsky, *Ginkgo yimaensis* Zhou and Zhang and *Ginkgo biloba* L. *Ginkgoites tigrensis* from the Lower Creta-



Figs. 26–34. *Sphenobaiera huangii* (Sze) Hsü from the Lower Jurassic Hsiangchi Formation in Hubei, China. Transmission electron microscopy (TEM) photos of the lower cuticle. Specimen no. PB20045. 26–29. Transverse sections. Specimen no. PB20045. **26.** Detail of Fig. 22, showing guard cell (GC) and the lower part of the subsidiary cell (SC) cuticle. Negative no. gtx373. Scale bar = 2 μm. **27.** Detail of Fig. 26, showing the outer part of the guard cell cuticle with layer A. Negative no. gtx376. Scale bar = 100 nm. **28.** Detail of Fig. 26, showing the middle part of the guard cell cuticle with granules. Negative no. gtx377. Scale bar = 100 nm. **29.** Detail of Fig. 26, showing the inner part of the guard cell cuticle with layer B containing fibrils. Negative no. gtx378. Scale bar = 100 nm. 30–34. Longitudinal sections of ordinary cell of the lower cuticle. **30.** General view of an ordinary epidermal cell cuticle, showing layers A and B. Negative no. gtx389. Scale bar = 2 μm. **31.** Detail of Fig. 30, showing the innermost part with layer B and part of layer A. Negative no. gtx383. Scale bar = 500 nm.

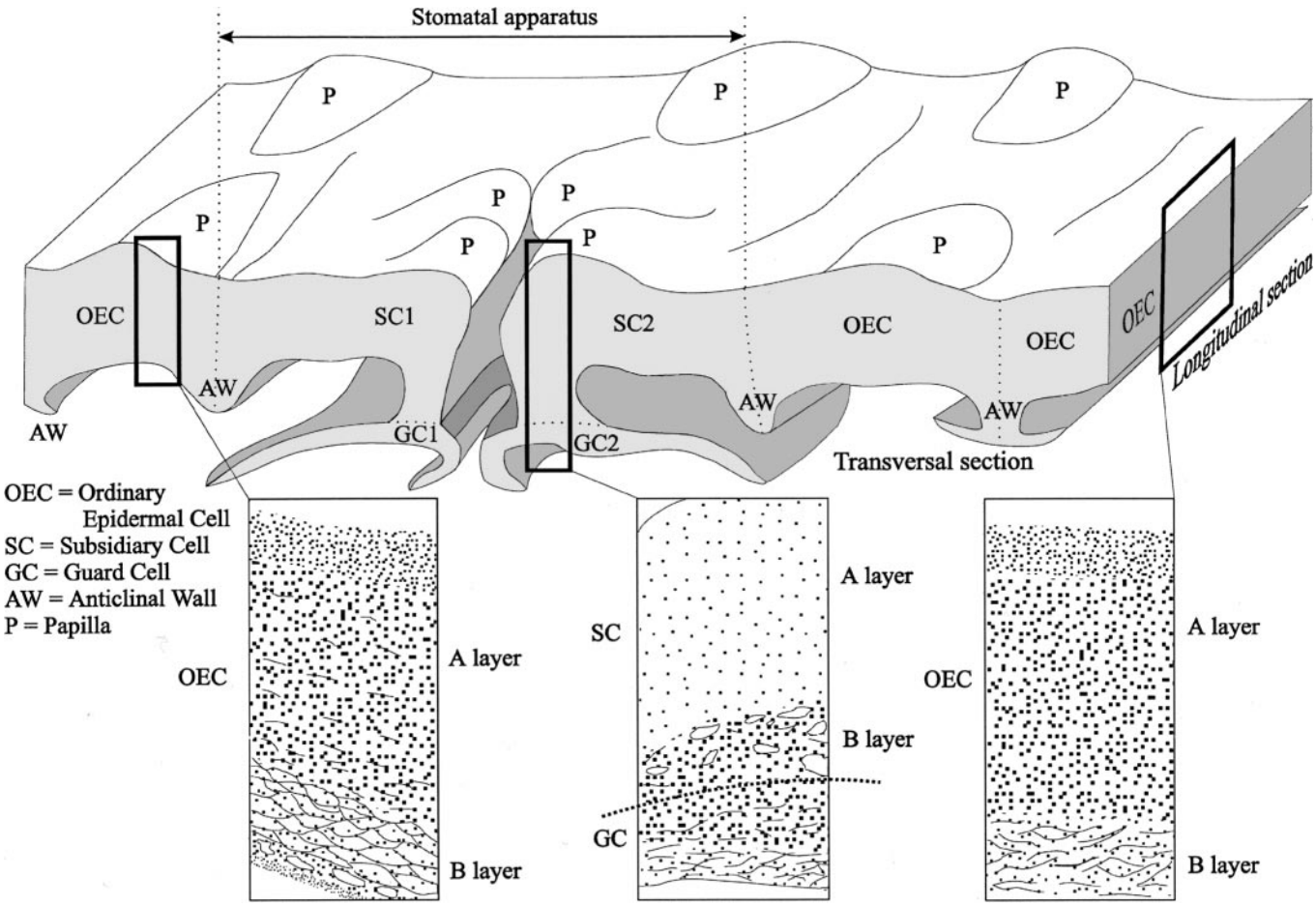


Fig. 35. A suggested three-dimensional reconstruction of the cuticular anatomy of *Sphenobaiera huangii* (Sze) Hsü, based on transverse and longitudinal sections in various parts of the cuticle, including ordinary epidermal cell (OEC), anticlinal wall (AW), papillae (P), stomatal complex region with guard cell (GC), and subsidiary cell (SC).

ceous of Argentina is a representative member of the Karkeniaceae. Available data demonstrate that the cuticular ultrastructure of *S. huangii* shows a closer affinity with that of *G. tigrensis*. According to a recent study by Villar de Seoane (1997a), the cuticular ultrastructure of *G. tigrensis* from Argentina closely resembles that of *S. huangii* from China. The outer part of the *G. tigrensis* cuticle is compact and homogeneous, comparable to the outer granular layer of *S. huangii*. The inner part of the cuticle is slightly reticulate and is structurally similar to the heterogeneous inner layer with fibrils of *S. huangii*. The polylamellate layer in *G. tigrensis* is absent (Villar de Seoane, 1997a). So far, the leaf cuticular ultrastructure is known for only one fossil taxon belonging to Ginkgoaceae of Ginkgoales. According to Guignard and Zhou (in press), the leaf cuticle of *Ginkgo yimaensis*, the oldest Ginkgo from the Jurassic of China, is obviously distinguished from *S. huangii* in ultrastructural level by having a distinct outer polylamellate layer. The leaf cuticle of living *Ginkgo* is also different from that of *S. huangii*. Taylor et al. (1989) and Guignard and Zhou (in press) demonstrated that the cuticle of *G. biloba* is characterized by an outer polylamellate layer and inner granular and fibrillar layers, differing from *S. huangii* of China at the ultrastructural level.

The studies on the fossil leaf cuticular ultrastructure using transmission electron microscopy started with the pioneer work of Archangelsky et al. (1986). Since then, the leaf cuticular ultrastructure is known for a number of fossil taxa or groups, including pteridosperms (Taylor et al., 1989; Baldoni and Barale, 1996; Labe and Barale, 1996; Maheshwari and Bajpai, 1996; Bajpai, 1997; Guignard et al., 2001), bennettitaleans (Barale and Baldoni, 1993; Villar de Seoane, 2001), cycadaleans (Artabe and Archangelsky, 1992; Villar de Seoane, 1997b), ginkgoaleans (Taylor et al., 1989; Villar de Seoane, 1997a; Guignard and Zhou, in press), czekanowskialeans (Zhou and Guignard, 1998), as well as conifers (Archangelsky and Taylor, 1986; Archangelsky et al., 1986; Del Fueyo et al., 1990; Barale et al., 1992; Guignard et al., 1998; Villar de Seoane, 1998; Zhou et al., 2000). Most of the cuticle is marked

←

Figs. 26–34. Continued. **32.** Detail of Fig. 30, showing the outermost part of the cuticle with layer A. Negative no. gtx381. Scale bar = 100 nm. **33.** Detail of Fig. 30, showing the innermost part of the cuticle with fibrils of layer B. Negative no. gtx385. Scale bar = 100 nm. **34.** Detail of Fig. 30, showing the middle part of the cuticle with layer A. Negative no. gtx382. Scale bar = 100 nm.

TABLE 1. Comparisons between *Sphenobaiera huangii* and other related species of *Sphenobaiera* in different localities.

			Leaf morphology		Cuticle structure							
					Thickness (μm)		Papillae		Stomata density (/mm²)			
Species	Locality	Horizon	Leaf/lobe size	Number of veins (per cm)	Upper	Lower	Upper	Lower	Upper	Lower	Ultrastructure	References
S. huangii (Sze) Hsü	Hubei, China	Lower Jurassic	leaf 7.5–25 cm long; lobe 8-(14)-21 mm wide; lobe angle 10°–25°	10–11	4–6.5	3–5	usually bear papillae	with developed papillae	13-(20)-25	20-(32)-48	Composed of two layers: outer layer A and inner layer B. Layer A homogeneous and composed of granules; layer B heterogeneous with mixture of granules and fibrils variable in density and thickness	This paper
S. biloba Prynada	Siberia	Lower Cretaceous	leaf 13 cm long, lobe 18–20 mm wide	10–13	thicker	#	*	#	no stomata	#	*	Prynada, 1938; Samylina, 1967
S. biloba Prynada	Fuxin, Liaoning, China	Lower Cretaceous	leaf up to 17 cm long, lobe 13 mm wide; lobe angle 10°	12	thicker	thinner	with indistinct papillae	no papillae	rare	few	*	Chen et al., 1988
S. juncta Zhou	Shaqiao, Hunan, China	Upper Triassic	leaf 6–10 cm long, lobe 4 mm wide	15–26	2.5	3–3.5	sometimes with papillae	sometimes with papillae	29–58	69–72	*	Zhou, 1989
S. pulchella (Heer) Florin	Eastern Siberia	Upper Jurassic	leaf >11 cm long, lobe 6–12 mm wide	13–16	cuticle structures are unknown for this species							Heer, 1876, 1878; Samylina, 1963
S. ikorfatensis (Seward) Florin	Western Greenland; Inner Mongolia, China;	Lower Cretaceous	leaf 13–15 cm long; 4–6 lobes, each lobe 8–10 mm wide	20–30	4–7	3–5	with or without papillae	no distinct papillae	6–8	20–30	*	Lydon et al., 2003; Sun et al., 2003

Note: Upper = Upper cuticle; Lower = Lower cuticle; * = No data or records. # = Lower cuticle in this species not observed and described.

by an outer polylamellate zone, similar to type 1 of Holloway's (1982) cuticle classification (six types based on the leaf ultrastructure of living plants). It is noteworthy that Holloway (1982) is very careful to point out the lamellate structure of the cuticle proper; where it occurs in the cuticular layers, it is difficult to illustrate. Some results may depend upon the staining technique, which can alter the appearance of the cuticle. In this study, *S. huangii* cuticle is stained using a method similar to that used for *G. yimaensis* and *G. biloba* (Guignard and Zhou, in press), with osmium tetroxide and a post-stain with uranyl acetate and lead citrate. It is evident that the outer polylamellate layers are reported in *G. yimaensis* and *G. biloba* (Ginkgoaceae), but were not found in *S. huangii*, though similar staining was used in both cases.

The cuticle of *S. huangii* from the Lower Jurassic of Hubei, China, has some affinities with both Holloway's type 3 and type 6. In type 3, the cuticle is partly reticulate without the granular layer in *S. huangii*. Type 6 has many different layers, but they are very different from *S. huangii*. It is known that a cuticle with an outer homogeneous layer as described in *S. huangii* is very distinct and rarely reported in living and fossil records. A more or less similar structure was reported in two fossil cycadalean leaves from the Lower Cretaceous of Argentina (Villar de Seoane, 1997b) and in *Phoenicopsis* and *Arctobaiera* leaves of the Czekanowskiales from the Jurassic of Henan, central China (Zhou and Guignard, 1998), but the cuticle of these taxa are otherwise very different in general structure. No known fossil ginkgoalean member bears a cuticle similar in ultrastructure to *S. huangii*; only *G. tigrensis* (Karkeniaceae) has a close affinity with *S. huangii* at the ultrastructural level.

Previous and recent studies show that some species of *Sphenobaiera* are associated with the ovule *Karkenia*, belonging to the family Karkeniaceae (Archangelsky, 1965; Krassilov, 1972; Schweitzer and Kirchner, 1995; Zhou et al., 2002), whereas other species of *Sphenobaiera* are associated with *Ginkgo*-type ovules. However, in most species of *Sphenobaiera*, their ovule-bearing organs are still unknown. Obviously, the genus *Sphenobaiera* is difficult to place into any known family within the Ginkgoales, based upon either leaf morphology and/or general cuticular features. According to this investigation, the ultrastructural data of *S. huangii* cuticle may imply a potential affinity to the family Karkeniaceae of Ginkgoales. We have provided useful information for exploring the relationship of the leaf cuticle construction among different taxa and about the extent of variation in a given taxon and for assessing the significance of cuticular structure in plant taxonomy. Further work is obviously needed in order to provide more reliable data on reproductive organs associated with *S. huangii* and to confirm its systematic status.

In summary, this investigation of *S. huangii* from the Early Jurassic in Hubei, China, provides new insights into the cuticular anatomy, as well as the variation in leaf morphology. Many features are described for the first time for this species, based upon light and electron microscopic observations, including general structure of lower and upper cuticle, stomata, and papillae. At the ultrastructural level, two layers have been distinguished in both lower and upper cuticle, including a homogeneous outer layer with granules and a heterogeneous inner layer with fibrils. Comparison with literature between *S. huangii* and other relevant species of *Sphenobaiera* indicate that this species from the Lower Jurassic of China may represent the best-known taxon in the genus *Sphenobaiera* in both leaf morphology and cuticular structures. Particularly, this study provides the first detailed ultrastructural data on the leaf cuticle of *Sphenobaiera*, one of the oldest foliage taxa of ginkgoales. This offers further evidence for potential discussion on the taxonomic relationships with other ginkgoalean taxa.

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