



Studies on plant cuticles from the Lower–Middle Devonian of China



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ARTICLE INFO

Article history:

Received 15 May 2015

Received in revised form 29 October 2015

Accepted 3 November 2015

Available online 4 December 2015

Keywords:

Cuticle

Epidermis

Stoma

Early plant

Devonian

China

ABSTRACT

Numerous plant cuticles were collected from five sections in the Lower–Middle Devonian of Yunnan and Sichuan provinces, China. Based on these cuticles and published data, we recognize five types of stomata or stoma-like pores in Devonian plants, i.e., anomocytic, rosette and complex types of stomata, pores like in *Nematothallus*, and pores within thick cuticle. Anomocytic and/or rosette types of stomata are more common in some hornophytopsids, rhyniopsids, renalioids, zosterophylloids, lycopsids and a progymnosperm. Complex type found only in the Middle Devonian likely occurred in *Orestovia* and *Schuguria*. Pores like in *Nematothallus* and pores within thick cuticle are documented in both the Lower and Middle Devonian and are usually observed on dispersed cuticles which have relationship with non-vascular plants. The various plant species share only five types of stomata and stoma-like pores. It is difficult to understand the exact affinities of epidermises without other macrofossil information.

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1. Introduction

Vascular plants began to diversify in the late Silurian and Early Devonian and then their morphological complexity increased significantly in the Devonian (Boucot, 1990; Edwards and Berry, 1991; Taylor et al., 2009; Hao and Xue, 2013), which includes the evolution of cuticles and stomata (Edwards et al., 1982, 1998). Since the 1930s, abundant cuticles of early plants have been documented from many localities around the world (e.g., Lang, 1932; Ergolskaya, 1936; Chaloner et al., 1974; Edwards et al., 1979; Ishchenko and Ishchenko, 1980; Krassilov, 1981; Edwards and Rose, 1984; Strother, 1993). Fossil cuticles, in situ or dispersed, are especially useful to know the details of epidermal and stomatal features (e.g., Gensel et al., 1990; Taylor et al., 2009), which are helpful for taxonomy, ecological interpretations and have been used to estimate paleoatmospheric carbon dioxide concentration (e.g., McElwain and Chaloner, 1995).

Here, we present a comprehensive study of numerous cuticles of the Lower–Middle Devonian plants from Yunnan and Sichuan provinces, China, from where various megafossil plants have been documented that document a high taxonomic diversity (Wang et al., 2007; Hao and Xue, 2013). On the basis of these newly found cuticles and data from previously published articles, early plant epidermises with five types

of stomata or stoma-like pores are recognized and discussed in relation to Devonian plant groups.

2. Material and methods

2.1. Locality and geology

The cuticles are from five Devonian localities in South China (Fig. 1): 1. The Xujiachong Section (13 km NW of Qujing City, Yunnan Province) – Two pieces of cuticle of *Drepanophycus* sp. were obtained from gray and yellow-green argillaceous siltstone in the middle-lower part of the Xujiachong Formation, Pragian, Lower Devonian (Fig. 1 in Wang et al., 2002; Fig. 3 in Liu et al., 2004; Wellman et al., 2012). 2. The Longhuashan Section (2 km SW of Zhanyi County, Yunnan Province) – Six pieces of cuticle of *Drepanophycus* sp. and six dispersed cuticles were obtained from gray and green-yellow argillaceous sandstone in the upper part of the Xujiachong Formation, Emsian, Lower Devonian (Fig. 1 in Wang et al., 2002). Since the 1960s, comprehensive studies on stratigraphic sequences, spore assemblages, flora and faunas (fish and bivalves) of the Xujiachong Formation in Qujing area have been continuously performed (e.g., Wang et al., 2002; Hao and Xue, 2013). 3. The Yuguang Section (2 km NE of Zhanyi County, Yunnan Province) – Two pieces of cuticle of *Yuguangia ordinata* and more than five hundred of dispersed cuticles were obtained from white-gray mudstones and siltstones of the Haikou Formation, Givetian, Middle Devonian (Fig. 1 in Hao et al., 2007). This section contains the fish *Bothriolepis* sp. and the plant *Y. ordinata*, *Minarodendron cathaysiense* and *Lepidodendropsis* sp. (Hao et al., 2007). 4. The Wujian

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Fig. 1. Map showing positions of the sites where cuticles were collected.

Section (20 km N of Luquan County, Yunnan Province) – More than hundred dispersed cuticles were obtained from an organic-rich intercalation between yellow-gray sandstone and shale beds, in the upper part of the Haikou Formation. Assemblages of plants and spores indicate that the Haikou Formation in this section is Givetian, Middle Devonian in age (Sun et al., 2007). 5. The Damaidi Section (20 km W of Panzhihua City, Sichuan Province) – Eight dispersed cuticles were obtained from coal beds of the Lagude Formation, Givetian, Middle Devonian (Fig. 2 in Wang et al., 1997). This section contains dispersed cuticles and spores and some plant fragments (Wang and Han, 1998).

2.2. Methods and storage

To isolate cuticles from the rock matrix, the specimens were first treated with hydrochloric acid (HCl) and subsequently with hydrofluoric acid (HF) (sensu Kerp, 1990). Then the specimens were rinsed in water to wash out the remaining soluble substances. Bleaching was not necessary, because cuticles are yellow-orange in color. Finally, the cuticles were embedded in slides, which were observed and photographed with a digital microscope. Terminology for describing epidermal features follows that of Stace (1965). The SI is calculated as: $SI(\%) = [SD / (SD + ED)] * 100$, where SI(%) represents the stomatal index, SD the stomatal density per mm^2 , and ED the non-stomatal epidermal cell density per mm^2 . All specimens and slides are housed in Department of Geology, Peking University (Beijing, China).

3. Description

Plant cuticles are preserved as small pieces and yellow-orange in color, and their size ranges from 0.2–211.3 mm^2 and mostly are c. 4.4 mm^2 .

3.1. Cuticles from the Lower Devonian, China

Cuticles of *Drepanophycus* sp. stems from the Xujiachong and Longhuashan sections display rectangular to elongate epidermal cells

with the long axes oriented parallel to the stem length (Plate I, 1, 2). Epidermal cells are 144–(180)–226 μm long and 30–(35)–40 μm wide, being several times longer than wide. Elliptical stomata are randomly distributed, and are 62–(83)–110 μm long and 45–(53)–62 μm wide. The stomatal density and index are 5.0 to 13.0 mm^{-2} and 1.7 to 6.5, respectively. Each stoma consists of two reniform guard cells with cuticular thickening near the outer (and perhaps the inner) rim (Plate I, 2, arrows, and 3; Fig. 2A).

Dispersed cuticles from the Longhuashan Section show polygonal or nearly isodiametric epidermal cells, 12–(25)–38 μm long and 11–(12)–19 μm wide (Plate I, 4, 5). These cuticles lack stomatal apparatus but possess round pores, which are c. 15 μm in diameter, randomly distributed and more or less appear as ruptures of epidermal cells (Fig. 2D). Some pores are surrounded by a ring of five to eight epidermal cells (Plate I, 5, arrows).

3.2. Cuticles from the Middle Devonian, China

Cuticles of *Yuguangia ordinata* (Plate I, 6–8) and abundant dispersed ones (Plate I, 9–11; Plate II, 1–5) from the Yuguang and Damaidi sections show rectangular to elongate epidermal cells, 91–(192)–368 μm long and 17–(38)–66 μm wide, with elliptical or semicircular stomata, 52–(98)–216 μm long and 32–(64)–134 μm wide. Stomata are randomly distributed. The long axes of the stomatal pores and guard cells are oriented parallel to the long axes of the epidermal cells. The stomatal density and index are 1.0 to 26.0 mm^{-2} and 0.3 to 13.3, respectively. Each stoma consists of two reniform guard cells (Plate I, 7–8; Plate II, 1–4, 5, arrows; Fig. 2A). Guard cells show different extents of cuticular thickenings near the outer rims, and/or at the ‘T’ parts representing the contacts of two guard cells, and even on the whole guard cell surface (Plate I, 7–11; Plate II, 1–5).

Some dispersed cuticles from the Wujian Section have polygonal, rectangular or nearly isodiametric epidermal cells, 47–(91)–138 μm long and 25–(33)–44 μm wide (Plate II, 6–8). Cells near the stoma are smaller than other epidermal cells. Semirounded to rounded

Plate I. Cuticles from Xujiachong (Early Devonian), Longhuashan (Early Devonian) and Yuguang (Middle Devonian) sections in Yunnan Province, China (see on page 44).

1. Cuticle showing epidermis of *Drepanophycus* sp. with elongate epidermal cells and anomocytic stomatal apparatus; Xujiachong Section, scale bar = 200 μm .
2. Cuticle showing epidermis of *Drepanophycus* sp. with rectangular to elongate epidermal cells and anomocytic stomatal apparatus (arrows); Longhuashan Section, scale bar = 100 μm .
3. Detail of Plate I, 1 (arrow) showing anomocytic stomatal apparatus with two reniform guard cells bearing cuticular thickening, scale bar = 50 μm .
- 4, 5. Dispersed cuticles (*Nematothallus* type) showing epidermises with polygonal, nearly isodiametric epidermal cells and randomly distributed round pores (e.g., arrows); Longhuashan Section, scale bars = 50 μm .
6. Cuticle showing epidermis of *Yuguangia ordinata* with epidermal cells and anomocytic stomatal apparatus; Yuguang Section, scale bar = 200 μm .
- 7, 8. Stomatal apparatus of *Yuguangia ordinata* with two reniform guard cells; scale bars = 50 μm . 9–11. Dispersed cuticles showing epidermises with epidermal cells and anomocytic stomatal apparatus; Yuguang Section, scale bars = 250 μm , 300 μm and 300 μm , respectively.

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