



Ultrastructure and development of sporoderm in *Aristolochia clematitis* (Aristolochiaceae)

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ABSTRACT

The purpose of this study was to investigate the sporoderm development of inaperturate pollen grains in *Aristolochia clematitis* (Aristolochiaceae). During successive microsporogenesis several types of tetrads are formed; no tetrahedral tetrads were observed. In the tetrad period, the primexine is observed around the perimeter of microspores. In the free microspore period, a thick lamellar endexine develops around the perimeter of the microspore; the thick tubular intine appears later in this period. At the maturation of pollen grains, the intine is stratified into two layers: an outer tubular ectintine and an inner homogeneous endintine. Finally, the intine forms an aperture thickening. The thickened intine deforms and displaces the endexine and tears the ectexine apart. This shows that pollen grains of *A. clematitis* are aperturate. The apertures are colpi.

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1. Introduction

The Aristolochiaceae belong to basal angiosperms, order Piperales. About 500 species of this family are incorporated into four main genera: *Aristolochia* L., *Asarum* L., *Saruma* Oliver and *Thottea* Rottboll (Neinhuis et al., 2005). These taxa are widespread in the tropics and subtropics. Some species occur in temperate regions of the Northern Hemisphere. Successive and simultaneous types of microsporogenesis are known in the members of the family; different types of tetrads are formed (Gonzalez et al., 2001; Furness et al., 2002). The simultaneous microsporogenesis results in all tetrad types of microspores including tetrahedral tetrads. The successive microsporogenesis results in several types of tetrads except tetrahedral tetrads (Albert et al., 2011). *Aristolochia clematitis* L. has successive microsporogenesis and isobilateral, decussate, T-shaped and linear tetrad types. The secretory tapetum is typical for this family. Orbicules are formed during microsporogenesis (Gonzalez et al., 2001).

Pollen grains of all investigated *Aristolochia* species are considered to be inaperturate including *A. clematitis* (Erdtman, 1952; Kuprianova and Alyoshina, 1972; Gonzalez et al., 2001; Mulder, 2003; Perveen and Kaiser, 2008). It has been observed, however, that pollen grains of *A. clematitis* have a colpous aperture (Advocat, 2004). Pollen grains of *Asarum* species can be 2–3–6–porate (Kuprianova and Alyoshina, 1972; Yamaji et al., 2006). Pollen grains of *Saruma* species are mononosulcate (Erdtman, 1952; Dickinson, 1992). Since the Aristolochiaceae comprise genera with different aperture types, and the aperture type in *A. clematitis* was differently interpreted as inaperturate or colpate, the investigation of the sporoderm development can help to solve this

contradiction. Sporoderm development of inaperturate pollen in basal angiosperm taxa is of special interest. This inaperturate pollen type can be formed from both polar and equatorial aperture types. Although some information was published by Furness et al. (2002, Fig. 4, E and F) and Gonzalez et al. (2001, Fig. 101–109), our study is the first that deals with the sporoderm development in *A. clematitis* in detail.

2. Material and methods

Flower buds of *A. clematitis* at different developmental stages were collected in the Moscow State University botanical garden on 26 May 2011, 19 May 2012 and 27 May 2014. Four samples of mature pollen grains were investigated with a light microscope. The first sample was cultivated in botanical garden of MSU (Moscow), and three samples were collected in native habitat of *A. clematitis*: Ryazan region (54.706343 N, 40.860328 E), 01 July 1994; Voronezh region (51.812164 N, 39.385424 E), 23 June 2007; and the Republic of Mordovia (54.181899 N, 46.192865 E), 11 June 1986.

The material was prepared as follows.

For light microscopy (LM), parts of flowers with stamens were prepared according to the acetolysis method of Erdtman (1952). The unstained pollen grains were mounted in glycerin jelly and observed with a Nikon Eclipse Ci microscope (E40, 0.75).

To prepare samples for fluorescent microscopy (FM), mature pollen grains were extracted from anthers and put into a drop of medium, using dissecting needles. The standard medium included 1.6 mM H_3BO_3 , 3 mM $Ca(NO_3)_2$, 0.8 mM $MgSO_4$, 1 mM KNO_3 and 0.25 M mannitol added to 25 mM MES–Tris buffer, pH 5.9. A part of the material was

Table 1

Morphometry of acetolized mature pollen grains of *Aristolochia clematitis* from different native localities, LM.

Locality	Major axis, (μm)	Minor axis, (μm)	Exine thickness, (μm)
Mordovia region	38.9* (33.2–43.7)	32.1 (24.7–36.4)	1.49 (0.94–1.8)
Moscow	43.0 (38.4–49.8)	34.0 (27.4–40.7)	1.71 (1.28–2.31)
Ryazan region	39.6 (33.6–59.4)	31.5 (25.7–40.6)	1.22 (0.88–1.91)
Voronezh region	43.4 (29.6–49.3)	32.7 (28.3–38.1)	1.41 (1.11–1.75)

* Average value, minimal and maximal values in brackets.

stained with 0.01% solution of Calcofluor White M2R (Fluorescent Brightener 28, Sigma), which reveals the presence of β -glucans (most commonly cellulose). The rest of the material was used for the study of sporopollenin autofluorescence. Vital preparations of pollen grains were analyzed and photographed using an Axioplan 2 imaging MOT research microscope equipped with an AxioCam HRc digital camera and AxioVision 4.7 software (Carl Zeiss, Germany). Fluorescence was excited with a mercury lamp at 359–371 nm, detected at wavelengths >397 nm.

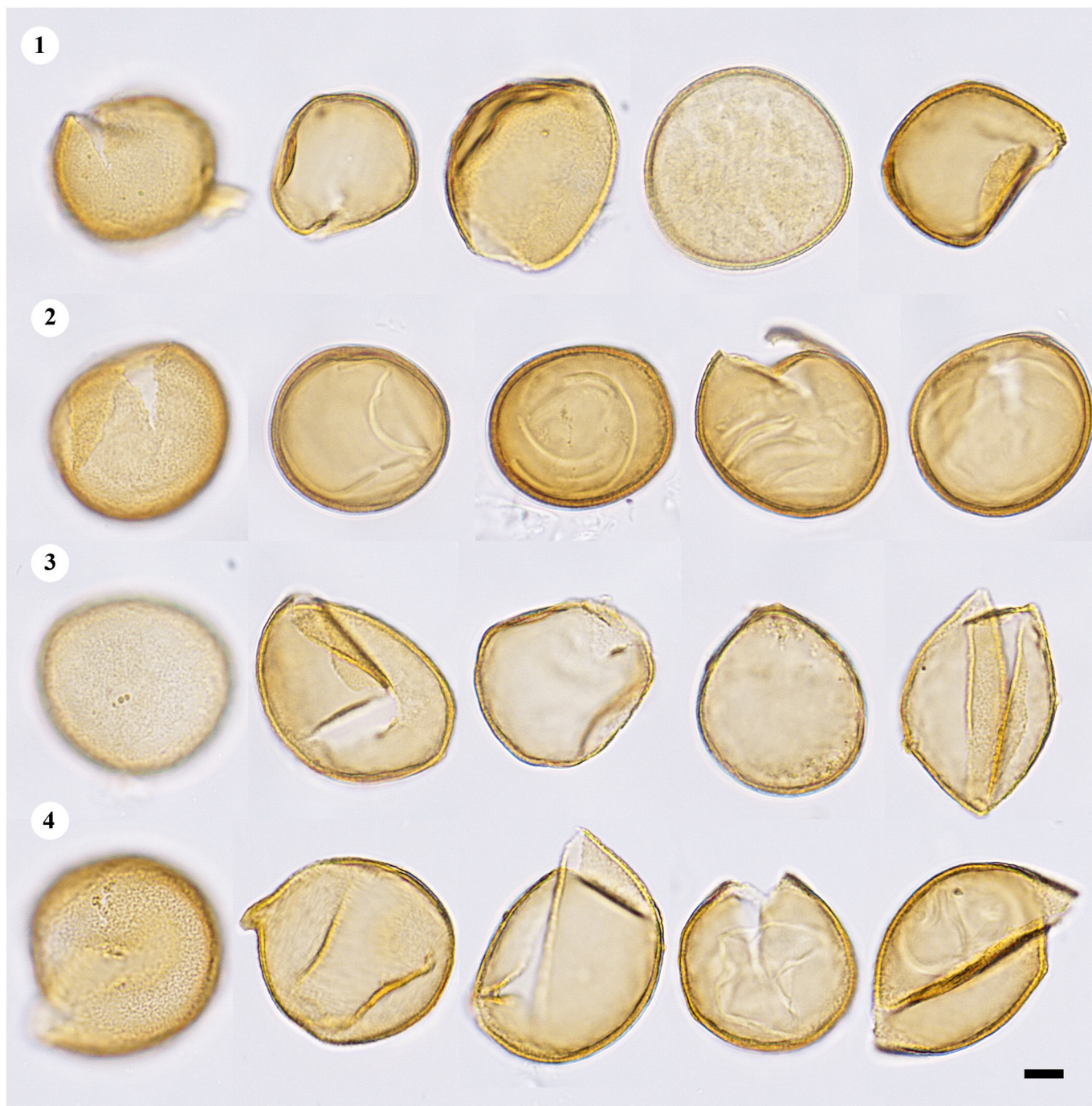


Plate I. Acetolized pollen grains of *Aristolochia clematitis* from different regions, LM.

1. Mordovia region.
2. Moscow.
3. Ryazan region.
4. Voronezh region. Scale bar 10 μm.

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