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Ontogeny of the flowers in *Paulownia tomentosa* – A contribution to the recognition of the resurrected monogeneric family Paulowniaceae

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ABSTRACT

Disintegration of the Scrophulariaceae due to molecular data resulted in re-circumscriptions, resurrection and new descriptions of families to encompass the monophyletic lineages. In some of these families floral morphological/ontogenetic data, however, are largely missing, as, for example, in Paulowniaceae. This study reveals a set of distinctive features that were up to now unknown in Paulowniaceae: In the lateral flowers of the inflorescence, initiation sequence in calyx and corolla is unidirectional in identical direction, starting at the adaxial side; the formation of sympetaly is late but ledges connecting the separate petals arise relatively early. Of importance are particularly the occurrence of: crescent-shaped archespore and pollen sacs with a pollen sac placentoid, secretory tapetum, a several cell layers thick endothecium, endothecium-like cells situated all over the tissue of the theca except in the placentoid, undivided placenta originating in each locule on the septum only, a tubular stigma with papillae inside a dilated chamber (in this character *Paulownia* differs from all other members of the Lamiales-clade!), nectary in the basal part of the superior ovary, and small, winged seeds whose testa possesses protrusions that laterally expand into several sinuate wings, gradually increasing in extension towards the two margins.

When continuing to resolve and stabilize the relationships of clades, it should be one of the goals to find new, visually perceptible data that enable easy identification of clades. For Paulowniaceae, these distinctive characters are the peculiar shape of the multi-winged seeds with their lateral wings gradually increasing in size and the tubular stigma with papillae inside a dilated chamber.

Introduction

The Lamiales are a well-supported order in the euasterids I (=lamiids; e.g. Bremer et al., 2002; Judd and Olmstead, 2004), in which classification is under ongoing revision. Currently, the order comprises 23 families (APG III, 2009). With the tools of molecular systematics, the identification of many monophyletic groups of the former Scrophulariaceae alliance has been possible. Especially the Scrophulariaceae have been disintegrated based on a series of molecular systematic studies (dePamphilis et al., 1997; Olmstead and Reeves, 1995; Olmstead et al., 2001; Oxelman et al., 2005). The studies resulted in re-circumscriptions, resurrection as well as new descriptions of families to encompass these monophyletic lineages.

Whereas the amount of molecular phylogenetic studies continues to grow, detailed morphological/ontogenetic data are largely missing or the existing data have to be valued anew. One of the resurrected families are the Paulowniaceae, comprising one genus and between six and ten species native to East Asia. The woody *Paulownia* was usually classified in Scrophulariaceae (e.g. Bentham, 1876; Takhtajan, 1997; Wettstein, 1891), but also positioned at the borderline between Scrophulariaceae and Bignoniaceae (Armstrong, 1985; Campbell, 1930) or even transferred to Bignoniaceae (Cronquist, 1981; Takhtajan, 1980), although Nakai (1949) treated it already as its own family, Paulowniaceae.

Native to central and western China, the princess tree, *Paulownia tomentosa*, is primarily grown in other regions as an ornamental tree for its profuse spring bloom of attractive flowers and its large catalpa-like green leaves. It has escaped cultivation and now is naturalized in many areas of the world. In spite of the frequent cultivation of the tree, detailed information on its morphology is largely missing and a floral ontogenetic study has never been done.

Material and methods

Flowers and flower buds of *Paulownia tomentosa* (Thunb.) Steud. have been collected in the University campus in Heidelberg (Germany) and in the garden of Hotel Juliane in Meran (Italy). Vouchers of the collected material are deposited in the herbarium

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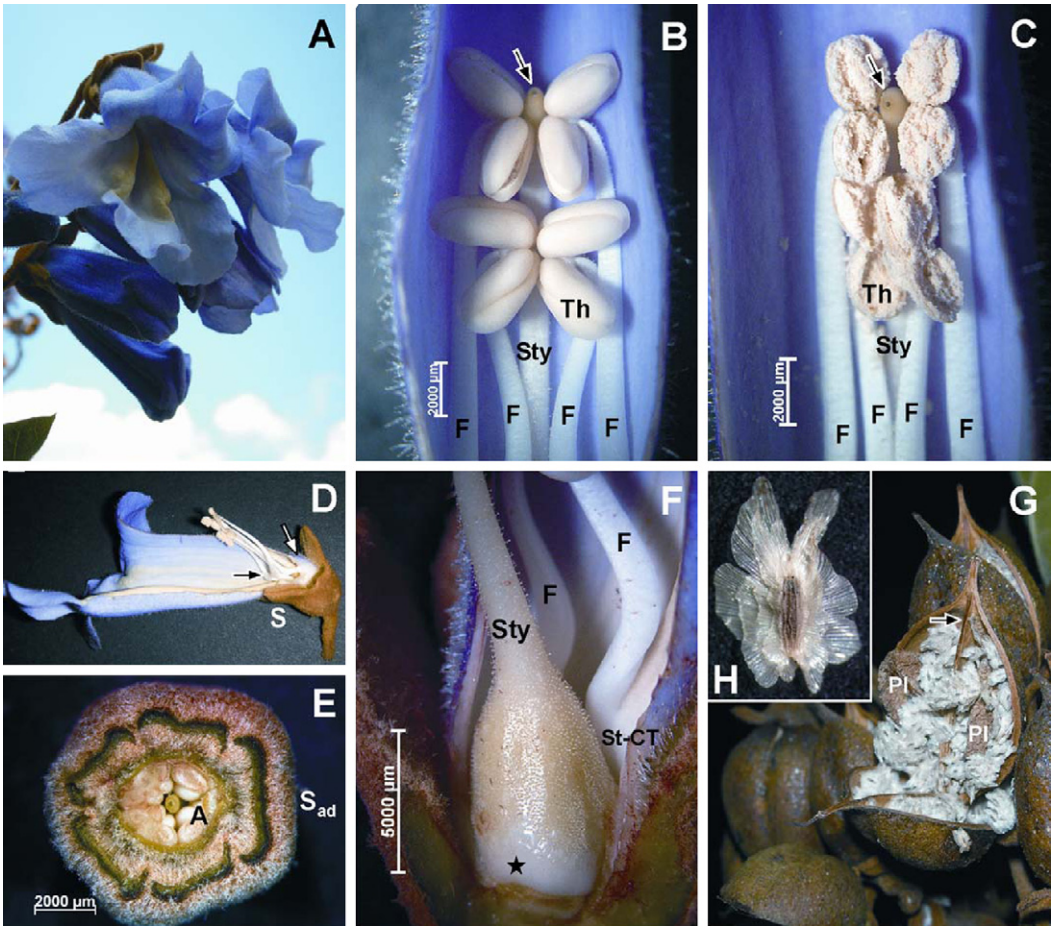

Fig. 1. (A) Flowers of *Paulownia tomentosa*. (B and C) Flowers cut open to show the arrangement of 4 stamens and the style, arrows point to the top of the style (entrance into the tubular stigma cavity). (D) Flower cut open, white arrow points to the short stamen-corolla tube, black arrow points to the bends in the filaments. (E) Overwintering flower bud cross-sectioned with valvate aestivation of the sepals, note the green sepals with their dense indumentum on the outer and inner side. (F) Ovary of an adult flower, the asterisk marks the position of the nectary. (G) Ripe loculicidal capsule artificially opened to show the numerous seeds and the detached placentae, arrow points to the septal ledge in the symplicate zone. (H) Multi-winged seed. A, anther; F, filament; Th, theca; Pl, placenta; S, sepal; S_{ad}, adaxial sepal; St-CT, stamen-corolla tube; Sty, style. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of the Botanical Garden of the University of Heidelberg (HEID: Erbar 58/2007, Erbar 60/2007, Erbar 41/2008, Erbar 72/2009).

Flower buds were fixed in FAA (formalin, acetic acid, alcohol). For samples studied using SEM techniques, the buds were dehydrated in dimethoxymethane, critical-point dried using liquid CO_2, mounted onto stubs, coated with gold and studied in a Leitz (AMR 1200B) scanning electron microscope (software: Digital Image Processing System 2.6). For sections examined using light microscopy (Zeiss, Software: AxioVision 4), the flower buds were dehydrated in an alcohol series, transferred into the infiltration medium and embedded in a methacrylate resin (Kulzer, Technovit 7100). The resin blocks were cut with a rotary microtome (using disposable blades) at a thickness of 6 µm, and the microtome sections were then stained with toluidine blue.

Results

Description of the species

Paulownia tomentosa is a deciduous tree with large leaves (15–30 cm long and 10–20 cm wide), arranged in opposite pairs. The inflorescence is a large (15–30 cm long), erect panicle with 5–6 cm long, pale violet gullet-blossoms (resembling a foxglove flower; Fig. 1A). The thick, somewhat fleshy synsepalous calyx is densely covered with brown indumentum (Fig. 1E). The calyx lobes are as long as the calyx tube. In the zygomorphic flowers, the adaxial bilobed lip of the corolla is slightly shorter than the abaxial trilobed lip. The lower part of the corolla tube bears two cream (to yellow) protrusions running the length of the corolla (Fig. 1A). They can be interpreted as floral guides, namely as anther dummies, which replace the non-visible real stamens ("signal-dummy theory" sensu Osche, see Leins and Erbar, 2010). Indeed, four stamens (2 longer and 2 shorter) are only about half as long as the corolla and are thus hidden within the corolla tube. At the base, the filaments are twisted, so that the anthers with their divergent thecae (sagittate anthers) become positioned in the upper flower half (Fig. 1D). Consequently, pollen deposition is nototribic (dorsal side pollination). Below the long corolla tube, a short stamen-corolla tube is formed. The superior ovary is bilocular, and the pistil with its tubular style has almost the same length as the stamens (Fig. 1B and C). It develops into an oval, woody loculicidal capsule (additionally, the large placentae break off from the septum) whose apex is shortly beaked. The capsule contains small, numerous winged seeds in great number (Fig. 1G). The colour changes from sticky green to brown. The sticky capsules, together with the persistent calyx, may remain on the tree for long periods. The mature seeds are minute, oval and tightly packed one above the other like roof tiles. The seed surface is covered by protrusions that ventrally (side facing the placenta) and dorsally are only flat, whereas laterally they are expanded into several sinuate wings, gradually increasing in extension. At the micropylar and chalazal ends the wings are unequally extended (Fig. 1H).