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Morphogenesis and Structure of Hairs of *Tetrapanax papyriferus* (Hook.) K. Koch (Araliaceae)

Morphogenese und Struktur der Haare bei *Tetrapanax papyriferus* (Hook.) K. Koch (Araliaceae)

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K e y w o r d s : *Tetrapanax papyriferus,* multicellular hairs, morphogenesis, structure

Summary

The green parts of *Tetrapanax papyriferus* (Hook.) K. Koch (Araliaceae) are covered by complex, morning star like, multicellular trichomes. These trichomes initially appear as papilla-like cells of the epidermis, which develop into multicellular, sometimes biseriate stalks. At maturity the stalks are crowned by a star-like structure, consisting of many cells with ray-like protrusions in a globose arrangement, the protrusions radiating into all directions. Already in early stages of the hairs, these heads are present as morula-like cell agglomerations. The central part of the head eventually appears brownish, caused by secretory activity.

The hair cover is most prominent on both sides of young leaves, the abaxial sides of older leaves and bracts, on peduncle, pedicels, the upper third of the abaxial side of petals as well as the hypanthium of the inferior ovary. The hair cover on the adaxial surfaces of the older leaves, bracts and petals as well as the upper part of the ovary around the styles is less dense to absent. At the upper part of the ovary the hairs are additionally characterized by having shorter stalks but more rays.

The irritant indumentum, covering the susceptible young and reproductive organs, particularly the lower sides of the leaf organs protecting the buds, is discussed as an adaptation primarily against herbivores.

Zusammenfassung

Die grünen Teile von *Tetrapanax papyriferus* (Hook.) Koch (Araliaceae) sind von komplexen, morgensternartigen, vielzelligen Trichomen bedeckt. Diese Trichome erscheinen zunächst als papillenartige Zellen der Epidermis, welche sich zu viel-

zelligen, manchmal zweizeiligen Stielen entwickeln. Schon in jungen Stadien sind diese Stiele von Morula-artigen Zellhaufen gekrönt. Letztere entwickeln sich zu sternförmigen Strukturen, indem die Zellen des Haufens strahlenartig in alle Richtungen weisende Auswüchse bilden. Die Zentren der sternförmigen Haarköpfe werden schließlich durch sekretorische Aktivität bräunlich gefärbt.

Die Behaarung ist auf beiden Seiten der jungen Blätter, den abaxialen Seiten der älteren Blätter und Tragblätter, auf den Blüten- und Blütenstandsstielen, dem oberen Drittel der abaxialen Seite der Petalen und dem Hypanthium am dichtesten. Auf der adaxialen Oberfläche der älteren Blätter, Tragblätter und Petalen, und dem oberen Teil des Fruchtknotens um die Griffel, ist die Behaarung weniger dicht. Auf dem oberen Teil des Fruchtknotens sind die Haare zusätzlich durch kürzere Stiele aber mehr strahlige Zellauswüchse charakterisiert.

Die Behaarung, welche besonders die in Knospe schützenden morphologischen Unterseiten der Blatt- sowie die empfindlichen Reproduktionsorgane bedeckt, und dessen Sekrete Dermatitis hervorrufen können, wird vor allem als Anpassung gegen Fraßfeinde diskutiert.

Introduction

Tetrapanax papyriferus (Hook.) K. Koch (Araliaceae), Chinese name: Tong-Tuo-Mu, or Tong-Cao, is the only species of its genus, occurring in Southern and Western China, in the provinces of Shanxi and to the south of the Yangtze River at elevations lower than 2,800 m above sea level. It is a shrub, 1–2 m tall, with large, palmately 7–12-lobed leaves, preferring moist but well-drained, humus-rich soil in full sun or semi-shaded. The inflorescence is an about 50 cm long and up to 50 cm wide terminal compound panicle with umbellules as inflorescences of second order. The green to yellowish white, fragrant flowers have 3–5 petals of 2 mm length, and the 3–5 stamens have 3 mm long filaments. The ovary is 2-carpellate with 2 free styles, which are erect at first, but later recurved at their tips (Li 1942).

The 'rice-paper-plant', *Tetrapanax papyriferus,* is much cultivated in China for the pith obtained from the stems and for its medicinal properties. Thin slices of the spongy tissue of stem pith are used to prepare pith paper, which is soft, white, and spongy, with a velvety feel. It has been used for making flowers in China for centuries, and also as a substrate for watercolour paintings (Tsai 1999). Medically it is used as a diuretic, lactogen, for the treatment of dysuria, oliguria, and edema (Qian 1996). Nowadays, it is widely planted for ornament in East-Asia, Europe, North America, and South America. One of its attractive aspects is the dense indumentum, forming a light brown cover on the leaves, stems and inflorescence. However, the hairs hover down when the plant sways gently in the wind or when shaken. Clinical history and patch tests revealed an irritant nature of those hairs for human skin. Also other Araliaceae were

shown to cause dermatitis by their secretions (HAUSEN 1999). Either the mechanical penetration or the glandular hair secretion, but most effectively its combination can cause dermatitis (GIANNATTASIO et al. 1996). Despite the broad usage of this species, a description of the conspicuous hairs is missing. Hence, this paper will focus on morphogenesis and structure of the multicelluar trichomes of *T. papyriferus*. An ultrastructural investigation of the hairs will be subject of future studies.

Materials and Methods

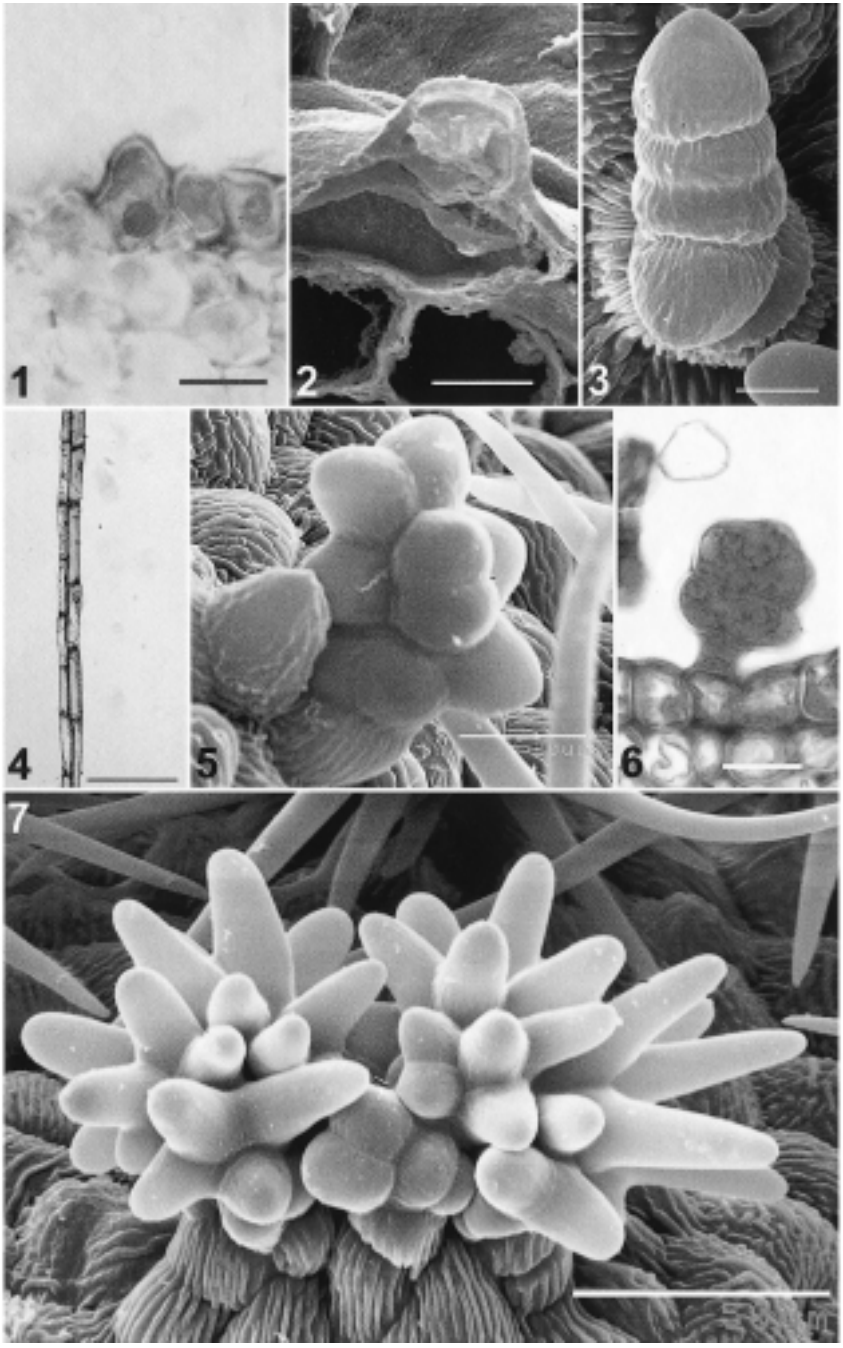
Plants of *Tetrapanax papyriferus* (Hook.) K. Koch were collected from Hangzhou Botanical Garden (China) and Leipzig Botanical Garden (Germany), parts of it immediately fixed in FPA (Formalin (37 %) : Propionacid : 50 %-Ethanol at 0,5 : 0,5 : 9) and later transferred in to 70 % ethanol for storage. Some fixed material of inflorescences was collected from Komarov Botanical Institute, St. Petersburg (Russia).

Samples of leaves, stem, inflorescence were dehydrated in an ascending buthanolseries and embedded in Paraffin (Merck, melting point 56°–58°C), in order to prepare 10–15 μm sections using a Leitz 1512 microtome. The sections were stained with astrablue/auramine/safranine and preserved in Corbit-Balsam as permanent slides (GERLACH 1984). Samples for scanning electron microscopy (SEM) were dehydrated through ethylene glycol monoethyl ether, washed twice in acetone, dried by the "critical point method" (ANDERSON 1951), and coated with gold in a Balzers Union Sputter Coater.

For light microscopy we used a Leitz DMRB-microscope with a photographic camera. Scanning electron microscopy was done with Hitachi S-530 SEM.

Results

Hairs of *Tetrapanax papyriferus* are glandular trichomes, consisting of three different parts: a basal cell, stalk cells and cells forming a stellate head. They initially appear as papilla-like cells in the epidermis (Fig. 1 + 2), with thicker outer periclinal walls compared to their neighbouring cells. The papilla cells contain big nuclea and dense cytoplasma (see Fig. 1). From these basal cells the multicellular stalk develops by numerous cell divisions (Fig. 3), the cells of which have thinner walls than the basal cell. When two papillae occurred closely together, biseriate stalks may develop (Fig. 4). However, already in early stages, when the stalk is still short, the cells forming the star like head may already be present as a knobby, roundish cell complex at the apical tip of the stalk. They have developed by anticlinal as well as periclinal divisions from the apical cell of the young stalk, building a morula-like aggregation of cells (Fig. 5 + 6). These cells produce protrusions radiating into all directions (Fig. 7), which later will be 100–300 μm long and sharply tipped,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crowning the stalks with a star-like structure (Fig. 8). During the development, hairs may increase in length (see Fig. 8). Due to the thin walls of the stalk cells these hairs are flexible, often contorted and interwoven with the numerous other trichomes, building a dense indumentum (Fig. 9). The longest hair found was about 1 cm long and consisted of 34 stalk cells.

While the trichome develops, the colour of the central part of stellate-head always becomes brownish, due to the accumulating of the secretory substance (Fig. 10). Sometimes also the head rays as well as the stalk cells, in the latter concentrated close to the cross walls, show storage of secretions. The cell walls of the stalk are subject to disintegration when the hairs age or when the plant is exposed to physical forces. The shedding of the hairs is due to disconnection of two stalk cells, mostly close to the stellate head.

The indumentum is particularly dense on young stems, the peduncle, the pedicels, the margins of leaves, both sides of young leaves, the abaxial surfaces of old leaves, bracts (see Fig. 9), and the upper third of the abaxial side of the petals (Fig. 11). Also the hypanthium is heavily covered (Fig. 12). The hair cover is less dense to absent on the adaxial faces of the mature leaves, bracts, petals and the ovary around the styles (Fig. 13). The hairs around the styles also differ compared to all other organs by having consistently shorter stalks but more rays (see Fig. 13).

Morphogenesis of the hairs of *Tetrapanax papyriferus*

Fig. 1. Longitudinal section through a papilla having dense cytoplasm and a large nucleus. Bar = 20 μm.

Fig. 2. SEM-picture of a papilla. Bar = 10 μm.

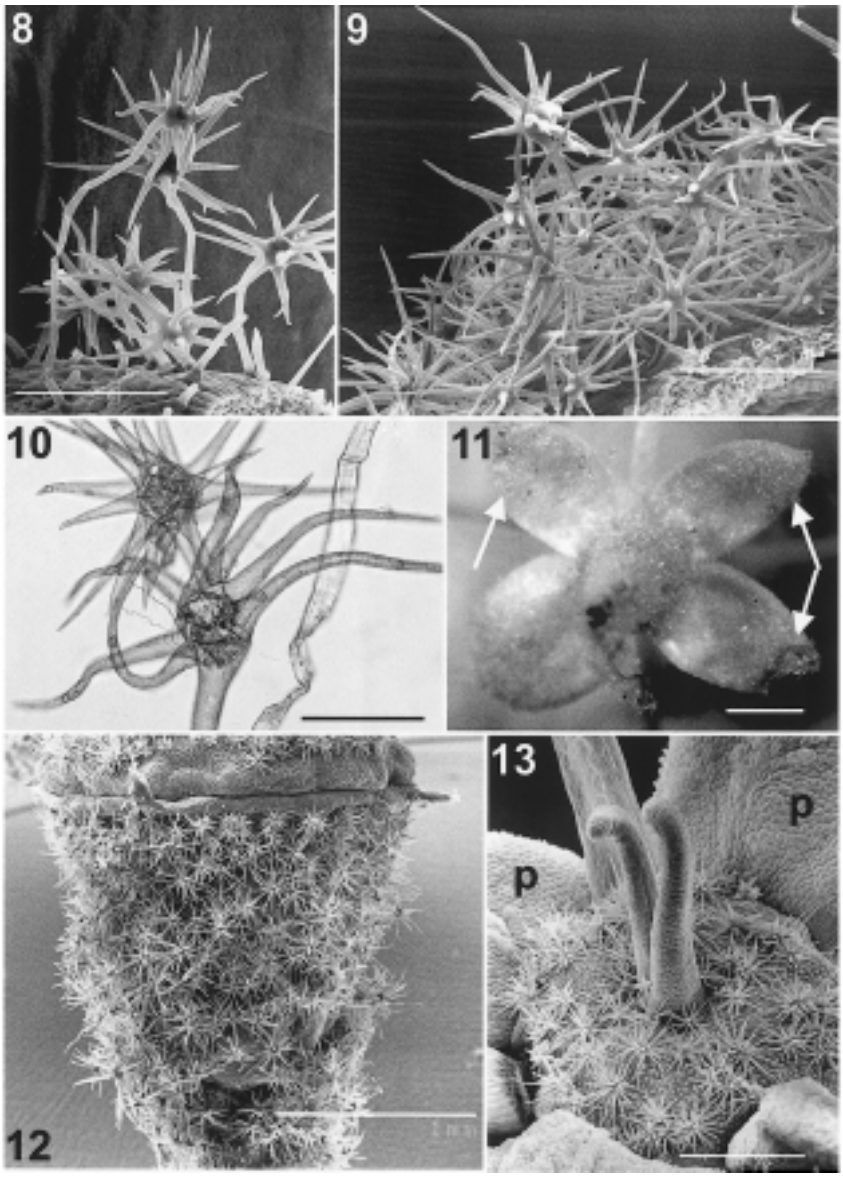
Fig. 3. Young stalk, yet formed by five cells plus papilla. Bar = 10 μm.

Fig. 4. Biseriate stalk. Bar = 100 μm.

Fig. 5. SEM-picture of a morula-like young stage of a stellate head. The stalk is still short. Bar = 20 μm.

Fig. 6. Light microscopy picture of a morula-like stage of a stellate head. Bar = 20 μm.

Fig. 7. Development of the ray-like protrusions of the cells forming the stellate head. The protrusions did not yet attain their final length nor their sharp tips. Bar = 50 μm.



Mature hair structures of *Tetrapanax papyriferus*

Fig. 8. Mature hairs consisting of long stalks and stellate heads with sharply pointed protrusions. Bar = 200 μm.

Fig. 9. Dense indumentum comprising of interwoven stellate hairs. Bar = 200 μm.

Fig. 10. Secretions stored in the central part of the stellate head, visible by the darker colour. Bar = 100 μm.

Discussion

Many flowering plants produce multicellular glandular trichomes. Multicellularity allows trichomes to function as miniature organs, with functional differentiation within the trichomes (FAHN 1990). Often, they consist of a stalk and an enlarged terminal portion, which may be referred to as the gland, secreting a variety of compounds (e.g. UPHOF & HUMMEL 1962; HAMMOND & MAHLBERG 1977; WEBER 1981; MAHLBERG 1985; WERKER et al. 1985; SEITHE & SULLIVAN 1990). This also holds for the hairs of *T. papyriferus,* which have not been described in the literature before. Only a single figure in GIANNATTASIO et al. (1996) has been shown, whereas the text concentrates on the harmful effects of the hairs secretion. Structurally the trichomes are strikingly similar to the hairs of *Miconia chrysophylla* Urban and *Calygonium calyopteris* Urban (Melastomataceae) as well as the Asteraceae *Olearia* ssp. and *Andryala cheiranthifolia* Link. (METCALF & CHALK 1979). This is an unambiguous hint for a convergent evolution in microstructure, the more so as the closer related species *Panax ginseng* C. A. Meyer, *Aralia cachemirica* and *Hedera helix* (Araliaceae) have different hair types (ZEUSKE 2000; BERNHARDT 2001; WICHTL 2002).

Secretory hairs can accumulate secretions, gathering the potentially harmful compounds outside the plant body, thus serving as a shield against herbivores (WAGNER 1991). When touched, the stellate heads of the hairs of *T. papyriferus* will break off from their long stalks and penetrate the skin with their numerous sharp points. The combination of the mechanical penetration and the injected substance is probably responsible for the irritating effect (see GIANNATTASIO et al. 1996). A dense layer of trichomes also can represent a protection against the effects of radiation as well as irradiation, against water loss through transpiration, helping to maintain the water balance, or absorb gases by living trichomes (UPHOF and HUMMEL 1962). At the rather sunny sites where *Tetrapanax papyriferus* occurs, the hairs, in fact, may protect the plant from radiation. However, taking the moist conditions of its habitat into account, and considering the peculiar structure of its trichomes, the conspicuous indumentum probably serves primarily as a protection against herbivores. The most tender and susceptible parts, especially the young

Fig. 11. Flower from below, showing the dense hair tufts on the tips of the lower side of the petals (arrows). Bar = 1 mm.

Fig. 12. Hypanthium with dense hair cover (petals detached). Bar = 1 mm.

Fig. 13. Upper part of the ovary, with less densely distributed and short stalked hairs. The upper sides of the petals (p) are devoid of hairs. Bar = 500 µm.

leaves and reproductive organs, have the densest hair cover. Interestingly, at those parts where visitors are desired, like the inner faces of the petals and the upper part of the ovary around the styles, hairs are eigther missing or without stalks. The same holds for the upper surface of older, photosynthetically active leaf blades, where a dense hair cover would interfere with effective assimilation. The flower bud, however, is particularly protected by the dense hair tuft at the upper third of the abaxial face of the petal curving over the ovary: an amazingly specific adaptation.

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