Epicuticular wax ultrastructure and classification of *Ranunculiflorae*

WILHELM BARTHLOTT and INGE THEISEN

Received November 11, 1994

**Key words:** Angiosperms, *Ranunculiflorae*, cuticle, wax, scanning electron microscopy, wax ultrastructure, systematics, taxonomy.

**Abstract:** Epidermal surfaces of about 199 species from 66 genera of ranunculiflorous families are examined by scanning electron microscopy. The micromorphology of their epicuticular wax crystals is presented and discussed under taxonomic aspects. All families of the *Ranunculiflorae* s. str. (*Ranunculales, Papaverales*) prove to be highly uniform: apart from a few exceptions they are characterized by the presence of clustered wax tubules (*Berberis* type), chemically dominated by the secondary alcohol nonacosan-10-ol in the species analysed. This is in marked contrast to the *Magnoliidae* s. str. (*Aristolochiales, Laurales* s. l., *Magnoliaceae*), which are almost uniformly defined by transversely ridged crystals of the *Aristolochia* type, chemically characterized by the presence of palmitone and the absence of nonacosan-10-ol. However, the *Canellaceae, Nelumbonaceae,* and *Winteraceae* produce the *Berberis* type tubules similar to *Ranunculiflorae*. This suggests a reconsideration of the position of these families and in particular for *Nelumbo* a close relation to the *Ranunculiflorae* also based on other chemical data. Within the polyphyletic *Hamamelididae* the “lower” families *Cercidiphyllaceae, Daphniphyllaceae,* and certain genera of *Hamamelidaceae* are also characterized by *Berberis* type waxes.

Over the last decades systematically relevant information on structure and composition of the plant cuticle based on SEM studies have been published (reviews in BEHNKE & BARTHLOTT 1983, JEFFREE 1986, BARTHLOTT 1990). The cuticles of the majority of higher plants are covered with epicuticular wax secretions. Epicuticular “waxes” occur throughout bryophytes, pteridophytes, gymno- and angiosperms. They are chemically diverse mixtures of lipophilic substances like long-chain fatty acids (true waxes), alkanes, ketones, esters, and cyclic compounds like pentacyclic triterpenes, phytosterols, and flavonoids. These substances occur usually as local projections of crystalline nature (JEFFREE & al. 1975) exhibiting surprisingly a high ultrastructural diversity. The micromorphology of epicuticular wax crystals revealed by SEM has provided valuable new criteria for the classification of angiosperms (BARTHLOTT 1993, DITSCH & BARTHLOTT 1994, FRÖLICH & BARTHLOTT 1988, HENNIG & al. 1994, THEISEN & BARTHLOTT 1994).
The monocots are characterized by the presence of two wax types: parallel oriented platelets (Convallaria type) within most liliiflorous families including Triuridales. The subclasses Commelinidae, Zingiberidae, and Arecidae are characterized by aggregated rodlets with longitudinal striations (Strelitzia type). The core group of Magnoliidae (Aristolochiales, Annonales, Laurales, Magnoliales) as well as Paeoniaceae are defined by the occurrence of transversely ridged rodlets (Aristolochia type) chemically containing a considerable amount of palmitone. Canellaceae, Nelumbonaceae, and Winteraceae share epicuticular wax features with the Ranunculiflorae and they are discussed below.

The data presented in the present paper are based on our comprehensive survey of Magnoliidae, Ranunculidae, and Hamamelididae (Hennig & al. 1994), which we also refer to for material examined and methods of high resolution SEM. The conclusions are based on the examination of some 199 species of 66 genera of almost all families; they are interpreted in comparison with data of about 13,000 species of angiosperms analysed in the last 18 years. It became obvious, that both Ranunculiflorae s. str. and Magnoliiflorae s. str. each are characterized by highly specific uniform wax types – but share no common features under this aspect.

Results

Epicuticular wax crystal ultrastructure of Ranunculiflorae

Micromorphology of ranunculiflorous waxes. Thin wax films forming continuous layers are present in many taxa: they are not detectable by SEM and under systematic aspects they are not relevant.

Within the subclass treated here only two types of epicuticular crystals (apart from a minor exception in Podophyllum) occur. The dominating Berberis type of hollow tubular waxes occurs throughout the order (Fig. 1c–h). They chemically consist in the few examples analysed (e.g., Papaver) of the secondary alcohol nonacosan-10-ol. The tubules are often branched, and they are frequently not uniformly arranged on the outer cuticular surface, but show a specific “clustered” distribution characteristic for this wax type (Fig. 1c–d). This is not easily detectable in some taxa.

The second wax type occurring only within certain taxa of few families are irregular platelets (Fig. 1b) of differing size and shape, but without the specific parallel orientation of the liliiflorous monocotyledons (Convallaria type). These platelets occur throughout all major orders of angiosperms and they are of less systematic significance.

Systematic survey of waxes in the Ranunculiflorae. The circumscription of the families listed alphabetically follows Cronquist (1988); tentatively related families are added. Enlisted are several additional families of the Magnoliidae and Hamamelididae which produce Berberis type waxes. The numbers in brackets indicate the numbers of genera and species examined within the family (gen./spp.).

Berberidaceae (8/29) (incl. Leonticaceae): Uniformly characterized by the Berberis type apart from one Epimedium species with irregular platelets. Podophyllum differs significantly (see Podophyllaceae).