



## Systematic significance of tepal surface morphology in tribes Persicarieae and Polygonae (Polygonaceae)

SUK-PYO HONG FLS

*Laboratory of Plant Systematics, Department of Biology, Kyung Hee University, Seoul 130-710, Korea*

L. P. RONSE DECRAENE\* FLS AND E. SMETS FLS

*Laboratory of Plant Systematics, Botanical Institute, Katholieke Universiteit Leuven, Kard. Mercierlaan 92, B-3001, Heverlee, Belgium*

*Received June 1997; accepted for publication December 1997*

In order to improve understanding of the systematic relationships between taxa and of tepal-pollinator and tepal-habitat relationships, a detailed scanning electron microscopy (SEM) study of the adaxial tepal surface of 135 taxa belonging to c. 14 genera in the tribes Persicarieae and Polygonae (Polygonoideae–Polygonaceae) was carried out. The tepal surfaces have revealed some striking differences among the genera studied. Three main patterns of sculpturing and cell shape can be recognized. Type I: mostly rectangular to elongate cells with straight or undulating anticlinal walls; the cuticles smooth or striate in longitudinal direction and often continuous (*Persicaria*, *Bistorta*, *Aconogonon*, *Koenigia* and some species of *Fagopyrum*). Type II: irregular tesselated to elongated cells, rarely rectangular with mostly sinuate anticlinal walls; the cuticles rarely with longitudinal striation, but with strong orthogonal to reticulate ridges or striae, often without correlation between cells (*Polygonum* s.s., *Polygonella*, *Fallopia*, *Paraptenopyrum*, *Pteropyrum*, *Atraphaxis* and *Calligonum*). Type III: mostly irregular, mammilliform, papillose cells with either longitudinal tightly pressed or randomly ridged cuticles (some species of *Fagopyrum* and *Oxygonum*). The present data generally support the division of Polygonae and Persicarieae by Ronse Decraene & Akeroyd. The mammilliform, papillate epidermis of tepals in *Oxygonum* and some *Fagopyrum* is probably well-adapted to entomophily either as a foothold or even as a light-trap, and also shows some correlation with heterostyly. It is noteworthy that the tepal structure of *Polygonella* (tesselated form) is highly similar to that of *Polygonum* s.s. (especially *P.* sect. *Duravia*). Cuticular striation alone does not appear to have much systematic value, but has a mechanical function in affording extra strength to the cell walls. Some correlations between the degree/shape of cuticles and the pollination mechanisms or the habitat of each taxon are also briefly discussed.

\*Correspondence to: Dr L. P. Ronse DeCraene.

It is concluded that the studied tepal characters can be useful in improving the classification of tribes Persicarieae and Polygoneae, and give additional support at the infrageneric level.

© 1998 The Linnean Society of London

ADDITIONAL KEY WORDS:—cuticle — generic delimitation — micromorphology — pollination — Polygonoideae — SEM — systematics.

## CONTENTS

Introduction . . . . .	92
Material and methods . . . . .	93
Results: Taxonomic distribution of tepal characters . . . . .	94
Tribe Persicarieae . . . . .	94
Tribe Polygoneae . . . . .	101
Discussion . . . . .	104
Acknowledgements . . . . .	110
References . . . . .	110
Appendix: Species and specimens examined . . . . .	112

## INTRODUCTION

The Polygonaceae is one of those families which give major problems for classification in many floras (Brandbyge, 1993). Several proposals for classification have been presented since the nineteenth century. The subdivision of the large genus *Polygonum* L. s.l. into more natural units at generic, subgeneric or sectional rank seems to be especially problematic, and it is still a matter of debate which rank should be used (cf. Haraldson, 1978; Ronse Decraene & Akeroyd, 1988).

The use of various characters, such as vegetative anatomy (Haraldson, 1978; Lersten & Curtis, 1992), pollen morphology (Hedberg, 1946; Nowicke & Skvarla, 1977; Hong & Hedberg, 1988), chromosome numbers (Jaretzky, 1928; Fedorov, 1969) and phytochemistry (Jaretzky, 1925; Hegnauer, 1969), has greatly contributed in recognizing several segregates in the genus *Polygonum* L. Ronse Decraene & Akeroyd (1988) investigated a number of floral characters (stamen insertion, tepal morphology and morphology of floral nectaries, etc.) in order to elucidate the relationships within *Polygonum* and several of its segregate genera. In addition, Ronse Decraene & Smets (1991) clarified the position and morphology of the floral nectaries of *Polygonum* and related genera. The delimitation of the tribes Polygoneae and Persicarieae seems to be justified by the above-mentioned studies of Haraldson (1978), Ronse Decraene & Akeroyd (1988) and Ronse Decraene & Smets (1991).

The micromorphology of the perianth (called ‘tepals’ in this study) in the flowering plants has been of interest to many botanists. Gale & Owens (1983) suggested that epidermal features are useful for determining the mechanisms of floral protection and pollinator attraction. In addition, Kevan & Lane (1985) suggested that the microtexture of flower and petal might have a tactile role (i.e. providing a microtextural nectar-guide for pollinators). The morphology of the epidermal cells and cuticular surface of the tepals is directly related to the capture of incident light to produce maximum brilliance of the pigments. The optical effect of light is dependent on the angle of incidence and the shape of the barrier it strikes (Brehm & Krell, 1975; Kay, Daoud & Stirton, 1981).

Barthlott (1981, 1990), in a general review of epidermal characters of plants,

confirmed the systematic significance of epidermal characters. The remarkable and distinctive surface structures of the epidermis of petals have recently been investigated with the scanning electron microscope (SEM) in many taxa such as Compositae (Baagøe, 1977, 1978, 1980), Fabaceae (especially Papilioideae: Stirton, 1981), Orchidaceae (Ehler, 1976), Asclepiadaceae (Ehler, 1975), Commelinaceae (Gale & Owens, 1983), Rubiaceae (Robbrecht, 1988) and Polygonaceae (Ronse Decraene & Akeroyd, 1988; Brandbyge, 1990; Hong, 1992, 1993).

Although a comparative study of the tepal surface in *Polygonum* s.l. and some related genera has been made (Ronse Decraene & Akeroyd, 1988), our present study is intended to amplify these observations from additional material and to establish new types of detailed surface ornamentation with descriptive-diagnostic value. The aim of the present investigation is to report on micromorphological data for the two tribes, i.e. Persicarieae Dum. and Polygoneae emend. Haraldson, and to evaluate their use in solving taxonomic problems. Further, Ronse Decraene & Akeroyd's (1988) classification is assessed in the light of these new results. At present it is the opinion of the first author that the genera *Aconogonon* and *Bistorta* should be recognized within the tribe Persicarieae, contrary to Ronse Decraene & Akeroyd (1988) who retain these as sections of *Persicaria*. Differences of rank are a matter of opinion with little importance for this study. In the results all differing formally named sections of *Persicaria* and *Polygonum* will be analysed, notwithstanding the status given to them by Ronse Decraene & Akeroyd (1988).

#### MATERIAL AND METHODS

The study of inner tepals was conducted mostly on material taken from herbarium specimens on loan from the following herbaria (abbreviations according to Holmgren, Holmgren & Barnett, 1990): BM, BR, E, G, GB, K, KHUS, LD, LV, PE, RNG, and UPS, but also partly on living material. A list of all species and specimens investigated is given in the Appendix.

For examination of tepal epidermis, well-developed, open flowers were selected. Material was examined with the dissecting microscope, light microscope (LM) and scanning electron microscope (SEM). Most of the material from the herbarium specimens was directly mounted on aluminium stubs, and coated and photographed as outlined below. The flowers, which were collected from living plants, were prepared for the SEM as follows. The samples were either osmicated using an osmium tetroxide ( $\text{OsO}_4$ )-solution or dehydrated using formaldehyde-dimethylacetal (see also Ronse Decraene & Akeroyd, 1988; Gerstberger & Leins, 1978). Critical point drying was carried out, using a CP-Drier (CPD 030, Balzers). The dried samples and those taken from the herbarium specimens were mounted on aluminium stubs and coated with c. 30 nm layer of Au or Au/Pd before being studied under the SEM (JEOL T-20, JEOL-5200 and JEOL-6200), operating at 15 kV, respectively in Seoul, Reading and Leuven. Some material was also treated with aerosol-OT (dioctyl sodium sulfosuccinate) following Erbar (1995) with variable results. Additional material was checked under the light microscope.

Standard terminology mainly follows Gale & Owens (1983), Ronse Decraene & Akeroyd (1988) and Barthlott (1990) for the cell types and surface sculpturing patterns.

## RESULTS: TAXONOMIC DISTRIBUTION OF TEPAL CHARACTERS

## Tribe Persicarieae

Genus *Persicaria* Mill.

[including Sects. *Persicaria* (Mill.) Gross, *Echinocaulon* (Meisn.) H. Gross, *Cephalophilon* (Meisn.) H. Gross, *Rubrivena* (M. Král) S.-P. Hong, *Tovara* (Adans.) H. Gross, *Amblygonon* Meisn.]

In *Persicaria* sect. *Persicaria*, the tepal epidermis has rectangular cells with straight to sinuate anticlinal walls (Figs 1–5). Sometimes, the cell shape of the epidermis is fairly long, as in *P. minus* Huds. [length (L): 150 µm, width (W): 32 µm], while in *P. hydropiper* L. it is shortly rectangular (L: 35 µm, W: 13 µm). The anticlinal walls of the cells are smooth and usually have well-developed longitudinal cuticular striae. In some taxa a few stomata occur (Fig. 1).

In most investigated taxa of *P. sect. Echinocaulon*, the tepal epidermis is of a similar type as in sect. *Persicaria*, i.e. rectangular cells, mostly with straight anticlinal walls and usually smooth (Figs 6–8), but rarely with irregularly, weakly developed longitudinal cuticular striae (e.g. in *P. persfoliata*).

Most of the taxa in *P. sect. Cephalophilon* have a rectangular cell shape, straight anticlinal walls with smooth striae which are not deep (Figs 9, 10) or sometimes weakly longitudinal to oblique cuticular striae (e.g. in *P. glaciale* (Meisn.) Hook.). In *P. chinense* L., however, the epidermal cells are rectangular (L: c. 20 µm, W: c. 80 µm), and the striation of the cuticle is deep and longitudinal (Fig. 11).

The small section, *P. sect. Rubrivena*, has a short rectangular cell shape and weakly sinuate anticlinal walls with longitudinal cuticular striae (in *P. wallichii* Greuter & Burdet, cf. Fig. 12).

In *P. neofiliformis* Ohki (*P. sect. Tovara*), the epidermal cells are rectangular with sinuate anticlinal walls (L: c. 20 µm, W: c. 70 µm). The cuticles show longitudinal, discontinuous striae (Fig. 14), while in *P. virginiana* L. cuticular striae are more or less irregular to straight (Fig. 13).

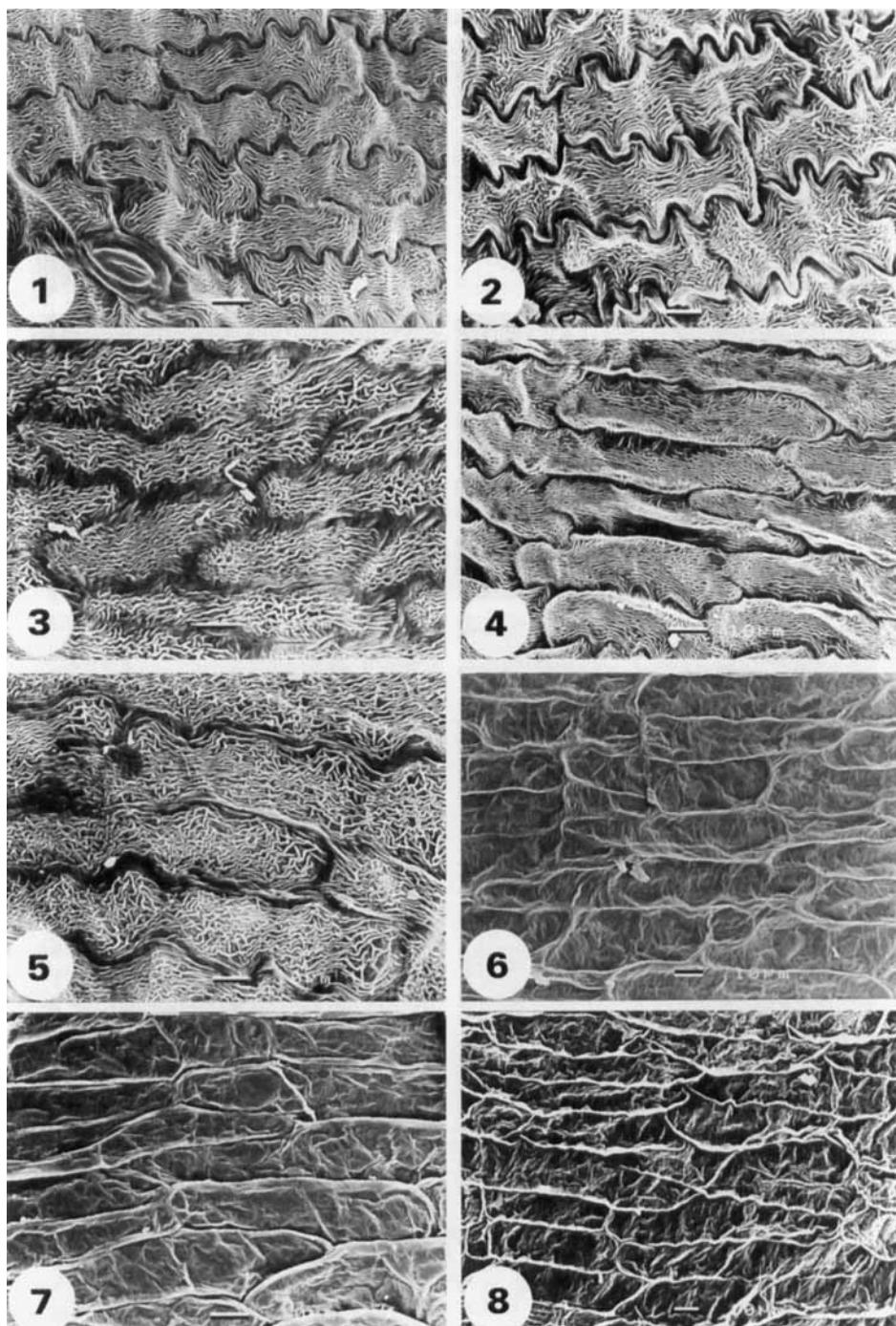
In *P. sect. Amblygonon* most tepal epidermal cells are rectangular with straight to slightly undulating anticlinal walls (Figs 15, 16).

Genus *Bistorta* Mill.

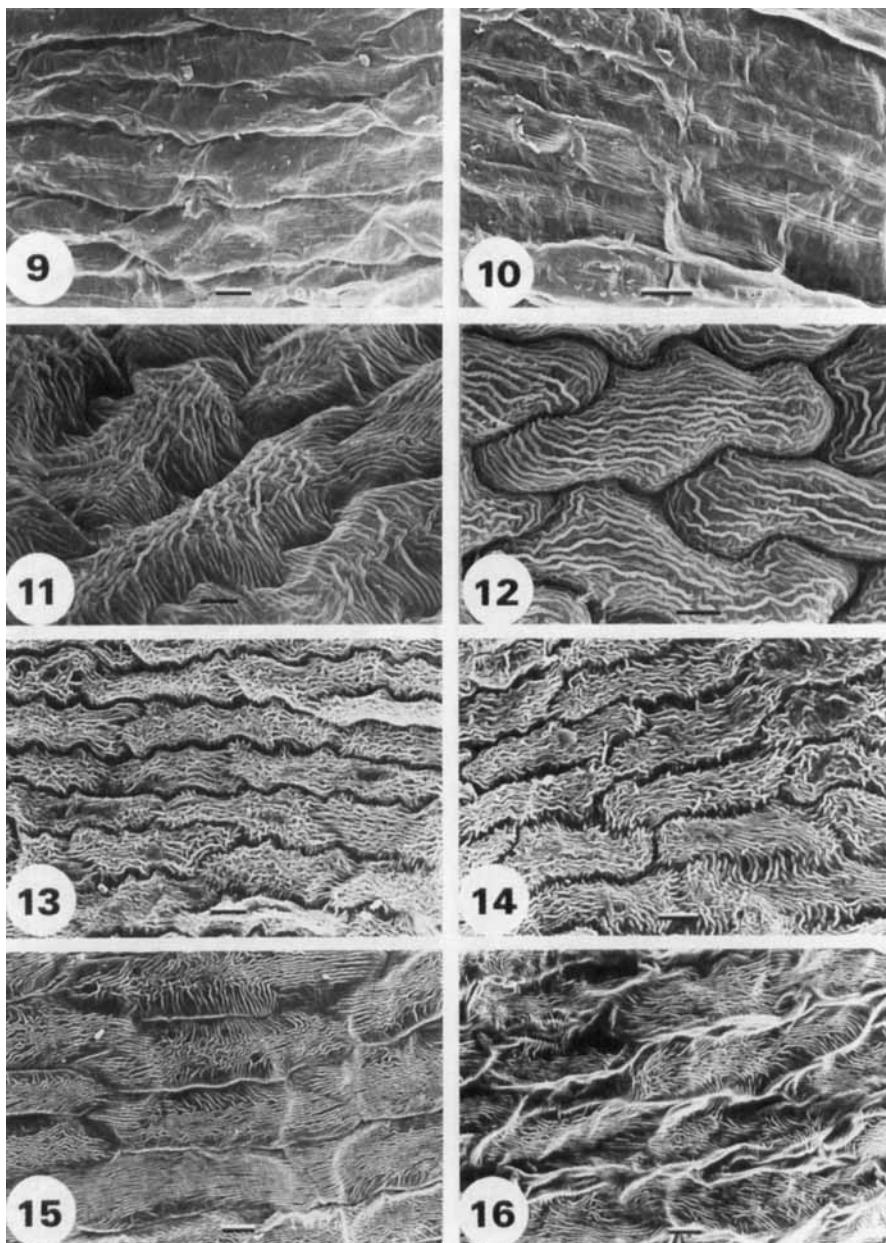
The tepal epidermis consists of elongated to rectangular cells (L: 50–90 µm, W: 15–22 µm) with straight (Fig. 24) to undulating (Figs 18, 19) or sinuate (Figs 17, 21–23) anticlinal walls. The cuticles show mostly well-developed straight to undulating longitudinal striae, as in *B. affinis* (D. Don) Greene (Fig. 23). A few rare stomata occur in *B. suffulta* (Maxim.) Greene ex H. Gross (Fig. 18).

Genus *Aconogonon* (Meisn.) Reichenb.

The surface of the tepals consists mainly of rectangular cells with smooth (Figs 25, 28) or slightly longitudinal striae (Figs 26, 27) or sometimes with a strongly ridged cuticle (in *A. campanulatum* (Hook. f.) Hara var. *campanulatum*, Cf. Fig. 29). The cuticle mostly shows a longitudinal striation (Figs 26, 27, 29), but in *A. molle* (D. Don) Hara var. *rude* (Meisn.) Hara, striae run more or less horizontally, sometimes longitudinally at the extremities (Fig. 30). Usually the cell length exceeds the cell

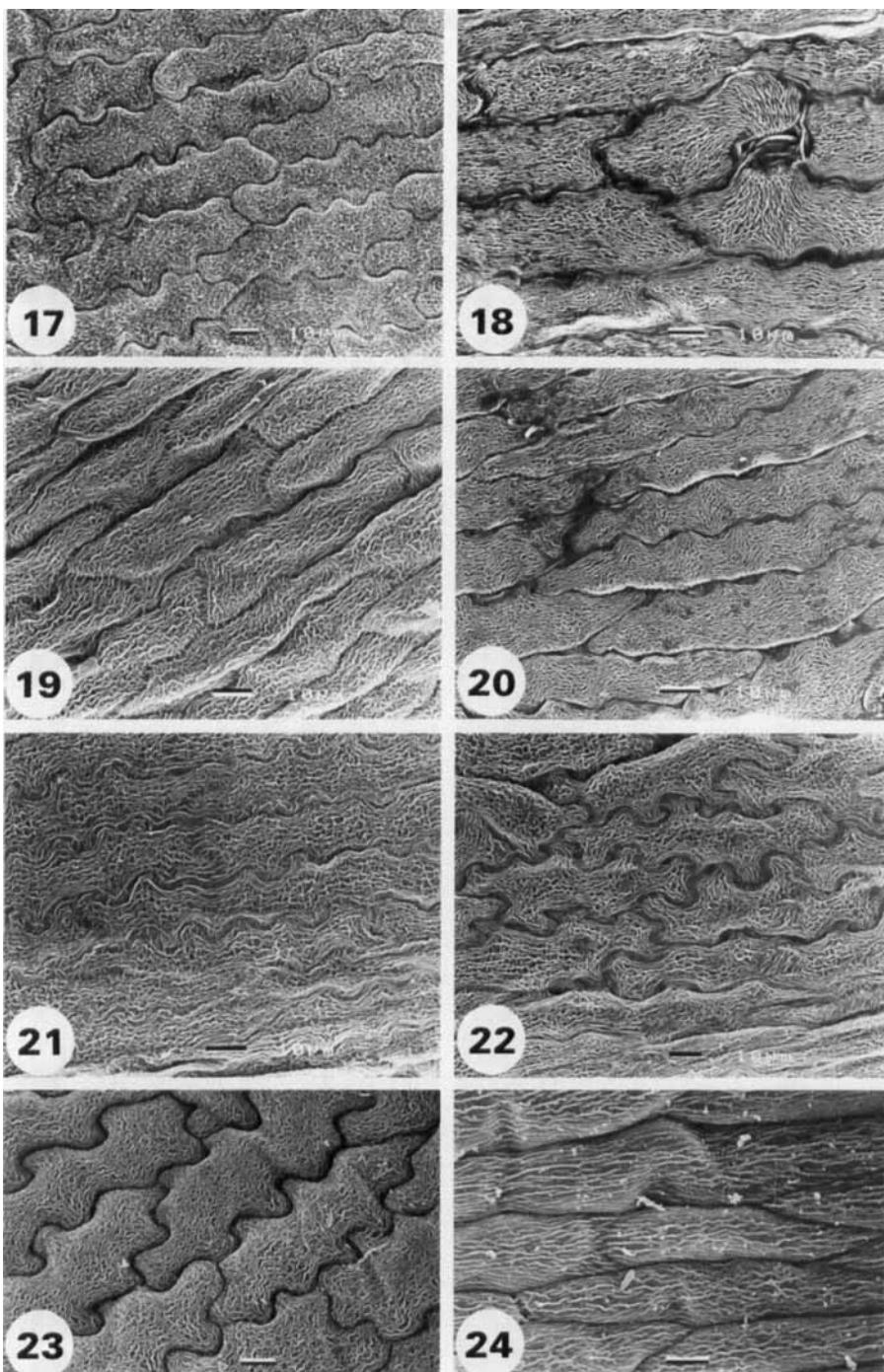


Figures 1–8. SEM micrographs of the inner tepal epidermis cells of *Persicaria* (Figs 1–5: *P. sect. Persicaria*, Figs 6–8: *P. sect. Echinocaulon*). Fig. 1. *P. coccinea* (Cooperrider 3236). Fig. 2. *P. pulchra* (Mohoro 588). Fig. 3. *P. viscosa* (Ryding 322). Fig. 4. *P. hydropiperoides* (Mealme 1482). Fig. 5. *P. yokusaiana* (Ohwi 9077). Fig. 6. *P. artifolia* (Bodin s.n.). Fig. 7. *P. sagittata* (Einarsson *et al.* 3915). Fig. 8. *P. hastato-sagittata* (Kanai 10383). Scale bars = 10 µm.

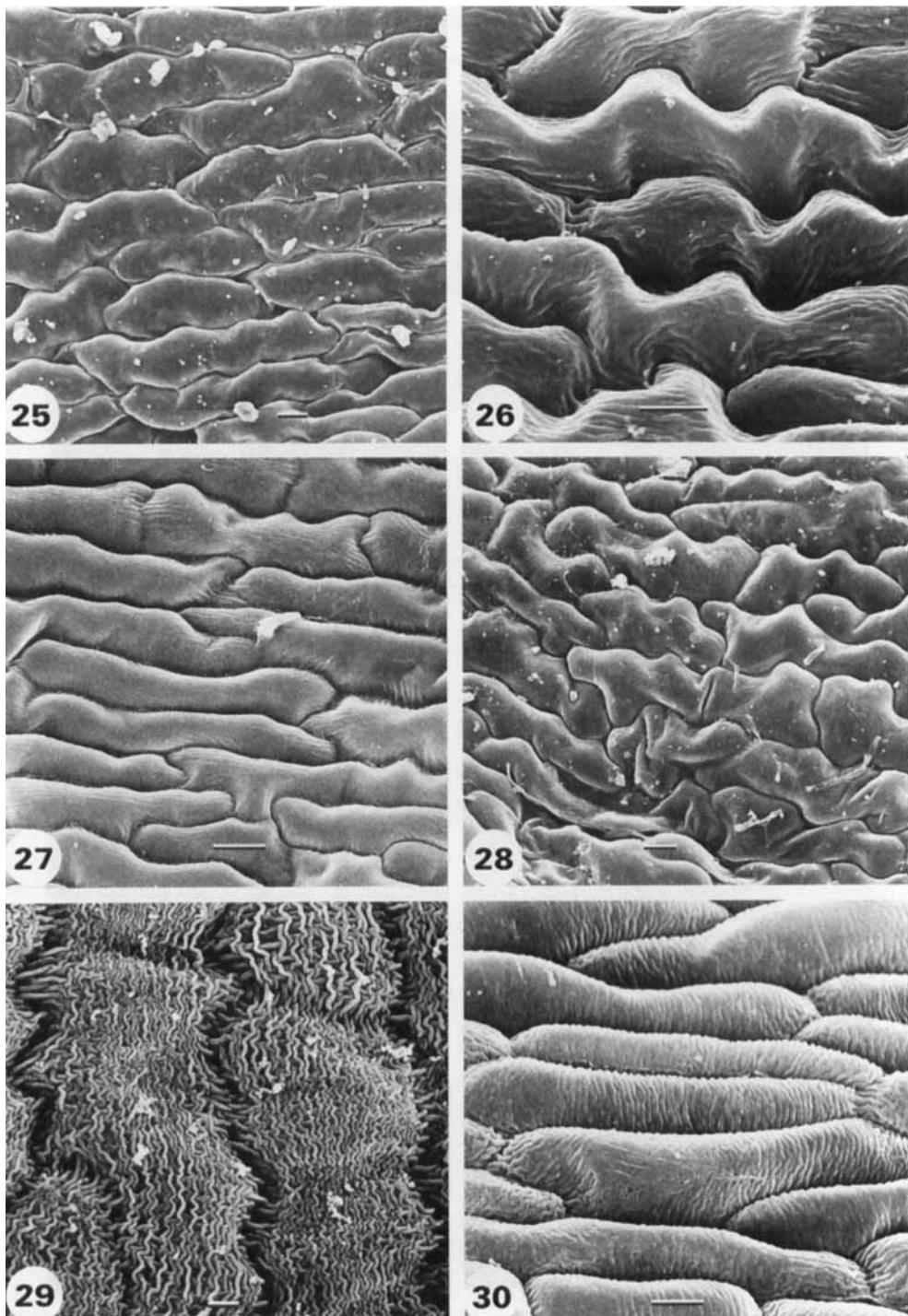


Figures 9–16. SEM micrographs of the inner tepal epidermis cells of *Persicaria* (Figs 9–11: *P. sect. Cephalophilon*, Fig. 12: *P. sect. Rubrivena*, Figs 13, 14: *P. sect. Tovara*, Figs 15, 16: *P. sect. Amblygonon*). Fig. 9. *P. runcinata* (Ludlow & Sherriff 8250). Fig. 10. *P. alata* (Hedberg s.n.). Fig. 11. *P. chinensis* (Vennning 88). Fig. 12. *P. wallichii* (Ronse Decraene 15 Le). Fig. 13. *P. virginiana* (McDonald s.n.). Fig. 14. *P. neofiliformis* (Ohwi 331). Fig. 15. *P. orientalis* (Brumbach 6921). Fig. 16. *P. senegalensis* (Lye 2816). Scale bars = 10 µm.

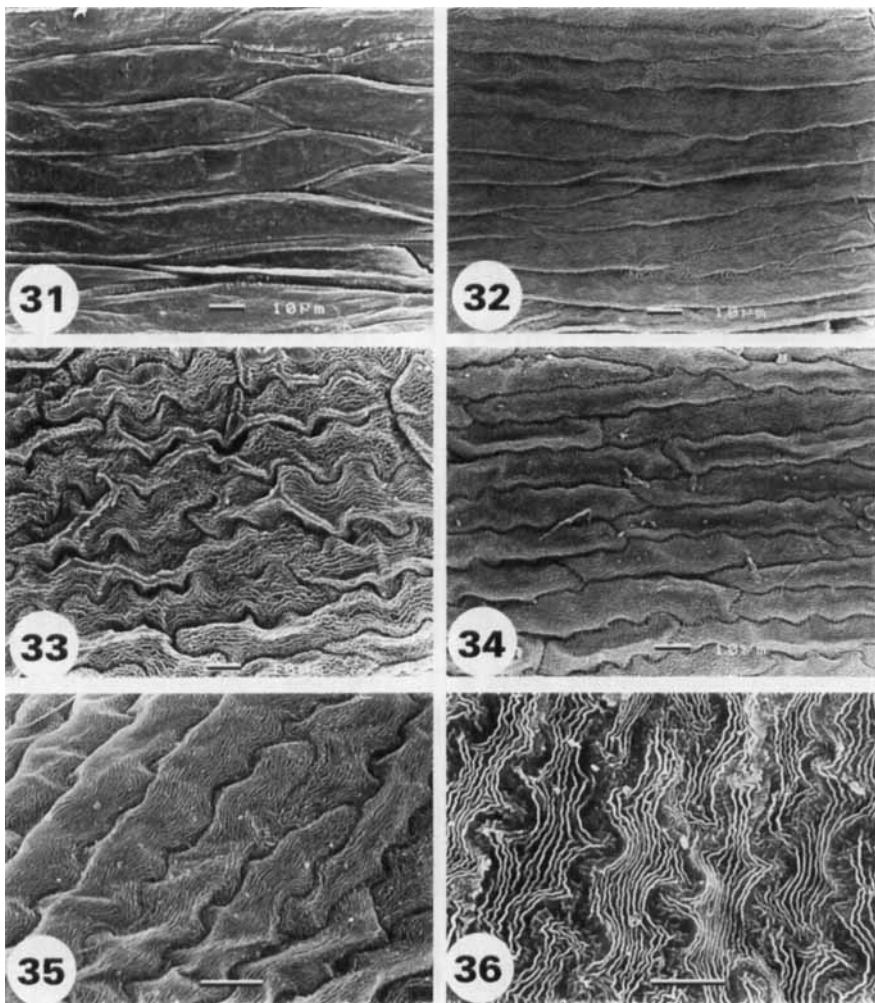
width (L: 50–180 µm, W: 13–25 µm). The anticlinal walls of the epidermal cells are undulate to almost straight. Rarely a few stomata occur in the upper tepal epidermis of *A. tortuosum* (D. Don) Hara var. *pubitepalum* S.-P. Hong.



Figures 17–24. SEM micrographs of the inner tepal epidermis cells of *Bistorta*. Fig. 17. *B. griffithii* (Ludlow *et al.* 13097). Fig. 18. *B. suffulta* (Yahara *et al.* 6998). Fig. 19. *B. purpusella* (Ludlow *et al.* 21115). Fig. 20. *B. macrophylla* (H. Smith 10932). Fig. 21. *B. vivipara* (Hedberg 3168). Fig. 22. *B. major* (Murbeck s.n.). Fig. 23. *B. affinis* (Ludlow & Sherriff 8203). Fig. 24. *B. vaccinifolia* (Ludlow *et al.* 17136). Scale bars = 10 µm.



Figures 25–30. SEM micrographs of the inner tepal epidermis cells of *Aconogonon*. Fig. 25. *A. coriarium* (Hedge & Wendelbo 5148). Fig. 26. *A. rumicifolium* (Forrest 29864). Fig. 27. *A. hookeri* (Rock 14376). Fig. 28. *A. rhombifolium* (Forrest 29864). Fig. 29. *A. campanulatum* var. *campanulatum* (Ronse Decraene 12 Lb). Fig. 30. *A. molle* var. *rude* (Hong-cult. 89-K1). Scale bars = 10 µm.



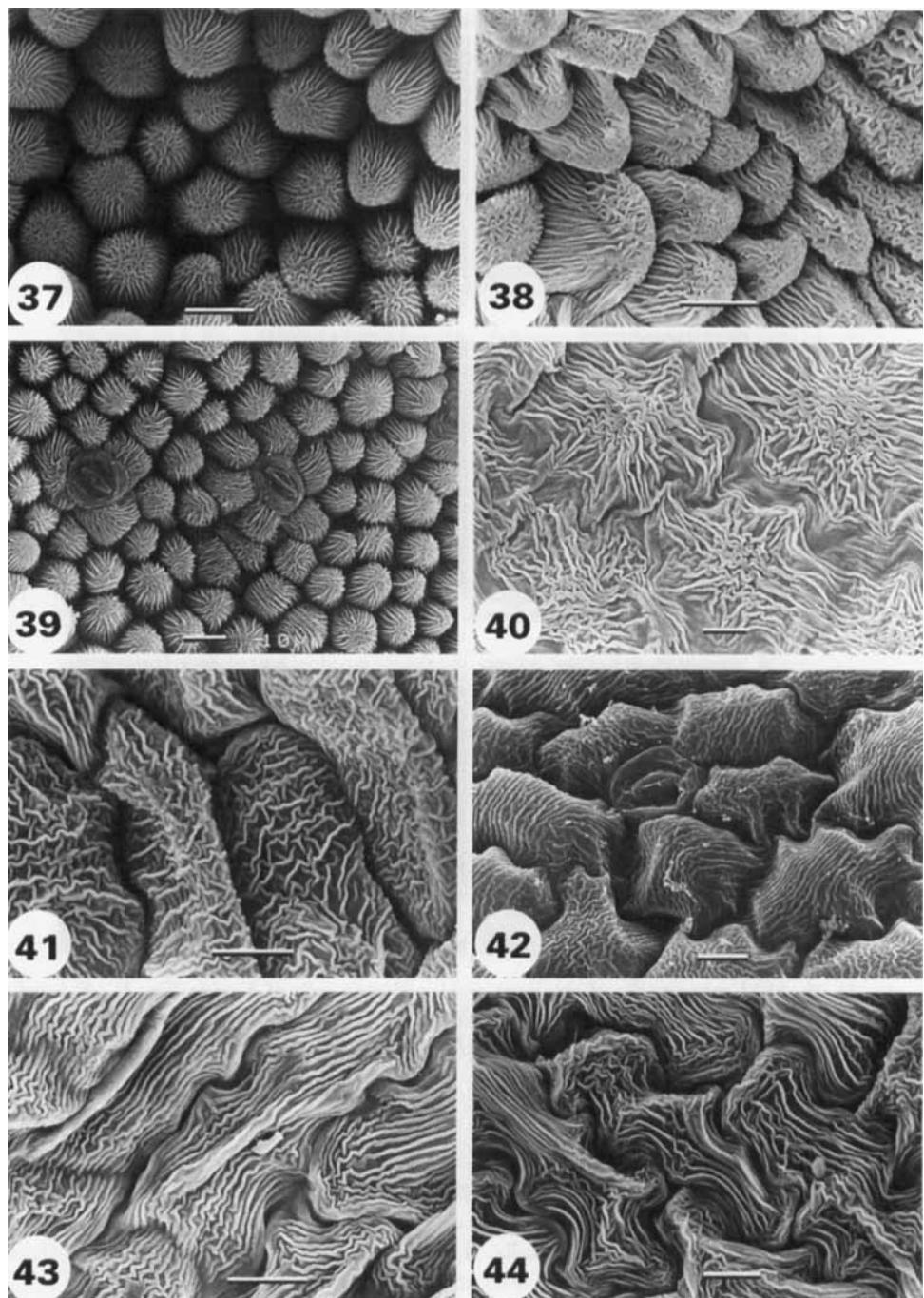
Figures 31–36. SEM micrographs of the inner tepal epidermis cells of *Koenigia*. Fig. 31. *K. islandica* (Nielsen 69). Fig. 32. *K. nepalensis* (Einarsson et al. 3394). Fig. 33. *K. delicatula* ssp. *reducta* (Forrest 25042). Fig. 34. *K. nummularifolia* (Duthie 3337). Fig. 35. *K. filicaulis* (Kingdon Ward 8612). Fig. 36. *K. delicatula* ssp. *delicatula* (Gould 1586). Scale bars = 10 µm.

#### Genus *Koenigia* L. emend. Hedb.

The surface of the tepals consists of rectangular to elongated cells (L: 39–150 µm, W: 13–36 µm) with mostly strongly sinuate (Figs 33, 36) to rarely straight (e.g. in *K. islandica* L., cf. Fig. 31) anticlinal walls. The cuticles have deep longitudinal striae (Figs 32–36), or are rarely more or less smooth (Fig. 31).

#### Genus *Fagopyrum* Mill. emend. Hong (including *Harpagocarpus* Hutch. & Dandy)

The cells of the inner tepal epidermis are papillate in this genus (e.g. *F. esculentum* Moench, *F. tataricum* (L.) Gaertn., Figs 37–39) more or less rectangular (*F. leptopodium* (Diels) Hedberg, *F. giraldii* (Dammer ex Diels) Haraldson, *F. snowdenii* (Hutch. & Dandy) S.-P. Hong; L: 50–90 µm, W: 13–25 µm) to broadly irregular mammilliform-like (*F. megacarpum* Hara). The anticlinal walls of the cell are either irregular (Figs



Figures 37–44. SEM micrographs of the inner tepal epidermis cells of *Fagopyrum*. Fig. 37. *F. esculentum* (Brumbach 6902). Fig. 38. *F. dibotrys* (Cave s.n.). Fig. 39. *F. tataricum* (Ronse Decraene 626 Ln). Fig. 40. *F. giraldii* (Hedberg 7321). Fig. 41. *F. lineare* (Handel-Mazzetti 8569). Fig. 42. *F. snowdenii* (Kabuye 72). Fig. 43. *F. leptopodium* ssp. *grossii* (Marie 3). Fig. 44. *F. gilesii* (Handel-Mazzetti 8017). Scale bars = 10  $\mu\text{m}$ , except Fig. 39 = 100  $\mu\text{m}$ .

37–39) or undulating (Figs 40, 42–44), or rarely somewhat straight (Fig. 41). In *F. snowdenii*, they are sinuate (Fig. 42). The cuticle is formed in various ways, e.g. either longitudinally tightly pressed (Figs 37–39), randomly ridged (Figs 40, 41), short-reticulately to horizontally ridged (Fig. 42), or with undulating to longitudinal cuticular striae (Figs 43, 44). In *F. tataricum* we observed a transition from more or less rectangular cells with straight anticlinal walls and horizontal striae lower on the tepal surface to typically mammilliform cells with contracted striae higher up (Fig. 39). This indicates that the mamillae probably arose by contraction of the cells.

### Tribe Polygoneae

#### Genus *Polygonum* L. s.s.

(including Sects. *Polygonum*, *Pseudomollia* Boiss., *Duravia* S. Watts., *Tephis* (Adans.) Meisn. emend. Haraldson)

The tepal epidermis is similar in most species of section *Polygonum* [including *P. moliaeforme* Boiss. (often treated as sect. *Pseudomollia*) Fig. 49], consisting of irregular, elongated cells with sinuate outline [L: 40–50 (–90) µm, W: 13–15 (–30) µm]. They mostly have a tessellated cell shape. The cuticle is often deeply and irregularly ridged or has sometimes randomly placed short striations (in most taxa of the *P. aviculare* L. group, Figs 45, 46). Often a few stomata occur in some taxa of sect. *Polygonum* (Figs 45, 46).

In general, the tepal cells of sect. *Tephis* are elongated to rectangular and the cell length exceeds the cell width (L: c. 60 µm, W: c. 15 µm). The anticlinal walls are sinuous, their periclinal walls low-domed, and longitudinally covered with convoluted cuticular striae (Fig. 48). Many stomata are scattered over the surface of the tepal (Figs 47, 48).

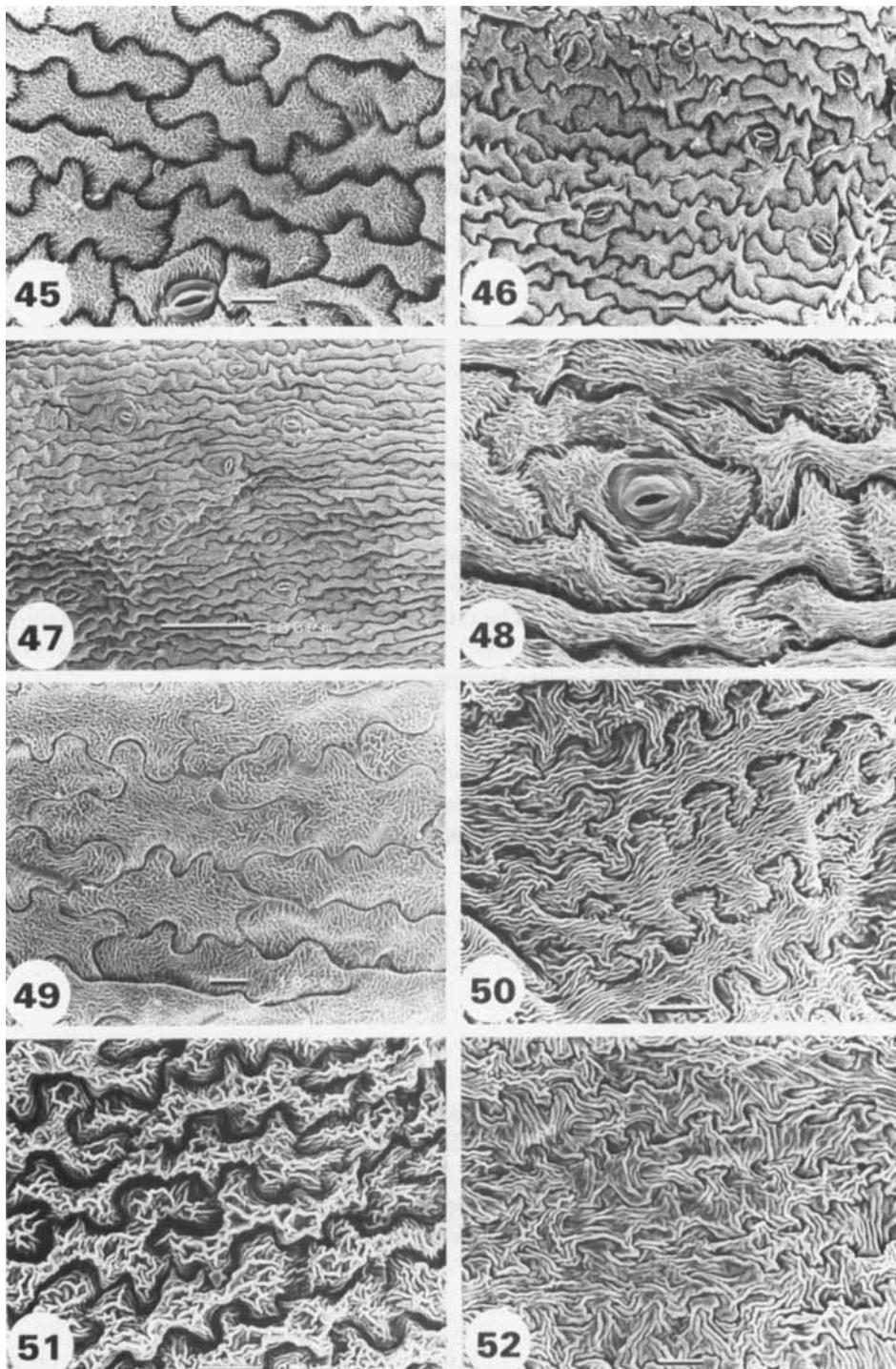
In sect. *Duravia* the inner tepal cells have mostly long rectangular cells with strongly sinuous anticlinal walls (L: c. 100 µm, W: 10–15 µm) covered by a strongly compacted, irregularly ridged cuticle, with the striations mostly orthogonal to the long axis (Figs 50–52).

#### Genus *Polygonella* Michx.

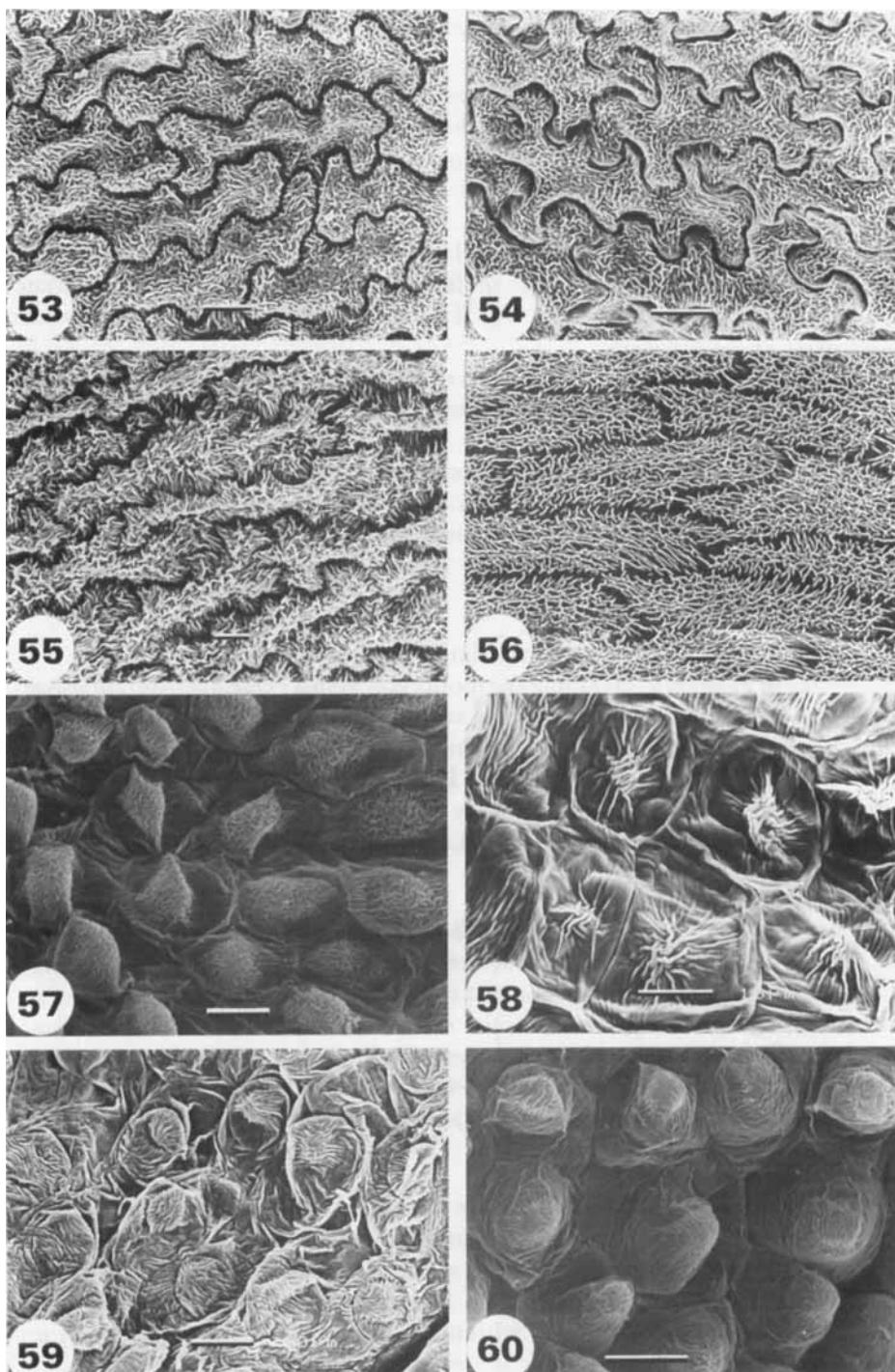
The tepal epidermis has mostly irregular, rectangular cells with sinuate outlines (Figs 53–55), but rarely regular cells with straight anticlinal walls (Fig. 56, e.g. *P. americana* (Fisch. & Mey) Small). The cell lengths are c. 50–110 µm and widths are 16–20 µm. The cuticles are irregularly deeply ridged (Figs 53–55) or randomly to orthogonally ridged, especially in *P. americana* (Fig. 56).

#### Genus *Oxygonum* Burch.

The tepal cells are irregular (c. 15 µm in diameter) in shape and are mostly covered with mammilliform-like papillae having a randomly ridged cuticular striaion (Figs 57–60). Rarely the cells are rectangular to broadly irregular, producing irregular mamillae with random to longitudinal tightly pressed striae (e.g. in *Oxygonum dregeanum* Meisn.). A transition between irregular and more rectangular cells was observed in *O. atriplicifolium* (Fig. 57).



Figures 45–52. SEM micrographs of the inner tepal epidermis cells of *Polygonum*. Figs 45, 46: *Polygonum* sect. *Polygonum*, Figs 47, 48: *P.* sect. *Tephis*, Fig. 49: *P.* sect. *Pseudomollia*, Figs 50–52: *P.* sect. *Duravia*. Figs 45, 46. *P. aviculare* ssp. *aequale* (Koh 48/455). Figs 47, 48. *P. afromontanum* (Hedberg 1622). Fig. 49. *P. molliaeforme* (Kotschy 778). Fig. 50. *P. kelloggii* (Holm 273). Fig. 51. *P. douglassii* (Sandberg & Leiberg 434). Fig. 52. *P. californicum* (Howell s.n.). Scale bars = 10 µm.



Figures 53–60. SEM micrographs of the inner tepal epidermis cells of *Polygonella* and *Oxygonum* (Figs 53–56: *Polygonella*, Figs 57–60: *Oxygonum*). Fig. 53. *Polygonella articulata* (Long 11563). Fig. 54. *P. gracilis* (Vestulund s.n.). Fig. 55. *P. fimbriata* (Blanton 6825). Fig. 56. *P. americana* (Fischer 10). Fig. 57. *Oxygonum atriplicifolium* (Haraldson 401). Fig. 58. *O. stuhlmannii* (Mhoro & Backeus 2236). Fig. 59. *O. delagoense* var. *strictum* (Fries 1258). Fig. 60. *O. sinuatum* (Zumer 56). Scale bars = 10 µm.

Genus *Fallopia* Adans. emend. Ronse Decr.

(including Sects. *Fallopia* (Adans.) Holub, *Pleuropterus* (Turcz.) Haraldson, *Parogonum* Haraldson, *Reynoutria* (Houtt.) Ronse Decr.)

The tepal cells have an irregular to elongated shape [Figs 61–63, *F. scandens* (L.) Holub and *F. convolvulus* (L.) A. Löve], but sometimes the outline of cells is more or less irregular to rectangular, as in *F. aubertii* (L. Henry) Holub, *F. baldschuanica* (Regel) Holub and *F. pterocarpa* (Meisn. in Wall.) Holub (L: 35–42 µm, W: 16–20 µm). The anticinal cell walls are more or less straight to sinuate and the cuticles are irregularly reticular-ridged (*F. scandens*, Fig. 61) or finely irregular to longitudinally striate (*F. convolvulus*, *F. pterocarpa*, cf. Figs 62, 64). The cuticle consists of rare long randomly placed striae (*F. baldschuanica*).

In *Fallopia cilinodis* (Michx.) Holub (sect. *Parogonum*), the tepal cells are elongated and the anticinal walls are slightly undulate with elongated striae. A few stomata are found (Fig. 64).

The tepal cells of sect. *Reynoutria* are irregularly rectangular (Fig. 66; L: 10–14 µm, W: 10–17 µm). The anticinal wall of the cells are mostly undulating or rarely slightly straight (Figs 65, 66). The cuticles are mostly longitudinal, but vary from cell to cell; the cuticle is often rough with random striae (*F. sachalinensis* (F. Schmidt) Ronse Decr., cf. Fig. 66).

Genus *Pteropyrum* Jaub. & Spach (including *Parapteropyrum* A. Li)

Most taxa of *Pteropyrum*, including the monotypic genus *Parapteropyrum* (*Parapteropyrum tibeticum* A. Li, Fig. 72), have irregular to polygonal tepal cells and the anticinal walls are mostly sinuate (Figs 69–72) or undulate (Figs 67, 68) with a strongly ridged, randomly striate cuticle (cf. Figs 67–72; L: 45–54 µm, W: 13–20 µm). The cells of *P. scoparium* Jaub. & Spach are irregularly elongated with deep, almost longitudinal or sinuate striation with scattered stomata (Figs 67, 69).

Genus *Atrapaxis* L.

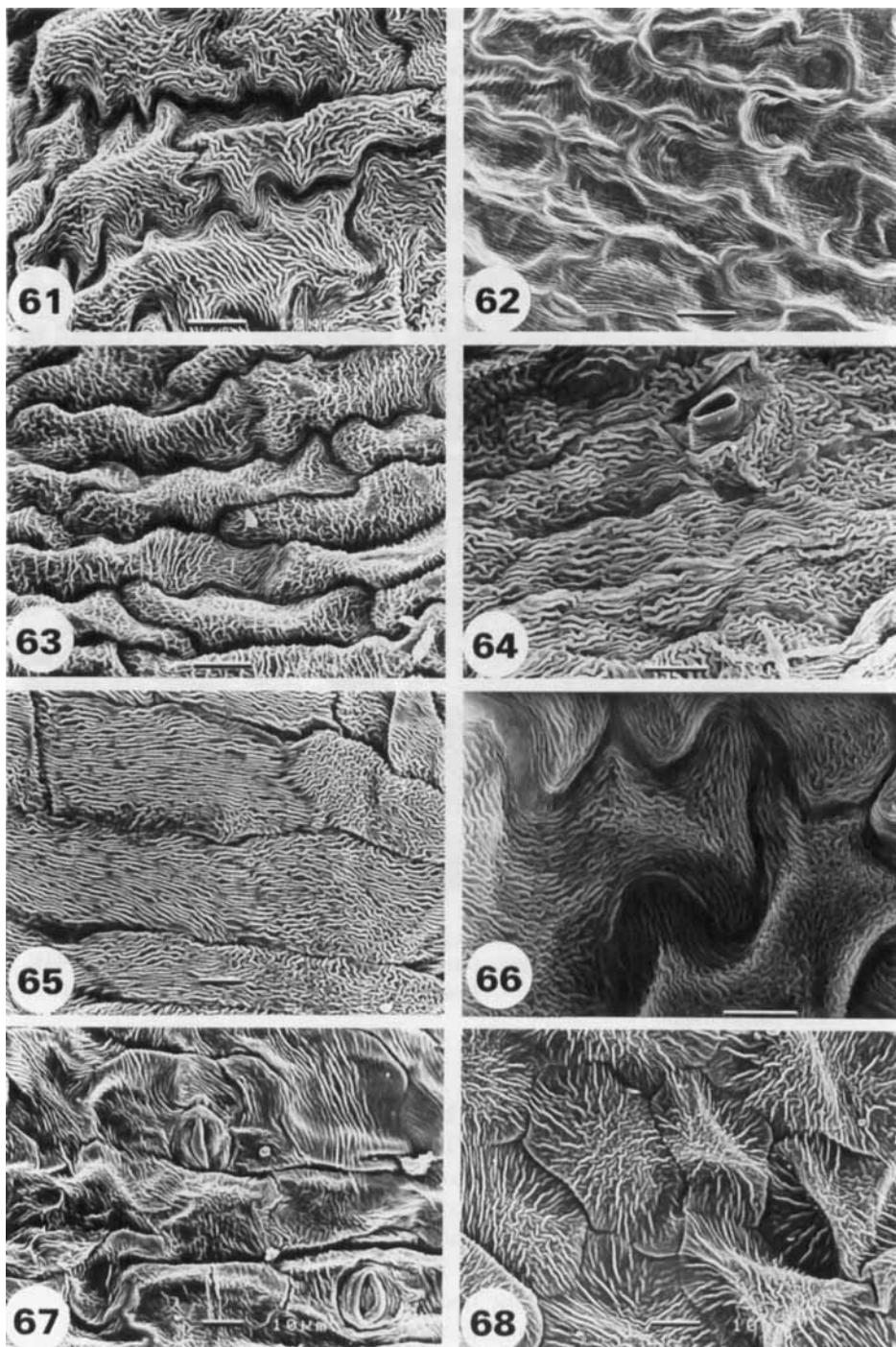
In most taxa investigated, the tepal cells are elongated and more or less irregular. The cuticles are generally densely covered with longitudinal to random striae. The anticinal cell walls are usually sinuate to undulate or almost straight (Figs 73–76). In *A. buxifolia* Jaub. & Spach, the tepal cells are irregular to rectangular and the anticinal walls are sinuate with thick, longitudinal or random striation, with scattered stomata (Fig. 73). The cell sizes in *A. billardieri* Jaub. & Spach are approximately 100 µm or even longer and c. 18 µm wide respectively (cf. Fig. 74).

Genus *Calligonum* L.

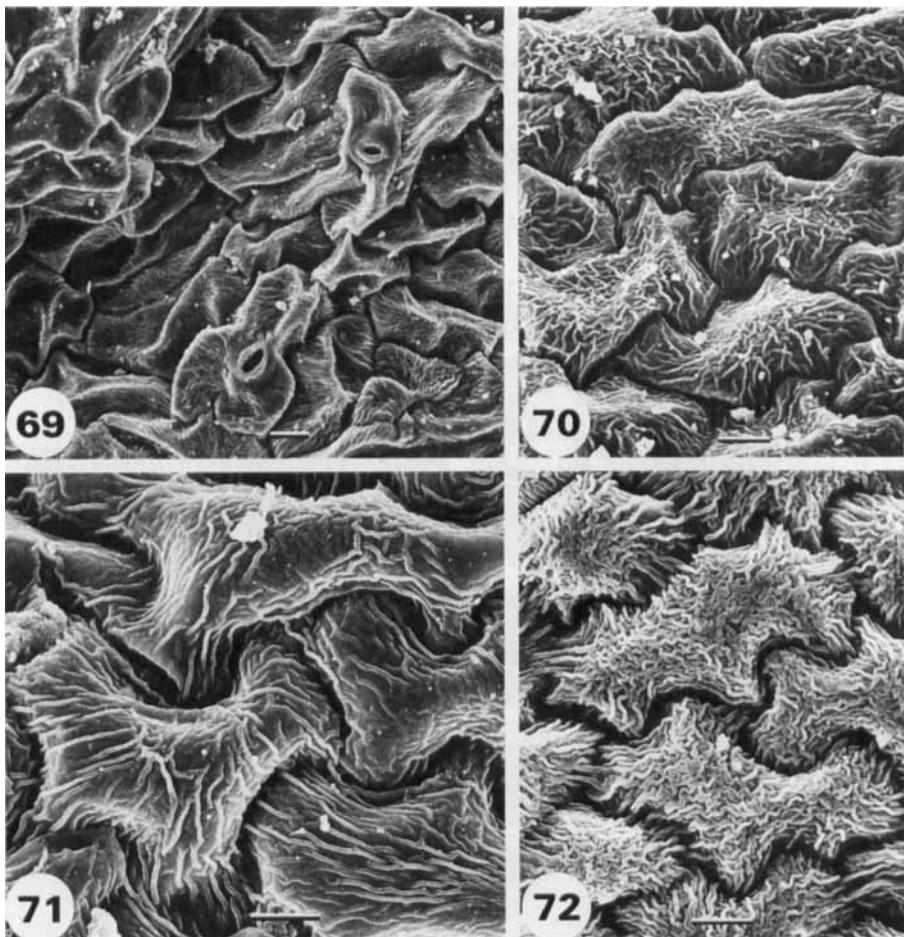
The tepal epidermal cells are irregular to more or less elongated (Figs 77–80) or sometimes broadly rectangular to irregular (*C. microcarpum* Borshch., cf. Fig. 77). The anticinal walls are more or less straight, sometimes slightly undulate (L: 30–40 µm, W: 15–20 µm). The cuticles have deep longitudinal striations (Figs 78–80, in *C. comosum* L'Hérit., *C. caput-medusae* Schrenk and *C. eriopodium* Bunge) or a random striation extending from the middle (*C. microcarpum*, cf. Fig. 77).

## DISCUSSION

SEM studies of tepal surfaces have revealed some significant differences among several genera of the tribes Persicarieae and Polygoneae of Polygonaceae as delimited

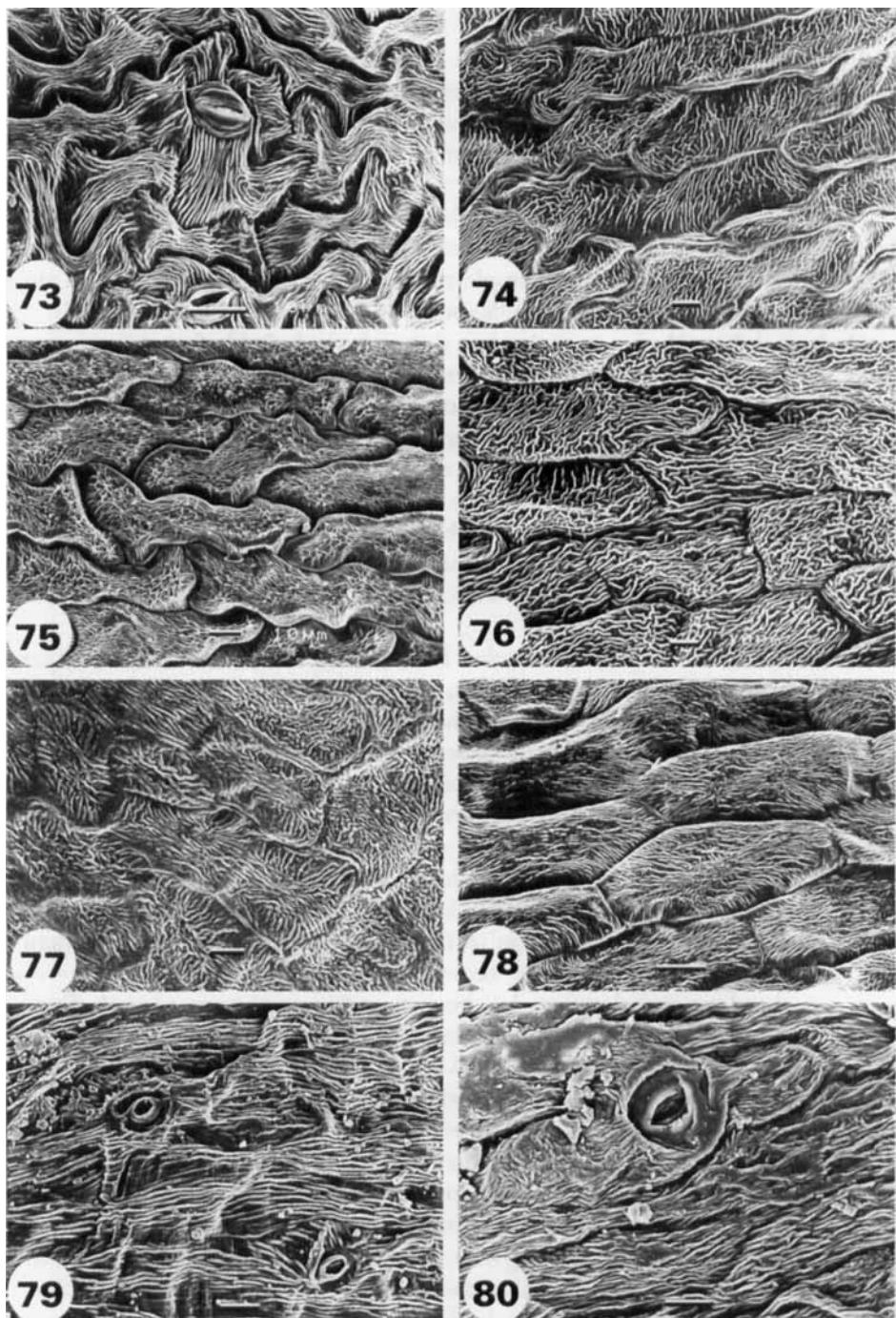


Figures 61–68. SEM micrographs of the inner tepal epidermis cells of *Fallopia* and *Pteropyrum* (Figs 61–63: *Fallopia* sect. *Fallopia*, Fig. 64: *F.* sect. *Paragonum*, Figs 65, 66: *F.* sect. *Reynoutria*, Figs 67, 68: *Pteropyrum*). Fig. 61. *F. scandens* (Ludlow et al. 7059). Fig. 62. *F. convolvulus* (H. Smith 4372). Fig. 63. *F. dumetorum* (Cardvso s.n.). Fig. 64. *F. cilinodis* (Mexon & Weatherby 1045). Fig. 65. *F. japonica* (Barley 1218B). Fig. 66. *F. sachalinensis* (HE & ST Parks 24448). Fig. 67. *Pteropyrum scorpiarium* (Miller 6677). Fig. 68. *P. gracile* (Straus s.n.). Scale bars = 10 µm.



Figures 69–72. SEM micrographs of the inner tepal epidermis cells of *Pteropyrum* (Figs 69–71) and *Parapteropyrum* (Fig. 72). Fig. 69. *Pteropyrum gracile* (Straus s.n.). Fig. 70. *P. aucheri* (Rechinger 27441). Fig. 71. *P. noéanum* (Horsain & Horsain 53). Fig. 72. *Parapteropyrum tibeticum* (Qing-zang Exped. Suppl. Group 750657). Scale bars = 10 µm.

by Ronse Decraene & Akeroyd (1988). Three main patterns of sculpturing and cell shape can be recognized. The first group (Type I) mostly has rectangular to elongated cells. The anticlinal walls of the cell are usually straight or undulating. The cuticles are smooth or striate in longitudinal direction and often continuous. A reticulate pattern is absent and individual cells do not differ much from each other. This type is found in the genera *Persicaria* (Figs 1–16), *Bistorta* (Figs 17–24), *Aconogonon* (Figs 25–30), *Koenigia* (Figs 31–36) and some taxa of *Fagopyrum* (Figs 40–44), which belong to the tribe Persicarieae. The second group (Type II) has irregular to elongated, rarely rectangular cells. The anticlinal walls of the cells are mostly sinuate. The cuticles rarely show a longitudinal striation, but have strongly orthogonal to reticulate ridges or striae, often without correlation between cells. The individual cells vary much in size and shape. This type occurs in *Polygonum* s.s. (Figs 45–52), *Polygonella* (Figs 53–56), *Fallopia* (Figs 61–66), (*Para*)*Pteropyrum* (Figs 67–72), *Atraphaxis* (Figs 73–76) and *Calligonum* (Figs 77–80). The third type (Type III) has mostly irregular cells with



Figures 73–80. SEM micrographs of the inner tepal epidermis cells of *Atraphaxis* (Figs 73–76) and *Calligonum* (Figs 77–80). Fig. 73. *Atraphaxis buxifolia* (Grossbein? 20). Fig. 74. *A. billardieri* (Balansa 1289). Fig. 75. *A. frutescens* (Alm s.n.). Fig. 76. *A. muschketovii* (Anonym. s.n.). Fig. 77. *Calligonum microcarpum* (Sintenis 2202). Fig. 78. *C. comosum* (Bougeau 43). Fig. 79. *C. caput-medusae* (Anonym. s.n.). Fig. 80. *C. eriopodum* (Michelson s.n.). Scale bars = 10  $\mu$ m.

mammilliform papillae and either longitudinal tightly pressed or randomly ridged cuticles. Type III is considered a unique cell structure, which occurs in some taxa of *Fagopyrum* (cf. Figs 37–39) and *Oxygonum* (Figs 57–60).

In the genus *Persicaria*, Ronse Decraene & Akeroyd (1988) lumped sects. *Echinocaulon*, *Amblygonon* and *Cephalophilon* within a single section *Persicaria*. Most taxa of sect. *Echinocaulon* and *Cephalophilon* share a smooth or rarely weakly striate cuticle. Following the cladogram of the genus *Persicaria* presented by Hong (1993: 110), *P.* sect. *Persicaria* is the sister group of *P.* sect. *Echinocaulon*, which is supported by two synapomorphies (the presence of simple multiseriate or stellate hairs and a similar phytochemistry, such as methylated flavonoids). This is not well supported by tepal morphological data. However, more data should be included before definite answers can be reached for the delimitation and recognition of sections. Similar patterns are found in the genus *Bistorta*, but striations are mostly well-marked. In the genus *Aconogonon* the cuticles mostly show a longitudinal striation, which is well-marked in some cases (*A. campanulatum*, Fig. 29), or cuticles are almost smooth (e.g. *A. coriarium*, Fig. 25, *A. rhombitepalum*, Fig. 29). Only in one taxon, *A. molle* var. *rude*, cuticles show a more or less transversal pattern, which is never found in other genera (cf. Fig. 30). However, the striae at the cell extremities tend to run longitudinally. Horizontal patterns of the striae also occur in some species of *Fagopyrum* (e.g. *F. tataricum*, *F. lineare*, *F. snowdenii*, cf. Figs 41, 42).

In conclusion, all taxa placed under *Persicaria* by Ronse Decraene & Akeroyd (1988) show the same pattern of variation, with a more or less pronounced tendency to stability to one kind of epidermis. The shape of cells, strictly rectangular with straight or undulating margins, the absent, faintly present to strongly developed cuticular striae converge to one basic type.

It was interesting to find that the tepal shape and surface of the investigated *Oxygonum* taxa are more or less similar to those of some species of *Fagopyrum*. It is probable that these mammilliform papillae with either longitudinal tightly pressed or randomly ridged cuticles in *Oxygonum* and some taxa of *Fagopyrum* have probably been acquired as a better adaptation to the insect-pollination mechanism than the tepal surface structures of any other taxon in these two tribes. It is also noteworthy that a heterostylous sexual system has been found in some taxa of both *Fagopyrum* (Ye & Guo, 1992; Hong, unpublished data) and *Oxygonum* (Graham, 1957, 1958). Some of the heterostylous taxa from both general have mammilliform papillae with either longitudinal tightly pressed or randomly ridged cuticles, but this is not so in all heterostylous taxa (most of the studied taxa in *Oxygonum*, except *O. delagoense*, which is hermaphrodite). However, other species of *Fagopyrum* are similar to the *Persicaria* type (Figs 40–42; Ronse Decraene, unpubl.). In *F. tataricum* and perhaps *F. dibotrys* both types may be present, as transitions were found from bottom to top of the tepal surface. Contrary to *Fagopyrum* the mammillae are a constant feature in *Oxygonum*. It is therefore possible that the similar tepal structure of *Fagopyrum* and *Oxygonum* represents a homoplasy, as both genera show important differences, such as tepal vasculature, nectaries, etc. (Ronse Decraene & Smets, 1991).

The general impression is that the tessellated tepal structure of the genus *Polygonella* is highly similar to that of the genus *Polygonum* s.s., especially *P.* sect. *Duravia* which is interesting phylogenetically. Pollen morphology (cf. Hedberg, 1946; Horton, 1963; Hong & Oh, 1996 and unpublished SEM data), floral morphology (Ronse Decraene & Akeroyd, 1988), tepal structure (ibid., this study), some seed characters (Hong &

Oh, unpublished SEM and anatomical data), and the anatomical evidence (Haraldson, 1978) support the phylogenetic proximity of these two taxa as one natural group, even though Hedberg (1946) speculated that these resemblances probably evolved by convergence. A detailed nomenclatural proposal, however, will be delayed until we get more data (such as molecular data and others) to clarify the phylogenetic relationship between *Polygonum* and *Polygonella* (Ronse Decraene & Hong, in prep.).

The genus *Pteropyrum* produces mostly short, more or less rectangular cells with a deeply reticulate, randomly striate cuticle. Almost the same type is found in the closely related taxa *Atraphaxis* and *Calligonium*, although the tepal shape of some species of *Atraphaxis* tends to approach type I (*A. billardieri*: Fig. 74). They have been considered closely related to each other phylogenetically (cf. Haraldson, 1978; Ronse Decraene & Akeroyd, 1988). Some authors proposed that these three taxa should be treated as one tribe (Dammer, 1893) or subtribe (Gross, 1913; Jaretzky, 1925). However, on the basis of the tepal characters found in these three genera it may be difficult to separate them from other genera in the tribe Polygoneae. It is also true that the monotypic genus *Parapteropyrum*, being endemic to the Xizang Plateau (South-east Tibet) of China, has a similar tepal surface to that of *Pteropyrum*. Pollen morphological data also suggest a close relationship between *Pteropyrum* and *Parapteropyrum* (Hong, 1995).

In general, the present data support Ronse Decraene & Akeroyd's (1988) system which divided the genus *Polygonum* L. s.l. into two tribes (i.e. Persicarieae and Polygoneae), except for the taxonomic position of the genus *Fagopyrum* for which it is still not clear whether it belongs to Persicarieae or Polygoneae. Traditionally, *Fagopyrum* is placed closely to the genus *Fallopia* (Gross, 1913), because of a similar habit and superficial resemblance. However, on the basis of some floral characters (e.g. stamen morphology, the vasculature of the tepals and nectaries), Ronse Decraene & Akeroyd (1988) did not support a relationship of both genera, which we continue to maintain. Thus, on the basis of the inner tepal surface characters alone, the genus *Fagopyrum* could be considered as paraphyletic. It may also be speculated that these differences are possibly caused by the variety of habitats. *Fagopyrum* also shows numerous floral characters which place the genus at the base of evolution in the Persicarieae (see also Ronse Decraene & Akeroyd, 1988; Ronse Decraene & Smets, 1991).

Most of the taxa studied here occasionally have a few stomata occurring on the epidermis of the tepals. Some taxa, such as *Polygonum* s.s. (especially sections *Polygonum* and *Tephis*), *Fagopyrum*, *Pteropyrum* and *Calligonium*, have stomata on the tepal surface on a more frequent basis. The occurrence of stomata on the floral parts has been reported earlier in some angiosperm families (Maercker, 1965), but may have a wider distribution. In Polygonaceae Brandbyge (1990) and Hong (1992) demonstrated the presence of stomata on the tepal epidermis of two *Coccoloba* species and on two *Aconogonon* species respectively. However, stomata found on the tepals are usually non-functional (cf. Fahn, 1990).

The studied tepal characters tend not only to improve intrageneric classification but also to clarify plant-plant as well as plant-pollinator relationships. The optical geometry of a smooth lenticular tepal surface does not enable it to function as a light-trap, and smooth (unstriated) lenticular tepal surfaces usually show fairly strong surface reflections. According to Baagøe (1977) the papillate epidermal cells compensate for the increase in volume by increasing the surface area of the anticlinal cell walls which are in contact with neighbouring cells, thereby allowing a better

nutrient exchange to take place. In addition, the cuticular striations appear to afford extra strength to the cell walls (cf. Gale & Owens, 1983).

The cuticular striations do not appear to have much taxonomic value. However, it seems that there are some correlations between the degree or shape of cuticles on the tepal surface and the pollination mechanisms and the habitat of the plants, at least to some degree. The genus *Oxygonum* and some *Fagopyrum* taxa show a typically insect-adapted inner tepal surface (mammilliform papillae) which acts as a foothold for a specific pollination vector or even as a light-trap for incident light (cf. Kay *et al.*, 1981). The rest of the taxa in the two tribes Persicarieae and Polygoneae seems to be adapted to various pollination mechanisms, not only to a specific vector. For example, *Koenigia islandica*, the tiny self-pollinated arctic plant, has a fairly smooth inner tepal surface, while the other Himalayan taxa of *Koenigia* mostly have deep longitudinal striae, which are probably linked to entomophily. A highly striate cuticle may also be habitat-dependent, viz. taxa of dry or ruderal places.

It can be concluded that tepal characters in the tribes Persicarieae and Polygoneae can be useful in improving tribal classification, and give additional support at the infrageneric level.

#### ACKNOWLEDGEMENTS

We are grateful to the directors/curators of the following herbaria for the loan of specimens: BM, BR, E, G, GB, K, KHUS, LD, LV, PE, RNG, and UPS. We acknowledge the SEM and Photography Unit of the Plant Science Laboratories, University of Reading for permission to publish photographic material from Ronse Decraene's (1986) unpublished work. We are also thankful to Prof. Dr R. Swennen at the laboratory of Physico-Chemical Geology of Katholieke Universiteit Leuven for technical assistance with the SEM. This work was supported by a Junior Postdoctoral Fellowship from the Research Council of Katholieke Universiteit Leuven (Belgium) and, in part, by 'Non-Directed Research Fund (1995: No. 01-D-0425)' from the Korea Research Foundation to S.-P.H., which are gratefully acknowledged. This research was also supported by the FWO (Fund for Scientific Research, Flanders; Project no. 2.0038.91, SEM and Project no. G.0143.95, General research project). LPRDC is a postdoctoral fellow of the FWO.

#### REFERENCES

- Baagøe J.** 1977. Taxonomic application of ligule microcharacters in Compositac. *Svensk Botanisk Tidsskrift* 71: 193–223.
- Baagøe J.** 1978. Taxonomic application of ligule microcharacters in Compositae. II. Arctotidæ, Astereæ, Calenduleæ, Eremothamneæ, Inuleæ, Liabeæ, Mutisieæ, and Senecioneæ. *Svensk Botanisk Tidsskrift* 72: 125–147.
- Baagøe J.** 1980. SEM-studies in ligules of Lactuceæ (Compositæ). *Svensk Botanisk Tidsskrift* 75: 199–217.
- Barthlott W.** 1981. Epidermal and seed surface characters of plants: systematic applicability and some evolutionary aspects. *Nordic Journal of Botany* 1: 345–355.
- Barthlott W.** 1990. Scanning electron microscopy of the epidermal surface in plants. In: Clapham D, ed. *Scanning electron microscopy in taxonomy and functional morphology*. Systematic Association Special Volume No. 41. Oxford: Clarendon Press, 69–94.

- Brandbyge J.** 1990. The diversity of micro-morphological features in the genus *Coccocloba* (Polygonaceae). *Nordic Journal of Botany* **10**: 25–44.
- Brandbyge J.** 1993. Polygonaceae. In: Kubitzki K, Rohwer JG, Bittrich V, eds. *The families and genera of vascular plants. II. Flowering plants (Dicotyledons): Magnoliid, Hamamelid and Caryophyllid families*. Berlin, Heidelberg: Springer-Verlag, 531–544.
- Brehm BG, Krell D.** 1975. Flavonoid localization in epidermal papillae of flower petals: a specialized adaptation for ultraviolet absorption. *Science* **190**: 1221–1223.
- Dammer U.** 1893. Polygonaceae. In: Engler A, Prantl K, eds. *Die natürlichen Pflanzenfamilien*, 3(1a). Leipzig: Engelmann Verlag, 1–36.
- EHler N.** 1975. Beitrag zur Kenntnis der Mikromorphologie der Coroll-Epidermen von Stapelieen und ihre taxonomische Verwendbarkeit. *Tropische und Subtropische Pflanzenwelt* **14**: 83–139.
- EHler N.** 1976. Struktur und Funktionen der Oberflächen von orchideenblüten. In: Senghas K, ed. *Tagungsbericht der 8. Welt-orchideen-Konferenz, Palmengarten, Frankfurt am Main: Deutsche Orchideen-Gesellschaft*, 456–462.
- Erbar C.** 1995. On the floral development of *Sphenoclea zeylanica* (Sphenocleaceae, Campanulales)—SEM-investigations on herbarium material. *Botanische Jahrbücher für Systematik* **117**: 469–483.
- Fahn A.** 1990. *Plant anatomy*. 4th ed. Oxford: Pergamon Press.
- Fedorov AA.** 1969. *Chromosome numbers of flowering plants*. Leningrad: Nauka.
- Gale RMO, Owens SJ.** 1983. Cell distribution and surface morphology in petals, androecia and styles of Commelinaceae. *Botanical Journal of the Linnean Society* **87**: 247–262.
- Gerstberger P, Leins P.** 1978. Rasterelektronenmikroskopische Untersuchungen an Blütenknospen von *Physalis philadelphica* (Solanaceae)—Anwendung einer neuen Präparationsmethode. *Berichte der Deutschen Botanischen Gesellschaft* **91**: 381–387.
- Graham RA.** 1957. A revision of *Oxygonum* (Polygonaceae-Polygoneae). *Kew Bulletin* **1**: 145–172.
- Graham RA.** 1958. Polygonaceae. In: Turrill WB, Milne-Redhead E, eds. *Flora of Tropical East Africa*. London: Crown Agents for Oversea Governments & Administrations, 1–40.
- Gross H.** 1913. Beiträge zur Kenntnis der Polygonaceen. *Botanische Jahrbücher für Systematik* **49**: 234–339.
- Haraldson K.** 1978. Anatomy and taxonomy in Polygonaceae subfam. Polygoideae Meisn. emend. Jaretzky. *Symbolae Botanicae Upsalienses* **22**: 1–95.
- Hedberg O.** 1946. Pollen morphology in the genus *Polygonum* L. s.l. and its taxonomic significance. *Svensk Botanisk Tidskrift* **40**: 371–404.
- Hegnauer R.** 1969. *Chemotaxonomie der Pflanzen*, Vol. 5. Basel: Birkhäuser-Verlag.
- Holmgren PK, Holmgren NH, Barnett LC.** 1990. *Index Herbariorum. Part I: The herbaria of the world*, 8th ed. New York: New York Botanical Garden.
- Hong SP.** 1992. Taxonomy of the genus *Aconogonon* (Polygonaceae) in Himalaya and adjacent regions. *Symbolae Botanicae Upsalienses* **30**: 1–118.
- Hong SP.** 1993. Reconsideration of the generic status of *Rubrivena* (Polygonaceae, Persicarieae). *Plant Systematics and Evolution* **186**: 95–122.
- Hong SP.** 1995. Pollen morphology of *Parapteropyrum* and some putatively related genera (Polygonaceae-Atraphaxideae). *Grana* **34**: 153–159.
- Hong SP, Hedberg O.** 1988. Parallel evolution of aperture numbers and arrangement in the genera *Koenigia*, *Persicaria* and *Aconogonon* (Polygonaceae). *Grana* **29**: 177–184.
- Hong SP, Oh IC.** 1996. The preliminary study of the palynological variation in *Polygonum* L. s. str. and the relationship of this group to *Polygonella* Michx. (Polygonaceae). In: The Korean Association of Biological Sciences, ed. *The abstract from the 50th anniversary meeting of the KABS*. Seoul: KABS, 68.
- Horton IH.** 1963. A taxonomic revision of *Polygonella*. *Brittonia* **15**: 177–203.
- Jaretzky R.** 1925. Beiträge zur Systematik der Polygonaceae unter Berücksichtigung des Oxymethyl-anthrachinon-Vorkommens. *Feddes Repertorium Specierum Novarum Regni Vegetabilis* **22**: 49–83.
- Jaretzky R.** 1928. Histologische und karyologische Studien an Polygonaceen. *Jahrbücher für Wissenschaftliche Botanik* **69**: 357–490.
- Kay QON, Daoud HS, Stirton CH.** 1981. Pigment distribution, light reflection and cell structure in petals. *Botanical Journal of the Linnean Society* **83**: 57–84.
- Kevan PG, Lane MA.** 1985. Flower petal microtexture is a tactile cue for bees. *Proceedings of the National Academy of Sciences of the United States of America* **82**: 4750–4752.
- Lersten NR, Curtis JD.** 1992. Foliar anatomy of *Polygonum* (Polygonaceae): survey of epidermal and selected internal structures. *Plant Systematics and Evolution* **182**: 71–106.
- Maercker U.** 1965. Über das Vorkommen von Stomata in der Epidermis bunter Perianth-blätter. *Zeitschrift für Pflanzenphysiologie* **53**: 422–428.

- Nowicke JW, Skvarla JJ.** 1977. Pollen morphology and the relationship of the Plumbaginaceae, Polygonaceae and Primulaceae to the order Centrospermae. *Smithsonian Contributions to Botany* 37: 1–64.
- Robbrecht E.** 1988. Tropical woody Rubiaceae. *Opera Botanica Belgica* 1. Meise: Nationale Plantentuin van Belgie.
- Ronse Decraene LP, Akeroyd JR.** 1988. Generic limits in *Polygonum* and related genera (Polygonaceae) on the basis of floral characters. *Botanical Journal of the Linnean Society* 98: 321–371.
- Ronse Decraene LP, Smets E.** 1991. The floral nectaries of *Polygonum* s.l. and related genera (Persicarieae and Polygoneae): position, morphological nature and semophytes. *Flora* 185: 165–185.
- Stirton CH.** 1981. Petal sculpturing in papilionoid legumes. In: Polhill RM, Raven PH, eds. *Advances in Legume Systematics*. Volume 2. Kew: Royal Botanic Gardens, 771–788.
- Ye N, Guo G.** 1992. Classification, origin and evolution of genus *Fagopyrum* in China. In: Lin R, Zhou MD, Tao Y, Li J, Zhang Z, eds. *Proceedings of the 5th International Symposium on Buckwheat*. Taiwan: Agricultural Publishing House, 19–28.

#### APPENDIX: SPECIES AND SPECIMENS EXAMINED

The herbarium of origin of the material indicated by the abbreviations used in Holmgren *et al.* (1990). Species are listed alphabetically within genera/sections. For facility and comparative purposes all sections are listed, notwithstanding our acceptance of these.

#### Tribe Persicarieae Dumortier

##### *Persicaria* Mill.

###### Sect. *Persicaria* Mill.

- Persicaria amphibia* (L.) Gray: France, Berck, Pas-de-Calais, *de Bullemon* s.n. (LV); Russia, Jenisei, *Lundström* s.n. (UPS); USA, Minnesota, Swede Lake, *Bodin* S.V. (UPS).
- Persicaria bungeana* (Turcz.) Nakai: China, Chili Prov., Cho-kou-tien, *Bohlin* 268 (UPS).
- Persicaria coccinea* (Mehlenb.) Greene: USA, Iowa, Clinton Co., *Cooperrider* 3236 (UPS).
- Persicaria hydropiper* (L.) Opiz: China, Szechuan, Hsu-tsing, *H. Smith* 4778 (UPS).
- Persicaria hydropiperoides* Michx.: Brazil, Rio Grande, *Mealme* 1482 (UPS).
- Persicaria hispida* (H.B.K.) M. Gomez: Ecuador, El Oro Prov., *Asplund* 15861 (UPS).
- Persicaria lanigera* (R. Br.) Soják: Ghana, mouth of Volta River, *Ryding* 77 (UPS).
- Persicaria lapathifolia* (L.) Gray: China, Shansi Prov., *H. Smith* 7984 (UPS).
- Persicaria maculata* (Raf.) Löve & Löve: Belgium, Bruges, *Ronse Decraene* 24 Lb (LV).
- Persicaria minus* (Huds.) Opiz: UK, Sussex, *Sandwith* s.n. (K).
- Persicaria nodosa* (Pers.) Opiz: UK, *Lousley* 1671 (RNG).
- Persicaria pulchra* (Blume) Soják: Tanzania, Iringa distr., Kidatu, *Mohoro* 588 (UPS).
- Persicaria viscosa* (Buch.-Ham. ex D. Don) H. Gross: Nepal, Bagmati, Kathmandu, *Ryding* 332 (UPS).
- Persicaria yokosaiana* (Nakai) Makino: Japan, Hondo, Kyoto, *Ohwi* 9077 (UPS).

###### Sect. *Echinocaulon* (Meisn.) H. Gross

- Persicaria artifolia* (L.) Haraldson: USA, Minnesota, Chicago, *Bodin* s.n. (UPS).
- Persicaria hastato-sagittata* (Nakai) Nakai: Japan, Nikko, *Kanai* 10383 (UPS).
- Persicaria perfoliata* (L.) H. Gross: China, Szechuan, Iping, *H. Smith* 10000 (UPS).
- Persicaria sagittata* (L.) H. Gross: Nepal, Jumla, *Einarsson et al.* 3915 (UPS).
- Persicaria sieboldii* (Meisn.) Ohki: Korea, Ditaku, *Ohwi* 2569 (UPS).
- Persicaria thunbergii* (Siebold & Zucc.) H. Gross ex Nakai: Japan, Hondo, Musashi, *Ohwi* 170 (UPS).

###### Sect. *Cephalophilon* (Meisn.) H. Gross

- Persicaria alata* (Buch.-Ham.) Nakai: Kenya, cult. Uppsala Bot. Gard., *Hedberg* s.n. (UPS).
- Persicaria capitata* (Buch.-Ham. ex D. Don) H. Gross: Nepal, Muga Karnali, *Polunin et al.* 5248 (UPS).
- Persicaria chinensis* (L.) H. Gross: Without country name, Chin Hill, *Venning* 88 (K).

*Persicaria nepalensis* (Meisn.) H. Gross: Nepal, Muga Khola, *Polunin et al.* 3017 (UPS); Korea, Kangwon-Do, Mt. Kwangduk, *Hong* 96-79 (KHUS).

*Persicaria runcinata* (Buch.-Ham. ex D. Don) Masamune: India, Kashmir, *Ludlow & Sherriff* 8250 (UPS).

Sect. *Rubrivena* (M. Král) S.-P. Hong

*Persicaria wallichii* Greuter & Burdet: Cultivated in Reading Bot. Gard. *Ronse Decraene* 15 Le (RNG).

Sect. *Tovara* (Adans.) H. Gross

*Persicaria neofiliformis* Ohki: Japan, Hondo, Koshigaya, *Ohwi* 331 (UPS).

*Persicaria virginiana* (L.) Gaertn.: USA, Illinois, Peoria, *McDonald* s.n. (UPS).

Sect. *Amblygonon* Meisn.

*Persicaria limbata* (Meisn.) Hara: Clulkana, near Lakarumpour, *Herb. Hookerianum* s.n. (K).

*Persicaria orientalis* (L.) Spach: USA, Pennsylvania, Reading, *Brumbach* 6921 (UPS).

*Persicaria senegalensis* (Meisn.) Soják: Uganda, Busiro Co., Bukiberu, *Lye* 2816 (UPS).

*Persicaria tomentosa* (Willd.) Sasaki: India, Dacca Station, *Clarke* 8144 (UPS).

*Bistorta* Mill.

*Bistorta affinis* (D. Don) Greene: India, Kashmir, Mantnar Nullab, *Ludlow & Sherriff* 8203 (UPS).

*Bistorta amplexicaulis* (D. Don) Greene: Nepal, Chiong, *Dhawij* 108 (UPS).

*Bistorta major* Gray: Hercegovina, *Murbeck* s.n. (UPS).

*Bistorta griffithii* (Hook.) Grierson: SE Tibet, Showa Dzong, *Ludlow et al.* 13097 (UPS).

*Bistorta macrophylla* (D. Don) Soják: China, Sikang, Kngting, *H. Smith* 10932 (UPS).

*Bistorta perpusella* (Hook.) Greene: Bhutan, Shingh, *Ludlow et al.* 21115 (UPS).

*Bistorta suffulta* (Maxim.) Greene ex H. Gross: Japan, Honshu, Nagano Pref., *Yahara et al.* 6998 (UPS).

*Bistorta vaccinifolia* (Wall. ex meisn.) Greene: Bhutan, Thampe La, *Ludlow et al.* 17136 (UPS).

*Bistorta vivipara* (L.) A. Gray: Canada, NW Territory, Baffin Island, *Hedberg* 3168 (UPS).

*Aconagonon* (Meisn.) Reichenbach

*A. alpinum* (All.) Schur: India, Himachal Pradesh, *Stewart* 200 (K).

*A. angustifolium* (Pall.) Hara: UK, Aberdeen, *Poget* s.n. (RNG).

*A. campanulatum* (Hook. f.) Hara var. *campanulatum*: Seed from Edinburgh Bot. Gard., *Hong-cult.*, 89-A3 (UPS); *Ronse Decraene* cult., 12 Lb (LV).

*A. coriarium* (Grig.) Soják: Afghanistan Parwan, Panjahir Valley, Mukeni, *Hedge & Wendelbo* 5148 (E).

*A. divaricatum* (L.) Nakai ex Mori: China, Hsiao Wutaishan, *King* 1165 (K).

*A. hookeri* (Meisn.) Hara: China, Yunnan, Likiang, Mt. Haba, *Rock* 9642 (E); Tibet, Dzomo La, *Rock* 14376 (K).

*A. molle* (D. Don) Hara var. *nude* (Meisn.) Hara: Originally cultivated in Kew Bot. Gard., *Hong-cult.* 89-K1 (UPS); cult. in Kew, 267-72.02550 B.L.&M., *Ronse Decraene* 624 Le (LV).

*A. rhombifolium* S.-P. Hong: China, Yunnan, near Tali, *Forrest* 29864 (E).

*A. rumicifolium* (Royle ex Bab.) Hara: Pakistan, Ushu-Tales, *Em* 7620—*Hong-cult* 89-D1 (UPS).

*A. sericum* (Pall.) Hara: Originally cultivated in Cambridge Univ. Bot. Gard. *Anonym.* 52.96 (K).

*A. tortuosum* (D. Don) Hara var. *tortuosum*: Seed from Kew Bot. Gard., *Hong-cult.*, 89-K1 (UPS).

*A. tripterocarpum* (A. Gray) Hara: Ex. Herb. Hort. Bot. Imper. Petropolitani, *Nowicz* s.n. (K).

*A. weyrichii* (F. Schmidt) Hara: Cult. Oxford Bot. Gard., *Ronse Decraene* 19 Le (LV).

*Koenigia* L.

*K. delicatula* (Meisn.) Hara ssp. *delicatula*: Nepal, Annapurna, *Stainton et al.* 8603 (UPS); Tibet, Upper Chhami Valley, *Gould* 1586 (K).

*K. delicatula* (Meisn.) Hara ssp. *relicta* Hedberg: Upper Burma, N'Maikha-Salwinn, *Forrest* 25042 (UPS).

*K. filicaulis* (Wall. ex Meisn.) Hedberg: India, Assam, Delei Valley, *Kingdon Ward* 8612 (K).

*K. forrestii* (Diels) Hedberg: China, Yunnan, Isekon, *Monberg* 82 (K).

*K. islandica* L.: Greenland, E. Sukkertoppen, *Hornsen* 601 (UPS); *Nielsen* 69 (RNG).

*K. nepalensis* D. Don: Nepal, Jangla, *Einarsson et al.* 3394 (UPS).

- K. nummularifolia* (Meisn.) Mesicek & Soják: Nepal, Arun Valley, *Stainton* 728 (UPS); India, Kumain, Ralam Valley, *Duthie* 3337 (K).
- K. pilosa* Maxim.: China, Szechuan, Sung Pan Hsien, *Fang* 4419 (K).

*Fagopyrum* Mill.

- F. dibotrys* (D. Don) Hara: China, Hong Chow, Ling Ying, *Clung?* 3791 (UPS); cult. in Hyde Park, *Anonym. s.n.* (K); *Cave s.n.* (E).
- F. esculentum* Moench: Bhutan, Thimphu, *Grierson & Long* 1272 (E); China, Shansi, Chieh-hsiuh distr., Sung-lin-miao, *H. Smith* 7666 (UPS); USA, Monroe Co., Delaware Water Gap, *Brumbach* 6902 (K); Korea, Kangwon-Do, Pyungchang-gun, *Hong* 96-84 (KHUS).
- F. gilesii* (Hemsley) Hedberg: China, Yunnan, Londjre, *Handel-Mazzetti* 8017 (S).
- F. giraldii* (Dammer ex Diels) Haraldson: China, Szechuan, Drogochi, *H. Smith* 4521: 2 (UPS); N. China, *Licent* 4078 (K); *ibid.*, Shansi (seed collected by H. Smith 79), cultivated in Uppsala Bot. Gard., *Hedberg* 7321 (UPS).
- F. leptopodium* (Diels) Hedberg ssp. *leptopodium*: China, Yunnan, *Forrest* 6168 (E).
- F. leptopodium* (Diels) Hedberg ssp. *grossii* (H. Lév.) Lauener & Ferguson: China, Yunnan, *Schneider* 2015 (K); *ibid.*, La-kon, *Maire* 3 (E).
- F. lineare* (Sam.) Haraldson: China, Yunnan, Talifu, *Handel-Mazzetti* 8569 (S).
- F. megacarpum* Hara: Nepal, Muju Karnali Valley, *Polunin et al.* 3033 (UPS); *ibid.*, Suli-Gad, Stainton 5493 (BM).
- F. snowdenii* (Hutch. & Dandy) S.-P. Hong: Kenya, Embu distr., *Kabuye* 72(UPS); Tanzania, *Kerfoot* 1546 (K); Rwanda, Gikungu, *Troupin* 15254 (BR).
- F. statice* (H. Lév.) H. Gross: China, Ma-hong, *Maire s.n.* (G).
- F. tataricum* (L.) Gaertn.: China, Yang-tao-li, *Anonym.* 649 (UPS); cult. Leuven, *Ronse Decraene* 626 Ln, seeds from Botanische Garten Göttingen, no. 1385 (LV).
- F. uropyrum* (Bureau & Franch.) H. Gross: China, Yunnan, Mengtze, *Henry* 9133 (E).

Tribe Polygoneae emend. Haraldson

*Polygonum* L.

Sect. *Polygonum* L.

- P. aviculare* L.: Korea, Kyunggi-Do, Kwachun-si, *Hong* 96-33 (KHUS).
- P. aviculare* L. ssp. *aequale* (Lindm.) A. & G.: Switzerland, St. Gallen, *Koch* 48/455 (UPS).
- P. arenastrum* Boreau: Czechoslovakia, Moravia, *Unar* 1525 (UPS).
- P. bellardii* All.: Greece, Pharsalum, *Heldreich* 877 (UPS).
- P. equisetiforme* Sibth. & Sm.: Palestine, Bethlehem, *Linder s.n.* (UPS).
- P. floribundum* Schlr. ex Sprengel: Russia, Seratov prov., *Kasakeviev s.n.* (K).
- P. maritimum* L.: France, Gallica, *Nordin* 102 (UPS); Portugal, Barboa Sines, *Grandvaux* 13573 (RNG).
- P. oxyspermum* Meyer & Bunge ex Ledeb. ssp. *raii* Bab.: UK, without precise locality, *Jury & Rumsey* 4650 (RNG).
- P. patulum* M. Bieb.: Afghanistan, Tashkargan, *Furse* 7793 (K).
- P. plebeium* R. Br.: Tanzania, Dodoma, *Hedberg* 4724 (UPS); India, Karnataka, Belgain, *Rao* 27 (K).

Sect. *Pseudomollia* Boiss.

- P. molliaeforme* Boiss.: Without exact country name, Kuh-Daëna, *Kotschy* 778 (UPS); Iran, Denawand, *Bornmüller* 8181 (K).

Sect. *Tephis* (Adans.) Meisn. emend. Haraldson

- P. afromontanum* Greenway: Kenya, Nanyuki distr., Mt. Kenya, *Hedberg* 4320 (UPS); Ethiopia. Kaffa Prov., *Danish-Ethiopian Bot. Exped.*, 1622 (K).

Sect. *Duravia* S. Wats.

- P. californicum* Meisn.: USA, Oregon, Grant's Pass, *Howell s.n.* (LV); California, Stanislaus Co., *Hoover* 2392 (K).

- P. douglassi* Greene: USA, Washington, Kittitas Co., *Sandberg & Leiberg* 434 (UPS).

- P. douglassi* Greene ssp. *spergulariiforme* (Meisn. ex Small) J. Hickman: Oregon boundary Commission, Saturne Is., *Lyall* s.n. (K).  
*P. kelloggii* Greene: Canada, British Columbia, Whipsaw Creek, *Holm* 273 (UPS).  
*P. minimum* S. Wats.: USA, Washington, Cascade, *Sandberg & Leiberg* 799 (UPS).  
*P. shastense* Brewer: USA, California, Siera Nevada, *Sonne* s.n. (LV).

*Polygonella* Michx.

- P. americana* (Fisch. & C.A. Mey.) Small: USA, Texas, Cat Springs, *Fischer* 10 (UPS); Arkansas, Hot Springs Co., *Palmer* 8473 (K).  
*P. articulata* (L.) Meisn.: USA, Albany Co., *Wibbe* s.n. (LV); Virginia, Nansemond Co., *Long* 11563 (K).  
*P. fimbriata* (Elliott) Horton: USA, Florida, Tampa, *Blanton* 6825 (S).  
*P. gracilis* (Nitt.) Meisn.: USA, Florida, orange Co., Killarney, *Vestulund* s.n. (UPS).  
*P. parksii* Cory: USA, Texas, Leon Co., *Correll & Correll* 36649 (K).  
*P. polygama* (Vent.) Engelm. & Gray: USA, Indian River, *Curtis* 2433 (LV); California, Brunswick Co., Godfrey 1046 (K); Florida, Palm Beach, *Curtis* 5525 (K).

*Oxygonum* Burch.

- O. alatum* Burch.: S. Africa, Cape Prov., Irquatown, *Pole-Evans* 27 (K).  
*O. atriplicifolium* (Meisn.) Martel: Kenya, Eastern Prov., *Strid* 2405 (UPS); Kenya, Eastern Prov., Macharos Distr., *Haraldson* 401 (UPS).  
*O. delagoense* Kuntze var. *strictum* Wright: Rhodesia, Aborecorn, *Fries* 1258 (UPS); S. Africa, Bulfonein, O'connor 79 (K).  
*O. dregeanum* Meisn.: Tanzania, Ufipa distr., *Napper* 1054 (UPS).  
*O. dregeanum* Meisn. var. *canescens* (Send.) R.T. Craig: S. Africa, Pretoria, *Burll Davy* 2528 (K).  
*O. sinuatum* (Meisn.) Dammer: Ethiopia, Genale Gorge, *Friis et al.* 2696 (UPS); Kenya, Coast. Prov., Zumer 56 (UPS).  
*O. stuhlmannii* Dammer: Tanzania, Moshi distr., *Mhoro & Backus* 2236 (UPS).

*Fallopia* Adans.

- Sect. *Fallopia* (Adans.) Holub  
*F. convolvulus* (L.) A. Löve: China, Szechuan, Matang, *H. Smith* 4372 (UPS); UK, without detailed locality, *White* 49 (RNG).  
*F. dumetorum* (L.) Holub: Portugal, Coimbra, *Cardoso* s.n. (UPS).  
*F. scandens* (L.) Holub: China, SE Tibet, Monyul Prov., *Ludlow et al.* 7059 (UPS); USA, Philadelphia, Bowen U5 (RNG); China, Shantung Prov., *Chiao* 3140 (K).

Sect. *Pleuropterus* (Turcz.) Haraldson

- F. aubertii* (L. Henry) Holub: China, Szchuan, Wen-Chuan-Hsien, *H. Smith* 2316 (UPS); Ala Mt., Ning-Hsia, *Pai* 110 (K).  
*F. baldschuanica* (Regel) Holub: Turkestan, *Lundquist* s.n. (UPS); without detailed locality, *Watson* 47 (RNG).  
*F. multiflora* (Thunb.) Haraldson: China, Hong Chow, *Ching* 3843 (UPS).  
*F. pterocarpa* (Meisn. in Wall.) Holub: India, Darjeeling, *Gamble* 8520 (K).

Sect. *Pangonum* Haraldson

- F. cilinodis* (Michx.) Holub: USA, Maine, Hancock Co., *Mexon & Weatherby* 1045 (UPS).

Sect. *Reynoutria* (Houtt.) Ronse Decr.

- F. sachalinensis* (F. Schmidt.) Ronse Decr.: Japan, Sachalin, *Anonym* s.n. (LV); UK, Oxon, Marslow, *Druce* s.n. (LV); USA, California, cult.?, Humbolt Co., S. of Elk River Bridge, *HE & ST Parks* 24448 (UPS).  
*F. japonica* (Houtt.) Ronse Decr.: Japan, Hondo, Yamamoto, *Togashi* 1264 (UPS); SE Glamorgan, Oystermouth, *Barley* 1218B (LV).

*Parapteropyrum* A.J. li

*Parapteropyrum tibeticum* A.J. Li: China, Xizang, Gyaca, *Qing-zang Exped. Suppl. Group 750657* (PE).

*Pteropyrum* Jaub. & Spach

*Pteropyrum aucheri* Jaub. & Spach: Pakistan, Baluchistan, Kalat, *Rechinger 27441* (LD); Iraq, Sulermanrya, Al-Raddi 5282 (K).

*P. gracile* Boiss.: Persica, Snetunabad, *Straus s.n.* (LD).

*P. noéanum* Boiss. ex Meisn.: Iraq, Koisanjak, *Horsain & Horsain 53* (UPS).

*P. olivieri* Jaub. & Spach: Iran, Teheran, *Bowles Scholarship Bot. Exped. 2001* (K).

*P. scoparium* Jaub. & Spach: Oman, Masandam, *Miller 6677* (UPS); ibid., *Maconochie 3273* (K).

*Atraphaxis* L.

*A. aucheri* Jaub. & Spach: China, Chili, Hsiao-wu-tai-shan, *H. Smith 297* (UPS).

*A. billardieri* Jaub. & Spach: Without exact country name, Mt. Hymeto, *Balansa 1289* (UPS); Turkey, Erzerum Prov., Karaugan, *Davis & Hedge D30731* (K).

*A. buxifolia* Jaub. & Spach: Transcauc., Tiflis, *Grossbein? 20* (UPS); ibid., *Woronow & Schelkownikow 3* (K).

*A. frutescens* (L.) Koch: Cultivated in Uppsala Bot. Gard., *Alm s.n.* (UPS).

*A. lanceolata* Meisn.: Ex. Hort. Mus. Paris, *de Bullemonet s.n.* (LV).

*A. muschketovii* Krasn.: Cultivated in Berlin Bot. Gard., *Anonym. s.n.* (GB).

*A. spinosa* L.: Russia, Herb. Nom., Komarov, *Avetisian s.n.* (RNG).

*A. suaedifolia* Jaub. & Spach: Iran, Azerbaijan, Miaveh, *Wendelbo & Assadi 28026* (GB).

*Calligonum* L.

*C. arborescens* Litw. ex Komarov.: Russia, Buchara, *Samokish s.n.* (UPS).

*C. caput-medusae* Schrenk: Turkemenistan, *Anonym. s.n.* (GB).

*C. comosum* L'Herit.: Algeria, d'Oran Prov., *Bougeau 43* (UPS); Arabia, Ormein, *Oldfield 183* (K).

*C. eriopodum* Bunge: Russia, Transcasparian, *Michelson s.n.* (GB).

*C. litwinowii* Drobov: Uzbekistan, Kokangom, *Pjachin s.n.* (GB).

*C. microparum* I.G. Borshch.: Russia, Transcaucasia, Aschabad, *Sintenis 2202* (UPS); Turcomania, Beliavina & Proskwiakova 136 (RNG).