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***Under the microscope: plant anatomy and systematics.***
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# Systematic significance of fruit morphology and anatomy in tribes Persicarieae and Polygoneae (Polygonaceae)

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Fruits of Polygonaceae have a basically similar construction of indehiscent nuts or achenes. Sections of fruits, coupled with surface patterns were studied with SEM and LM in all genera of the tribes Persicarieae and Polygoneae (Polygonoideae-Polygonaceae). The outer layer of the pericarp is usually thickened and its anatomy can be used consistently to delimit genera more than any other character of the fruit. Cells are most often puzzle piece-shaped in surface view, but the shape of the cells may become polygonal with straight anticlinal walls towards the endocarp. The primary sculpture of the cells is highly variable and has value at the specific level, rarely at the generic level. No strict correlation exists between the external surface patterns and the anatomy. Two main cell types can be recognized in cross- and longitudinal section, correlated with the straight or undulating outline of the anticlinal walls. No distinction can be made between sections *Persicaria*, *Tovara*, *Echinocaulon*, and *Cephalophilon* of the genus *Persicaria*; all share narrow rectangular cells with undulating anticlinal walls. *Aconogonon* and *Bistorta* can be delimited by the square to rectangular cells with a narrow dichotomously branching lumen and straight anticlinal walls; both genera are best grouped as a single genus with two sections. A similar arrangement is found occasionally in species of *Polygonum s.s.*, *Polygonella*, *Atraphaxis*, *Fallopia* and *Calligonum*. Fruit anatomy of *Pteropyrum* is distinctive. The genus *Polygonum s.s.* shows a wide range of integrating patterns, ranging from straight to undulating anticlinal walls and cannot be separated from *Polygonella*. *Fagopyrum* is aberrant in having a parenchymatic exocarp and a thickened mesocarp; other evidence supports its isolated position. Different fruit anatomical patterns have arisen several times in evolution and have a limited value at tribal level but are useful at generic level. It is suggested that an arrangement with straight anticlinal walls and a broad lumen, eventually with dendritic branching towards the periphery, is ancestral.



ADDITIONAL KEYWORDS:– achene – anticlinal walls – exocarp – generic delimitation – pericarp – surface patterns – tribal classification.

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## INTRODUCTION

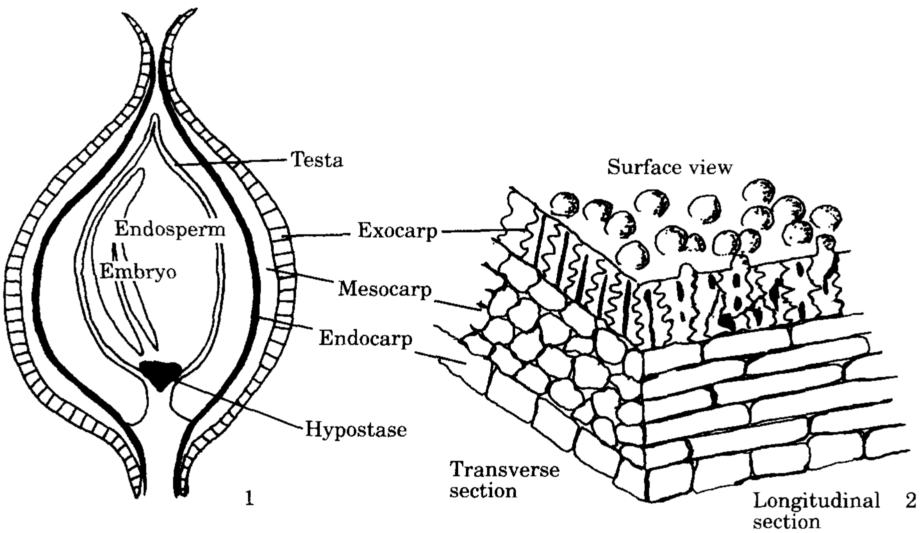
Subdivision of the large, heterogeneous genus *Polygonum* into a number of smaller, more natural units is a current necessity with a number of recent proposals (cf. Haraldson, 1978; Ronse Decraene & Akeroyd, 1988; Hong, 1992). This paper is the second in a series aiming to critically analyse and improve the delimitation and infrageneric relationships of tribes Persicarieae and Polygoneae presented by Ronse Decraene & Akeroyd (1988). In a previous investigation, Hong, Ronse Decraene & Smets (1998) studied the adaxial tepal epidermis of a number of species belonging to both tribes. Two main types could be recognized, corresponding to the tribes Persicarieae and Polygoneae, plus a third type of papillose cells, shared by some species of *Fagopyrum* and *Oxygonum*.

Classification of *Persicaria* at the sectional level is still not fully clarified, and recognition of genera such as *Aconogonon*, as accepted by Hong (1992), and *Bistorta*, separated from *Persicaria*, needs further investigation. The affinities of *Polygonella* to *Polygonum s.s.* have been recently investigated by Ronse Decraene, Hong & Smets (in press); palynology, fruit anatomy, and the general flower structure are overwhelming evidence for treating *Polygonella* as a section of *Polygonum*.

The taxonomic value of fruit morphology has been recognized early (see e.g. Marek, 1954, 1958; Kanai, Takeno & Taniguchi, 1983; Wolf & McNeill, 1986; Yang, Li & Wang, 1991; Hong, 1992, 1993; Hedberg, 1997), although fruit characters have mostly been investigated locally for a limited number of taxa and not at the level of entire tribes. In order to increase our knowledge of fruit morphology and anatomy in *Polygonum* s.l. and critically assess the classification of Ronse Decraene & Akeroyd (1988), we studied a representative number of species of tribes Persicarieae and Polygoneae.

### *General description of fruit in Polygonaceae*

Fruits of Polygonaceae are invariably indehiscent achenes or nuts formed by three carpels (pyramidal or triangular: Figs 21, 36, 55, 60, 61, 70) or two carpels (lenticular fruits: Fig. 16). Rarely, there are four carpels, which is a constant feature for the genus *Calligonum*. The number of styles or stigmatic lobes corresponds with the number of carpels. The fruit is enclosed by the persistent perianth, which may play an important role in the dispersal mechanisms. For example, the tepal lobes can become accrescent and covered with hooks in *Rumex* and *Emex*. In *Persicaria* sect. *Tovara* tepals are undifferentiated but dispersal occurs through the hooked persistent

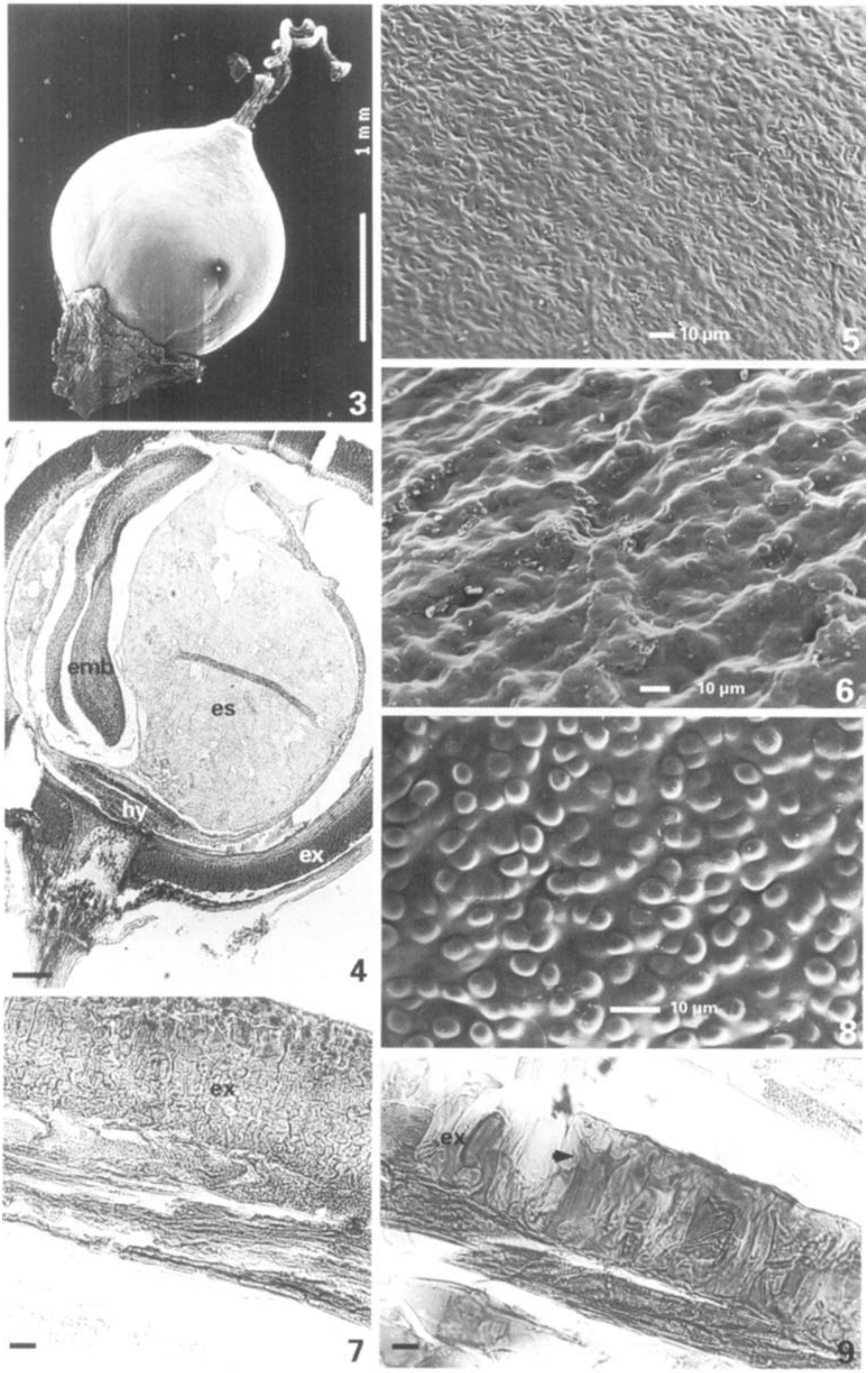



Figures 1, 2. Fig. 1. Schematic LS fruit of Polygonaceae. Fig. 2. Details of transverse section (TS) and longitudinal section (LS) of pericarp. Different shapes are shown for exocarp cells in TS and LS. However, both sections are similar for a given species.

styles (Fig. 16). In *Persicaria lapathifolia* (sect. *Persicaria*) the vasculature of the disintegrating tepals enclosing the fruit functions as an agent of dispersal, developing as anchor burrs (Wisskirchen, 1991).

The morphological configuration of the fruit (an achene) is relatively simple and basically similar in all Polygonaceae (Fig. 1; e.g. Dammer, 1893; Graham & Wood, 1965; Roth, 1977; Brandbyge, 1993). The three or two carpels enclose an orthotropous ovule arising from the apical meristem of the flower. Vautier (1949) studied the vascular arrangement of several taxa using a clearing treatment for whole flowers. The vasculature in the ovary is represented by three dorsal traces running into the styles; they are located in the mesocarp and may be flanked with marginal traces. The single placental trace (rarely three, as in *Fagopyrum*) is well-developed. The vasculature is sometimes interrupted (especially in younger stages) by a non-lignified zone at the level of the hypostase (Figs 1, 4). There has been discussion in the past about the origin of the free-central placentation (e.g. Laubengayer, 1937; Vautier, 1949). While the ovule develops as a seed, the carpel wall differentiates as the pericarp (Figs 1, 2).

The most conspicuous feature of the pericarp is the exocarp or epidermis, which is sclerified in most cases (Figs 1, 2). The young fruit consists of a well developed exocarp (epidermis), several layers of parenchymatous mesocarp cells (sometimes subdivided in an outer and inner portion, depending on the inclusion of cell contents) and an endocarp. During maturation the inner layers of the fruit wall (mesocarp and endocarp) become mostly flattened or destroyed. Only the exocarp increases in size and becomes heavily sclerified. Thickenings most commonly occur on the anticlinal (radial) walls, but not on the inner tangential (periclinal) walls. As thickening of the anticlinal walls increases from the inner tangential wall to the outer, the lumen often takes a triangular to trapezoid shape in section. The thickening is often U-shaped or horseshoe-shaped (cf. Roth, 1977). Very often small canals branch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from the triangular lumen into the surrounding sclerenchymatous tissue. Due to space constraints the anticlinal walls can become variously convoluted or bent in cross- or longitudinal sections (Fig. 2). As convolutions of the anticlinal walls may also occur tangentially this gives the cells a star- or puzzle piece-shape in surface view or in paradermal section, or the cells appear polygonal if no convolutions occur. Shifts in shape may occur within the cells from the periphery to the mesocarp (cf. Lonay, 1922). The outer surface of the epidermis represents interesting systematic characters, as emphasized by Barthlott (1981, 1990). Barthlott distinguished between primary cell sculpturing (including cell shape, cell boundaries and curvature of outer periclinal wall), secondary sculpturing (including microscopic sculpturing of an often cuticular nature), and tertiary sculpturing (epicuticular wax secretions). These characteristics apply equally for the fruit surfaces of Polygonaceae, which can be highly variable. However, in the past the descriptive terminology has often been vague, ill-defined and sometimes technically incorrect (cf. Wolf & McNeill, 1986). SEM studies reveal smooth, pitted surfaces, surfaces with a reticulate thickening, or surfaces covered with tubercles (Fig. 2). Wolf & McNeill (1986) recognized four surface patterns: smooth, roughened, papillose and striate-papillose. The achene can sometimes be supplied with spines and wings (e.g. *Fagopyrum giraldii*, *Oxygonum*, *Pteropyrum*).

Seeds are small and the testa is reduced to the outer integument with little specialization. The seed develops an outer layer of rectangular cells (exotesta), surrounding a mealy or horny endosperm and embryo. The embryo is mostly straight with incumbent cotyledons and is positioned excentrically in one corner of the seed. The outer layer of the endosperm is differentiated as a nutritional layer (Neubauer, 1971), which is a rare feature in dicotyledons. Seed and fruit development are little known in Polygonaceae (Corner, 1976), except for detailed studies by Neubauer (1971) on *Persicaria pennsylvanica* and Lonay (1922) on *Polygonum aviculare*. Corner (1976) was uncertain whether the seeds are truly exotestal or merely undeveloped because they are enclosed in indehiscent syncarpous fruits.

## MATERIAL AND METHODS

The study of fruits was conducted mostly on material taken from herbarium specimens on loan from the following herbaria (abbreviations according to Holmgren, Holmgren & Barnett, 1990): BOL, BM, BR, E, GB, K, LD, LV, S, and UPS, but also partly from pickled material. A list of all species and specimens investigated is provided in the Appendix.

Figures 3–9. Fruits of *Persicaria* sect. *Persicaria* (Figs 3–8) and sect. *Rubrivena* (Fig. 9). Figs 3, 5, 6, 8: SEM. Figs 4, 7, 9: LM. Fig. 3. Lateral view of mature fruit of *P. attenuata* (Mohoro 588) with twisted styles and globular fruit. Scale bar = 1 mm. Fig. 4. *P. viscosa* (Ryding 322). LS mature fruit; note thick pericarp. Scale bar = 100 µm. Fig. 5. *P. attenuata* ssp. *pulchra* (Mohoro 588). Detail of fruit outer surface with pits arranged in star-like pattern. Scale bar = 10 µm. Fig. 6. *P. hydropiper* ssp. *microcarpum* (H. Smith 4778). Detail of fruit outer surface with irregular ridges on anticlinal cell walls. Scale bar = 10 µm. Fig. 7. *P. acris* (Rosas 362). LS pericarp. Scale bar = 10 µm. Fig. 8. *P. orientalis* (Brumbach 6921). Detail of fruit outer surface with tubercles more or less set on anticlinal cell walls. Scale bar = 10 µm. Fig. 9. *P. wallichii* (Ronse Decr. 15Lc). LS pericarp. Arrow points to dendritic branching of cell lumen. Scale bar = 10 µm. Abbreviations: emb = embryo; es = endosperm; ex = exocarp; hy = hypostrase.

The following fruit characters were investigated:

*(1) External structure.* This includes fruit shape (correlated with carpel number), presence versus absence of a beak (e.g. in *Aconogonon campanulatum*: Hong, 1992) on which the style is inserted, presence of one or more styles which are free or fused at the base, and whether fruits are stipitate versus non-stipitate (the achene can have a stalk or be sessile).

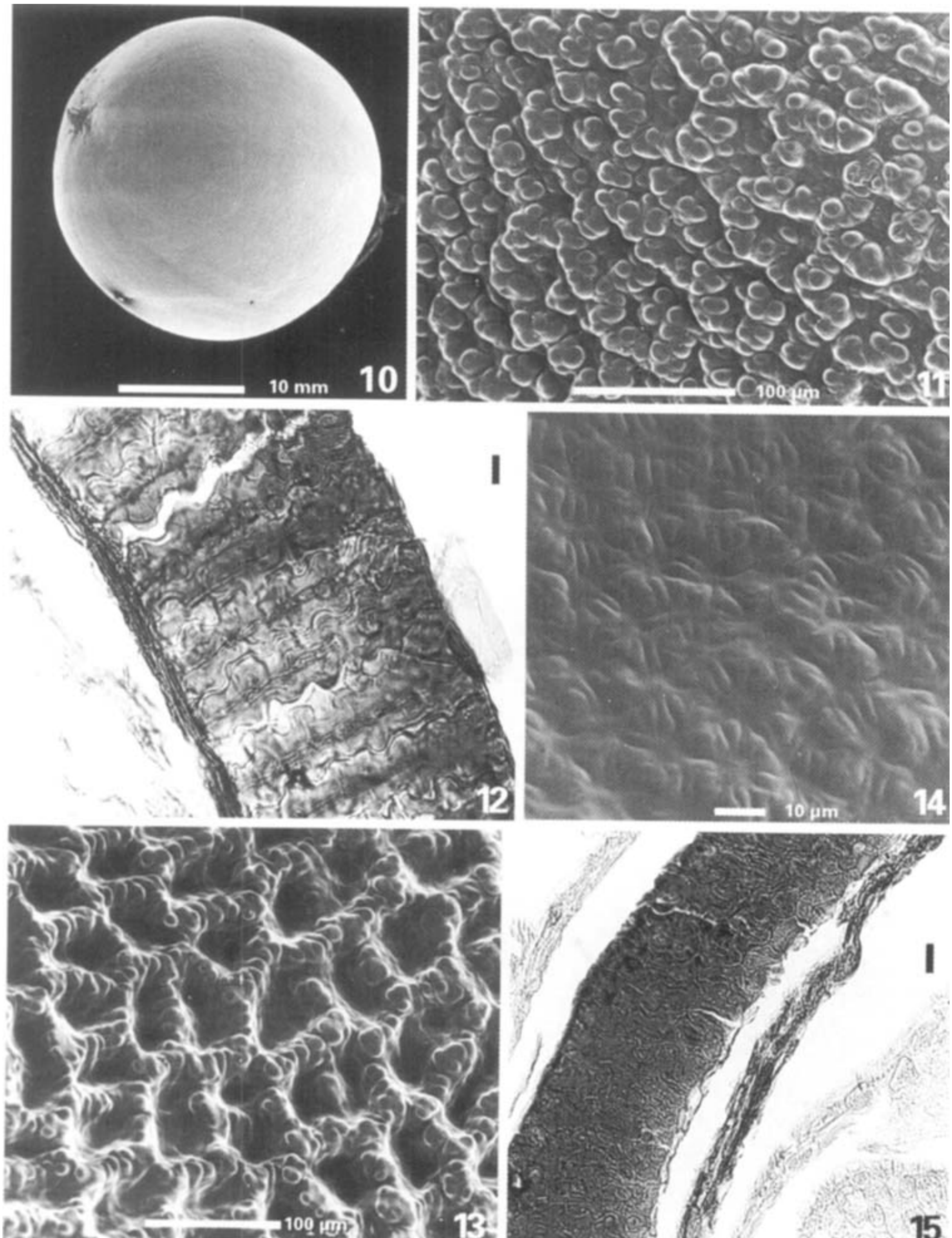
*(2) Perianth structure* (accrescent versus non accrescent). For example, in species of *Fagopyrum* the perianth persists as small basally inserted appendages, while the inner perianth whorl becomes strongly accrescent in *Rumex.*

*(3) Fruit surface patterns.* We follow the terminology of Barthlott (1981, 1990). Cell shape (primary sculpturing) is hardly visible externally, as cell boundaries are often unclear. Cells are most often isodiametric, rarely elongated (Fig. 28). Anticlinal walls are either straight or undulating, giving a puzzle piece-shaped pattern to the surface. At one extreme the anticlinal walls are not visible externally and the whole fruit surface is smooth (Figs 3, 10, 54, 60); in other cases the walls are collapsed and present as small pits lying radially around the cell (Figs 5, 17), as a continuous ridge or folds (Figs 6, 22, 24, 28, 30, 43, 51, 68, 78), or high walls giving a reticulate pattern to the surface (Figs 13, 46). Papillae (with a diameter below 10 μm: Figs 8, 11, 13, 14, 71) or strongly developed tubercles (with a diameter exceeding 10 μm: Figs 37, 50, 62) may be superimposed on the anticlinal walls, in some cases delimiting the boundaries of the cells when no ridge is visible (Fig. 37). In other instances the tubercles appear set in radial lines (Fig. 62; striate-papillose according to Wolf & McNeill, 1986). Papillae or tubercles are not necessarily linked with convoluted anticlinal walls, and their number may be variable. Ridges are not necessarily connected with the cell boundaries (Fig. 49). The outer periclinal wall of the cell is either flat (Figs 32, 46), or convex (Fig. 35), although this may be related to the collapsing of the wall. In *Oxygonum* short trichomes are present (Fig. 74).

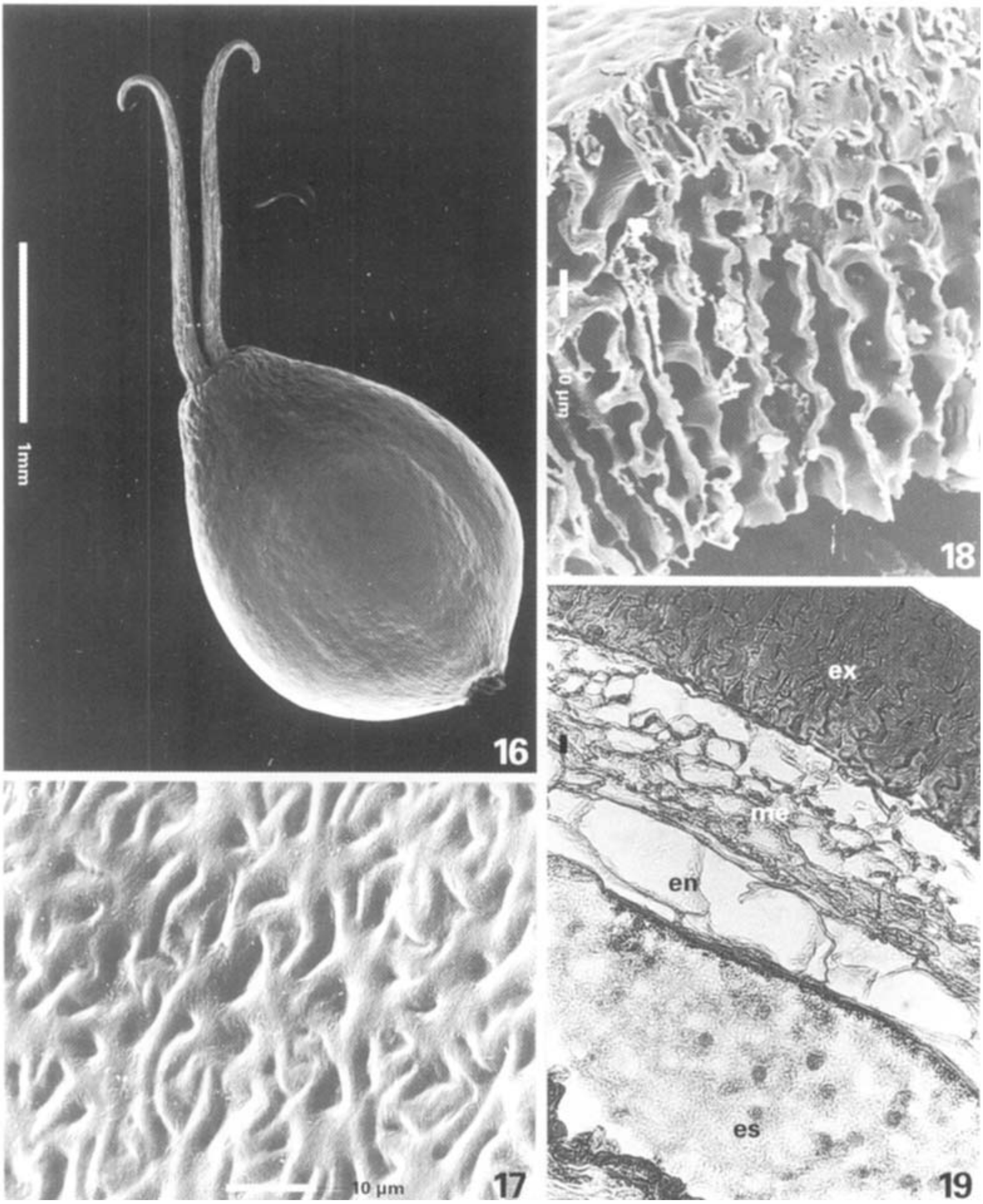
The secondary sculpturing of the cell wall consists in some cases of longitudinal cuticular striae, which may be weakly or strongly developed (Figs 54, 59). The limits between micropapillae (which are part of the secondary sculpture according to Barthlott), papillae, and tubercles are a matter of degree. Epicuticular wax secretions are only occasionally present (e.g. *Polygonum undulatum, P. minimum*).

*(4) Anatomical structure of pericarp.* In the simplest case we found one layer of cells aligned in parallel, the exocarp, resembling a palisade. These were normally stone cells, with a variable distribution of pit channels. Mesocarp and endocarp were often torn apart and were therefore mostly not included in the observations. Characters of testa and embryo were also not studied here.

Exocarp cell shape (in longitudinal or cross section) was square (isodiametric), shortly rectangular, or elongated-rectangular. Anticlinal walls were either straight (resembling 'corrugated sheets': Figs 20, 23, 25, 26, 29, 48, 54, 58, 64, 66, 69, 72), or undulating (resembling 'egg cartons': Figs 7, 12, 15, 18, 19, 38, 44, 50, 57, 65, 76, 78). Cell lumen size depends on cell wall thickening, which may be weak (limited to the outer tangential and radial walls, leading to a broad lumen: Figs 9, 42, 48, 52, 56), trapezoid or triangular (narrowing towards the periphery: Figs 29, 41, 47, 54, 63, 73), completely enclosed by thickenings (also with thickenings of the inner tangential wall: Figs 79, 80), or narrow with or without connection to the periphery (Figs 12, 19, 57, 64, 65, 66, 69, 72, 76, 77). In addition the lumen may show branches




Figures 10–15. Fruits of *Persicaria* sect. *Echinocaulon* (10–12) and sect. *Cephalophilon* (13–15). Figs 10, 11, 13, 14: SEM. Figs 12, 15: LM. Fig. 10. *P. perfoliata* (H. Smith 10000). Apical view of globular fruit. Scale bar = 10 mm. Fig. 11. *P. sieboldii* (Ohwi 2569). Surface detail with tubercled anticlinal cell walls. Scale bar = 10 µm. Fig. 12. *P. hastato-sagittata* (Kanai 10383). LS exocarp. Scale bar = 100 µm. Fig. 13. *P. alata* (Hedberg s.n.). Fruit surface; polygons surrounded by tubercled wall. Scale bar = 100 µm. Fig. 14. *P. runcinata* (Ludlow & Sherriff 8250). Detail of fruit with shallow papillae on anticlinal cell walls. Scale bar = 10 µm. Fig. 15. *P. capitata* (Polunin *et al.* 5248). TS fruit. Scale bar = 10 µm.




Figures 16–19. Fruits of *Persicaria* sect. *Tovara*. Figs 16–18: SEM. Fig. 19: LM. Fig. 16. Mature fruit of *P. neofiliformis* (Ohwi 331); fruit lenticular with long hooked styles. Scale bar = 1 mm. Figs 17–18. *P. virginiana* (Ronse Decr. 214 Lb). Fig. 17. Surface, with pits set in a star-like pattern. Scale bar = 10 µm. Fig. 18. TS pericarp showing cells with convoluted anticlinal walls and 'swiss cheesc'-holes. Scale bar = 10 µm. Fig. 19. *P. virginiana* (McDonald s.n.). LS fruit. Scale bar = 10 µm.

or canals situated at the outer limits of the lumen and branching dichotomously or trichotomously (Figs 9, 23, 25, 26, 40, 41, 63, 64, 66, 73), or as dendritic ramifications along the anticlinal sides of the lumen (as a result of the convolutions of the wall: Fig. 65). As seen in paradermal (tangential) section the shape of the palisade may change at different levels of the cell. Near the outer surface the cells often have undulating anticlinal walls (as discerned in surface view); towards the mesocarp the same cell may be polygonal with straight anticlinal walls. However, in cross or longitudinal sections the anticlinal walls may appear straight, although undulating in surface view (e.g. *Aconogonon, Bistorta, Fallopia, Koenigia*). One must distinguish between the undulations of the anticlinal walls seen in cross or longitudinal sections from those seen in paradermal section, confirming the existence of two different patterns.

For examination of fruits, well-developed, mature flowers were selected. Material was examined with the dissecting microscope, light microscope (LM) and scanning electron microscope (SEM). Most material from herbarium specimens was directly mounted onto aluminum stubs, coated and photographed as outlined below. A number of fruits was also treated with aerosol-OT (dioctyl sodium sulfosuccinate) following Erbar (1995) in order to compare dried fruits with rehydrated fruits. Sectioning of fruits was problematical, as the material was too hard to cut or became overstained. A solution to this was soaking the fruits in warm 10% KOH for a couple of hours, and the use of Stockwell's bleach (Schmid, 1977) to remove extra tannins. Material was subsequently treated with aerosol-OT and stored in 70% ethanol before sectioning.

Fruits collected from pickled material were prepared for the SEM as follows. Samples were dehydrated using formaldehyde-dimethylacetal (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 mm layer of Au or Au/Pd before being studied under the SEM (JEOL T-20, JEOL-5200 and JEOL-6200), operating at 15 kV, in Seoul, Reading and Leuven respectively.

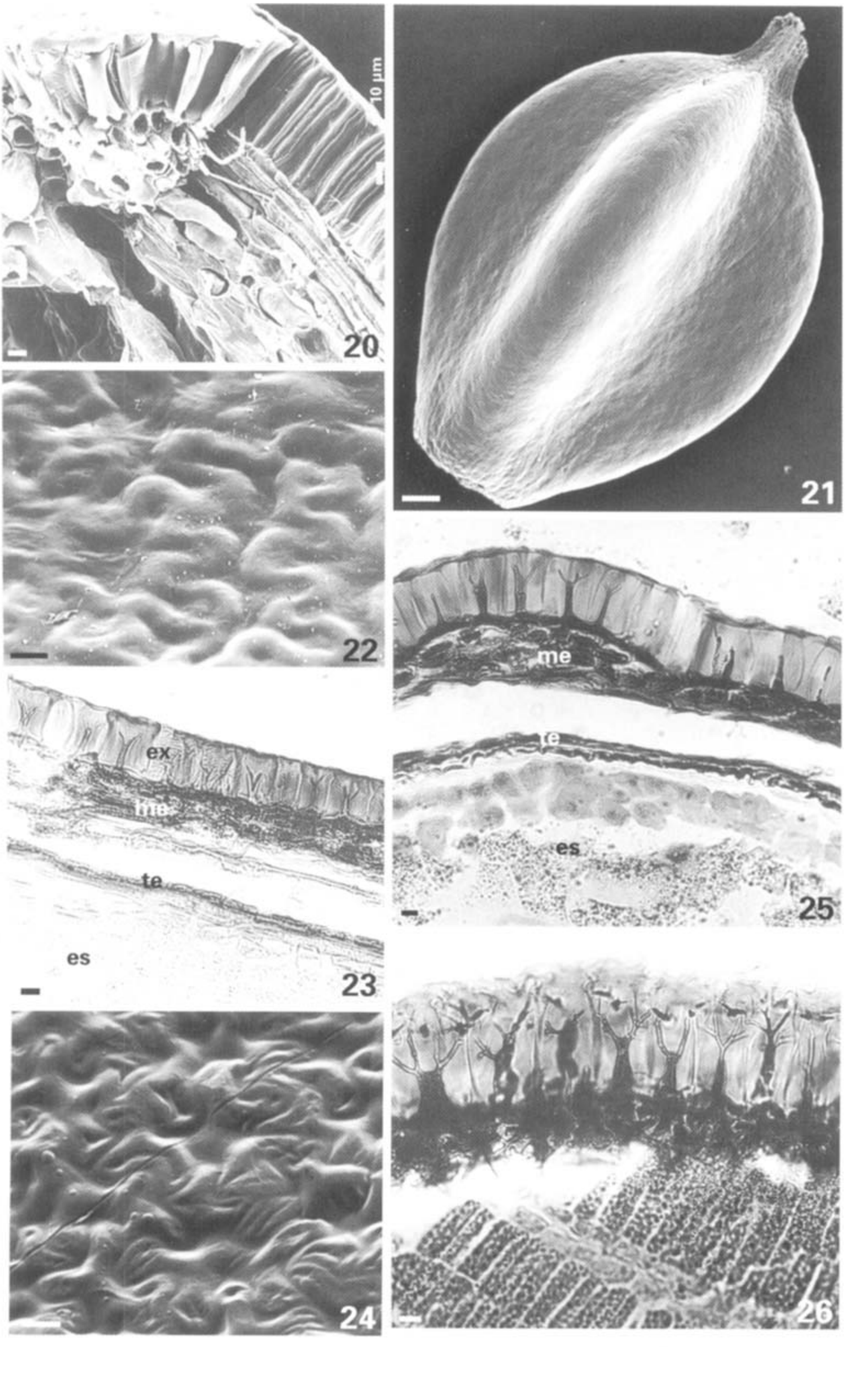
## RESULTS

### 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] (Figs 3–19)

In all taxa of *Persicaria* investigated except *P. wallichii* (Fig. 9), the epidermal cells are considerably higher than wide in cross section, with sinuate anticlinal walls (Figs 7, 12, 15, 18, 19). The thickness of the exocarp varies between 50 and 120 μm. The surface is rarely smooth, often pitted along the cell walls or with anticlinal walls covered by papillae or tubercles. The lumen of the cells is very narrow, running straight towards the periphery and is without branching.

Globular fruits are found in section *Persicaria* (*Persicaria attenuata*: Fig. 3, *P. viscosa*: Fig. 4, *P. strigosa*), or contrary to other sections the fruit is often elongated with a short beak (e.g. *P. acris*), bicarpellate and with almost no stipe, embedded in the perianth bases (Fig. 4). The fruit surface pattern is almost smooth (eventually with small pits set radially around the cells: *P. attenuata*: Fig. 5), with a variable number of papillae set on anticlinal ridges (*P. viscosum*), in *P. hydropiper* with the ridges following a longitudinal pattern (Fig. 6), or it consists of numerous tubercles delimiting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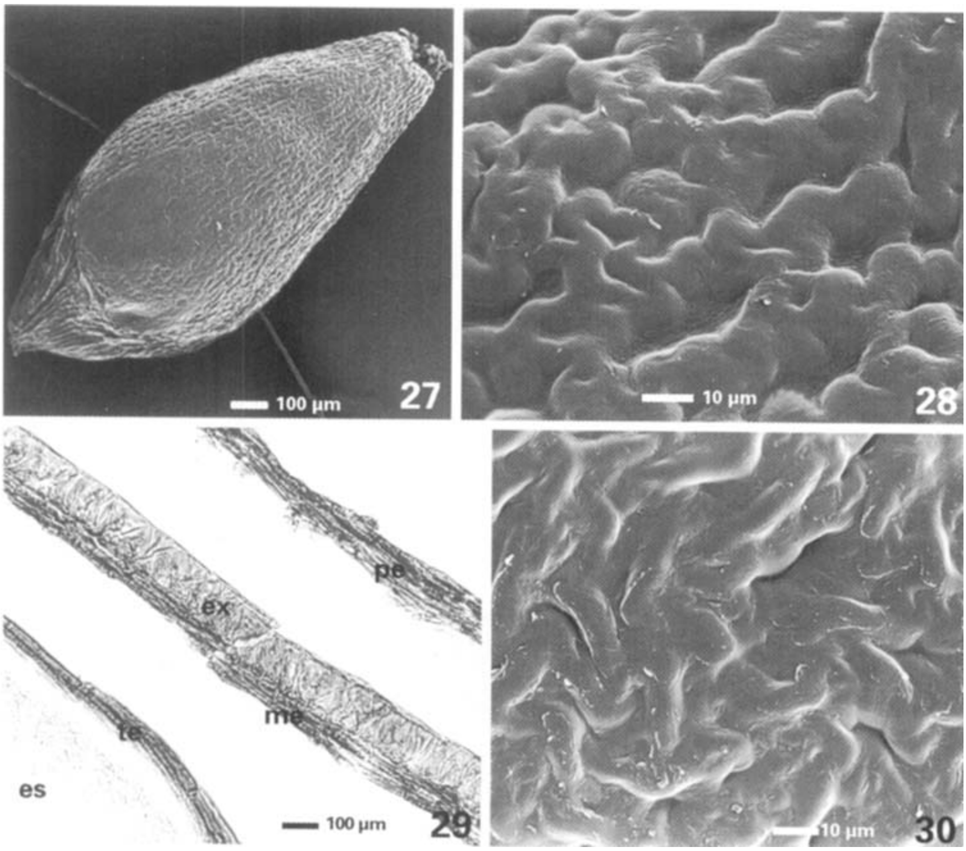



Figures 27–30. Fruits of *Koenigia*. All scale bars = 10 µm, except Fig. 27 = 100 µm. Figs 27, 28, 30: SEM. Fig. 29: LM. Fig. 27–28. *K. islandica* (Horsen 601). Fig. 27. Lateral view of mature fruit. Fig. 28. Surface detail; elongated cells with folded anticlinal cell walls. Fig. 29. *K. nepalensis* (Einarsson *et al.* 3394). LS fruit wall. Fig. 30. *K. nummularifolia* (Stainton 728). Surface detail. Abbreviations: es = endosperm; ex = exocarp; me = mesocarp; pe = perianth; te = testa.

individual cells (*P. bungeana, P. orientalis*: Fig. 8). The exocarp cells are narrowly rectangular (70–150 µm thick), with undulating anticlinal walls and narrow unbranched lumina (Fig. 7).

Fruits of sect. *Echinocaulon* are broadly triangular (e.g. *Persicaria sieboldii, P. hastato-sagittata*), rounded to almost globular (*Persicaria perfoliata*: Fig. 10), shortly stipitate, with a narrow beak. Tepals are not accrescent and shrivel at fruiting. Externally the surface consists of randomly grouped tubercles separated by small pits or deeper

Figures 20–26. Fruits of *Aconogonon* (*Persicaria* sect. *Aconogonon*) and *Bistorta* (*Persicaria* sect. *Bistorta*). All scale bars = 10 µm, except Fig. 21 = 100 µm. Figs 20–22, 24: SEM. Figs 23, 25, 26: LM. Fig. 20. Section through pericarp of *A. molle* var. *rude* (Ronse Decr. 642 Le). Fig. 21. Lateral view of fruit of *B. purpusella* (Ludlow *et al.* 21115). Fig. 22. *A. molle* var. *rude* (Ronse Decr. 642 Le). Surface detail with folded puzzle piece-like cell walls. Fig. 23. *B. griffithii* (Ludlow *et al.* 13097). LS fruit. Fig. 24. *B. macrophylla* (H. Smith 10932). Surface detail. Fig. 25. *A. hookeri* (Smith 4172). LS fruit. Fig. 26. *A. molle* var. *rude* (Hooker & Thompson s.n.). Section of fruit. Abbreviations: es = endosperm; ex = exocarp; me = mesocarp; te = testa.

invaginations. The number of tubercles ranges from a few large papillae arranged on the anticlinal wall (*P. hastato-sagittata*) to a high number of papillae grouped in polygons around depressions (*P. sieboldii*: Fig. 11). Anatomically one finds similar exocarp cells as in previous section (Fig. 12).

In section *Cephalophilon* one finds identical rectangular cells with undulating anticlinal walls (Fig. 15). The external fruit surface is constructed along the same pattern as in sect. *Echinocaulon* and consists of depressions (the periclinal wall of the cells) bordered by ridges covered with tubercles (*P. alatum*: Fig. 13, with a reticulate pattern, *P. nepalensis*). In *P. runcinata* the papillae are weakly developed in a position similar to the tubercles in other species (Fig. 14). Tepals are not accrescent but are larger than in section *Echinocaulon*. Fruits are more elongated and rounded in outline with a short stipe.

Section *Tovara* has bicarpellate lenticular fruits without beak and topped by two long styles with curved apex (Fig. 16). There is almost no stipe and the fruit surface is almost smooth, consisting of scattered small pits (in *P. virginiana*: Fig. 17) or shallow depressions in rows (in *P. neofiliformis*: Fig. 16), representing the collapsed anticlinal walls. In cross-section one finds a narrowly elongated exocarp with undulating tangential walls (Figs 18, 19). The mesocarp is loose and in some cases an endocarp of large cells is visible (mostly torn apart). The outer layer of the seed consists of darkly staining cells (Fig. 19). With the SEM one can observe holes in the undulating anticlinal walls which are connections between the lumina of adjacent cells.

Section *Rubrivena* was erected by Hong (1993) to include two polymorphic species *P. wallichii* Greuter & Burdet and *P. pinetorum* (Hemsley) H. Gross. Ronse Decraene & Akeroyd (1988) included *P. wallichii* in their section *Aconogonon* (as *Persicaria polystachya* (Wall. ex Meisn.) H. Gross). The exocarp of *P. wallichii* consists of rectangular cells with straight anticlinal walls and broad ellipsoidal lumen, branching dichotomously towards the outer tangential wall (Fig. 9). External fruit morphology and fruit surface are illustrated by Hong (1993).

*Aconogonon* (Figs 20, 22, 25, 26)

Data have been partly obtained from Hong (1989, 1992). In *Aconogonon* exocarp thickness varies between 30 and 65 μm. Fruits are trigonous, often with prominent ribs and almost no beak (except in *A. campanulatum*). Styles are short and topped with a cap-like stigma. The achenes are included, slightly exserted to well exserted above the persistent tepals.

Fruit surfaces have cells with undulating anticlinal walls, and are smooth (*A. coriarium*), sometimes slightly rough with weak depressions (*A. hookeri*, *A. campanulatum*, *A. angustifolium*), or with weak undulating ridges following the cell wall (*A. molle*: Fig. 22); there is no secondary sculpturing and rarely dispersed epicuticular wax secretions (*A. hookeri*). The pericarp is uniform in LM view with an exocarp of rectangular to square cells with straight anticlinal walls (Figs 20, 25, 26) and cylindrical lumina often branching dichotomously towards the outer periclinal wall. Dichotomous branching may be repeated (Fig. 26).

*Bistorta* (Figs 21, 23, 24)

Fruits are similar to those of *Aconogonon* with well developed ribs, but often more elongated (Fig. 21). There is virtually no stipe but the beak is well developed. Styles are short and topped with a cap-like stigma. The achenes are included, slightly exserted to well exserted above the persistent tepals. Fruit surfaces are smooth with tesselated cell outline, sometimes slightly pitted (*B. perpusella*), rough with weak folds (*B. griffithii*), or with undulating ridges along the anticlinal walls (*B. macrophylla*: Fig. 24). The exocarp consists of narrowly rectangular cells with straight anticlinal walls, and with a narrow lumen branching dichotomously towards the periphery (Fig. 23).

*Koenigia* (Figs 27–30)

Compared with *Persicaria* the exocarp anatomy of *Koenigia* is less elaborate and consists of one layer of more or less isodiametric cells in cross section (see also Hedberg, 1997). The cells show weak anticlinal thickenings delimiting a trapezoid lumen (Fig. 29). The mesocarp is flattened. Fruits are either elongated or globular with a short beak; there is a short stipe present (Fig. 27). The epidermal surface is either nearly smooth with inconspicuous ridges (*K. nepalensis*) or convolute with few to many folds on the anticlinal walls of the cells (*K. nummularifolia, K. islandica*: Figs 28, 30). In *K. islandica* the convolutions run in longitudinal rows and suggest an elongated shape of the cells (Figs 27, 28). Hedberg (1997) described the surface of the cells as smooth; otherwise his description corresponds with our data.

*Fagopyrum* (Figs 31–35)

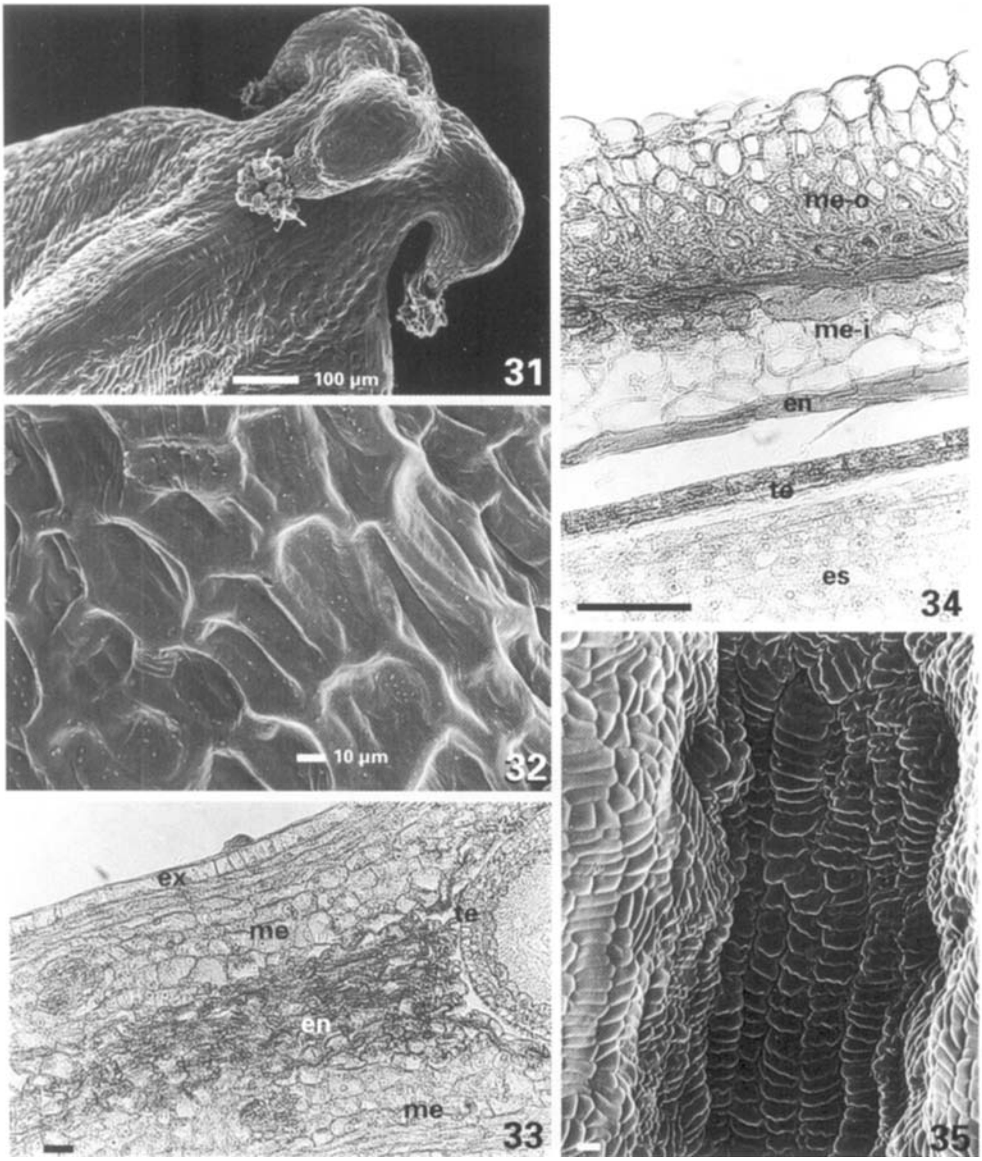
Mature fruits of *Fagopyrum* are readily recognizable by their massive triangular body with well developed ribs and alternating depressions, a non-accrescent perianth which persists at the base of the fruit, and the short tripartite style split to the base with reflexed, persistent style branches and small stigmas (Fig. 31). Fruit surface patterning is non-differentiated and thin-walled, and consists of rectangular cells which are collapsed in dry state (Figs 32, 35). Cell size may differ between the ribs and the intervening regions (Fig. 35). In section the pericarp consists of several layers (Figs 33, 34). The exocarp (epidermis) is thin-walled and isodiametric to rectangular in shape. The mesocarp consists of several cell layers: an outer mesocarp has small cylindrical cells occasionally becoming thickened towards the inner layers (Fig. 34), a transitional zone consisting of tannin-filled cells, and an inner mesocarp of parenchymatous cells containing starch. In other cases no thickenings are found (Fig. 33). There are several vascular bundles distributed in the mesocarp. The endocarp consists of larger parenchymatous cells disintegrating on the internal side of the fruit (Figs 33, 34).

## Tribe Polygoneae

*Polygonum L. s.s.* [including sect. *Polygonum, Pseudomollia, Duravia, Tephis*, and *Polygonella*] (Figs 36–59)

A detailed description of fruit structure and anatomy is given in Ronse Decraene, Hong & Smets (in press).

Fruits of sect. *Polygonum* are variously included or exserted from the perianth. The shape of the fruit is ellipsoidal-pyriform, often unequally triangular with one side broader than the other two, with a short stipe and long beak (Fig. 36). Styles are basally fused with capitate stigmas. Several species of sect. *Polygonum* and some of sect. *Duravia* have a distinctively tubercled surface pattern. Tubercles may be equidistant and sparsely covering the fruit (e.g. *P. bellardi, P. equisetiforme*), crowded




Figures 31–35. Fruits of *Fagopyrum*. All scale bars = 100 µm, except Fig. 32 = 10 µm. Figs 31, 32, 35: SEM. Figs 33, 34: LM. Fig. 31. *F. esculentum* (Reekmans s.n.). Detail of mature fruit; three hooked styles with terminal stigmas clustered with pollen. Fig. 32. *F. cymosum* (H. Smith 13315). Detail of collapsed cells on fruit surface. Fig. 33. *F. esculentum* (Ronse Decr. 30 Le). TS fruit; scattered bundles in mesocarp, crushed endocarp and absence of inner space between opposite wall-layers. Figs 34, 35. *F. tataricum* (Ronse Decr. 1335). Fig. 34. LS fruit and outer surface of fruit. Note the mesocarp with thickened walls. Fig. 35. Fruit surface with detail of interrib region. Abbreviations: en = endocarp; ex = exocarp; me = mesocarp (inner and outer); te = testa.

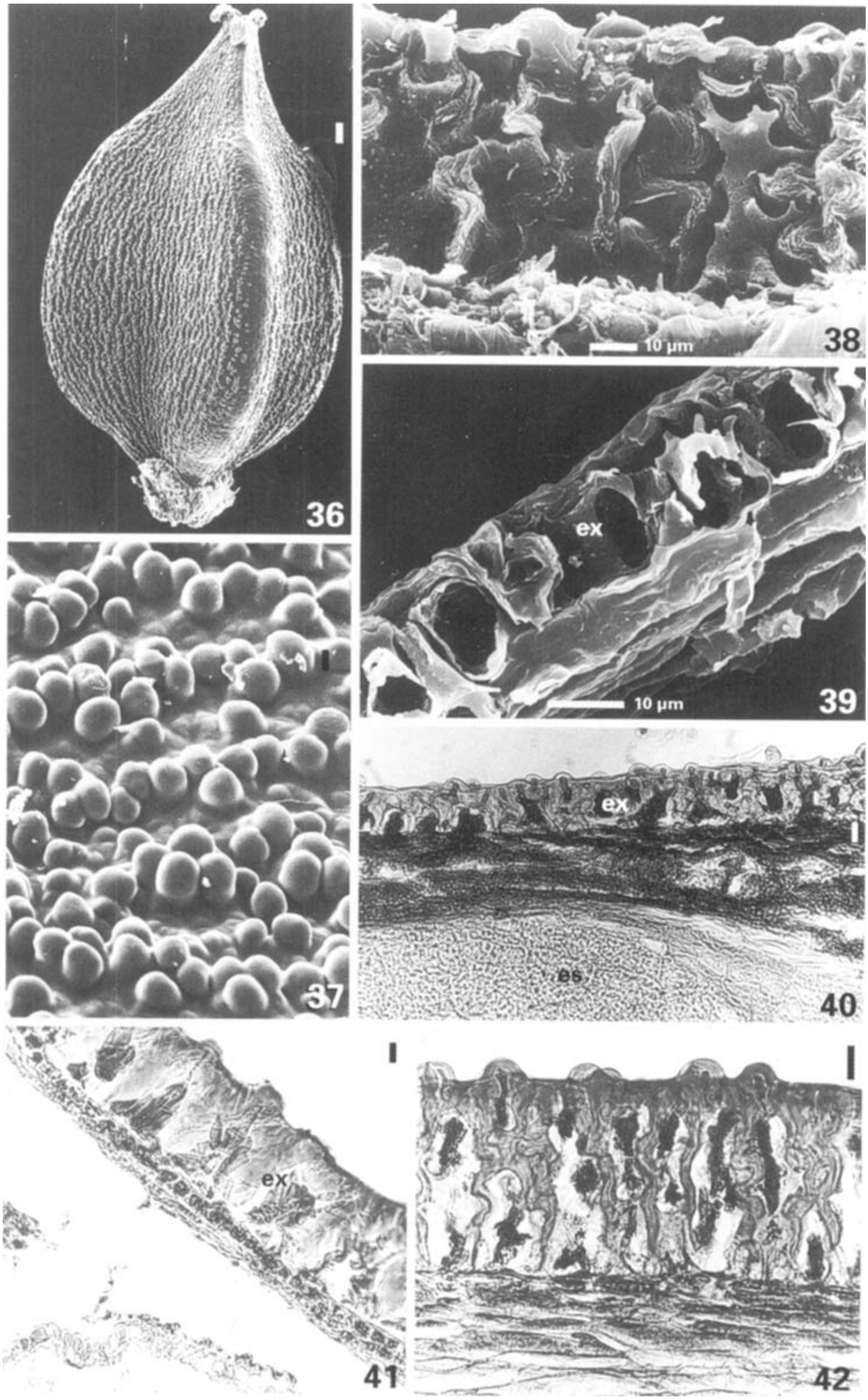
on the anticlinal ridges (e.g. *Polygomum achoreum, P. erectum*: Fig. 37), or in longitudinal rows without connection to the anticlinal walls of the cells (e.g. *P. arenastrum, P. aviculare*: Fig. 36). Tubercles may be associated with pits, but never with superficial striae. In other species the fruit surface is smooth (e.g. *P. maritimum*) or the upper half of the fruit is tubercled and the lower half smooth (e.g. *P. oxyspermum*, *P. arenastrum*). In the exocarp of sect. *Polygonum* two kinds of cell structure were observed. In several species the anticlinal walls are strongly convolute with numerous folds and gaps in the walls (Figs 38, 44). The lumen of the cells is broadly rectangular with dendricular branching along the sides (e.g. *P. ramosissimum*, *P. tubulosum*, *P. equisetiforme*, *P. bellardi*). The exocarp is usually thick (above 60 μm). The second cell type consists of smaller, isodiametric or shortly rectangular cells with a broad lumen, triangular to trapezoid in shape with the smallest side towards the periphery. The lumen is often dichotomously or trichotomously branching towards the periphery (Figs 39, 40; e.g. *P. oxyspermum* var. *raii*, *P. arenastrum*, *P. aviculare*). The exocarp is thinner (less than 40 μm). Some species have exocarps that are intermediate between both types (e.g. *P. bellardi*: Fig. 41), depending on the origin of the material.

*P.* sect. *Tephis* (with two species *P. afromontanum* and *P. undulatum*) is distinctive in its lenticular cells with long styles and capitate stigmas. The fruit surface is almost smooth or the outer periclinal walls are curved with slightly undulating anticlinal walls filled with epicuticular secretions (Fig. 43). In section, the exocarp consists of long rectangular cells (about 70 μm thick) with undulating anticlinal walls and a narrow lumen (Figs 44, 45).

The fruit surface of *P. molliaeforme* (sect. *Pseudomollia*) is distinctive with a roughly reticulate surface formed by the straight anticlinal walls (Fig. 46) along the wings lining the beak of the fruit; the reticulation is more compact and is covered with tubercles in some places (see also Ronse Decraene, Hong & Smets, in press). In section the exocarp consists of square cells with straight anticlinal walls and tangential lumina, similar to species of *Polygonella* and sect. *Duravia* (Fig. 47).

*P.* sect. *Duravia* shows the same variability as sect. *Polygonum*. Smooth fruit surfaces are found in *P. minimum* and *P. paronychia*. The fruit surface is almost smooth with low ridges (*P. bolanderi*) or with pits (*P. shastense*, *P. californicum*) along the anticlinal walls depending on the material, and there is an occasional superficial cuticular striation present. The fruit surface of *P. polygaloides s.l.* (including *P. kellogii*, *P. confertiflorum*) is the most distinctive and shows a reticulation of longitudinally running ridges bridged at regular intervals (Fig. 49). These ridges do not necessarily correspond with the anticlinal cell walls. *P. douglasii* and *P. tenue* are polymorphic in having some materials with a smooth surface and others with tubercles more or less following the anticlinal walls (Figs 50, 51, 53). The exocarp is most often narrow with isodiametric cells, straight anticlinal walls, and a broadly trapezoid lumen (Figs 48, 52). In a few species (e.g. *P. douglasii*, *P. tenue*: Figs 50, 53), the exocarp resembles that of sect. *Polygonum* in being rectangular with undulating anticlinal walls.

In *Polygonella* the outer surface of the fruit is most often smooth (*P. americana*, *P. gracilis*, *P. polygama*: Figs 54, 55, 59), or with weak depressions along the anticlinal walls (*P. articulata*). Longitudinal cuticular striae are often present (Figs 54, 59), but not in *P. fimbriata* or *P. gracilis*. *P. fimbriata* has a combination of a close packing of tubercles in the upper part of the fruit (without relation to the anticlinal walls), and a roughly pitted surface in the lower part (see also Ronse Decraene, Hong & Smets, in press). The shape of the fruit is narrowly triangular with prominent ribs, a long beak and short stipe. The short styles with globular stigmas drop early. Most species have a narrow exocarp (40 μm thick) of square cells with straight anticlinal walls and limited thickening (Figs 54, 56, 58). The only exception with rectangular cells, a narrow dendritically branching lumen, and undulating anticlinal walls is *P. americana* (Fig. 57).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*Fallopia* (Figs 60–66)

Three to four sections are recognized (see Holub, 1970; Haraldson, 1978; Ronse Decraene & Akeroyd, 1988). Fruits are triquetrous with strong equal ribs, a beak is virtually absent or very short (except for sect. *Reynoutria*: Fig. 60) and styles are short and fused with capitate stigmas (Fig. 61; except for sect. *Reynoutria* with free styles and fimbriate stigmas). Both sect. *Reynoutria* and sect. *Sarmentosae* possess winged, enlarged outer tepals surrounding the fruit.

The fruit surface is either smooth (e.g. *F. cilinodis, F. sachalinensis, F. multiflorum*), with unequal ridges following the anticlinal cell walls (*F. japonica*), or covered with tubercles without link to the anticlinal walls (e.g. *F. convolvulus, F. dumetorum, F. aubertii*: Figs 60–62). Tubercles may be distributed without apparent order (e.g. *F. dumetorum*) or in regular sequences or lines (*F. convolvulus*: Fig. 62, *F. scandens, F. aubertii*). The exocarp is often represented by rectangular cells with straight anticlinal walls and a narrow lumen dichotomously or trichotomously branching towards the periphery (Figs 64, 66). There is a gradation towards cells with undulating anticlinal walls. In *Fallopia convolvulus* we found a dendritically branching lumen (probably the result of the convoluting radial walls: compare with Roth, 1977: fig. 12b) and anticlinal walls were slightly undulating (Fig. 65). Section *Reynoutria* differs in the more isodiametric exocarp cells with broad trapezoid lumen (Fig. 63) reminiscent of those found in some species of sect. *Polygonum.*

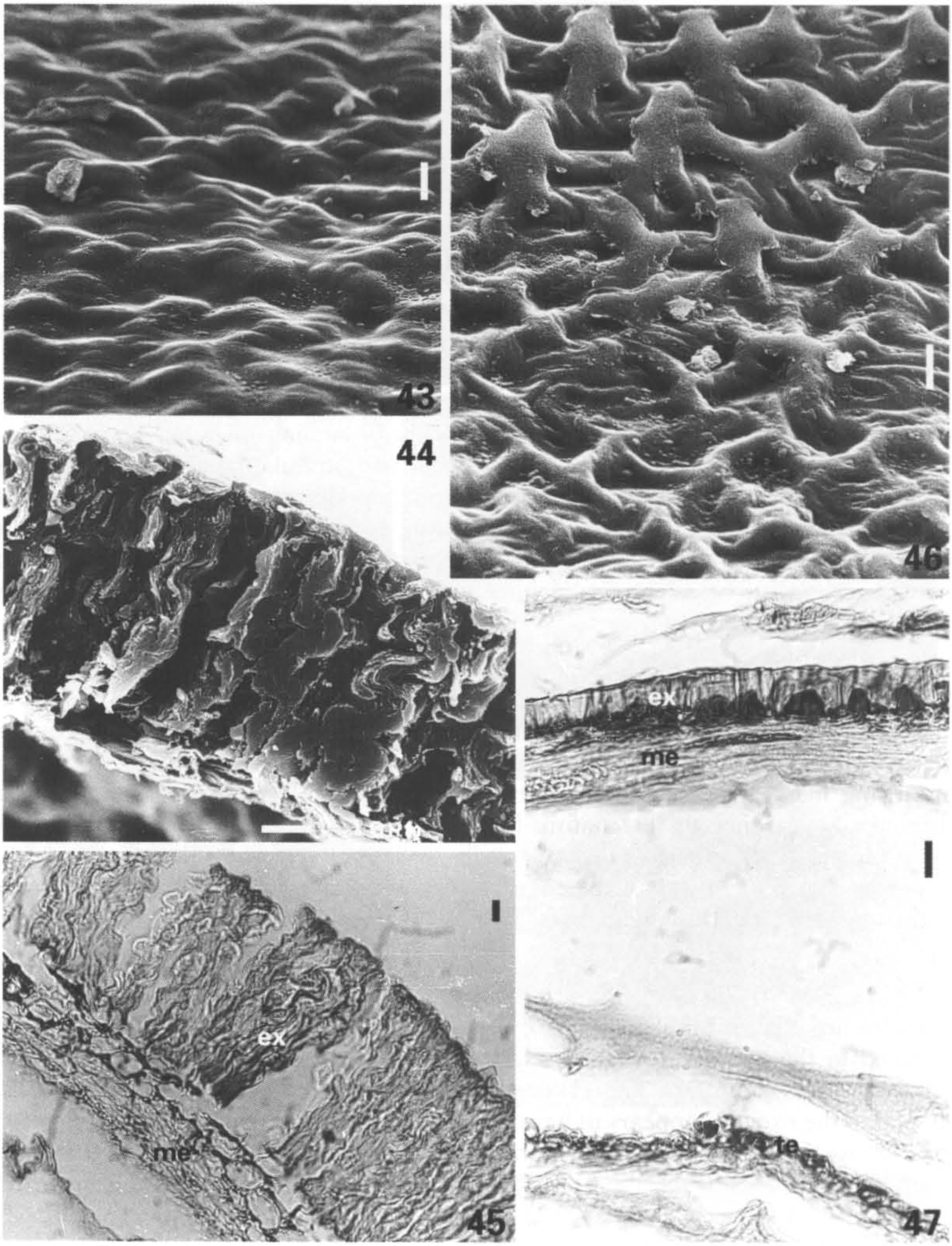
*Calligonum* (Figs 67–69)

Fruits are tetramerous, with a peculiar dispersal mechanism. Perianth segments are deflexed in the fruit and the achene surface is covered with strong dendritically branching hairs or cristae, arising along the ribs of the young fruit and giving a shrublike appearance to the mature fruit (Fig. 67). In between the ribs, the fruit surface consists of smooth polygonal cells (collapsed: Fig. 68). The exocarp (*C. eriopodum*: Fig. 69) consists of rectangular cells with narrow lumina dichotomously branching and straight anticlinal walls.

*Atraphaxis* (Figs 70–73)

Fruits are 'hazelnut'-like (Fig. 70: *A. suaedifolia*) or lenticular (e.g. *A. spinosa*), enclosed in the accrescent inner perianth parts. The fruit surface is covered with small papillae. (*A. buxifolia*: Fig. 71) or pits (*A. frutescens*) set along the anticlinal walls. In section the exocarp appears to have rectangular cells with narrow (e.g. *A. pyrifolia*: Fig. 72) to broad lumina (*A. billardieri*: Fig. 73), dichotomously or trichotomously branching towards the periphery. In the latter species the shape of the lumen is trapezoidal.

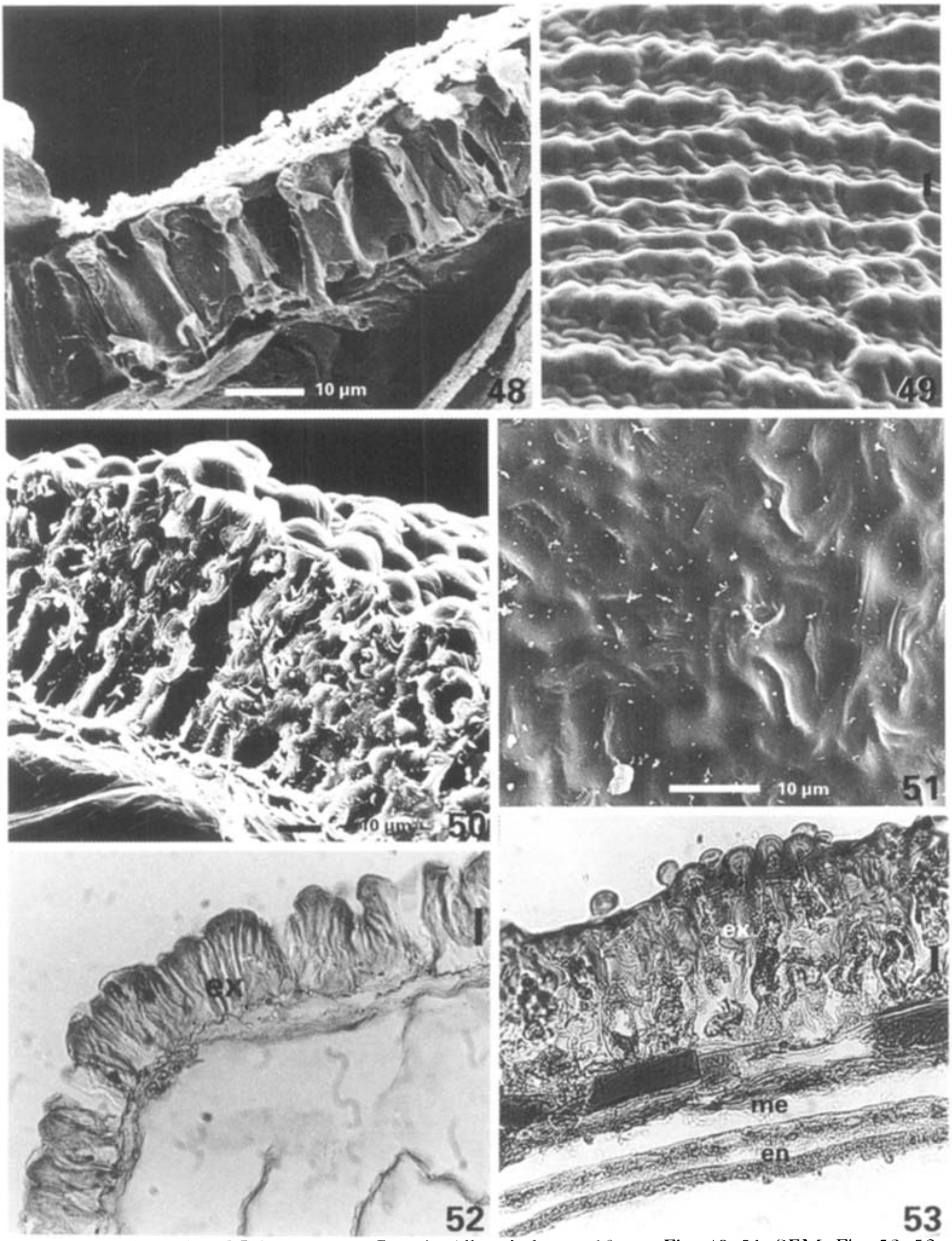
Figures 36–42. Fruits of *Polygonum* sect. *Polygonum*. All scale bars = 10 μm, except Fig. 36 = 100 μm. Figs 36–39: SEM. Figs 40–42: LM. Fig. 36. *P. aviculare* var. *aequale* (Ronse Decr. 25 Lb). Lateral view of mature fruit; tubercles arranged in longitudinal rows. Fig. 37. *P. erectum* (Bebb s.n.). Surface detail. Fig. 38. *P. ramosissimum* (Puissant s.n.). Section through exocarp. Note strong convolution and holes in anticlinal walls. Fig. 39. *P. arenastrum* (Ronse Decr. 1157). Section through exocarp. Note nearly isodiametric cells and straight anticlinal walls. Fig. 40. *P. oxyspermum* var. *raii* (Corbière 5306). LS fruit wall. Fig. 41. *P. bellardi* (Heldreich 877). LS pericarp. Fig. 42. *P. ramosissimum* (Puissant s.n.). LS pericarp; note surface tubercles and convoluted anticlinal walls. Abbreviations: es = endosperm; ex = exocarp.



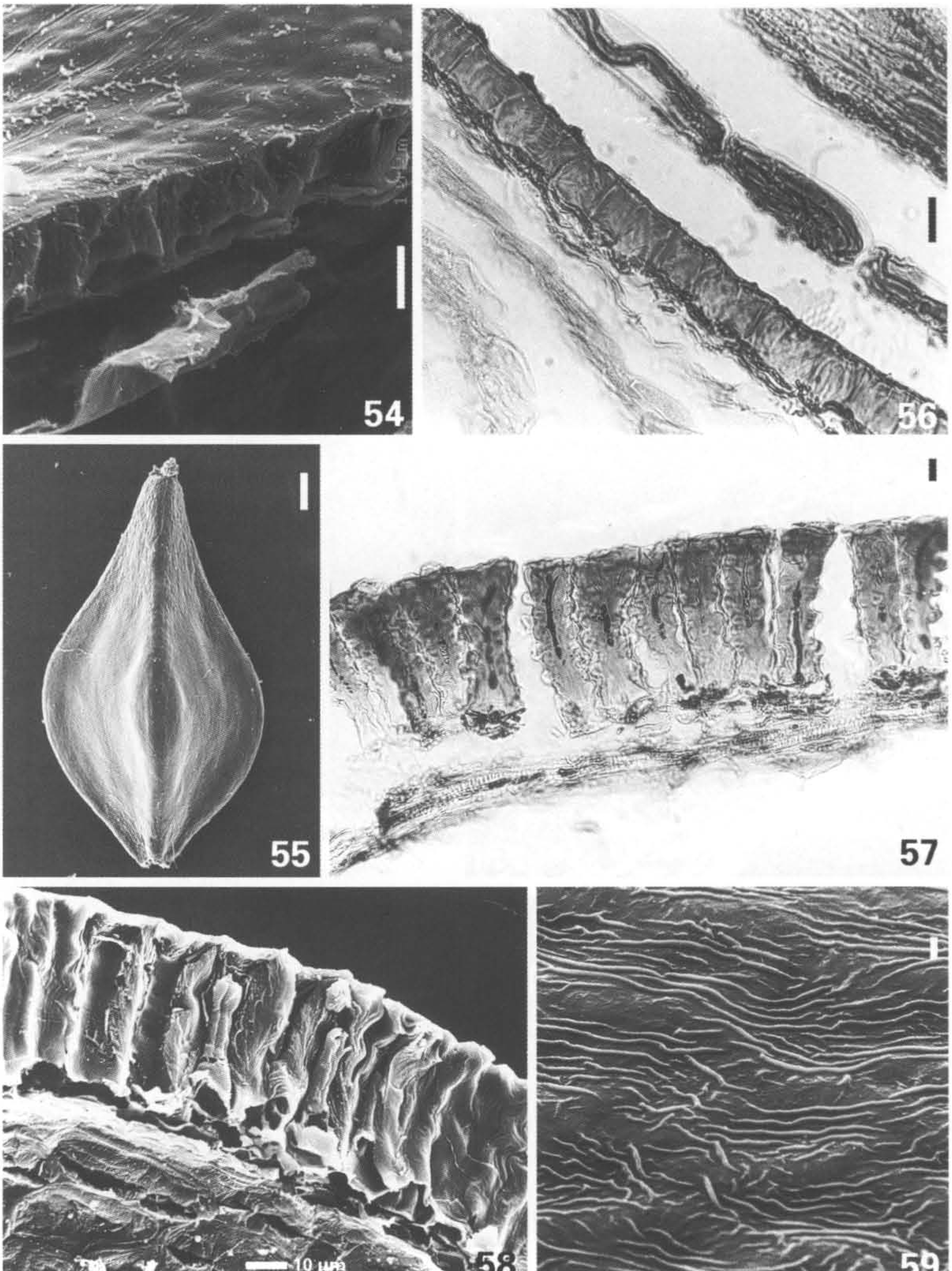

Figures 43–47. Fruits of *Polygonum* sect. *Tephis* (43–45) and sect. *Pseudomollia* (46–47). Scale bars = 10 µm. Figs 43, 44, 46: SEM. Figs 45, 47: LM. 43. *P. afromontanum* (Hedberg 4320) Surface detail. Figs 44–45. *P. undulatum* (Fourcale 5962). Fig. 44. LS exocarp. Fig. 45. LS pericarp. Figs 46–47. *P. molliaeforme* (Kotschy 778). Fig. 46. Detail of fruit surface. Fig. 47. LS fruit. Abbreviations: ex = exocarp; me = mesocarp.

*Oxygonum* (Figs 74–77)

Achenes are tightly enclosed within the fused perianth and receptacle. Several fruits of *Oxygonum* appear cross-like in longisection (Fig. 75). This is caused by the




Figures 48–53. Fruits of *Polygonum* sect. *Duravia*. All scale bars = 10 µm. Figs 48–51: SEM. Figs 52, 53: LM. Fig. 48. *P. shastense* (C.F. Sonne s.n.). Section through pericarp. Note large lumen and erect anticlinal walls. Fig. 49. *P. polygaloides* (Nelson & Nelson 6463). Surface detail; ridges run between puzzle piece-like cells in longitudinal rows. Fig. 50. *P. douglasii* (Howell s.n.). Section through pericarp; note tubercles on surface of fruit and strong convolutions. Fig. 51. *P. douglasii* var. *latifolium* (Howell s.n.). Detail of fruit surface. Fig. 52. *P. polygaloides* (Howell s.n.). Section through fruit wall. Fig. 53. *P. tenue* (Puissant s.n.). Section through fruit wall. Abbreviations: en = endocarp; ex = exocarp; me = mesocarp.




Figures 54–59. Fruits of *Polygonella*. All scale bars = 10 µm, except Fig. 55 = 100 µm. Figs 54, 55, 58, 59: SEM. Figs 56, 57: LM. Figs 54–56. *P. polygama*. 54. Detail of fruit surface and exocarp (Curtiss 2433) with surface striations. Fig. 55. Lateral view of mature fruit (Curtiss s.n.). Fig. 56. LS fruit wall; thick exocarp with straight anticlinal walls (Curtiss s.n.). Fig. 57. *P. americana* (Meisner 1845). LS fruit wall with convoluted anticlinal walls. Figs 58–59. *P. articulata* (Bodin s.n.). Fig. 58. Section through pericarp seen from inside of fruit. Note slightly convoluted anticlinal walls. Fig. 59. Surface detail with cuticular striations.

presence of spines or wings in the middle of the fruit. Fruits have a trigonous shape and are elongated-pyriform. The fruit surface appears fimbriate to wrinkled and is covered with short trichomes (e.g. *O. stuhlmannii*, *O. delagoense*: Fig. 74) which may resemble spines (*O. sinuatum*). The exocarp consists of narrowly rectangular cells with undulating anticlinal walls. The lumen is narrow without dichotomous branching (Figs 76, 77).

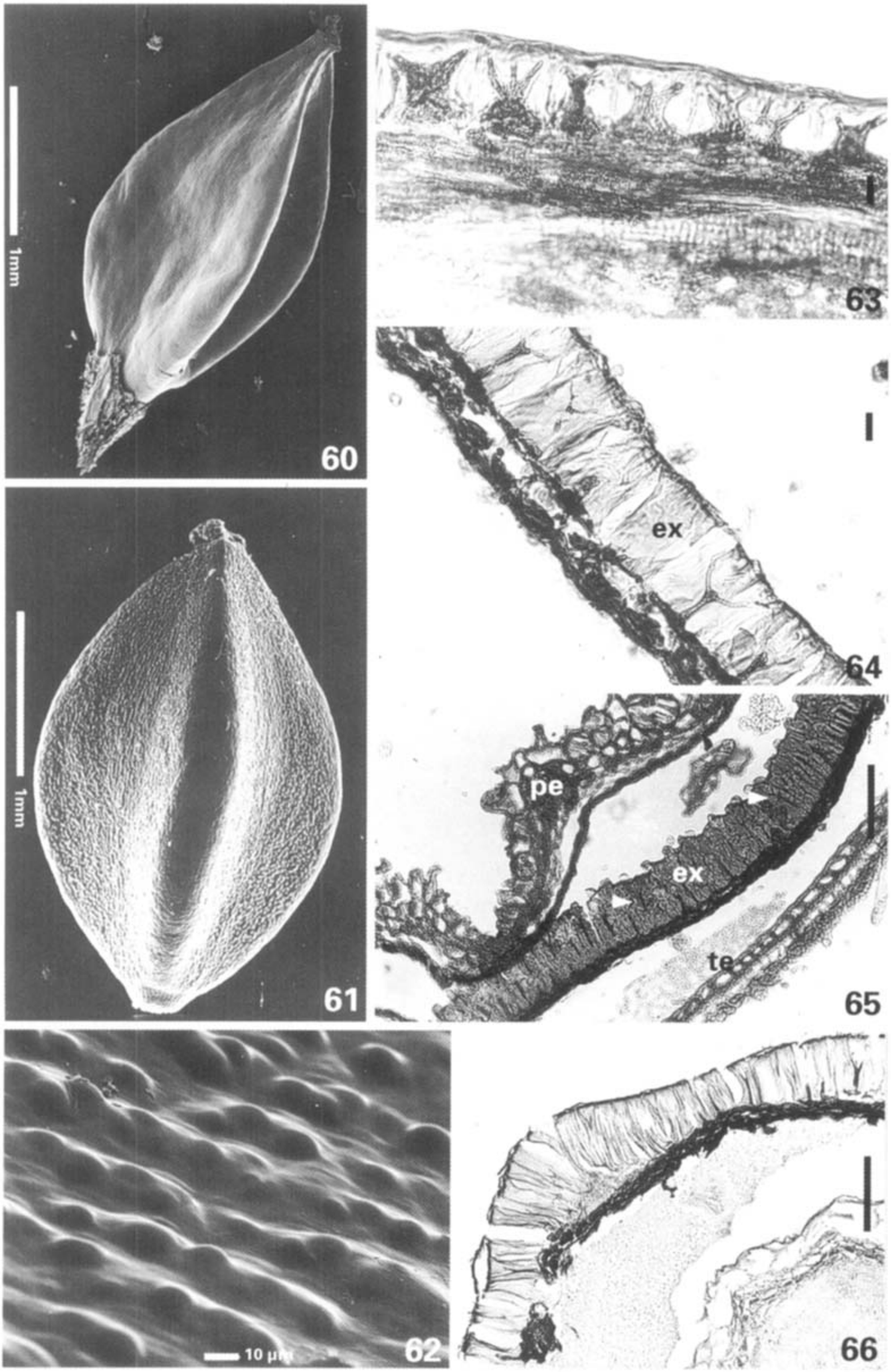
*Pteropyrum* (Figs 78–80)

Fruits are surrounded by two strongly winged outer tepals and smaller inner tepals. The fruit is beaked and has three narrow wings covered by the folds of the outer tepals (Fig. 80). The wings are biparted by an invagination in the middle with appendages running alongside the fruit. The fruit surface has cells surrounded by ridges sparsely covered with papillae (Fig. 78: *P. noëanum*) or is almost smooth (*P. aucheri*). The exocarp is distinctive, consisting of square stone-cells with central lumina (Figs 79, 80).

## DISCUSSION

Table 1 lists the different fruit morphological and anatomical characters of the genera presented here. The anatomy of the outer epidermal cells (the exocarp) has more systematic value than any other fruit character in Persicarieae and Polygoneae. It can be used consistently to delimit genera. However, no clear-cut fruit characters were found to delimit tribes Persicarieae and Polygoneae. This lack of distinctive features may be related to the common *Bauplan* of the fruits in Polygonaceae.

Neubauer (1971) argued that development of the cell wall thickenings differs between *Polygonum aviculare*, as described by Lonay (1922), and *Persicaria pennsylvanica*. He described the former species as having anticlinal walls with smooth, flat outer surfaces and convoluted inner surfaces (formed by localized internal thickenings), contrasting with the entire anticlinal walls becoming convoluted in the latter species. Indeed, cell wall thickening of *Polygonum aviculare* is different, but not in the manner described by Neubauer. Lonay (1922) clearly showed (backed by illustrations) that the thickening of *P. aviculare* is different, stating "Les parois latérales sont aussi très épaissies; cependant ces épaississements vont en diminuant vers l'intérieur, tantôt progressivement, et alors la cavité cellulaire est conique, tantôt brusquement à partir du quart interne de ces parois, auquel cas la cavité cellulaire a la forme d'une cloche évasée vers ses bords" [There is also considerable thickening in the lateral walls; however, this diminishes towards the centre of the fruit, either progressively, resulting in a conical cavity, or abruptly about three quarters of the way through the cell wall, resulting in a splayed, bell-shaped cavity.] (Lonay, 1922: 15). This shows that at least in *P. aviculare*, anticlinal cell wall thickening is different from that of *P. pennsylvanica* and represents a different character state, as we describe in this paper. We found that the structure of the convoluted anticlinal fruit wall (the 'egg-case' type) is basically similar in all investigated species (e.g. *Polygonum*, *Polygonella*, *Persicaria*, *Oxygonum*) and is obviously the result of tangential pressures during fruit development. The exocarp with straight anticlinal walls (the 'corrugated sheet' type) appears to be more basic, although wall thickening is variable. Seen from the surface and in paradermal section, exocarp cell shape often changes from the periphery to the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mesocarp. In most genera the cells are puzzle piece- or star-shaped on the surface and become polygonal towards the centre of the fruit. We observed this transition in several species and it was beautifully illustrated by Lonay (1922) for *P. aviculare*. Anticlinal cells which are straight over their whole surface are restricted to *Fagopyrum*, *Calligonum* and *Polygonum* sect. *Pseudomollia*.

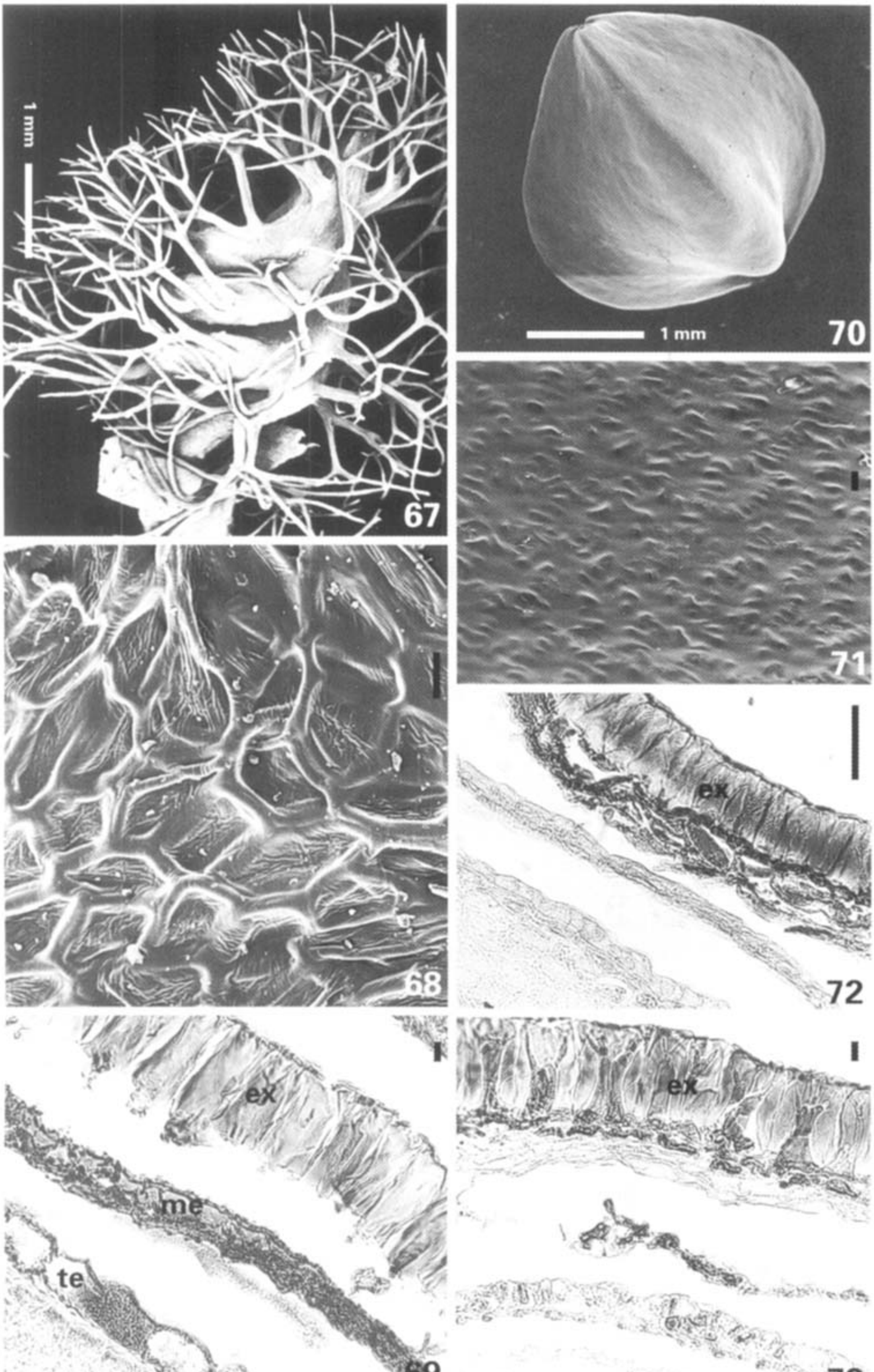
Primary sculpturing of fruit wall cells often includes ridges or folds following the outline of the anticlinal walls. In other instances the walls are collapsed and pits are visible. The ridges are often covered with papillae or tubercles, following the outline of the walls, even when the ridge is not visible, or running independently of the anticlinal walls in longitudinal lines. The association of tubercles with presence versus absence of convolutions in cross or longitudinal sections is incidental.

On the basis of fruit anatomy and the external cell surface, sections *Tovara*, *Cephalophilon* and *Echinocaulon* cannot be distinguished from sect. *Persicaria*. All share a similar thick exocarp of narrowly rectangular cells with undulating anticlinal walls. The lumen is narrow, eventually with short dendritic branches, but it does not show any dichotomous splitting towards the periphery. Differences are expressed in the thickness of the exocarp, being relatively thin in sections *Echinocaulon* and *Cephalophilon*, but thick in sections *Persicaria* and *Tovara* (Table 1). The thickest exocarp occurs in *Persicaria orientalis* with an upper limit of 150 μm. A frequently occurring surface pattern consists of a reticulate arrangement of ridges covered with tubercles running along the anticlinal walls of the cells, and there is a gradual transition from an almost smooth surface (e.g. *P. runcinata*) occasionally with pits, to weakly developed papillae and finally strongly developed tubercles. Section *Persicaria* is even more variable with a different extent of coverage with tubercles. Given the shared pattern of tepal epidermal cells (rectangular cells with straight to undulating anticlinal walls, and smooth surface or with longitudinal ridges: Hong, Ronse Decraene & Smets, 1998), the classification of Ronse Decraene & Akeroyd (1988) is supported. *Cephalophilon* and *Echinocaulon* cannot be distinguished from sect. *Persicaria* using the external morphology on fruit sections. However, section *Tovara* is readily recognizable macromorphologically by its dimerous fruits with long hooked styles.

*P. wallichii* (sect. *Rubrivena*) does not correspond with *Persicaria* in its fruit anatomy, but appears similar to *Aconogonon*. Section *Rubrivena* differs in pollen (granulated muri) and inflorescence structure from *Aconogonon* and from the other sections of *Persicaria* (Hong, 1993). However, exocarp morphology lends support to the inclusion of section *Rubrivena* in *Aconogonon*. This is also supported by floral characters (e.g. Ronse Decraene & Akeroyd, 1988).

*Aconogonon* differs anatomically from *Persicaria* in the almost isodiametric to short rectangular exocarp cells with lumina branching towards the outer tangential walls. Fruit anatomy and fruit surface pattern are almost identical to those of *Bistorta*. Fruit

Figures 60–66. Fruits of *Fallopia* sect. *Reynoutria* (60, 63), sect. *Fallopia* (61, 62, 65, 66) and sect. *Sarmentosae* (64). Figs 60–62: SEM. Figs 63–66: LM. Fig. 60. *F. sachalinensis* (Anonym). Lateral view of mature fruit. Scale bar = 1 mm. Fig. 61. *F. dumetorum* (Ronse Decr. 1309). Lateral view of mature fruit. Scale bar = 1 mm. Fig. 62. *F. convolvulus* (H. Smith 4372). Surface detail; note rows of tubercles. Scale bar = 10 mm. Fig. 63. *F. japonica* (Clément Aigret s.n.). Section through fruit wall. Scale bar = 10 mm. Fig. 64. *F. multiflorum* (Hers 813). Section through pericarp. Scale bar = 10 mm. Fig. 65. *F. convolvulus* (Kalheber 78-640). LS fruit wall; note dendritic branching in lumen (arrows). Scale bar = 100 μm. Fig. 66. *F. cilinodis* (Graxton 9631). TS fruit. Scale bar = 100 μm. Abbreviations: ex = exocarp; pe = perianth; te = testa.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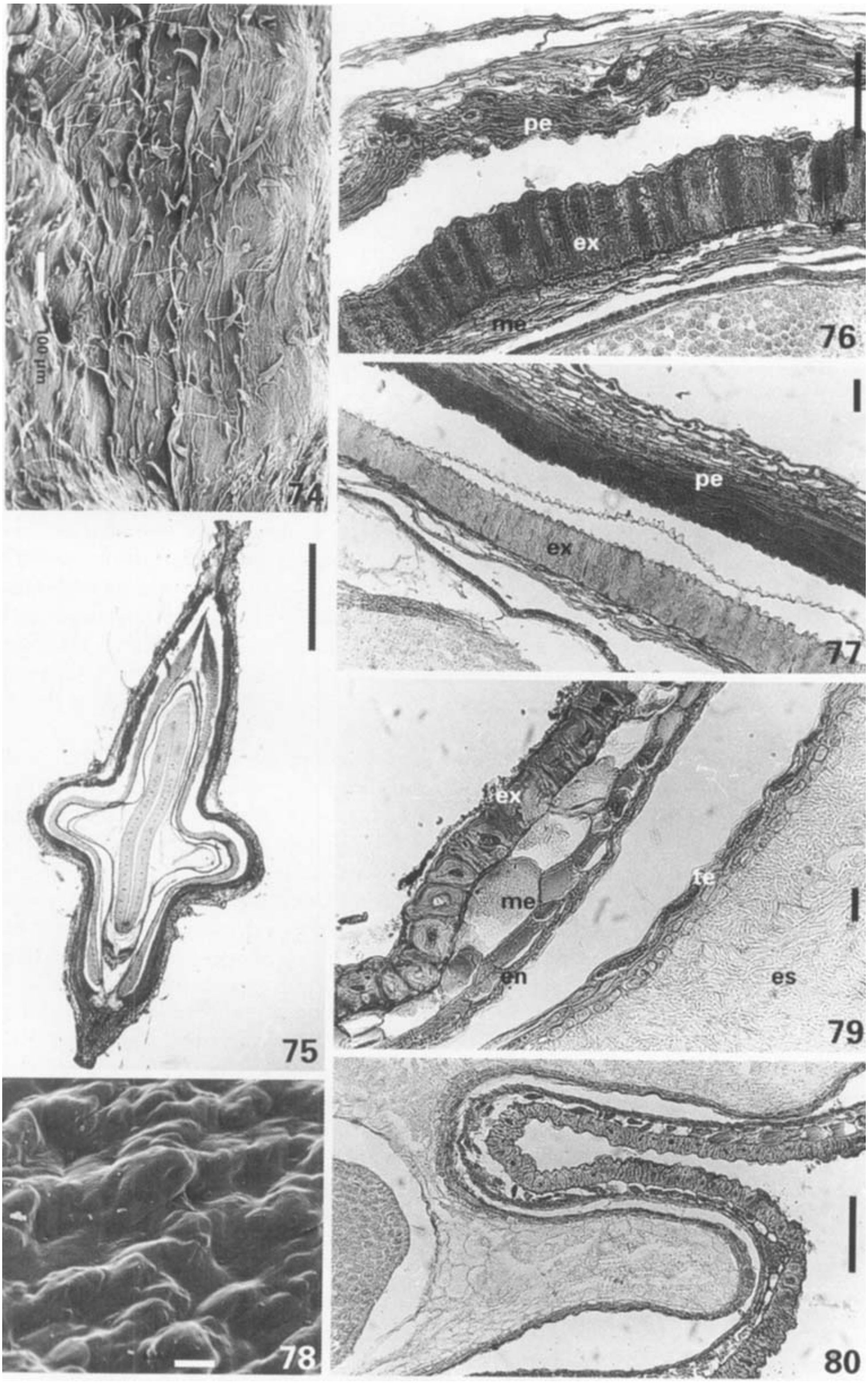
anatomy supports other evidence (see e.g. Haraldson, 1978; Ronse Decraene & Akeroyd, 1988) in assigning a close relationship between *Bistorta* and *Aconogonon*. They share the same pollen morphology (tricolpate with smooth exine covered with microspinules: see also Jaretzky, 1925), fusion of nectaries with stamen bases into a disc (Ronse Decraene & Smets, 1991), constant octomerous androecium, comparable inflorescence and sharing of anthraquinones (Jaretzky, 1925), and embryos with accumbent cotyledons. However, tepal epidermal cell structure is not much different from that of *Persicaria*. In our opinion the two genera show sufficient similarities to be grouped into a single genus as sister to *Koenigia* and *Persicaria*. *Koenigia* differs in fruit anatomy in the isodiametric cells with thinner thickening (see also Hedberg, 1997), but the external epidermal surface is strongly similar.

A similar exocarp structure to that of *Aconogonon* has been found in *Knorringia* (but see Hong, 1989). Hong (1989) erected *Knorringia* (formerly known as *Polygonum sibiricum*) as a genus separate from Persicarieae in tribe Coccolobeae on the basis of differential characters. He described the pericarp as distinctive and two-layered, with a lumen narrowing triangularly in cross section. However, in the material we studied (Table 1) the one-layered exocarp has straight anticlinal walls; the lumen is cylindrical, only branching at the surface. From the illustrations in Hong (1989) the external surface of the fruit appears rather smooth with shallow depressions. The achenes are included to slightly exserted above the tepals. Unfortunately little information is available on the structure of the flower (e.g. nectaries, tepal epidermis). *Knorringia* shares the dendritic venation of the tepals with tribe Polygoneae, and closely resembles the genus *Fallopia* in pollen morphology, exocarp structure, chemical substances (presence of anthraquinones) and chromosome number. Style and stigma shape are reminiscent of sect. *Reynoutria*. Haraldson (1978) placed *Fallopia* in the Coccolobeae.

There is strong overlap between some species of sect. *Duravia* and sect. *Polygonum* on the one hand, and between sect. *Duravia* and *Polygonella* on the other. Similar smooth fruit surfaces (eventually with pits aligning the anticlinal cell walls) are found in *Polygonum* sect. *Duravia* (e.g. *P. californicum, P. minimum*), and sect. *Polygonum* (e.g. *P. maritimum*). In some cases superficial cuticular striations are superimposed on the smooth surfaces as in some species of *Polygonella* and sect. *Duravia*. Smooth or rough surfaces with irregular ridges lining the anticlinal walls were found in sect. *Tephis*, sect. *Pseudomollia* and sect. *Duravia* (e.g. *P. douglasii*). In some cases fruits with smooth-pitted surfaces and with tubercles occur side by side in the same species (e.g. *P. arenastrum, P. douglasii*). More or less similar cell anatomy was observed in a few species of sect. *Duravia* (e.g. *P. douglasii, P. tenue*), sect. *Tephis* (although the convolution is more important and it lacks the dendritic branching), and exceptionally in *Polygonella* (e.g. *P. americana*). Almost straight anticlinal walls (less than 40 μm wide) with narrow lumina occur in most other species of sect. *Duravia* (e.g. *P. coarctatum, P.*

Figures 67–73. Fruit of *Calligonum* (67–69) and *Atraphaxis* (70–73). Figs 67–68. *C. microcarpum* (Sintenis 2202). Figs 67, 68, 70, 71: SEM. Figs 69, 72, 73: LM. Fig. 67. Part of fruit with branch-like extensions. Scale bar = 1 mm. Fig. 68. Surface detail between branches. Scale bar = 100 μm. Fig. 69. *C. eriopodum* (Michelson s.n.). LS fruit wall. Scale bar = 10 μm. Fig. 70. *A. suaedifolia* (Wendelbo & Assadi 28026), lateral view of fruit. Scale bar = 1 mm. Fig. 71. *A. frutescens* (Alm s.n.). Detail of fruit surface. Scale bar = 10 μm. Fig. 72. *A. pyrifolia* (Regel s.n.). LS fruit. Scale bar = 10 μm. Fig. 73. *A. billardieri* (Heldreich 617). LS fruit wall. Scale bar = 10 μm. Abbreviations: ex = exocarp; me = mesocarp; te = testa.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*shastense, P. californicum*), most *Polygonella* (e.g. *P. articulata, P. polygama*), and in sect. *Pseudomollia*. The lumen appears narrow-rectangular, x-shaped to triangular with the broad base on the inner tangential wall. Dendritic canals were not observed. Ronse Decraene, Hong & Smets (in press) could not find straightforward differences between *Polygonella* and *Polygonum s.s.* in fruit anatomy, flower structure, pollen and micromophological details. The identity of *Duravia* is not clear with some species closely related to *Polygonella*, and others to sect. *Polygonum*. The tribe is probably artificial.

A similar exocarp morphology is shared by some species of *Fallopia, Calligonum* and *Atraphaxis*. *Fallopia* is polymorphic with even more variation of cell shapes than in *Polygonum* sect. *Polygonum*. The distinctness of sect. *Reynoutria* is best supported by fruit anatomy, but sect. *Sarmentosae* and *Fallopia* have a strongly overlapping pattern, both in outer morphology and cell structure.

*Fagopyrum* is isolated in its fruit morphology and anatomy. Several characteristics link the genus to *Rheum*, such as the reflexed styles with central aperture, smooth and unthickened fruit surface, small undifferentiated perianth lobes in fruit, pollen and anther morphology, and tepal epidermis. However, *Rheum* differs in being trimerous and has a fused disc-like nectary, while there are free lobes in *Fagopyrum*. Ronse Decraene & Smets (1991) suggested that *Fagopyrum* occupies a basal position in the tribe Persicarieae, being primitive in many respects and forming a link with a *Rheum*-like ancestor. The suggestion of Marek (1958) to place *Fagopyrum* in a separate subfamily makes sense, but we are more inclined to assign it to its own tribe Fagopyreae. More study of related tribes as well as its sectional taxonomy are necessary to understand the relationships of this enigmatic genus.

### *Relationships between different pericarp types*

We have constructed a hypothetical scheme showing the relationships between different pericarp types (Fig. 81). An exocarp with trapezoidal to triangular lumina, relatively square cells and straight anticlinal walls can be considered as basal (Fig. 81C). Evidence supporting this assumption is the fact that such exocarp is found in the neighbouring tribe Rheae (e.g. *Rumex, Oxyria, Rheum*: Marek, 1954). Increased thickening of the exocarp leads to rectangular cells with straight anticlinal walls and dichotomous branching (e.g. *Bistorta, Aconogonon, Calligonum, Atraphaxis, Fallopia*: Fig. 81F). Due to constraints of development the cells often become undulating; this has occurred independently in several genera, with the two conditions often occurring side by side (e.g. *Polygonella, Polygonum, Fallopia, Oxygonum*: Fig. 81A,B). A limited thickening linked with isodiametric exocarp cells is found in *Koenigia, Polygonum* sect.

Figures 74–80. Fruits of *Oxygonum* (74–77) and *Pteropyrum* (78–80). Figs 74, 78: SEM. Figs 75–77, 79, 80: LM. Fig. 74. *O. delagoense* (Richards 14666). Surface detail with fimbriate tissue and trichomes. Scale bar = 100 µm. Fig. 75. *O. stuhlmannii* (Mhoro & Backeus 2236). LS entire fruit with cross-like median extensions of the fruit and coherent perianth. Scale bar = 10 mm. Fig. 76. *O. dregeanum* var. *strictum* (Napper 1054). Section of fruit wall. Scale bar = 100 µm. Fig. 77. *O. sinuatum* (Friis *et al.* 2696). Section of fruit wall. Scale bar = 100 µm. Fig. 78. *P. noëanum* (Horsain & Horsain 53). Detail of fruit surface. Scale bar = 10 µm. Fig. 79. *P. aucheri* (Rechinger 27441): TS fruit. Scale bar = 10 µm. Fig. 80. *P. gracile* (Strauss s.n.). TS fruit with strongly ribbed structure. Scale bar = 100 µm. Abbreviations: en = endocarp; es = endosperm; ex = exocarp; me = mesocarp; te = testa.

TABLE 1. Fruit morphological and anatomical characters of tribes Persicarieae and Polygoneae (Polygonaceae). Mostly from personal observations, also literature data from Dammer (1893), Hong (1989, 1992, 1993), Li (1952), Lonay (1922), Lousley & Kent (1981), Neubauer (1971), Marek (1954), Mitchell & Dean (1978), Ronse Decraene, Hong & Smets (in press), Steward (1930)

| Genus | Styles | Stigma | Fruit shape | Fruit surface | Tepals | Exocarp cell shape in cross-and longitudinal section | Exocarp thickness | Anticlinal walls of exocarp | Presence of dendritic branching |
|---|---|---|---|---|---|---|---|---|---|
| *Aconogonon* | free and short, rarely long, occ. heterostylous | capitate | triquetrous, strongly angular, not beaked | cells puzzle piece-shaped, almost smooth, with pits or inconspicuous folds along the anticlinal walls | achene included to exserted | square to rectangular cells, narrow lumen | 25–40 µm | straight | dichotomous |
| *Atraphaxis* | short, free or basally fused | capitate | triquetrous, lenticular, subangular | smooth, or with pits or papillae on the anticlinal walls | achene included by accrescence of inner tepals | rectangular, lumen narrow | 40–55 µm | straight | dichotomous or trichotomous |
| *Bistorta* | free, long, deciduous | capitate | triquetrous | cells puzzle piece-shaped, almost smooth, or with folds along the anticlinal walls | achene included to exserted | rectangular with narrow lumen | about 50 µm | straight | dichotomous, with 2nd order branching |
| *Calligonum* | very short to long, basally fused or free | capitate | tri- to often tetraquetrous, subangular | polygonal cells, forming reticulate pattern by collapse of cell wall; ribs covered with dendritic branching hairs | achene exserted | rectangular, lumen broad | 55–60 µm | straight | dichotomous |
| *Fagopyrum* | free, reflexed, persistent, heterostylous | small, capitate, converging towards a central aperture | sharply triquetrous, beaked, angles inflated-rounded with deep grooves, or subangular | aggregation of rectangular cells, 15–60 × 15–20 µm in LS or TS, polygonal in surface view, smooth and smaller in grooves | achene exserted, perianth typically persistent at the base of the fruit | unthickened, rectangular | 40–50 µm | straight to slightly undulating | absent |

*continued*

TABLE 1—*continued*

| Genus | Styles | Stigma | Fruit shape | Fruit surface | Tepals | Exocarp cell shape in cross-and longitudinal section | Exocarp thickness | Anticlinal walls of exocarp | Presence of dendritic branching |
|---|---|---|---|---|---|---|---|---|---|
| *Fallopia sect. Fallopia* | short to very short, basally fused | capitate | triquetrous, angular, not or slightly beaked, not stipitate | cells puzzle piece-shaped with tubercles, randomly scattered or in rows, or smooth to ribbed surface | achene included, outer tepals winged or not winged | square, lumen broadly triangular | 20–25 µm | straight | dichotomous to trichotomous |
| *Fallopia sect. Reynoutria* | short, basally fused | fimbriate | triquetrous, subangular to angular, beaked, not stipitate | smooth surface or with scattered tubercles on anticlinal walls | achene included, outer tepals winged | rectangular, narrow lumen | 30–50 µm | straight | dichotomous, with 2nd order branching |
| *Fallopia sect. Sarmentosae* | very short | capitate | triquetrous, subangular to more or less angular, shortly beaked, not stipitate | with tubercles forming interrupted ridges in longitudinal rows | achene included, outer tepals winged | rectangular, lumen narrow | 50–75 µm | occ. with undulations, or straight | dendritic or dichotomous branching |
| *Koenigia* | free, very short to absent | capitate | subangular, not beaked, triquetrous, lenticular | cells puzzle piece-shaped, sometimes elongated with folds along anticlinal walls | achene half included | square, with straight anticlinal walls and narrow lumen, x-shaped | 20–40 µm | straight | absent |
| *Knorringia* | deciduous, fused at base | (oblong)-capitate | triquetrous with ± prominent ribs, ovoid | apparently smooth to slightly folded | achene included in persistent tepals | rectangular, with narrow lumen | 100 µm | straight to slightly convoluted | dichotomous |
| *Oxygonum* | three short basally fused styles | capitate | triquetrous, often with three spines or wings, elongated with strong beak | with longitudinal ridges and trichomes | enclosed by floral tube and perianth | narrowly rectangular, lumen slitlike | 40–80 µm | undulating | absent |

*continued*

TABLE 1—*continued*

| Genus | Styles | Stigma | Fruit shape | Fruit surface | Tepals | Exocarp cell shape in cross-and longitudinal section | Exocarp thickness | Anticlinal walls of exocarp | Presence of dendritic branching |
|---|---|---|---|---|---|---|---|---|---|
| *Persicaria sect. Echinocaulon* | free or fused above or up to middle, deciduous | capitate | triquetrous, subangular, beaked, ovate to rounded | with tubercles on ridges along anticlinal walls forming a reticulate structure, or smooth | achene included | long rectangular, lumen narrow | 100–120 μm | strongly undulating | absent |
| *Persicaria sect. Cephalophilon* | fused above the middle, deciduous | capitate | triquetrous, subangular, beaked | with tubercles on ridges along anticlinal walls forming a reticulate structure, or almost smooth | achene included | narrowly rectangular, with (mostly) regularly undulating anticlinal walls, lumen slitlike | 70–150 μm | strongly undulating | absent |
| *Persicaria sect. Persicaria* | basally fused, long, deciduous | capitate | triquetrous to lenticular, beaked, ovate to rounded, subangular | cells with anticlinal walls collapsed as pits or as irregular ridges with scattered tubercles or papillae | achene included | rectangular with broad ellipsoid lumen | about 75 μm | strongly undulating | dichotomous |
| *Persicaria sect. Rubrivena* | deciduous, free, long | capitate | triquetrous, ovoid, ovoid-orbicular, not beaked, not stipitate | almost smooth (*P. wallichii*) to strongly folded (*P. pinetorum*) | achene included | broadly rectangular, lumen broadly trapezoidal | about 75 μm | straight | dichotomous |
| *Persicaria sect. Tovara* | free and persistent, hooked at tip | minute | lenticular, not beaked, not stipitate | puzzle piece-shaped cells; anticlinal walls collapsed as pits, or with pits aligned in longitudinal rows | achene included | narrowly to broadly rectangular with regularly undulating anticlinal walls, lumen slitlike | 70–80 μm | undulating | absent |
| *Polygonum sect. Duravia* | short to long, basally fused, erect | small, capitate | triangular, not beaked to conspicuously so, slightly stipitate | puzzle piece-shaped cells, with folds or tubercles along anticlinal walls, or almost smooth with longitudinal cuticular striae | included to slightly exserted | rectangular to isodiametric, lumen broad to narrow | 25–70 μm | straight or undulating | absent |

*continued*

TABLE 1—*continued*

| Genus | Styles | Stigma | Fruit shape | Fruit surface | Tepals | Exocarp cell shape in cross-and longitudinal section | Exocarp thickness | Anticlinal walls of exocarp | Presence of dendritic branching |
|---|---|---|---|---|---|---|---|---|---|
| *Polygonum sect. Polygonella* | erect, short to very short | small, capitate | narrow, elongated, subangular, beaked | surface smooth, covered with longitudinal cuticular striae, rarely with tubercles | achene surrounded by three inner accrescent tepals, or exserted | rectangular or isodiametric, lumen broad to slitlike | 25–75 µm | straight or undulating | absent |
| *Polygonum sect. Polygonum* | short to very short, free or basally fused | capitate | trigonous, beaked, subangular to angular, often with combinations of subequal convex and concave sides | surface smooth, with tubercles covering ridges of anticlinal walls, in longitudinal rows, or randomly distributed | perianth not accrescent, fruit variously inserted or exserted | rectangular to isodiametric, lumen variously narrow, triangular or trapezoid | 25–95 µm | straight or undulating | dichotomous, trichotomous, dendritic, or absent |
| *Polygonum sect. Pseudomollia* | erect, short, basally fused | capitate | triangular, angles winged in upper part | polygonal cells, collapsed with broad anticlinal wall segments, tubercles in the angles | included to slightly exserted | isodiametric, lumen triangular | about 16 µm | straight | absent |
| *Polygonum sect. Tephis* | erect, long, basally fused | capitate | lenticular, rounded | cells puzzle piece-shaped with anticlinal walls collapsed or with irregular ridges | achene included | rectangular, lumen narrow | 50–70 µm | strongly undulating | absent |
| *Pteropyrum* | basally converging, well developed | capitate | triquetrous, producing three wings or spines in alternation, in the middle interrupted | cells with anticlinal walls ridge-like covered with scattered tubercles | achene exserted | square, lumen large, central | 25–30 µm | straight | absent |

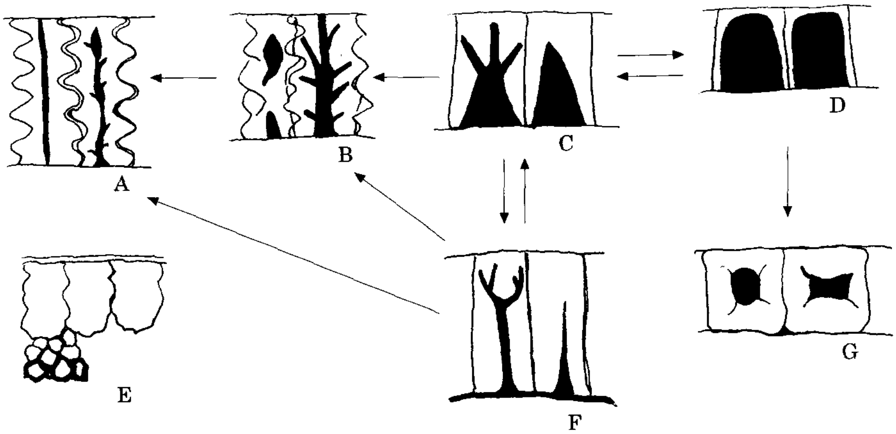


Figure 81. Schematic presentation of hypothetical evolutionary trends in exocarp anatomy. A. *Persicaria* sect. *Persicaria, P.* sect. *Echinocaulon, P.* sect. *Cephalophilon, P.* sect. *Tovara, Oxygonum, Polygonum* sect. *Polygonum* partly, *P.* sect. *Duravia* partly, *P.* sect. *Tephis, Polygonella* partly. B. *Polygonum* sect. *Polygonum* partly, *Polygonella* partly, *Fallopia* partly. C. *Polygonum* sect. *Polygonum* partly, *P.* sect. *Pseudomollia, Persicaria* sect. *Rubrivena, Atraphaxis, Fallopia* partly, *Aconogonon* partly. D. *Koenigia, Polygonella* partly, *Polygonum* sect. *Duravia* partly. E. *Fagopyrum.* F. *Fallopia* partly, *Aconogonon* partly, *Bistorta, Calligonum, Atraphaxis.* G. *Pteropyrum.*

*Duravia, P.* sect. *Pseudomollia,* and *Polygonella* (Fig. 81D). *Pteropyrum* (Fig. 81G) is distinctive in that the thickening also occupies the inner tangential walls. *Fagopyrum* (Fig. 81E) cannot be related to any of the previous types. *Persicaria* (except for sect. *Rubrivena* which does not belong here) is distinct in the association of narrow rectangular cells with undulating anticlinal walls and the absence of branching in the lumen. Also if there are papillae or tubercles, these are associated with ridges formed on the anticlinal cell walls. No distinction can be made between different sections of *Persicaria* on the basis of fruit anatomy. In *Polygonum* and *Fallopia* the presence of undulating anticlinal walls is often accompanied by dichotomous to dendritic branching of the lumen.

There is no correlation between anatomy and outer surface structure. Fruit anatomical characters appear more constant within separate sections, contrary to fruit surface characters, which may be strongly variable within genera. The value of external surface patterns is limited and must be sought at subgeneric level, as several conditions coexist in one genus, and even in a single species. However, there are recurring patterns, such as smooth surfaces with striae in *Polygonella* and *Polygonum* sect. *Duravia,* the reticulate pattern in the polymorphic *Polygonum polygaloides,* the presence of tubercles in sect. *Polygonum,* and the folded anticlinal walls of the epidermal cells shared by *Koenigia, Bistorta,* and *Aconogonon.*

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## APPENDIX: ORIGIN OF MATERIAL INVESTIGATED

*Aconogonon* (Meisn.) Reichenb.

*A. alpinum* (Allioni) Schur: India, Kashmir, Iragbel; *Clarke 292108* (K). *A. campanulatum* (Hook.f.) Hara var. *campanulatum* S.-P. Hong: China, Tibet, Tin To Shan; *McLaren 8313* (E). *A. coriarium* (Grigorjev) Soják var. *coriarium*: Kazakhstan, Kaskelen; *Roldugin & Tzagolova 5363* (S). *A. hookeri* (Meisn.) Hara: China, Szechuan, Tsipula; *Smith 4172* (UPS). *A. molle* (D.Don) Hara var. *rude* (Meisner) Hara: India, Mt. Khasia; *Hooker & Thompson s.n.* (BM); originally cultivated in Kew Bot. Gard. Kew, 267–72. *02550 B.L. & M., Ronse Decr. (spirit) 642 Le* (LV). *A. tortuosum* (D.Don) Hara var. *tibetanum* (Meisn.) S.-P. Hong: India, Kashmir, Lamayuru; *Koelz 2748* (E).

*Atraphaxis* L.

*A. billardieri* Jaub. & Spach: Syria, Hymetti, *Heldreich 617* (LV). *A. frutescens* (L.) Koch: cultivated in UPS, *Alm s.n.* (UPS). *A. pyrifolia* Bunge: Turkestan, Kokschar, *Regel s.n.* (UPS). *A. suaedifolia* Jaub. & Spach: Iran, Azarbayejan, Miaveh to Zanjan, *Wendelbo & Assadi 28026* (GB).

*Bistorta* Mill.

*B. amplexicaulis* (D.Don) Greene: Nepal, Chiong, *Dhwoj 108* (UPS). *B. griffithii* (Hook.) Grierson: SE Tibet, Showa Dzong, *Ludlow et al. 13097* (UPS). *B. macrophylla* (D.Don) Soják: China, Sikang, Kangting, *H. Smith 10932* (UPS). *B. major* Gray: Hercegovina, *Murbeck s.n.* (UPS). *B. perpusella* (Hook.) Greene: Bhutan, Shingh, *Ludlow et al. 21115* (UPS). *B. suffulta* (Maxim.) Greene ex H. Gross: Japan, Honshu, Nagano Pref., *Yahara et al. 6998* (UPS).

*Calligonum* L.
*C. eriopodum* Bunge: Russia, Transcasparian, *Michelson s.n.* (GB). *C. litvinowii* Drobov: Uzbekistan, Kokangom, *Prjachin s.n.* (GB). *C. microcarpum* Borszcz.: Russia, Transcaucasia, Aschabad, *Sintenis 2202* (UPS).

*Fagopyrum* Mill.
*F. cymosum* Meisn.: China, Sikang, Kangtung, Tachinlu, Vaszeko, *H. Smith 13315* (UPS); China, Yunnan, Tong-Achouan, *Maire s.n.* (G). *F. esculentum* Moench.: China, Shansi, Chieh-Hsiuh Distr., Sung-Lin-Miao, *Smith 7666* (UPS); USA, Pennsylvania, Monroe Co., Delaware Water Gap, *Brumbach 6902* (K); Burundi, Bururi Prov., Botare, *Reekmans s.n.* (UPS); cult. Reading Botanic Garden, *Ronse Decr. (spirit) 30 Le* (LV). *F. tataricum* (L.) Gaertn.: China, Fiouping-Route, Qutae, Yang Tao-Li (9vi 1925), *Anonymous 649* (UPS); Belgium, cultivated Nodebais, seeds from Bot. Gard. Göttingen 1385, *Ronse Decr. 1335 (spirit 626Ln)* (LV).

*Fallopia* Adans.
Sect. *Sarmentosae* (I. Grintz.) Holub
*F. aubertii* (L. Henry) Holub: China, Szchuan, Wen-Chuan-Hsien, *H. Smith 2316* (UPS). *F. baldshuanica* (Regel) Holub: Turkestan, cult. in Uppsala, *Lundquist s.n.* (UPS). *F. multiflorum* (Maxim.) Haraldson: China, Hunan, Changmau, *Herb. J. Hers 813* (BR).

Sect. *Reynoutria* (Houtt.) Ronse Decr.
*F. japonica* (Houtt.) Ronse Decr.: Japan, Hondo, Yamamoto, *Togashi 1264* (UPS); ex Hort. Mus. Paris, *Herb. L. de Bullemont* 206 (LV); *Herb. Clément Aigret s.n.* (LV); Belgium, cult. Bruges, *Ronse Decr. 1150 (spirit 11 Lb)* (LV). *F. sachalinensis* (F. Schmidt) Ronse Decr.: Japan, Sachalin, Anonym. S.n. (LV); FAA, *Leg. J. Bailey*, Cirencester.
Sect. *Fallopia* (Adans.) Holub
*F. cilinodis* (Michx.) Holub: Canada, Ontario, Black Bay, *Graxton 9631* (UPS); New York, N. of N. Hudson, off Rd 9, *Ronse Decr. 1342 (spirit 646 La)* (LV). *F. convolvulus* (L.) A. Löve: Germany, Hessen, *Kalheber 78–640* (UPS); China, Szechuan, Matang, H. Smith 4372 (UPS). *F. dumetorum* (L.) Holub: Austria, Vienna, Leopoldsberg, *Ronse Decr. (spirit) 447 Lo* (LV); Belgium, Oud-Heverlee, *Ronse Decr. 1309 (spirit 541 L1)* (LV). *F. scandens* (L.) Holub: China, SE Tibet, Mönyul Prov., Nyam Jang Chu, Ludlow *et al.* 7059 (UPS).

Knorringia (Czuk.) S.-P. Hong (*Aconogonon* sect. *Knorringia* (Czuk.) Soják)
*K. sibirica* (Laxm.) Tzvel. Ssp. *sibirica*: China, Hopeh, Peitaino Ho, Hopkinson 1620 (S).

*Koenigia* L.
*K. islandica* L.: Greenland, E. of Sukkertoppen, *Horsen 601* (UPS). *K. filicaulis* (Wallich ex Meisn.) Hedb.: Nepal Rambrong, *Stainton et al. 6014* (UPS). *K. nepalensis* D. Don: Nepal, Jangla, *Einarsson et al. 3394* (UPS). *K. nummularifolia* Meisn.: Nepal, Arun Valley, W. of Num, *Stainton 728* (UPS).

*Oxygonum* Burch.
*O. alatum* Burch.: Zimbabwe, Chipinga, *Goodier 861* (BR). *O. atriplicifolium* (Meisn.) Martel: Kenya, East. Prov., S. of Mtiti Andei, *Strid 2405* (UPS); Kenya, East. Prov., Machakos Distr. Near Embakasi Station, *Haraldson 401* (UPS). *O. delagoense* Kuntze: Nyamaland, Francis Town, *Richards 14666* (UPS); Rhodesia, Aborecorn, *Fries 1258* (UPS). *O. dregeanum* Meisn. var. *strictum* (C.H. Wright) R. Graham: Zimbabwe, Sipolilo. Nyamunyeche Estate, *Nyariti 588* (UPS); Tanzania, Mbizi Forrest, Ufipa Distr. *Napper 1054* (UPS). *O. sinuatum* (Meisn.) Dammer: Kenya, Coast. Prov. Taxa Distr., 8 km NE of Voz. *Zumer 56* (UPS); Ethiopia, Genale Gorge, *Friis et al. 2696* (UPS). *O. stuhlmanii* Dammer: Kenya, Eastern Prov., S. of Mtizo Andei, *Jonsson 576* (UPS); Tanzania, Moshi Distr., Nyumbaya, *Mhoro & Backeus 2236* (UPS).

*Persicaria* Mill.
Sect. *Persicaria* Mill.
*P. acris* (H.B. & K.) Gomez de la Maza: Mexico, Veracruz, N. of Alzacan, *Rosas 362* (UPS). *P. attenuata* (R. Br.) Soják ssp. *attenuata* [= *P. javanicum* De Bruyn]: Thailand, Kanchanaburi Prov. *Ryding 688* (UPS); ssp. *pulchra* (Blume) K.L. Wilson: Tanzania, Iringa Distr. Kidatu, *Mohoro 588* (UPS). *P. bungeana*

(Turcz.) Nakai: China, Chili Prov., Cho-kou-tien, *Bohlin 268* (UPS). *P. hydropiper* (L.) Opiz ssp. *microcarpum* Denser: China, Szechuan, Hsu-tsing, *H. Smith 4778* (UPS). *P. decipiens* (R. Br.) K.L. Wilson [=*P. salicifolia* (Brociss. Ex Willd.) Assenov]: Malawi, Southern Region, Blantyre, *Brummitt & Williams 9856* (UPS). *P. orientalis* (L.) Spach: U.K.? Reading, Penna, *Brumbach 6921* (UPS). *P. pubescens* Blume: Nepal, Jumla, *Einarsson et al. 3961* (UPS). *P. strigosa* (R.Br.) H. Gross: Tanzania, Iringa Distr., Mufindi, *Bidgood & Loveth 4* (UPS). *P. tinctoria* (Aiton) H. Gross): Japan, cultivated, *Togasi 1518* (UPS). *P. viscosa* (Buch.-Ham. ex D. Don) H. Gross: Nepal, Bagmati, Kathmandu, *Ryding 332* (UPS).

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

*P. hastato-sagittata* (Nakai) Ohki: Japan, Numanotaira, Nikko, *Kanai 10383* (UPS). *P. perfoliata* (L.) H. Gross: China, Szechuan, Iping, *H. Smith 10000* (UPS). *P. sagittata* (L.) H. Gross: Nepal, Jumla, *Einarsson et al. 3915* (UPS). *P. sieboldii* (Meisn.) Ohki: Japan, Hondo, Koshigaya in Musashi (1950), *Ohwi 110* (K); Korea, Daitaku, Ohwi 2569 (UPS). *P. thunbergii* (Sieb. & Zucc.) H. Gross ex Nakai: Japan, Hondo, Musashi, *Ohwi 170* (UPS).

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

*P. alata* (Buch.-Ham.) Nakai: Kenya, Aberdare Range, cult. in UPS, (*Hedberg s.n.* (UPS). *P. capitata* (Hamilt. Ex D. Don) H. Gross: Nepal, Muga Karnali Valley, *Polunin et al. 5248* (UPS). *P. chinensis* (L.) H. Gross: Nepal, Chin Hills, *Venning 88* (K). *P. nepalensis* (Meisn.) H. Gross: Nepal, Muga Khola, *Polunin et al. 3017* (UPS). *P. runcinata* (Buch.-Ham. ex D.Don) Roxb. var. *sinuata*: India, Kashmir, Kel, *Ludlow & Sherriff 8250* (UPS).

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

*P. neofiliformis* (Nakai) Ohki: Japan, Hondo, Koshigaya, Ohwi 331 (UPS). *P. virginiana* (L.) Gaertn.: Belgium, seed from Bot. Garden of Bordeaux, cult. Bruges, *Ronse Decr. (spirit) 214 Lb* (LV); USA, Illinois, Peoria, *McDonald s.n.* (UPS).

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

*P. wallichii* Greuter & Burdet: U.K., cult. Reading Bot. Gard., *Ronse Decr. (spirit) 15 Le* (LV).

*Polygonum* L.

Sect. *Polygonum* L.

*P. achoreum* Blake: USA, Wyoming, Crook Co., Sundance, *Porter & Porter 8384* (UPS). *P. arenastrum* Boreau: U.K., Devon, Prawle Point, E. Prawle, *Ronse Decr. 1157 (spirit 405 Le)* (LV). *P. aviculare* L.: Belgium, Bruges, *ssp. aequale; Ronse Decr. (spirit) 25 Lb* (LV). *P. bellardi* All. Greece, Thessalia, Pharsalum, *Heldreich 877*, ex Herb. *Bullemont 8369* (LV). *P. erectum* L.: USA, Illinois, Fountaindale, *Bebb s.n.* (UPS). *P. equisetiforme* Sibth. & Sm.: Tunisia, Jerba, near hotel Toumana, *Ronse Decr. 975 (spirit 309 Lt)* (LV). *P. maritimum* L.: France, Bouches-du-Rhône, Camargue, étang d'Iland, *Nordin 102* (UPS). *P. oxyspermum* Meyer & Bunge ex Ledeb. subsp. *raii* (Bab.) D.A. Webb & Chater: France, Manche, Vauville et Denneville, *L. Corbière 5306*, ex Herb. *Bullemont 8443* (LV). *P. ramosissimum* Michx., USA., Kansas, St. Mary's, *P.A. Puissant s.n.* (LV). *P. tubulosum* Boiss.: India, Kashmir, Sind Valley, *Ludlow & Sherriff 7948* (UPS).

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

*P. afromontanum* Greenway, Ethiopia, S. Bale, Ririka, *Hedberg 377* (UPS); Kenya, Nanyuki Distr., Mt. Kenya, *Hedberg 4320* (UPS). *P. undulatum* (L.) Bergius: South Africa, Humansdorp Distr., 2.6 miles from Assegaai Bosch, *Fourcale 5962* (BOL).

Sect. *Pseudomollia* Boiss.

*P. molliaeforme* Boiss.: Iran, Kuh-Daena, *Kotschy 778* (UPS); Iran. Denawand, *Bornmüller 8181* (K).

Sect. *Duravia* S. Wats.

*P. bolanderi* Brew. ex A. Gray: USA, California: Napa Hills, *C.G. Pringle s.n. ex Herb. Wibbe 7829* (LV). *P. californicum* Meisn.: USA, California, Eal River, *Jepson s.n. ex Herb. Wibbe 7830* (LV). *P. douglasii* E. Greene: USA, Oregon, Siskiyou Mountains, as var. *latifolium* E. Greene. *Howell s.n. ex Herb Wibbe 7842* (LV); Placer Co., Sierra Nevada Mts., *A.M. Carpenter s.n. ex Herb. Wibbe 7840* (LV); Wyoming, Southern Carbon Co., W slope of Sierra Madre, *Porter & Porter 9722* (UPS); Oregon, base of Stein's mountain, *Howell s.n. ex herb. Wibbe 7841* (LV). USA. Montana, as *P. douglasii montanum* Small, *Rydberg & Bessey 5364* (K). ssp. *spergulariiforme* (Meisn. ex Small) Hickman [=*P. coarctatum* Dougl. ex Meisn.]: USA, Oregon, Grant's Pass, *Howell s.n. ex Herb. Wibbe 7881* (LV); *Lyal 1858* (K). *P. minimum* S. Wats.: USA, Washington, Cascades, Sterens Pass, *Sandberg & Leiberg 799* (UPS). *P. paronychia* Cham. & Schlecht.: USA, California, San Francisco, Golden Gate Heights, *Rose 47103* (UPS). *P. polygaloides* Meisn.: USA, Oregon, *Howell s.n. ex Herb. Wibbe 7881* (LV); USA, Wyoming, Uinta Co., Snake River, *Nelson & Nelson 6463* (UPS). ssp. *kelloggii* (E. Greene) Hickman [=*P. kelloggii* Greene]; USA. Wyoming, Johnson Co., Big Horn Range, W. of Buffalo, Circle Park, *Porter & Porter 7555* (UPS). ssp. *confertiflorum* (Nutt. ex

Piper) Hickman [=*P. confertiflorum* Nutt. ex Piper]: USA, California, Modoc Co., 9 miles NW of Camby, *Bacigalupi & Smith 5982* (UPS). *P. shastense* Brewer: USA, California, E. North Peak, *Nygsen s.n.* (UPS); USA, California?, Placer Co., *A.M. Carpenter s.n. ex Herb. Wibbe 7880* (LV); USA, California, N. slopes above Coldsham, Sierra Nevada, *C.F. Sonne s.n. ex Herb. Wibbe 7879* (LV). *P. tenue* Michx.: USA, Massachussets, Milten Blue Hills, *Forbers 1346* (UPS); Baltic Co, *P.A. Puissant* (LV), USA.

*Polygonella* MICHX.
*P. americana* (Fisch. et Mey.) Small: USA, Texas, Cat. Springs, *Fischer 10* (UPS); Alabama, Blackwarrior Creek, Blount County, *Meisner 1845* (BR). *P. articulata* (L.) Meisn.: USA, Massachussets, *Oakes? s.n.* (UPS); New Jersey, Woodbury, *Henry S. Conard s.n.* (LV); New Jersey, Middlesex Co., South Amboy, *Bodin s.n.* (UPS). *P. fimbriata.* (Ell.) Horton: USA, Florida, Tampa, *Blanton 6825* (S). *P. gracilis* Meisn.: USA, Mississipi, Sandy barrens, Pass Christian, *A.B. Langlois 177, ex Herb. Wibbe 7817* (LV); Florida, Orange Co., Killarney, *O. Vestulund s.n.* (UPS). *P. polygama* (Vent.) Engelm. & Gray [=*Polygonella parvifolia* Michx.]: USA, N. Carolina, Brunswick Co., Orton Plantation Garden, *Godfrey 1046* (K); California, *Curtiss s.n.* (UPS); Florida, Indian River, *Curtiss 2433* (LV).

*Pteropyrum* JAUB. & SPACH
*P. aucheri* Jaub. & Spach: Pakistan, Baluchistan, Kalat, Rechinger 27441 (LD). *P. gracile* Boiss.: Iran, Snetaunabad?, *Strauss s.n.* (LD). *P. noëanum* Boiss. Ex Meisn.: Iraq, Koisanjak, *Horsain & Horsain 53* (UPS).