Ultrasculpture of achene surface in Polygonum section Polygonum (Polygonaceae) in Russia

O. V. Yurtseva


Based on SEM examination of 47 specimens and 33 species from Russia and Europe, this is a survey of achene surface ultrasculpture in 6 subsections of annual species of Polygonum. Early and late achenes detected in most species possess sound distinctions in achene shape, size, color and exocarp structure. Late achenes with early and fast seed germination preserve exocarp structure typical for premature achenes of both types: thin colorless walls and vast cavities, thin cuticle and insignificant wax deposits. Early achenes destined for long-term preservation in soil are thickwalled and covered with thick and smooth cuticles and wax layers. The structure of achene surfaces changes substantially during maturing, especially in early achenes: coarse or foveo-rugulate background becomes minutely rough, foveo-smooth or minutely reticulate. Verrucae are not obligatory ornaments. Depending on their location and arrangement of exocarp cells the surface is evenly verrucate (subsect. Patula Tzvel.), linear-verrucate (subsect. Salsuginea Tzvel.) or striate-verrucate (subsect. Humifusa Tzvel., most species in subsect. Polygonum). Smooth and glossy achenes are more common in permanently wet environments (subsect. Maritima Tzvel., Arenaria Tzvel., P. arenastrum and P. calcatum from subsect. Polygonum). In places with fluctuating availability of water the achenes have heavier sculpturing and thicker cutin and wax coverings. A broad range of surface sculptures in some species and their similarity across taxonomically distant taxa decrease the value of the characters for taxa identification.

O. V. Yurtseva, Department of Higher Plants, Biological Faculty, Moscow State University, Vorobjevy Gory, 119 899, Moscow, Russia.

Introduction

About 30 species from section Polygonum occur in Russia (Tzvelev 1979, 1996). Most of them are annuals with flowers clustered in axils of reduced bractlike or normally developed leaves, joined petioles and a basic chromosome number x=10 (Löve & Löve, 1956, Wolf & McNeill, 1986). They are weeds in a variety of habitats: from sea shores and saline marshes to dry, disturbed habitats along roadsides, footpaths and wastelaces.


Identification of Polygonum species is complicated by heterocarpy. Many species produce elongated, protruding "late" achenes appearing late in season, in addition to normal, "early" achenes, pro-
duced in the summer.

Problems in taxonomy and identification of species in section *Polygonum* have drawn attention to the characters of achene morphology and anatomy. Traditional taxonomy of the group was based on the characters of early achenes (size, colour, shape and surface texture), while late achenes were neglected.


The aim of this study is to investigate achene surfaces in section *Polygonum* in Russia and to evaluate diagnostic values of the characters. To understand exocarp structure we used SEM and LM studies of early and late achenes.

**Material and methods**

The study has been based on 47 specimens of 33 *Polygonum* species from Russia and Europe representing most subsections of section *Polygonum* (Tzvelev 1979, 1996). We used field collections and specimens from the Herbaria of Botanical Institute, St Petersburg (LE), Moscow State University (MW), National Museum of Natural History, Paris (P), Tartu University and Tartu Zoological-Botanical Institute. The specimens studied are listed in Appendix 1.

Early and late achenes, mature and premature, have been studied in *P. aviculare* and *P. calcatum*; in other species only mature early achenes. Ultrasculpture of the achenes has been investigated using SEM Hitachi S-405 A. The achenes were attached to brass stubs with one side in horizontal position and then covered with gold and platinum (1:1) in vacuum. The middle part of achene sides with the most distinct and typical ultrasculpture of the surface was photographed.

Mature achenes have been softened and stored in alcohol:glycerine:water (1:1:1). Sections cut 8-20 μm have been stained in sudan 3,4 and rutenium red. Achene structure has been studied in the middle part of the side and at ribs. Optical sections of exocarp cells have been studied with light microscopy without previous treatment.

The terminology of Murley (1951), Corner (1976), Barthlott (1981, 1984), Steam (1992), has been used for description of surface ultrasculpture and anatomy of achenes. The terminology of Kremp (1965) and Punt et al. (1994) elaborated for pollen grain surfaces has been used as well.

**Results**

**Achene morphology**

Many species of inland Russia with prolonged reproduction period produce both achene types. This happens in species from subsections *Polygonum L.*, *Humifusa* Tzvel., *Arenaria* Tzvel., *Salsuginea* Tzvel., and rarely in subsection *Patula* Tzvel. (Tzvelev 1979, 1996). The species of sea shores (subsect. *Maritimia* Tzvel.) produce only one type of achenes - large, inflated and glossy, looking as late ones, but with a thick pericarp, typical for early achenes.

Early and late achenes are substantially different from each other (Yurtseva et al. 1999). Early achenes are small, more or less equal in length to the perianth and hidden in it. They are ovate-trigonal, triangular in cross section, with thick hard pericarps, brown or dark-brown, often in shades of purple. They appear in July-August and ripen in 10-20 days. The seeds are characterized by deep innate dormancy which can be overcome during 2.5-3 months under wet conditions and low temperature (+5° C) (Yanishevsky 1927, Yurtseva & al. 1999). They are adapted for long-term preservation in soil, form soil bank and germinate through 5-8 years (Courtney 1968).

Late achenes are oblong-ovate, lanceolate or rarely crescent-shaped, 2-3 times as large as early ones, exserting from the perianth, oval in cross section. They possess thin scarious pericarps, straw-colored or olivaceous, sometimes with oblong purple spots. They appear in September-October and ripen in a month. During that time the premature pericarp and perianth assimilate, allocating nutrients into the seeds. They do not form seed banks and can partly germinate in a week under wet conditions and +25° C, but most of them germinate in the spring after 2-11 weeks under wet conditions at +5° C, a little earlier compared to early seeds.

Early and late achenes have similar biomass, but in early achenes the weight of seeds is only 1.5-2.7 times as much as the weight of pericarp, while in late achenes it is 5-12.5 times as much. Besides, seed biomass in early achenes is 1.3-1.4 times as much as that in late achenes. As a result late seeds develop faster and produce more powerful and twice as tall
plants (Yurtseva & al. 1999). The difference in size and mass of seeds and in time and conditions of germination contribute to morphological variability in populations, increasing resistance of the species to environmental fluctuations and their competition ability.

Early achenes of most species are trigonous, but the relative width of the sides depends on the presence of stamens opposite achene sides and the degree to which the perianth is divided into segments (Yurtseva 2000). The plants with 8 (5+3) stamens and perianth divided to 2/3-3/4 have 3 subequal concave sides (P. aviculare, P. patulum, P. maritimum etc.). The plants with 5 (3+2) stamens and perianth divided to 1/2 (P. arenastrum, P. calcatum, P. humifusum) have triangular achenes with two sides broad and convex, the third achene side being narrow and concave. It is opposite to the place, where a stamen was reduced from inner stamen circle. In P. calcatum and P. humifusum 7-10 % of flowers are dimerial with 4 stamens, digonous achenes and 2 stigmas. Late achenes of most taxa have more in common and hardly differ from each other, so the features of early achenes are more useful for the taxonomy of the group.

**Achene anatomy**

The study of exocarp anatomy helps to understand the ultrasculpture of achene surfaces better. Premature early and late achenes have similar structures. The pericarp consists of 40 layers of cells in the sides and 10-12 ones in the ribs: 1 layer of exocarp, several layers of parenchymatous mesocarp cells and 1-2 layers of endocarp. Exocarp cells are almost cubic, 20 × 20 × 20 μm, with thick walls and vast cavities. Anticlinal and outer periclinal walls are nearly straight or slightly undulate, colourless or light-rose.

Early achenes change exocarp structure during maturation. Exocarp cells are twice as high as in premature achenes. They are 30-40 μm, pericarp being 55-70 μm high (Fig. 1b).

Exocarp cells are isodiametric or tetra- to hexagonal in outline, 20 × 40 μm, slightly elongated across the side, smaller near the top and at the ribs of the achene. Anticlinal walls are almost straight or slightly curved at the base and regularly and prominently s-undulated near the surface, caused by prolonged growth of the cells (Miroslavov 1974). Interdigitated lobes provide firm connection of cells (Fig. 1a).

In cross section the anticlinal walls (AWs) are irregularly undulated, especially near the surface (Fig. 1b). The outer periclinal walls (OPWs) undulate too, forming numerous pits and projections (verrucae) on the surface (Fig. 1b). Their loops later merge, resulting in thickening of the outer periclinal walls with irregular reliefs (Fig. 1c). In mature achenes the cavities of the exocarp cells are rather vast at the base and extremely narrow in the upper part, where they form numerous pore canals (Fig. 1c, h-j). The canals in anticlinal walls connecting the cavities of adjacent cells later disappear. The canals branch dichotomically at the upper part of the cells (Fig. 1h), get to the surface and enter small hollow protuberances (verrucae) at the OPWs, where they become a little wider (Fig. 1c, g). In some cases bifurcate canals enter the pair of adjacent, incompletely separated verrucae. They are located on slightly raised central parts of exocarp cells (Figs 2, 4, 6) or on one of their lobes (Figs 3, 5, 7).

The walls of ripe fruits are thick and colored brown, while cell cavities containing tannins are dark-brown. The surfaces of the OPWs are impregnated with cutin and covered with a cuticle, 1-2 μm thick, and epicuticular waxes.

Mature late achenes exhibit an anatomical structure typical for premature achenes. In cross section the pericarp is 40 μm high, the exocarp being half of it (Fig. 1e). The OPWS are slightly undulated with few small invaginations and verrucae. The walls are rather thin, colourless or yellowish, impregnated with cutin from the surface and covered with cuticles and waxes, 1 μm thick.

Mesocarp and endocarp of both achene types have similar structures (Fig. 1c, f). Mesocarp includes 4-5 layers of chlorenchyma at the sides and 8-10 layers in the ribs. Isodiametric cells of two upper layers are a little larger. They contain suberin in the walls. Flattened cells of the two lowest layers are elongated in longitudinal direction, and obliterated in mature achenes. In the ribs the mesocarp includes large vascular bundles consisting of a few phloem and xylem elements with annular and helical thickenings.

The endocarp includes 1-2 layers of flat cells elongated in longitudinal direction, later obliterated. In mature achenes mesocarp and endocarp cells contain tannins.

A premature seed is covered with 2 integuments each composed of 2 layers of elongated cells. In mature seeds the upper layer (colored rose) of the first integument and both layers of the second are preserved. The endosperm, except 1-2 aleurone layers, is composed of cells containing simple and compound starch grains. The embryo with its two cotyledons and a radicle is located in one of the angles of the seed.
Fig. 1. *Polygonum aviculare*, pericarp structure in early (a-c, g-j) and late (d-f) achenes. – a, d: exocarp cells, view from the surface. – b, e: exocarp cells in cross section. – c, f: pericarp structure in cross section. – g: verrucae on the surface of exocarp cells. – h-j: exocarp (epidermal) cells near the surface, at the middle and at base in cross section. – ex – exocarp, m – mesocarp, en – endocarp, s – spermoderm, v – verrucae, end – endosperm.

**Achene surface texture**

The achene surface has been described in terms applicable at low magnification: smooth, glossy, shining, lustrous, dull, striate, granular, rugulate, punctate-rugulate etc.

Using SEM technics, Wolf & McNeill (1986) recognized four types of achene surface in 15 taxa of section *Polygonum* from Canada: smooth, roughened (with small irregular protuberances and depressions), papillose and striate-papillose (with papillae scattered evenly or arranged in longitudinal rows).

Figs 2-7. Arrangement of verrucae on the surface of exocarp cells in *Polygonum* species. – Fig. 2. *P. aviculare*. – Fig. 3. *P. neglectum*. – Fig. 4. *P. salsugineum*. – Fig. 5. *P. neglectum*. – Fig. 6. *P. patulum*. – Fig. 7. *P. retinerve*. 

516

Nord. J. Bot. 21(5) 2001
Watching achene surface in development, I have found foveo-recticate, foveo-rugulate, foveo-tuberculate, wavy, roughened or minutely rugulate textures as background. Round projections 15-20 μm in diameter, called “papillae” by Wolf & McNeill (1986), correspond rather to “verrucae” or “tubercles”, as their bases are wider or of the same diameter as their rounded tops. These projections make the surface tuberculate or verrucate, the background texture being different and usually neglected.

Arrangement of cells

Exocarp cells form longitudinal rows running from the base to the top of the achene. Near the base and the top the rows are regular, being formed by equal cells slightly elongated across the achene side. The horizontal anticlinal walls of the cells are parallel to each other. At the central part of the achene side the regularity of the rows is disturbed due to irregular cell divisions. As a result the cells of adjacent rows often alternate with lobes interdigitating at the surface. On the ribs exocarp cells are small and round.

Primary sculpture – Relief of cells

Ultrasculpture of the exocarp surface varies depending on achene type, maturity, cutin and wax covering and environmental conditions. Primary sculptures of premature achenes of both types are similar. Exocarp cells are isodiametric or tetra- to hexagonal in outline, 20 x 40-45 μm. Cell boundaries are clearly visible as narrow channeled depressions along s- undulating anticlinal walls. The relief of the OPWs is slightly convex or flat (Figs 8, 9). Later cutin and wax excreted on the surface mask invaginations and channeled depressions (Figs 10, 11), so that the cell boundary disappears.

In premature achenes of both types the invaginations of the OPWs often form a reticulate-recticate texture, especially if the achenes have dried before maturing (that is usual in herbarium material). Rather thin OPWs of exocarp cells are depressed in the centre, while s- undulated thickened anticlinal walls form elevated twisting ridge about 10 μm wide (Figs 12, 13) with small merging loops, invaginations and protuberances, the last becoming later verrucae (Figs 15, 16, 21-26, 28-29, 31).

Mature late achenes often preserve the primary sculpture from the early stages of development, but reticulate texture get smoother. The loops of twisting ridges merge and partly disappear under cutin and wax covering. Cutin produced on the surface masks the largest pits and hollows of the OPWS, making, however, its elevations or protuberances more prominent. As the result, the surface becomes either foveo-rugulate (Fig. 14) or foveo-tuberculate, rarely verrucate over foveo-rugulate background (Figs 15, 16).

In early achenes cutinization goes further on. Cell boundaries are never seen. Most of pits and hollows in the OPWs disappear under a thick covering of cutin and wax (Fig. 17). Only small oval or triradial pits from 2-3 to 10 μm in size are preserved (Fig. 18) or disappear completely. Depending on development of cuticle and size of OPWs elevations (10-25 μm in diameter), the surface of mature early achenes is foveo-rugulate (Fig. 14), foveo-tuberculate (Fig. 19), roughened (Fig. 20), or minutely rugulate, never being completely smooth.

Verrucae are not an obligatory ornament of the surface. They appear as hollow protuberances of the OPWs 5-7 μm in diameter, later becoming 12-20 μm. Often verrucae are located over the centres of exocarp cells (Figs 2, 4, 6) or over slightly raised interlocking lobes of adjacent cells (Figs 3, 5, 7). As exocarp cells form ordered lines, the verrucae run as longitudinal rows separated by concave grooves. This network is clearly visible at the centre of achene sides. At the margins, where regularity of lines is disturbed due to irregular divisions of exocarp cells, or if verrucae are located over the centre of cells, they are scattered more or less evenly over the surface. They densely cover the surface of achene sides, especially near the top, being usually absent from ribs. Sometimes verrucae are present at the protruding top, being absent from the base, hidden by the perianth (compare Figs 14-16). In rare specimens of P. aviculare. and P. arenstrum some achenes are verrucate, and some are smooth.

Verrucae are common in early achenes with thickwalled exocarp, covered by thick layers of cutin and wax. Otherwise, verrucae are rare or absent in

Figs 8-13. The surface of achene exocarp in development in Polygonum. – Fig. 8. P. robertii, s-undulated cell boundary in premature early achene. 380 x. – Fig. 9. P. calcarutum, s-undulated cell boundary in premature late achene. 750 x. – Fig. 10. P. aviculare, cutin excreted on the surface masks cell boundaries and pits (early achenes). 380 x. – Fig. 11. P. calcarutum, wax plates appearing on the surface of late achene. 750 x. – Fig. 12. P. aviculare, reticulate surface of premature late achene with depressed central parts of the OPWs (c) and thickened anticlinal walls (w). 500 x. – Fig. 13. P. aviculare, wavy ridge around the cells bears small invaginations (in), merging loops (l) and protuberances (p). 1000 x.
late achenes with thin OPWs and cuticle. A verrucate surface usually bears a lot of wax particles, often taking the shape of verrucae, so the last might serve for wax excretion.

**Secondary sculpture - Cuticle**

A secondary sculpture of the exocarp surface is conditioned by the micromorphology of the cuticle. Cutin excreted on the surface through the canals in cell walls mask channeled depressions along cell boundaries (Fig. 10), fills pits and invaginations of the OPWs, but the thin covering does not mask large invaginations and verrucae. Early in development of the achene a cuticle can be microwrinkled, but later it is usually smooth. Thick cuticles give polish to the surface of early achenes, especially those devoid of verrucae (Fig. 20). Late achenes covered with a thin cuticle preserve dull rugulate or reticulate surfaces (Fig. 14).

**Tertiary sculpture- Epicuticular excretions**

Tertiary sculpturing is formed by epicuticular deposits of waxes taking the shape of thin plates, flakes, powder or small particles (needles, granules, crystals) scattered over the surface (Figs 11, 18, 20, 26, 31). Wax excretions make the surface dull and partly mask invaginations of the OPWs. In mature achenes the verrucate surfaces are usually dull, being covered with wax particles.

**Achene surface of Polygonum section Polygonum**

**Subsection Polygonum**

Subsection *Polygonum* comprises plants from waste and trampled places, roadsides and open spots, with thin oblong-oblancoceolate or oval leafblades, the upper ones often diminished, but exceeding axillary flowers. Achenes are (1.2) 1.5 - 3.5 (4) mm long, early and late.

Scholz (1958) reported that in *P. arenastrum* ( = *P. aequale*) and *P. calcatum* the anticlinal walls of exocarp cells are straight, while in *P. aviculare* (= *P. heterophyllum* L.) they are undulate. Our observations showed undulate anticlinal walls in all the species.

A set of characters give reasons to subdivide subsection *Polygonum* into two groups. The first includes heterophyllous plants with perianth divided to 2/3-3/4, 8 stamens and 3 subequal achene sides. It includes *P. aviculare* (Figs 2, 10, 12, 20, 21), *P. agrestinum* (Fig. 23), *P. monspeliense*, *P. neglectum* (Figs 3, 5), *P. propinquum*, *P. patuliforme*, *P. rurivagum* (Figs 22, 26), and *P. retinerve* (Figs 7, 24-25). Their achenes have usually striate-verrucate surfaces, with verrucae arranged in longitudinal rows subdivided by concave grooves. Such pattern is conditioned by their location along longitudinal boards of adjacent cells at their interlocking lobes. Some individual verrucae are located between the rows over the centres of cells. If verrucae are rare, they form separate groups or are scattered evenly. Some specimens of many taxa have roughened surfaces without verrucae (Fig. 20).

Verrucae 5-7 μm in diameter appear on foveo-rugulate or foveo-roughened background, later becoming minutely rugulate or wavy. They grow to 14-18 μm (8-16 μm in Haberland 1963) and are located at mounds formed by the group of small cells or along the area of interdigitating lobes of adjacent cells. In mature early achenes cell boundary is invisible. Epicuticular waxes have the shape of small granules or crystals (Fig. 26).

Late achenes (Fig. 10) have rugulate or foveo-rugulate surfaces, with clearly visible cell boundaries, sometimes masked by cutin ridges. The cuticle is thin and smooth, covered by small granules and thin plates of wax.

The second group comprises homophyllous plants with perianth divided to 1/2-2/3, 5-6 stamens and 3 non-equal achene sides, *P. arenastrum*, *P. calcatum* (Figs 9, 11, 14-16, 18-19), and *P. aphyllum*.

Mature early achenes have usually foveo-rugulate, foveo-tuberculcate or roughened surface (Figs 18-20). The cell boundary is not seen. Cutin, covering pits and depressions, makes the surface plain and almost smooth (Fig. 18). Epicuticular waxes are represented by thin plates, granules, crystals or powder (Figs 11 and 18). Verrucae are rare in *P. calcatum*, but more usual in *P. arenastrum*, especially in the

---

Figs 14-19. The surface of achene exocarp in *Polygonum*. – Figs 14-16. *P. calcatum*, foveo-rugulate surface of a late achene, non-verrucate at the base (Fig. 14) and verrucate near the top (Figs 15, 16). 380 × (Figs 14, 15), 100 × (Fig. 16). – Fig. 17. *P. humifusum*, foveo-rugulate surface of early achene with rare verrucae. 380 ×. – Figs 18-19. *P. calcatum*, foveo-rugulate surface of early achene with round (r) or triradial (t) invaginations (Fig. 18), foveo-tuberculcate surface of early achene (Fig. 19). 2000 × (Fig. 18), 380 × (Fig. 19).
south of Russia. If present, they are scattered evenly or form groups of 2-5.

Late achenes preserve foveo-rugulate or foveo-rugphened surfaces with clearly visible cell boundaries (Figs 9, 14), rarely the surface is verrucose (Figs 15, 16). A smooth cuticle is sometimes covered by thin wax plates, granules and powder, more abundant near verrucae (Figs 9, 11).

Achene surface can vary from foveo-rugulate to smooth, can be verrucose or not within a species. But in some cases this variability seems to be a result of interspecies hybridization. A supposed hybrid has the surface of one of the parents (smooth or verrucose), taking the other characters (the number of stamens, the shape of perianth, leaves and habitus) from the other one. The examples are: P. arenastrum (a supposed hybrid of P. aviculare × P. calctatum; some specimens identified as P. neglectum and P. aequale subsp. oedocarpm (possible hybrids of P. aviculare × P. arenastrum); P. boreale (= P. aviculare × P. norvegicum), P. oxyspermum (= P. aviculare × P. raii), P. euxinum (= P. aviculare × P. maritimum). Chromosome numbers of some specimens of P. boreale (2n = 30, 50) confirm the hybrid nature of the taxa mentioned above.

**Subsection Humifusa Tzvel.**

Subsection *Humifusa* includes the plants of sandy river shallows and open places (roads). They have thin longpetiolate spathulate leaves, the basal ones often opposite; a short and sharply abrupted ochrea, small axillary flowers with 5 stamens and perianth divided to 1/2; achenes 2.2-2.7 mm, often digonous, smooth and glossy or striate-verrucate.

It includes P. humifusum and P. volchovense, a supposed hybrid of P. humifusum × P. aviculare (Tzvelev 1993), rather being a late-fruiting form of P. humifusum. Early and late achenes have foveo-rugulate or striate-verrucate surfaces with verrucose 8-14 μm in diameter (Fig. 17). In mature achenes cell boundaries are not visible. The cuticle is covered by small granules and thin plates of waxes. The surface is similar to that in subsection *Polygonum*, but the ochrea are quite different.

**Subsection Maritima Tzvel.**

Subsection *Maritima* comprises taxa of sandy and gravel sea shores with equal elliptic coriaceous bluish-gray leaves; large axillary flowers with 5-8 stamens; protruding achenes 3-5(6) mm, usually smooth and glossy, rarely striate-verrucate.

*Polygonum maritimum*, P. mesembricum, *P. raii*, *P. norvegicum*, *P. euxinum* and *P. robertii* have the only achene type, looking as the late type, but with the exocarp structure typical for early achenes. They are inflated, dark-brown and glossy, with nearly smooth surface, free of verrucae or foveo-rugulate, wavy, roughened. Cell boundaries, visible in premature achenes of *P. robertii* (Fig. 8), later disappears under a thick cuticle. Wax excretions in the form of granules and powder are insignificant. The survival of young plants at sea shores exposed to tidal and surf waves, depends on rapid germination and deep penetration of roots into the substrate. Large embryo and endosperm promote fast germination, air cavities in the achenes increase their buoyancy (Harper et al. 1970).

In contrast to Mediterranean plants, most specimens of *P. maritimum* from the Black Sea shores are annuals adapted to low-temperature water. They form hybrids with *P. aviculare*. The examples are *P. euxinum* and *P. mesembricum* from the Black Sea shores and *P. robertii* from the Atlantic ocean coast. The surface of their achenes varies from smooth to verrucate (Fig. 27).

*Polygonum oxyspermum* from the Baltic Sea shores has large inflated achenes with foveo-rugulate or minutely reticulate surfaces, but sometimes produces early achenes with verrucose or partly verrucose surfaces, nearly smooth at the base and evenly verrucose near the top. Verrucae are 10-14 μm in diameter. Verrucate surfaces in some specimens might confirm the hybrid nature of some plants of *P. oxyspermum*, a supposed hybrid of *P. raii* from Great Britain and the widely distributed *P. aviculare*.

*Polygonum boreale* from the White and Baltic Sea shores is often considered a variety or a subspecies of *P. aviculare* (Löve & Löve 1956; Wolf & McNeill 1986). It seems to be a hybrid of *P. norvegicum* × *P. aviculare*. It produces early achenes with various types of surface, foveo-rugulate, smooth and shiny, as in *P. norvegicum* from Northern Scandinavia, or covered with verrucae 13-17 μm in diameter, as in

Figs 20-25. The surface of early achenes in *Polygonum*. — Figs 20-21. *P. aviculare*, roughened surface of mature achenes without verrucae (Fig. 20), verrucae, scattered evenly over rugulate surface of premature achene (Fig. 21), 500 × (Fig. 20), 1500 × (Fig. 21). — Fig. 22. *P. rurivagum*, verrucae, arranged in groups and longitudinal rows on foveo-rugulate background, 500 ×, — Fig. 23. *P. agrestinum*, verrucae, arranged in groups and longitudinal rows on foveo-rugulate background, 500 ×. — Figs 24-25. *P. retinerve*, verrucae, arranged in groups and longitudinal rows, 200 × (Fig. 24), 500 × (Fig. 25).
subsection *Polygonum*. In mature achenes the cell boundaries are not visible under a thick smooth cuticle covered with granules of waxes.

**Subsection Salsuginea Tzvel.**

Subsection *Salsuginea* includes plants of dry saline or limestone soils with linear leaves, the upper ones diminished or completely reduced, equally toothed ochrea, small flowers with long perianth tube and narrow achenes, the early ones 1.3-2.5 mm, hidden in the perianth; the late ones 4-5 mm, sickle-like, protruding from the perianth. The surface of the achenes is verrucate. As a rule, each cell bears no more than one verruca.

*Polygonum salsugineum* has yellowish perianth lobes, sometimes tinted rose; the perianth divided to 1/2. In early achenes the cell boundaries are invisible. The surface is linear-verrucate with longitudinal rows of single verrucae 10-14 μm in diameter, located over the center of each cell and equally distant from each other (Figs 4, 28). The background is foveo-rugulate or smooth, covered with small granules of waxes.

*Polygonum ashersonianum*, a supposed hybrid of *P. salsugineum × P. aviculare*, has early achenes with linear-verrucate or striate-verrucate surfaces and late achenes with foveo-rugulate surface.

**Subsection Patula Tzvel.**

Subsection *Patula* includes plants of sandy or saline soils of steppe zones with linear or oblong-linear leaves, the upper ones much reduced; flowers in terminal inflorescences, perianths close-fitting to the light-brown, evenly verrucate or rarely smooth and glossy achenes. As a rule, each cell of the achene surface bears no more than one verruca. Early achenes appearing in summer are more common because the plants finish their flowering by the end of summer. The group includes *P. bellardii (= P. kitaibelianum)* (Fig. 29), *P. patulum* (Fig. 6), *P. novoascanicum (= P. bellardii var. gracilis)*, *P. argyrocoleon* and their numerous varieties. Their achene surfaces are covered by small verrucae homogeneously distributed over the surface (Fig. 29). Single verrucae 14-16 μm in diameter are located over the centre of exocarp cells being equally distant from each other or forming groups of 2-5 on foveo-rugulate or smooth background. Some specimens of *P. patulum* and most ones of *P. argyrocoleon* have foveo-smooth and glossy surface, devoid of verrucae and covered by smooth cuticle, small granules and rods of epicuticular wax.

**Subsection Arenaria Tzvel.**

Subsection *Arenaria* includes the plants of river banks or saline soil with thin, usually early deciduous, oblong or oblongate leaves, the upper ones diminished or completely reduced; flowers in dense terminal inflorescences, perianth short-tubed, broadly open; early achenes 1.2-2.5 mm, hidden in the perianth, and late protruding achenes 3-3.5 mm.

It includes *P. arenarium, P. junceum, P. pulchellum* with smooth and glossy early achenes. Their surface is usually smooth or minutely reticulate or rugulate (Fig. 30), rarely evenly covered with verrucae 12-16 μm in diameter (Fig. 31). In mature achenes cell boundary is hardly visible under smooth cutin and wax covering. In late achenes the surface is rugulate, cell boundary is channeled, s-undulated.

Two supposed hybrids, *P. psammophilum (= P. arenarium × P. patulum)* and *P. janta (= P. junceum × P. patulum)*, have evenly verrucate achene surfaces typical for *P. patulum* (Fig. 31). and perianth and inflorescence typical for *P. arenarium* or *P. junceum*. Subsections *Patula* and *Arenaria* have similar variants of achene surface, giving reasons to bring them together.

**Discussion**

Early and late achenes in *Polygonum* species in section *Polygonum* substantially differ from each other in achene shape, size, color and exocarp structure. Exocarp cells of late achenes preserve the characters typical for premature achenes of both types: rather thin, slightly undulated, colourless walls and large cavities, thin cuticle and insignificant wax deposits. This type of exocarp is not adapted for long-term preservation in soil. Instead, large embryos and endosperm promote early and fast germination. In

Figs 26–31. The surface of early achenes in *Polygonum*. – Fig. 26. *P. rurivagum*, striate-verrucate. Magn. 500 ×. – Fig. 27. *P. mesembricum*, foveo-rugulate. 500 ×. – Fig. 28. *P. salsugineum*, linear-verrucate (on the right) and evenly verrucate (on the left). 300 ×. – Fig. 29. *P. bellardii*, evenly-verrucate. 500 ×. – Fig. 30. *P. arenarium*, roughened or minutely rugulate, with raised central parts of OPWs (arrows). 500 ×. – Fig. 31 *P. janta*, evenly-verrucate. 500 ×.
contrast, exocarp cells of early achenes adapted for a long-term preservation in soil are thickwalled, firmly interlocked with the lobes, covered with a thick and smooth cuticle and wax layers. Such structures prevent the penetration of fungi and other pathogens into the cells, and enable germination over several years.

The types of achene surface detected in section Polygonum coincide with the results of Wolf & McNeill (1986), but the achene surface proved to be changing depending on achene type and stage of development.

Achene surfaces can be classified according to their primary sculpture and additional ornaments. As cuticle and wax deposits develop, foveo-rugulate background becomes minutely rough. In general, mature achenes possess thicker outer walls, cutin and wax layers, so they have a smoother exocarp surface. Nevertheless, they exhibit great individual and geographical diversity of the surface.

In mature achenes the following types of primary sculpture can be found: coarsely rugulate, foveo-rugulate, foveo-roughened, foveo-smooth, roughened, and minutely reticulate. They form transitional series, but if coarsely- and foveo-rugulate are typical for late achenes, the other types are typical for early ones. Verrucae can be present on any basic structure, but they are not obligatory elements.

Verrucae appear early in development as small protuberances of the OPWs 5-7 µm in diameter, later they attain a size of 12-16 (20) µm. Spreading of verrucae over the surface depends on their position on exocarp cells. If individual verrucae are located over the centres of exocarp cells arranged in chess-board order, the surface is evenly verrucate. If exocarp cells form longitudinal rows, running from the base to the top of the achene, the surface is linear-verrucate. The first variant seems to be more typical for subsection Patula, the second one for P. salsugineum. If right longitudinal rows are disturbed, both variants can be present in the same achene.

At last, small cells with individual verrucae over their centres form groups of 2-5 and, then, longitudinal rows. Otherwise, verrucae are located on interlocking lobes of adjacent cells, running from the base to the top of the achene. In both cases verrucae form groups and longitudinal rows, separated by flat or slightly concave grooves, equal to width of 1 or 2 exocarp cells, and the surface is striate-verrucate (subsect. Polygonum). Thus, the position of ornaments on the achene surface has some diagnostic value and may facilitate identification of hybrid specimens.

The functions of verrucae are not quite clear. The plants from more arid conditions possess achenes with thicker OPWs, cutin and wax covering. Thin-walled verrucae might provide wax excretion on their surface. The other probable function of verrucae is absorption of water necessary for germination. In contrast to thick and bold walls of exocarp cells, verrucae themselves possess rather thin walls, so they might serve for penetration of water to the inside of the cells, thus breaking dormancy in spring. Verrucae are common on the achene surfaces of plants from arid regions and habitats. In contrast, they are usually absent on the achene surfaces of plants from wet environments, sea shores (subsect. Maritima), sandy river banks or drying pools (P. arenarium, P. psammophilum). Hydrophobic smooth and glossy surfaces increase water repellency and decrease the ability to be attacked by fungi and other pathogens, what is especially important for early achenes adapted for long preservation in wet soils (Barthlott 1981).

In most xerophytic taxa of subsection Polygonum (P. rurivagum, P. neglectum, P. aviculare and some specimens of P. arenastrum), early achenes are usually striate-verrucate, in subsections Patula and Salsuginia evenly and linear-verrucate. Because of the position of exocarp cells in ordered lines, the arrangement of verrucae on the surface creates capillary networks of narrow channels running from the achene base to the top. It facilitates conduction of water along the achene surface.

Presence of achenes with verrucae top and smooth base hidden in perianth or smooth and verrucae achenes in the same plant may confirm that expression of the character is influenced by environment.

However, variable and dependent on environment the achene surface is, it can serve for taxa delimitation. Regular verruca surfaces are common in subsect. Patula, linear-verrucate in subsect. Salsuginia. In subsect. Polygonum and Humifusa the achene surface varies from foveo-rugulate or foveo-smooth (P. calcatum, P. aequale), to striate-verrucate (P. aviculare, P. neglectum, P. rurivagum and P. monspeliense).

Taxa and specimens of hybrid origin have achene surfaces typical for one of their parents. That is more obvious in hybrids between taxa from different subsections, such as P. boreale (= P. norvegicum x P. aviculare), P. psammophilum (= P. arenarium x P. patulum), P. patuliforme (= P. aviculare x P. novoascanicum).

Taking into account the great variability of achene surfaces, depending on achene maturity and environmental conditions, and the great similarity in the sculpturing of achene surfaces of rather distant groups, we can use these characters in the taxonomy of section Polygonum, but with great caution.
Acknowledgements – I thank E. V. Mavrodijev, T. E. Kramina, S. R. Majorov, D. D. Sokoloff, A. B. Schipunov, who kindly collected field specimens of some species; the curators of the herbaria of Botanical Institute, St Petersburg (LE), Moscow State University (MW), National Museum of Natural History, Paris (P), Tartu University, Tartu Zoological-Botanical Institute, who permitted using their collections; A. S. Kondrashov, who read the manuscript. The research was supported by RFFI foundation (99-04-48957).

References


Appendix 1

List of the specimens studied

P. agrestinum Jord. ex Bureau, France, Opel Berry prairie de Sateuat, 21 juin 1858, A. Bureau (P).

P. aphyllum Kroker, Ukraine, Charkov reg., prope Balaklea, left bank of the Volosskaya Balakleyka, salt meadow, 14.08.1974, n.12, N. N. Tzvelev (LE).


P. argyrocoleon Steudel ex Kunze, Russia, Udmurtia, dist. Kyzner, 3 km E from railway station Kyzner, between rails. 18.08.1984, A. N. Puzyrev, N. N. Tzvelev (LE).


P. aviculare L. s.str. (= P. heterophyllum Lindman), Russia, Moscow, Vorobyevy Gory, Moscow State University, on lawn, 30.08.1995, O. V. Yurtseva (MW).


P. boreale (Lange) Small, Russia, Karelia, Lokki dist., Pulonga, on shore of the White Sea, supralitoral, 27.07.1994, O. V. Yurtseva (MW).

P. calcatum Lindman, Russia, Olenetzkaya gub., Petrozavodsk dist., prope lake Sandal, Ivanova, Petrova. (LE); Russia, the White Sea, opposite Ustje, prope river Varsut, 30.08.1958, n. 656, N. N. Tzvelev (LE); Ukraine, Charkov reg., SW of Charkov, wet sandly slopes, n. 26, N. N. Tzvelev (LE).


P. humifusum Merk. ex C. Koch, Russia, Komi, prope Vorkuta, pr. pag. Varga-Shor, along road, 2.08.1982, V. V. Morevov, D. Milko (MW); Russia, Siberia, Omk reg., Berezovsk dist., Sarapnau, 10.08.1936, K. Igoschina (MW); Siberia, Tyumen reg., Yamal, on the bank of Hejek-river, prope mouth of the Nida-river, 4.08.1980, M. S. Ignatow (MW).


P. junceum Ledeb. (= P. divaricatum Pall.), Russia, Orenburg, lessing, 1892 (LE, isotype).


P. monspeliense Thieb. ex Persoon, Russia, Leningrad reg., prope Okkervil, n. 235, 11.08.1978, N. N. Tzvelev (LE).

P. neglectum Besser, [Ukraine], in arvis cultis, n. 2622, Besser (LE, isotype); Ukraine, Charkov reg., Zmiev dist., sandy open slopes in Pinenet, 21.09.1980, n.35, N. N. Tzvelev (LE); Ukraine, Cherson reg., Skadovsk dist., sandy sea shore, 13.08.1947, E. G. Pobedimova (LE); Russia, Moscow, Nakholim avenue, in fruit garden, 16.08.1996, O. V. Yurtseva (MW); Moscow, Vorobyevy Gory, Moscow State University, on lawn, 11.08.1995, O. V. Yurtseva (MW).


P. novoascacsicum Klokov (= P. bellardii var. gracilis) Ledecky) Klokov), Ukraine, Kiev, loco arenoso, 12.09.1910, A. Lonatschewsky (LE, Tartu University).


P. propinqua Ledecky. Russia, Astrachan, Ledebour, n. 818.26" (LE, type).


P. retinerve Worsocz., the Crimea, Sevastopol, prope Chersones, sandy sea shore, 1.08.1995, A. Belov (MW).

P. roberti Lois., France, Côte d'Azur, St. Tropez, sea shore, 4.10.1937, V. L. Komarov (LE).


P. volchovense Tzvel., Russia, Tver reg., Bezhetzk dist., prope pag. Esek, left bank of the Mologa, on sand, n. 2360, A. Ilyinsky (LE).