
WHAT IS THE TAXONOMIC STATUS OF *POLYGONELLA*? EVIDENCE OF FLORAL MORPHOLOGY¹

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ABSTRACT

A comparative morphological study of floral characters of the North American genus *Polygonella* and the four currently accepted sections of *Polygonum* s. str. (sect. *Polygonum*, sect. *Duravia*, sect. *Pseudomollia*, sect. *Tephis*) has been carried out with light microscopy (LM) and scanning electron microscopy (SEM). Flowers were investigated for macromorphological characters, tepal epidermal characters, pollen, and fruit morphology and anatomy. Results demonstrate that the limits between both genera become blurred through section *Duravia* of *Polygonum*, especially in characters of pollen and fruit morphology. *Polygonum* sect. *Duravia* and *Polygonella* share a wealth of intergrading floral and vegetative characters at the macroscopic, as well as ultrastructural, level (pollen morphology, fruit morphology, flower structure, vegetative anatomy). These characteristics, especially the pollen morphology, are sharply delimited from section *Polygonum*. Evidence presented here allows for a broader concept of *Polygonum* s. str. to be adopted, with an extended section *Duravia* including subsections *Duravia* and *Polygonella*. A cladistic analysis of morphological characters supports two distinct clades, section *Polygonum* with subsections *Polygonum* and *Tephis*, and section *Duravia* with subsections *Duravia* and *Polygonella*.

Key words: cladistic analysis, *Duravia*, floral morphology, fruit, pollen, Polygonaceae, *Polygonella*, *Polygonum*, sectional classification.

The genus *Polygonella* Michx. contains about 9 to 11 species native to eastern North America, with a few western outliers. The genus was originally erected by Michaux in 1803 to accommodate a single species, *P. parvifolia* Michx. Since that date a number of North American genera were described independently for the Polygonaceae. Fischer and Meyer (1840: 144) described the genus *Gonopyrum* Fisch. & Mey. ex C. A. Mey. with one species (*G. americanum*). Rafinesque described several new genera in the Polygonaceae, which were eventually transferred into *Polygonella*, such as *Lyonia* Rafin. (1808: 352), *Phyllepidum* Rafin. (1808: 356), *Lyonella* Rafin. (1818: 266), *Phylepidum* Rafin. (1836: 51), and *Stopinaca* Rafin. (1837: 11). Gray (1845: 232) recognized the genus *Thysanella* with one species (*T. fimbriata*) originally placed in *Polygonum*. Nieuwland (1914: 171) created the genus

Psamogonum for two species, *P. articulatum* Nieuwl. and *P. americanum* Nieuwl. Small (1896, 1909, 1913, 1924) described five new species in *Polygonella* and erected two additional genera (*Delopyrum* and *Dentoceras*). In 1933 he recognized 13 species under four distinct genera (*Polygonella*, *Delopyrum*, *Dentoceras*, and *Thysanella* A. Gray), while absorbing the other previously described genera. However, all were included by Horton (1963) under *Polygonella*, because he considered the differences used by Small (1896, 1909, 1924) to segregate these smaller genera not distinctive enough. The arguments used by Horton (1963) to recognize a single genus were mainly the homogeneity in anatomy and flower form against the heterogeneity in the neighboring genus *Polygonum*, although his views of the latter genus were doubtless much broader than in the present paper. An additional

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argument already used by Small (1897) is the fact that branching in *Polygonella* is internodal by adnation of the secondary axis to the main axis above a node, contrary to other members of the Polygonaceae. Eleven species are currently recognized. For population size and distribution we refer to Lewis and Crawford (1995). Horton (1963) did not consider the generic limits of *Polygonella*, nor did he make comparisons with taxa outside the genus. Meisner (1857) related *Polygonella* with *Atraphaxis* L. in a separate subtribe. Only later did authors consider it as related to *Polygonum* sensu lato (Bentham & Hooker, 1883; Dammer, 1893), although always as a distinct genus.

The most important distinctive characters of *Polygonella* enumerated in the literature are that the branches appear internodal by the fusion of their basal part to the main stem, the abruptly dilated inner filaments, the presence of solitary flowers on elongated pedicels at the nodes, the colored marcescent tepals, and conspicuous scarious bracts (Watson, 1873; Small, 1897; Rydberg, 1932; Graham & Wood, 1965; see Table 2). Horton (1963) added a few anatomical features, such as the very short vessel elements and a strongly reduced vascularization of the flower (as was observed by Vautier, 1949).

Horton recognized two subgenera in *Polygonella*, viz. subgenus *Polygonella* comprising the great majority of the species, and subgenus *Thysanella* with only one species (*Polygonella fimbriata* (Ell.) Horton) consisting of two varieties. Subgenus *Polygonella* was described as having two outer and three inner morphologically distinct tepals, pedicels without bracteoles within the ocreolae, and filaments that are dilated at the base, forming two lateral teeth. Subgenus *Thysanella* has two outer, one transitional, and two inner tepals, pedicels subtended by bracteoles within the ocreolae, and the filaments all alike and without teeth. Nesom and Bates (1984) considered the two varieties of *Polygonella fimbriata* as two valid species, *P. fimbriata* and *Polygonella robusta*. In a cladistic analysis, Lewis (1991, cited in Lewis & Crawford, 1995) found that *P. fimbriata* and *P. robusta* appear as a basal clade within *Polygonella*.

The circumscription of the genus *Polygonum* L. has changed considerably since its much broader circumscription by earlier authors. In recent approaches to the family Polygonaceae, the genus is currently segregated in the genera *Polygonum* s. str., *Fallopia* Adans., *Persicaria* Mill., with segregates *Aconogonon* (Meisn.) Rchb. and *Bistorta* Mill., and *Koenigia* L. (e.g., Haraldson, 1978; Ronse De Craene & Akeroyd, 1988; Brandbyge,

1993). Four sections are currently accepted within *Polygonum* s. str. (e.g., Dammer, 1893; Hedberg, 1946; Haraldson, 1978), viz. sections *Pseudomollia*, *Tephis*, *Polygonum* (= *Avicularia*), and *Duravia* (see Table 1). Ronse De Craene and Akeroyd (1988) recognized two sections only (*Polygonum*, *Tephis*), as they believed the distinctive characters to be unimportant in comparison to the inherent variability of section *Polygonum*. Haraldson (1978: 79) summarized the differences between the tribes of *Polygonum* s. str. in a table. She reported the presence of three staminodes besides five fertile stamens as a distinctive character for sections *Pseudomollia* and *Duravia*. Watson (1873) and Haraldson (1978) pointed out that section *Tephis* is more similar to section *Duravia* than to section *Polygonum*.

Section *Duravia* was erected by Watson (1873) for a single species, *Polygonum californicum*, on the basis of its supposedly distinctive achene structure (with a membranaceous pericarp). Small (1895) included four other species in his subgenus *Duravia* (*Polygonum bolanderi*, *P. greenei*, *P. parryi*, *P. bidwelliae*) on the basis of lacerate ochreae and spicate inflorescences. Greene (1904) elevated *Duravia* to generic rank on the basis of three distinctive characters (viz. solitary flowers, persistent styles, and absence of articulation at the base of the leaf blade). He accepted three other species (*D. bidwelliae*, *D. greenei*, and *D. bolanderi*) besides *D. californica*.

The taxonomy of North American *Polygonum*, sections *Polygonum* and *Duravia* alike, remains confused, as different populations tend to show wide gene flow and a high level of interbreeding (e.g., Mertens & Raven, 1965; Wheeler, 1938). Hickman (1984) tried to solve this problem by accepting two polymorphic species, *Polygonum polygaloides* and *Polygonum douglasii*, each with a number of subspecies that had been previously described under various species. He elevated section *Duravia* to the rank of subgenus with two sections, section *Duravia* with five species and section *Monticola* with the two heterogeneous species.

Hedberg (1946) described a distinct pollen type, the *Duravia*-type, for 18 species of *Polygonum* sensu lato, deviating from the other species of the genus, and including members of *Polygonella*. However, several species possessing the *Duravia*-type of pollen were placed by Small (1895) in his subgenus *Avicularia* (equivalent to sect. *Polygonum*). Based on the study of a limited number of species, Haraldson (1978) recognized section *Duravia* as distinct from section *Polygonum* by its petiole anat-

Table 1. Summary of the most important delimitations of *Polygonum* s. str. and *Polygonella* (full line indicates that certain sections were not considered by the authors).

Meisner (1857)	Bentham & Hooker (1883), Dammer (1893)	Small (1895, 1933)	Gross (1913)	Jaretsky (1925)
Sect. <i>Avicularia</i>	Sect. <i>Avicularia</i>	Subg. <i>Polygonum</i>	Sect. <i>Avicularia</i>	<i>Avicularia</i> sect. <i>Avicularia</i>
Sect. <i>Avicularia</i>	Sect. <i>Pseudomollia</i>	—	Sect. <i>Avicularia</i>	<i>Avicularia</i> sect. <i>Avicularia</i>
Sect. <i>Avicularia</i>	Sect. <i>Avicularia</i>	Subg. <i>Duravia</i>	Sect. <i>Avicularia</i>	<i>Avicularia</i> sect. <i>Avicularia</i>
Sect. <i>Tephis</i>	Sect. <i>Tephis</i>	—	Sect. <i>Tephis</i>	<i>Avicularia</i> sect. <i>Tephis</i>
<i>Polygonella</i>	<i>Polygonella</i>	<i>Polygonella</i> , <i>Dentoceras</i> , <i>Delopyrum</i>	<i>Polygonella</i>	<i>Polygonella</i>
—	—	<i>Thysanella</i>	—	—

omy and found it anatomically closer to *Polygonella* than to section *Polygonum*.

Other authors did not recognize the identity of section *Duravia*, mainly because of the observed existence of transitional forms between section *Duravia* and section *Polygonum* (see Dammer, 1893; Gross, 1913; Jaretsky, 1925; Graham & Wood, 1965; Ronse De Craene & Akeroyd, 1988; Table 1). Several North American species were retained in section *Polygonum* (Watson, 1873; Small, 1895), or no difference was made at the sectional level (Rydberg, 1932, 1954; Small, 1903, 1933; Kaul, 1986). Indeed, the taxonomy of section *Duravia* appears confusing and it is difficult to draw a sharp line between section *Polygonum* and section *Duravia*, especially in the annual species of section *Polygonum*. *Polygonella*, on the contrary, has been maintained as a distinct genus by all authors despite the fact that several distinctive features of *Polygonella* are found in *Polygonum* s. str., especially in the species that have been grouped under section *Duravia*. These characters include:

- The presence of a single unbranched vein in each tepal (Vautier, 1949; Horton, 1963; Graham & Wood, 1965; Ronse De Craene & Akeroyd, 1988);
- The corresponding vegetative anatomy of section *Duravia* and *Polygonella* (Haraldson, 1978);
- The lateral expansion of the (inner) filament bases does not occur in all species of *Polygonella*. In *Polygonella fimbriata* filaments are basally inflated as in *Polygonum* sect. *Polygonum* and section *Duravia*; the inner filaments of *Polygonella macrophylla* are intermediate (Horton, 1963);
- The similar epidermal cell morphology of the te-

pals (Ronse De Craene & Akeroyd, 1988; Hong et al., 1998);

- The pollen morphology of *Polygonella* and *Polygonum* sect. *Duravia* appears to be similar (Hedberg, 1946; Nowicke & Skvarla, 1977; Hong & Oh, unpublished). Hedberg (1946) found four species of *Polygonella* matching the pollen grains of *Polygonum* sect. *Duravia* (“*Duravia*-type”). However, he found one species, *Polygonella parvifolia* (= *Polygonella polygama*), that had pollen grains almost identical to section *Polygonum* (“*Avicularia*-type”), but he was not convinced of a close relationship, as important differences exist in habit and phytogeographical distribution. He concluded that there had been parallel development of the same pollen type in the two groups.
- The apparent trend for the outer stamens to become reduced or lost (a reduction of the total from eight to three; see also Ronse De Craene & Akeroyd, 1988); this trend is correlated with an expansion of the inner filament bases and occurs occasionally in *Polygonella* (Horton, 1963), *Polygonum* sect. *Duravia* (Wheeler, 1938), and section *Polygonum* (Trail, 1896; Ronse De Craene & Akeroyd, 1988). Gross (1913) mentioned one case of *Polygonella parvifolia* (= *Polygonella polygama*) with five stamens: three inner, and two outer (replacing the two pairs). An identical disposition is occasionally found in *Polygonum* sect. *Polygonum* (Vautier, 1949).

Ronse De Craene and Akeroyd (1988) briefly discussed the possibility of combining *Polygonella* and *Polygonum* s. str. into a single genus. In this paper we provide arguments for solving the problem, as more evidence has been gathered from dif-

Table 1. Extended.

Hedberg (1946)	Graham & Wood (1965)	Haraldson (1978)	Ronse De Craene & Akeroyd (1988)	Ronse De Craene & Hong (as proposed herein)
Sect. <i>Polygonum</i>	Sect. <i>Polygonum</i>	Sect. <i>Polygonum</i>	Sect. <i>Polygonum</i>	Sect. <i>Polygonum</i> subsect. <i>Polygonum</i>
Sect. <i>Pseudomollia</i>	—	Sect. <i>Pseudomollia</i>	Sect. <i>Polygonum</i>	Sect. <i>Pseudomollia</i>
Sect. <i>Duravia</i>	Sect. <i>Polygonum</i>	Sect. <i>Duravia</i>	Sect. <i>Polygonum</i>	Sect. <i>Duravia</i> subsect. <i>Duravia</i>
Sect. <i>Tephis</i>	—	Sect. <i>Tephis</i>	Sect. <i>Tephis</i>	Sect. <i>Polygonum</i> subsect. <i>Tephis</i>
<i>Polygonella</i> , <i>Gonopyrum</i>	<i>Polygonella</i> subg. <i>Polygonella</i>	<i>Polygonella</i>	<i>Polygonella</i> subg. <i>Polygonella</i>	Sect. <i>Duravia</i> subsect. <i>Polygonella</i>
<i>Thysanella</i>	<i>Polygonella</i> subg. <i>Thysanella</i>	—	<i>Polygonella</i> subg. <i>Thysanella</i>	Sect. <i>Duravia</i> subsect. <i>Polygonella</i>

ferent fields. The limits between the sections *Pseudomollia*, *Tephis*, *Duravia*, and *Polygonum*, relative to *Polygonella*, are also studied and clarified.

MATERIAL AND METHODS

A number of representative species of *Polygonella*, and species from all sections of *Polygonum* s. str., including sections *Duravia*, *Tephis*, *Pseudomollia*, and *Polygonum*, have been investigated. Material was either fixed in the field in FAA or removed from herbarium sheets. The origin of material is listed in Appendix 1. We studied selected characters considered to have systematic value based on previous studies, viz. pollen (Hedberg, 1946), fruit anatomy and surface patterns (Marek, 1954, 1958; Wolf & McNeill, 1986; Ronse De Craene et al., 2000), tepal epidermal structure (Ronse De Craene & Akeroyd, 1988; Hong et al., 1998), and gross floral morphology (Ronse De Craene & Akeroyd, 1988).

For LM observations herbarium material was either boiled in water or treated with sulfosuccinic acid 1,4-bis ester sodium salt (aerosol-OT; Ayensu, 1967). Flowers were first washed in a warm 10% KOH solution, before a treatment with Stockwell's bleach was applied to remove the excess of tannins (Schmid, 1977). Next material was run through an ethanol-tertiary butanol series and embedded in paraplast, sectioned at about 12 µm, and stained with saffranin and fast-green. The vasculature of a number of flowers was also studied after treatment with warm 10% KOH and clearing with lactic acid (Sporne, 1948).

Of the fruit wall only the exocarp (epidermis) survives at maturity and is usually lignified. As the cells are square, rectangular, or cylindrical they

have the same shape in cross or longitudinal section. However, tangential (paradermal) sections can vary from the epidermis toward the mesocarp. In surface view the cells may be puzzle piece- to star-shaped, and become polygonal deeper within the tissue (see also Ronse De Craene et al., 2000).

For SEM observations herbarium material was treated with aerosol-OT, stored in 70% alcohol (Erbar, 1995), and dissected before treatment with dimethoxymethane (Gerstberger & Leins, 1978) and critical-point drying. SEM observations were carried out either with a Jeol 6400 scanning electron microscope (LV) or Zeiss DSM 962 (E) at 5–15 kV.

We also studied a number of observable macro-morphological features of leaf, stem, inflorescence, and mature flowers and fruits, such as the overall shape of the flower, the shape of the tepals, tepal venation, the number of stamens and the filament shape, the number of carpels, and shape of the fruits. These characters were added to the micro-morphological characters to perform a cladistic analysis comprising 51 characters and 25 species (including one subspecies) (see Appendices 3, 4). Parsimony analysis was performed with PAUP* version 4.0 (Swofford, 1998).

Fallopia cilinodis (Michx.) Holub was used as outgroup, and characters were unordered and all had equal weight. *Polygonum molliaeforme* was initially included in the analysis, but was later removed because of strong morphological convergences (see discussion). Parsimony analysis was performed using a heuristic search with TBR swapping and the steepest descent option. Relative support for clades was assessed with a 50% majority-rule bootstrap and jackknife analysis.

Table 2. Diagnostic characters used to separate *Polygonella* and different sections of *Polygonum* (based on Graham, 1958; Haraldson, 1978; Hickman, 1984; Horton, 1963; Lousley & Kent, 1981; Mitchell & Dean, 1978; Ronse De Craene & Akeroyd, 1988; Small, 1897; Watson, 1873; Wheeler, 1938).

	<i>Polygonella</i>	<i>Polygonum</i> sect. <i>Duravia</i>	<i>Polygonum</i> sect. <i>Polygonum</i>	<i>Polygonum</i> sect. <i>Pseudomollia</i>	<i>Polygonum</i> sect. <i>Tephis</i>
Number of flowers per unit	1	1(2-4)-flowered fascicles	often 1(-)2-3(-)6-flowered fascicles	ochrea usually enclosing 1(2) flowers on each node	several flowers per node
Branch position	appearing intermodal through adnation	nodal	nodal	nodal	nodal
Pediceal orientation	often curved	curved or erect	erect	erect	erect
Flower sex	bisexual/unisexual	bisexual	bisexual	bisexual	bisexual
Style fusion	separate to the base	separate to the base (<i>Duravia</i>) or fused at base (<i>Monticola</i>)	separate to the base, or fused below middle	fused ca. 0.1 mm from the base, and divided into two	fused at the base
Beak	present	present or absent	absent or weakly developed	present	present
Number of carpels	3, rarely 2(4)	3	2-3	2	2
Fruit wall	smooth to shallowly pitted	smooth, (shallowly) pitted or tubercled, rarely reticulate	conspicuously tubercled or smooth	pitted (reticulate), more strongly at the wings (also tubercles)	smooth to shallowly pitted
Number of stamens	8	5-8	5-8	6	(5-)6-7
Filament shape	inner abruptly dilated, rarely progressively so	inner progressively dilated	inner progressively dilated	inner progressively dilated	inner progressively dilated
Inner/outer tepals	strongly differing from each other in size and shape, outer often smaller than inner and flattened	not differing, or outer slightly longer and keeled with cucullate tips	not differing, or outer incurved, inner flat, outer sometimes cucullate or keeled	outer angular to keeled, not differing in size	outer keeled, not differing in size
Tepal accrescence	inner distinctly to slightly accrescent	not to slightly accrescent	not accrescent	not accrescent	not accrescent
Achene	included in perianth, rarely exerted	included in perianth	included to often exerted above perianth	included in perianth	included in perianth
Chromosome numbers	N < 20	N < 20, N ≥ 20	N < 20, N ≥ 20	unknown	unknown

OBSERVATIONS

MACROMORPHOLOGY OF THE FLOWER (FIGS. 1, 2)

All tepals are similar in size and shape (Figs. 1D, 2C, D, F), or the outer tepals differ strongly from the inner ones (Fig. 1A, C, E). In some cases shape and size of tepals became increasingly different after anthesis. Outer tepals were found to be angular to keeled in species of sections *Polygonum*, *Duravia*, and *Tephis* (Figs. 1A, E, 2D). In section *Polygonum* the fruit tends to outgrow the perianth in size as to become increasingly exerted, and the tepals become appressed to the fruit. In sections *Tephis*, *Duravia*, and *Polygonella* the perianth loosely encloses the fruit, often becoming accrescent. A distinctive characteristic of some species of *Polygonella* (e.g., *Polygonella americana*, *Polygonella polygama*) is that the outer tepals become reflexed and are smaller than the accrescent inner ones (Fig. 1C).

The vasculature of the tepals is only rarely trifid (e.g., *Polygonum afromontanum*; Fig. 1A). In most cases it consists of a single dendritically branching vein (as a main trunk with short secondary ramifications along the trunk: most species of section *Polygonum* and some of section *Duravia*; Fig. 1B, D). In *Polygonella*, *Polygonum molliaeforme*, and some species of section *Duravia* there is only a single non-branching vein, or ramifications are few (Fig. 1C, E).

The most common arrangement of the stamens in the pentamerous Polygonaceae is of four equal stamens in two pairs opposite the two outer tepals, two unequal stamens opposite the intermediate tepal (one belonging to the inner whorl and one to the outer whorl), and single stamens opposite the two inner tepals (Fig. 1B, C; see, e.g., Laubengayer, 1937; Vautier, 1949; Ronse De Craene & Smets, 1991). Flowers are occasionally trimerous with six tepals (Fig. 1D). The transitional tepals have an intermediate shape and size (Figs. 1A, B, 2C, E) or are sometimes abnormally shaped (Fig. 1D). A single stamen is often found in sections *Tephis* and *Polygonum molliaeforme* instead of the usual stamen pair (Fig. 1A, E). Anthers are occasionally sterile, as in *Polygonum ramosissimum* (see also Ronse De Craene & Akeroyd, 1988). In all taxa studied the filaments of the inner stamens are inflated toward the base (Figs. 1A–E, 2A–E). In most species, the inflation is basipetally progressive from the middle of the filament, but in most species of *Polygonella* the filament abruptly widens in the lower half (Figs. 1C, 2A). However, this is not the case in *Polygonella fimbriata*, and its outer filaments are rarely inflated and are sometimes re-

duced (Horton, 1963). Nectar tissue is confined to the base of the inner filaments and extends onto the hypanthium surrounding the ovary. The nectary is not clearly visible, except for the epidermis that is not cutinized. Since no nectarostomata are visible, diffusion of nectar must take place through the non-thickened cell wall (cf. Ronse De Craene & Smets, 1991). Only in one species, *Polygonella articulata*, did we observe an apparently glandular rim (nectary?) of tissue surrounding the base of the gynoecium (see also Horton, 1963). For more details on nectaries in Polygonaceae we refer to Ronse De Craene and Smets (1991).

The shape of the gynoecium is either trigonous (three carpels) or lenticular (two carpels), and the fruit develops as an achene or nut. A condition with two carpels is consistently found in sections *Pseudomollia* (Fig. 6C) and *Tephis*, rarely in section *Polygonum*, and is almost absent in section *Duravia* and *Polygonella*. This may correspond with the loss of the intermediate tepal with accompanying stamens (Fig. 2D). Other differences between individual species exist in the presence (Figs. 6A, 7C, D) versus absence (Figs. 6C, 7A, B, F) of a basal stipe, the prolongation of the distal portion (beak) of the achene (Fig. 7C–F), as well as the development of the fruit angles or ribs (Figs. 6A, B, 7B, D, F). Fruits of *Polygonella* and several species of section *Duravia* are typically slender, triangular-ovoid with well-developed angles, stipitate, and beaked (Fig. 7C, D, F), although this is not always consistently so (Fig. 7A, E). The fruit of *Polygonum molliaeforme* is distinctive by the presence of a winged beak (Fig. 6C), although the wings may be variably developed. In section *Polygonum* the fruit is often disymmetric in transection, as two ribs are more prolonged compared to the third (Fig. 6B), or the opposite occurs (Fig. 2F).

POLLEN MORPHOLOGY (FIGS. 3, 4)

In all genera and sections investigated the pollen is prolate to spheroidal and tricolporate (Polar axis/Equatorial diameter = 1.11–1.68). The ektexine is the most variable feature, and is either reticulate (Fig. 3B–F, H, I), tectate (smooth and spinulose; Fig. 3A), or rough (Fig. 3G). In species with a reticulate exine, usually the area surrounding the colpi features smaller lumina than seen in the polar and intercolpal area.

Species of *Polygonum* sect. *Polygonum* and section *Tephis* (*Avicularia*-type sensu Hedberg, 1946) consistently have tricolporate, rarely hexa-pantocolporate (= hexarugate), prolate-spheroidal grains with the exine surfaces smooth with spinules (Figs.

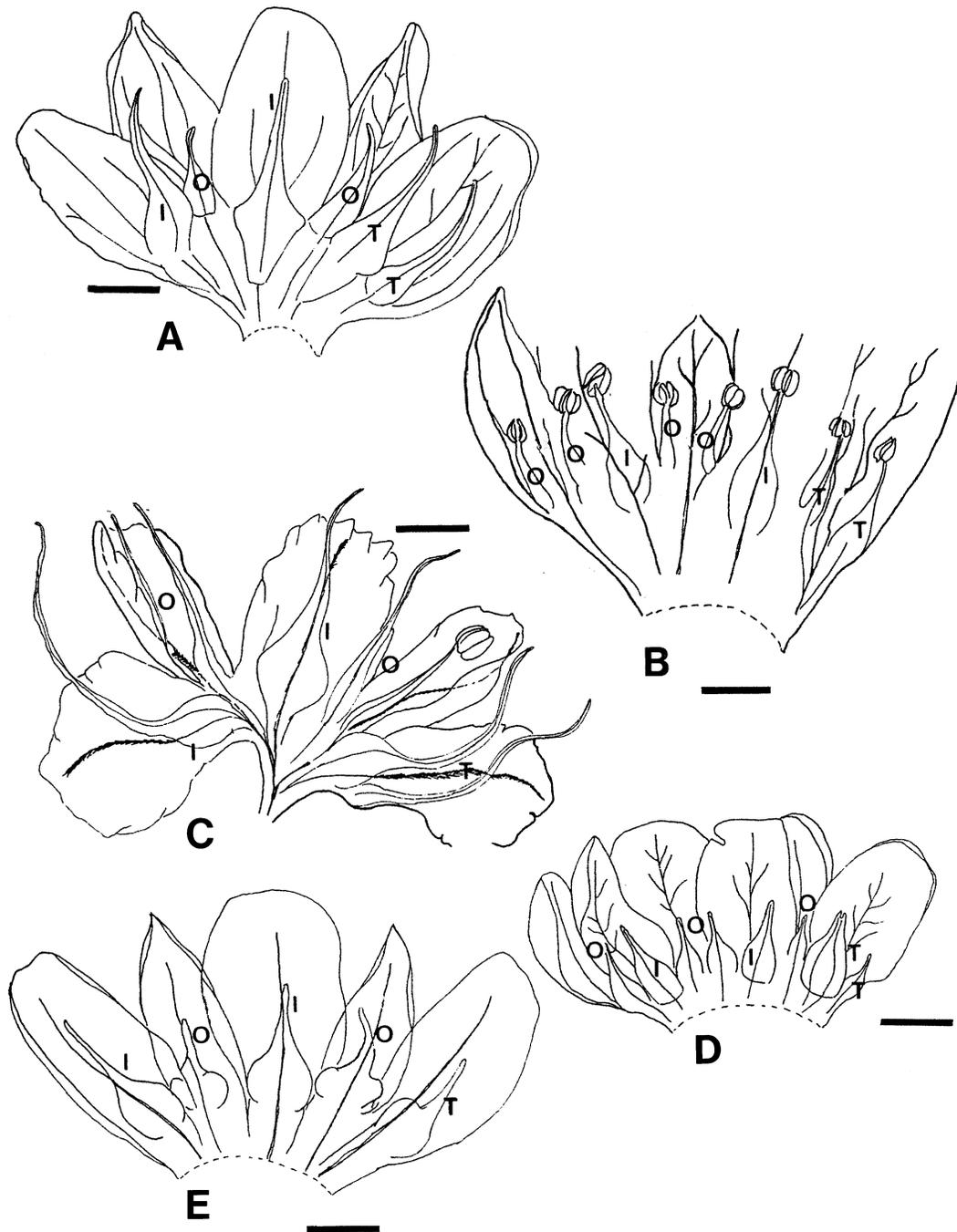


Figure 1. Floral shapes and structures, with flowers spread open and gynoecium removed (O, outer stamen; I, inner stamen; T, transitional stamen). —A. Section *Tephis*: *Polygonum afromontanum* (Danish-Ethiopian Bot. Exped. 1622). —B. Section *Duravia*: *Polygonum douglasii* (Rydberg & Bessey 5364). —C. *Polygonella polygama* (Godfrey 1046). —D. Section *Polygonum*: *Polygonum aviculare* (Ronse De Craene 25 Lb). —E. Section *Pseudomollia*: *Polygonum molliaeforme* (Bornmüller 8181). A, bar = 0.6 mm; B, C = 0.5 mm; D = 0.3 mm; E = 0.4 mm.

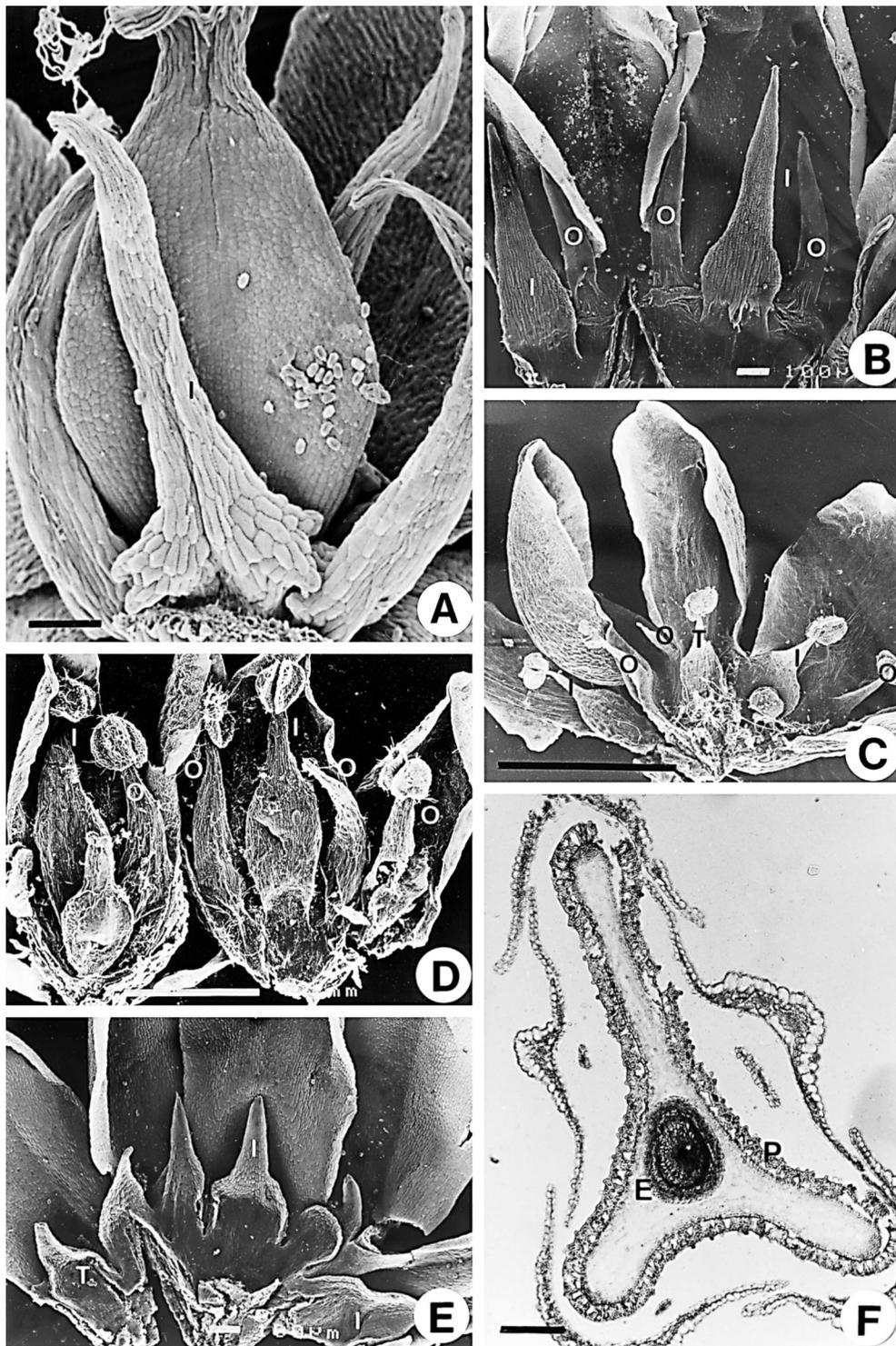


Figure 2. Flowers of *Polygonum* and *Polygonella*, SEM micrographs—A. *Polygonella parksii*: stamens and gynoecium; one inner tepal removed (Correll & Correll 36649). —B. *Polygonum californicum*: flower spread open (Jepson s.n.). —C. *Polygonum tenue*: flower spread open (Puissant s.n.). —D. *Polygonum undulatum*: flower spread open (Fourcade 5962). —E. *Polygonum aviculare*: flower spread open (Ronse De Craene 25 Lb). —F. *Polygonum aviculare*: transverse section of flower (Ronse De Craene 25 Lb). (E, embryo; I, inner stamen; O, outer stamen; P, pericarp; T, transitional stamen). Bars = 100 μ m, except C, D = 1 mm.

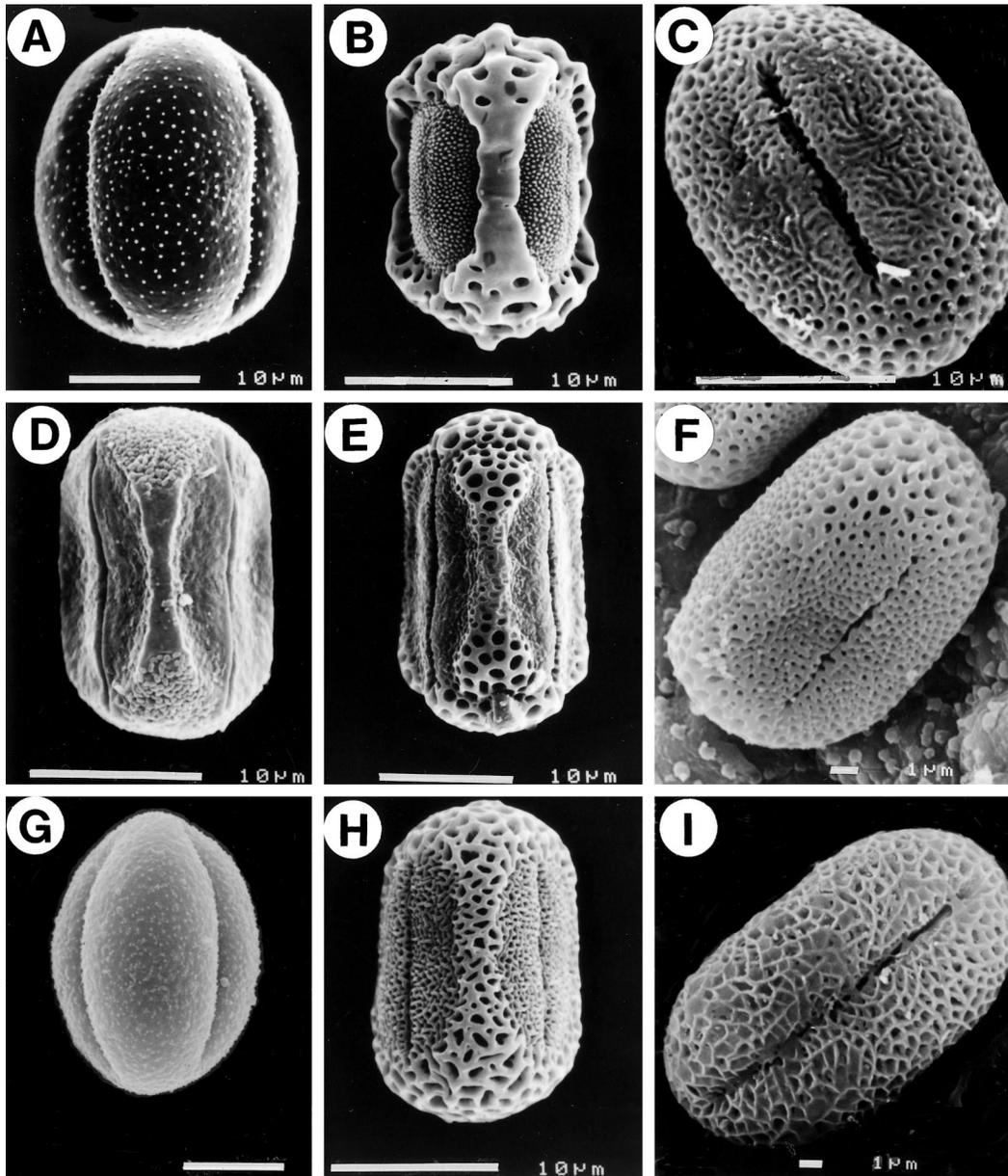


Figure 3. Equatorial view of pollen grains of *Polygonum* and *Polygonella*, SEM micrographs. —A. *Polygonum aviculare* (Nanfeldt 15203). —B. *Polygonum californicum* (Jepson s.n.). —C. *Polygonum douglasii* var. *latifolium* (Howell s.n.). —D. *Polygonum molliaeforme* (Kotschy 778). —E. *Polygonella americana* (Fischer 10). —F. *Polygonum tenue* (Puissant s.n.). —G. *Polygonum afromontanum* (Hedberg 4320). —H. *Polygonum minimum* (Sandberg & Leiberg 799). —I. *Polygonella polygama* (Godfrey 1046). Bars = 10 μm.

3A, 4A). In *Polygonum afromontanum* the exine surface is more or less roughened although comparable with section *Polygonum* (Figs. 3G, 4A).

Pollen of section *Pseudomollia* is tricolporate, prolate, and nearly triangular in polar view (Figs. 3D, 4D). It differs strongly from section *Polygonum* in its dimorphic exine, verrucose on both poles and

mesocolpium, but mostly psilate around the ectoaperture (Figs. 3D, 4D).

Several species of *Polygonella* (Fig. 3E) and of *Polygonum* sect. *Duravia* (Figs. 3B, 3H, 4B) have tricolporate, prolate grains with a dimorphic exine (*Duravia*-type sensu Hedberg, 1946). The exine is semitectate-reticulate at the mesocolpium and the

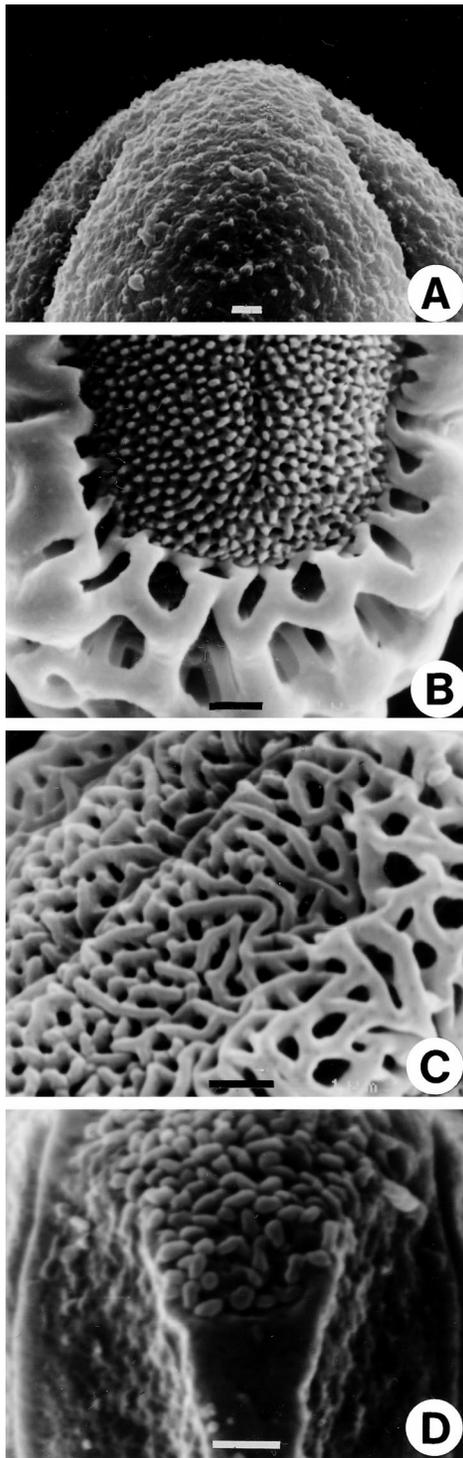


Figure 4. Details of ectexine of selected pollen grains of *Polygonum*, SEM micrographs. —A. *P. afromontanum* subsp. *soboliferum*: polar view (Hedberg 4320). —B. *P. californicum*: detail of alveoli and mesocolpium (Jepson s.n.). —C. *P. minimum*: detail of alveoli around colpus (Sandberg & Leiberger 799). —D. *P. molliaeforme*: detail of mesocolpium at pole and alveoli (Kotschy 778). Bar = 1 μ m.

poles, and rugulate/reticulate or sometimes foveolate with microspinules around the ectoapertures. For some (e.g., *Polygonella polygama*, *Polygonella articulata*, *Polygonum douglasii*, *Polygonum minimum*: Figs. 3C, F, I, 4C), the difference between the exine surface at the mesocolpium and the ectoapertures is a minor question of size, and is in some cases not distinguishable (Fig. 3I). Homogeneously distributed lumina are found in some *Polygonella* (Fig. 3I). As this difference increases, more typical *Duravia*-types occur (e.g., *Polygonum californicum*, *Polygonella parksii*, *Polygonella americana*: Fig. 3B, E). The distinction between zones of reticulations may be abrupt (*Polygonum bolanderi*) or progressive (*Polygonum tenue*: Fig. 3F). It is thus possible to construct a progressive transformation series between the typical *Duravia*-type with strict boundaries between the mesocolpal area and the ectoapertural area and strictly reticulate pollen with only a slight difference between these zones.

EPIDERMAL CELLS OF THE TEPALS (FIG. 5)

The adaxial epidermis of the inner tepals was analyzed by Hong et al. (1998). We add more observations here that are in agreement with the previous results. Tepal epidermal characters cannot be used to differentiate *Polygonum* s. str. from *Polygonella* (cf. Hong et al., 1998). Two types of epidermal cells can additionally be distinguished herein (Fig. 5): more or less rectangular with straight anticlinal walls (Fig. 5D), or puzzle piece-shaped to rectangular outlines with undulate anticlinal walls (Fig. 5A–C, E). Cuticular striae are mostly deep and randomly distributed, but sometimes aligned in one direction.

FRUIT MORPHOLOGY AND ANATOMY (FIGS. 6–9)

The value of fruit anatomy in Polygonaceae was recognized previously (e.g., Lonay, 1922; Marek, 1954, 1958; Neubauer, 1971) and has been used by us recently to delimit the tribes Polygoneae and Persicarieae (Ronse De Craene et al., 2000). Two parameters have been recognized as taxonomically significant: (1) fruit surface patterns (with SEM) (Figs. 6–8), and (2) pericarp anatomy (with SEM and LM) (Fig. 9).

A single bitegmic seed develops from an orthotropous basal ovule and becomes surrounded by a hardened pericarp. The pericarp consists of a sclerified exocarp, a mesocarp, and endocarp (see also Lonay, 1922; Marek, 1958; Neubauer, 1971; Ronse De Craene et al., 2000). The thickenings most commonly occur on the anticlinal (radial) walls, but not

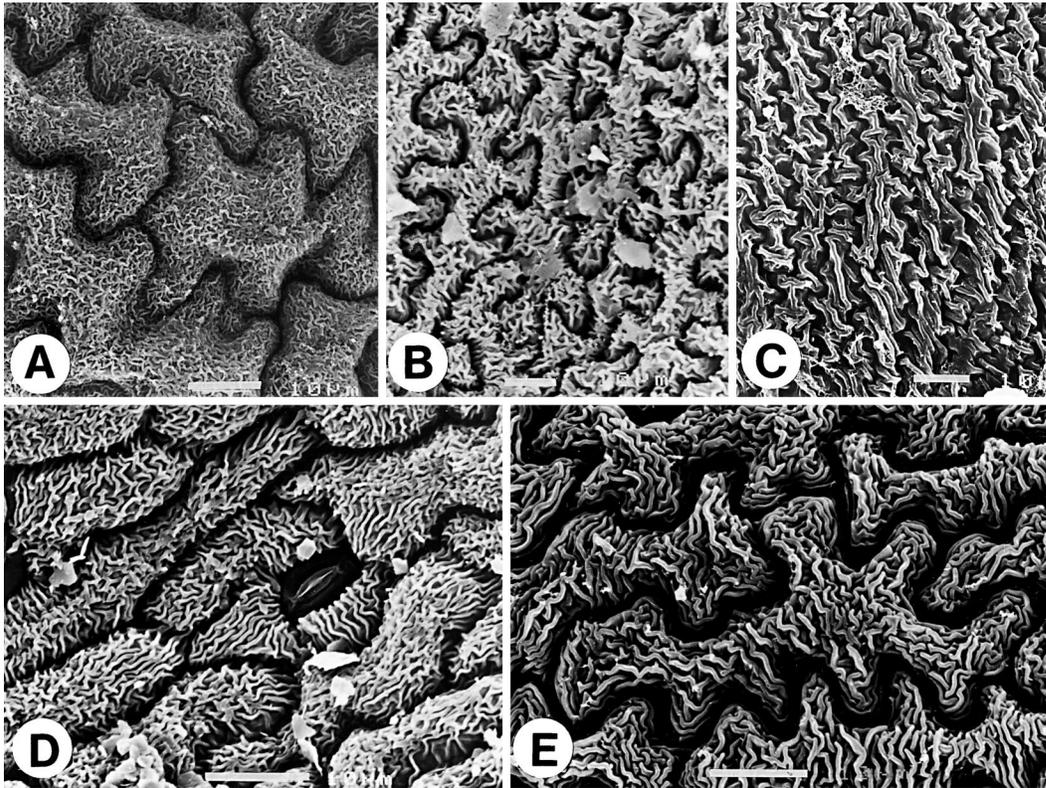


Figure 5. SEM micrographs of the inner tepal epidermis. —A. *Polygonella parksii* (Correll & Correll 36649). —B. *Polygonum douglasii* subsp. *spergulariiforme* (Lyal 1858). —C. *Polygonum bolanderi* (Pringle s.n.). —D. *Polygonum arenastrum* (Ronse De Craene 1157). —E. *Polygonum douglasii* var. *latifolium* (Howell s.n.). Bars = 10 μ m.

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 (Fig. 9B, E, F). In other instances the thickenings are more regular and the lumen appears narrowly rectangular (Fig. 9A, C, H, I). Very often small canals branch from the lumen into the surrounding sclerenchymatous tissue (Fig. 9A, B, H, I). Due to space constraints the anticlinal walls can become variously convoluted or bent in cross or longitudinal sections (Fig. 9A, G, I). 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 cell appears 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 Marek (1954, 1958), Wolf and McNeill (1986), and Ronse De Craene et al. (2000).

In *Polygonella* the outer fruit surface is smooth

(*Polygonella gracilis*, *Polygonella americana*: Fig. 7E, F), or with shallow pits (*Polygonella articulata*: Fig. 8I). Longitudinal cuticular striae are often present (Fig. 8I), but not in *Polygonella fimbriata* (Figs. 7D, 8H), or in *Polygonella gracilis*. *Polygonella fimbriata* has a mixture of a closely packed layer of “tubercles” on the upper fruit with a roughly pitted lower surface (Figs. 7D, 8H). Smooth surfaces are also found in *Polygonum* sect. *Duravia* (e.g., *Polygonum minimum*: Fig. 7A, *Polygonum paronychia*), and section *Polygonum* (e.g., *Polygonum maritimum*: Fig. 6A). In other species the upper half of the fruit can be tubercled and the lower half smooth (e.g., *Polygonum oxyspermum* subsp. *raii*, *Polygonum arenastrum*), and this is related with the pressure of the tepals at the base of the fruit. Smooth surfaces with pits representing the collapsed anticlinal walls of the cells were found in sections *Tephis* (Fig. 8G), *Pseudomollia*, and *Duravia* (e.g., *Polygonum shastense*, *Polygonum californicum*: Fig. 8D, *Polygonum coarctatum*, and *Polygonum tenue*: Fig. 8E). The fruit surface of *Polygonum polygaloides* s.l. (including subspecies

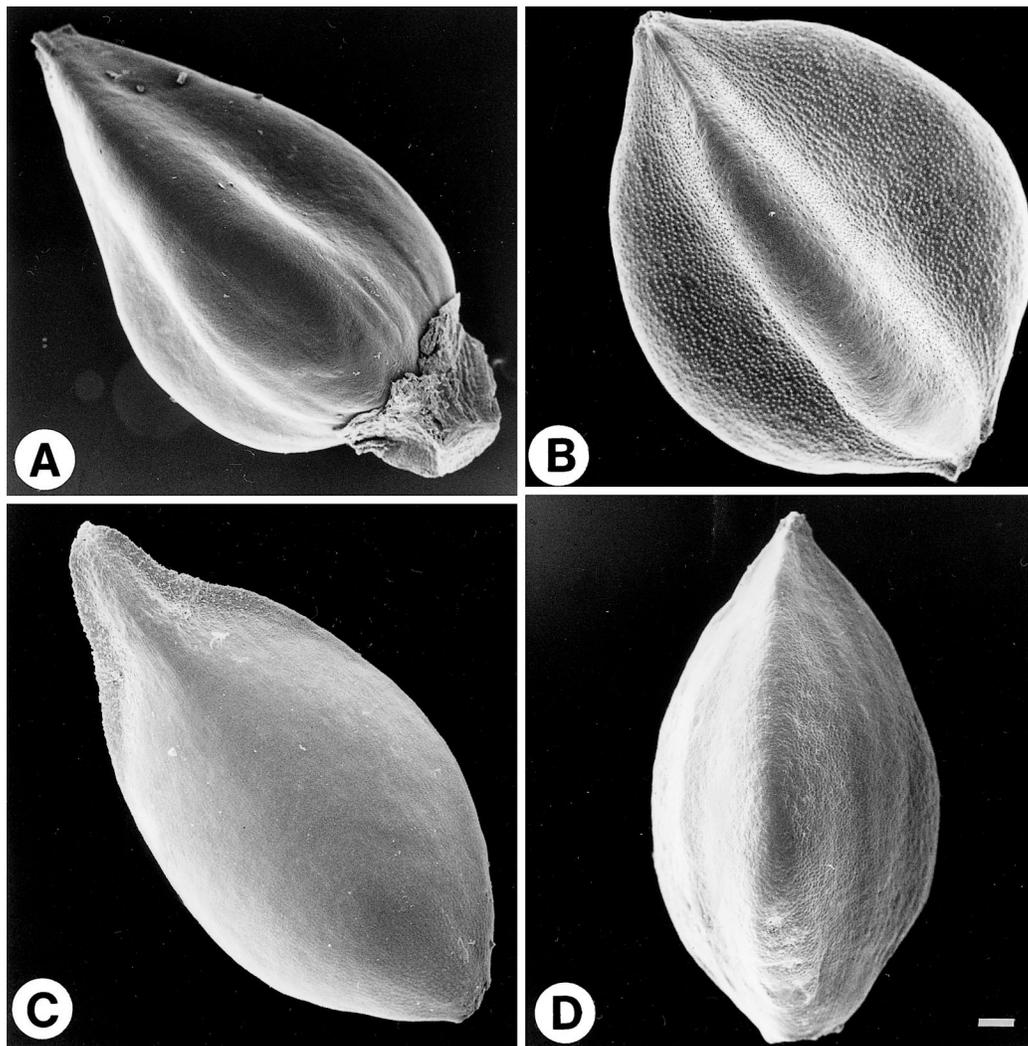


Figure 6. SEM micrographs of lateral views of entire fruits of *Polygonum* sects. *Polygonum*, *Molliaeforme*, and *Tephis* (tepals removed). —A. *P. maritimum*: smooth surface (Nordin 102). —B. *P. bellardii*: tubercled surface (Heldreich 877). —C. *P. molliaeforme*: foveate with short apical wings (Kotschy 778). —D. *P. afromontanum*: pitted surface (Hedberg 4320). Bar = 100 μ m.

kelloggii: Fig. 8F; subspecies *confertiflorum*: Fig. 7C) is unique and shows a scalariform-reticulate pattern with longitudinally running ridges bridged at regular intervals with variations depending on the samples or subspecies studied. These ridges do not necessarily correspond with the anticlinal walls of the cells.

Several species of section *Polygonum* and a few of section *Duravia* have a distinct surface pattern covered by tubercles. Tubercles may be equidistant and sparsely covering the fruit along the anticlinal walls of the cells (e.g., *Polygonum bellardii*: Figs. 6B, 8A), crowded on ridges formed by the anticlinal cell walls (e.g., *Polygonum achoreum*, *Polygonum*

equisetiforme: Fig. 8C), or in longitudinal rows or clusters without connection to the anticlinal walls of the cells (e.g., *Polygonum arenastrum*, *Polygonum aviculare*, *Polygonum douglasii*: Figs. 7B, 8B). Tubercles may be associated with pits, but never with superficial striae. *Polygonum douglasii* and *Polygonum tenue* differ markedly from most other species of section *Duravia* in the presence of tubercles arranged in short longitudinally placed rows (Fig. 8B). In some cases fruits with smooth-pitted surfaces and with globular emergences occur side by side in the same species (e.g., *Polygonum arenastrum*, *Polygonum douglasii*, *Polygonum spergulariforme*, *Polygonum kelloggii*, *Polygonum ten-*

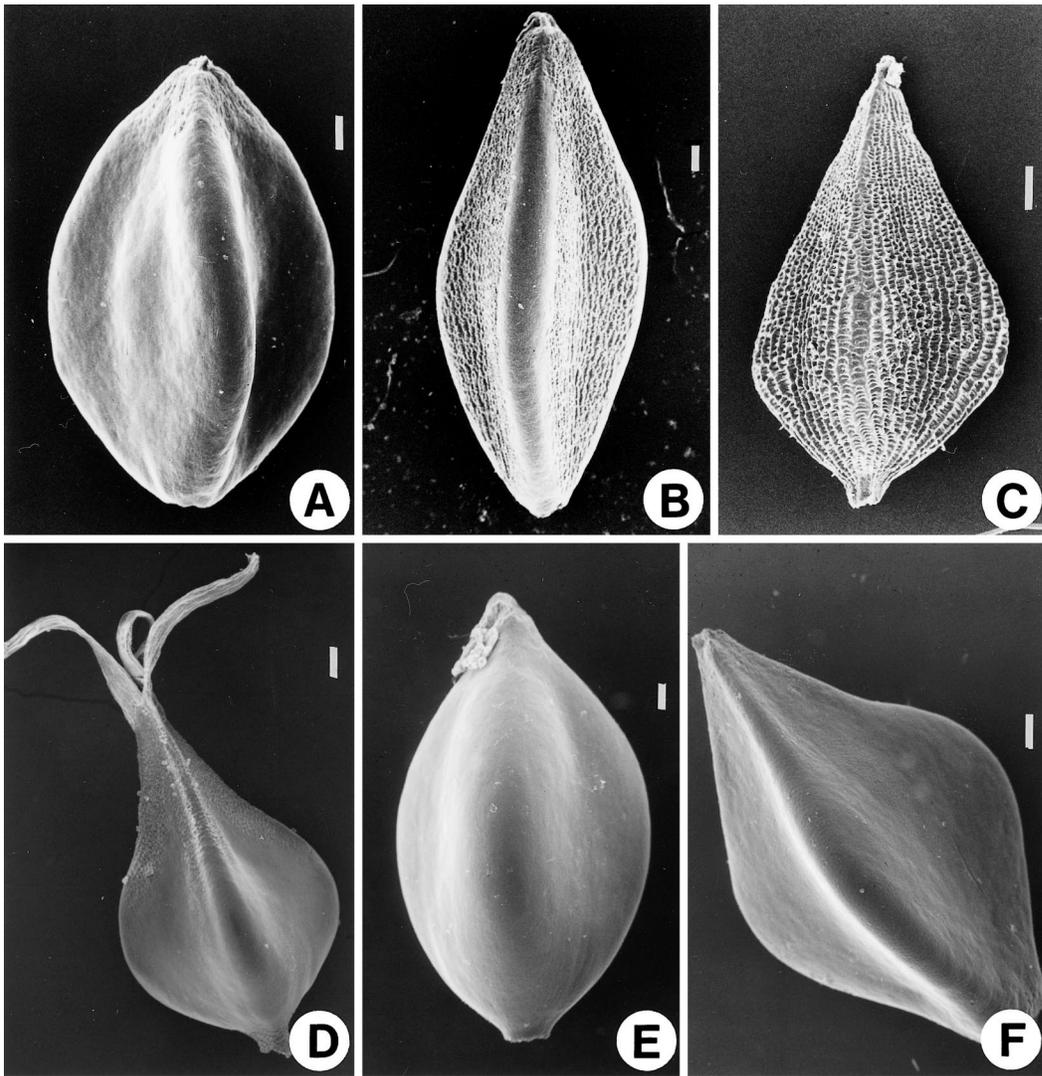


Figure 7. SEM micrographs of lateral views of fruits of *Polygonum* sect. *Duravia* and *Polygonella*. —A. *Polygonum minimum*: smooth surface (Sandberg & Leiberg 799). —B. *Polygonum douglasii*: tubercled surface (Porter & Porter 9722). —C. *Polygonum polygaloides* subsp. *confertiflorum*: reticulate surface (Bacigalupi & Smith 5982). —D. *Polygonella fimbriata*: smooth surface, apically pitted (Blanton 6825). —E. *Polygonella gracilis*: smooth surface (Vestlund s.n.). —F. *Polygonella americana*: smooth to pitted surface (Fischer 10). Bars = 10 μm .

ue: Fig. 8E). The lenticular fruit of *Polygonum molliaeforme* (sect. *Pseudomollia*) is distinctive with a roughly reticulate surface and deep pitting along the wings lining the beak of the fruit (Fig. 6C); the reticulation is more compact and is covered with tubercles at some places (see also Ronse De Craene et al., 2000). The extent of development of the angles of the fruit is correlated with a different surface pattern between the ribs and the angles. In some species this difference is well pronounced (e.g., *Polygonella fimbriata*, *Polygonum molliaeforme*: Figs. 6C, 7D, 8H).

Sections of the fruit have been made for a representative number of species (for details see also Ronse De Craene et al., 2000). In LS the exocarp consists of palisade-like cells (20–80 μm thick) with slightly undulate or straight radial walls. In section *Polygonum* the radial walls appear convolute because of irregular thickening on the inner wall (Lonay, 1922; Neubauer, 1971). The lumen of the cells is narrowly rectangular with dendritical branching toward the outer tangential wall (Fig. 9A, C). The wall is usually thick (> 60 μm) but sometimes thinner (< 40 μm as in *Polygonum oxysper-*

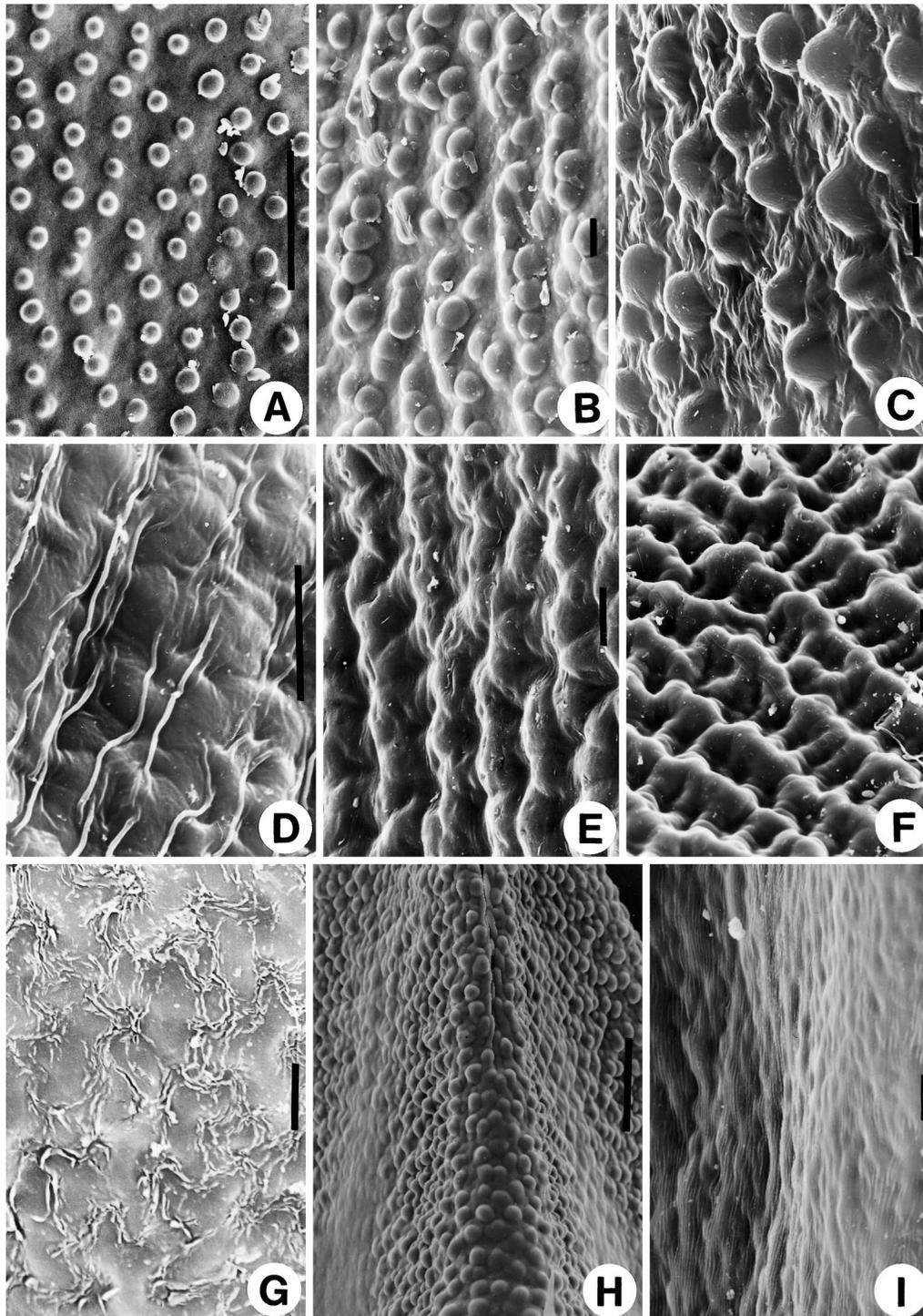


Figure 8. SEM micrographs with details of fruit surfaces of *Polygonum* and *Polygonella*. —A. *Polygonum bellardii*: tubercled (Heldreich 877). —B. *Polygonum douglasii*: tubercles in clusters (Porter & Porter 9722). —C. *Polygonum equisetiforme*: tubercles with pits (Ronse De Craene 975). —D. *Polygonum californicum*: smooth to pitted surface with striae (Jepson s.n.). —E. *Polygonum tenue*: pitted surface (Puissant s.n.). —F. *Polygonum polygaloides* subsp. *kelloggii*: reticulate surface (Porter & Porter 7555). —G. *Polygonum undulatum* (Fourcade 5962): smooth with pits. —H. *Polygonella fimbriata*: detail of granular rib (Blanton 6825). —I. *Polygonella articulata*: pitted surface with striae (Bodin s.n.). Bars = 10 μm , except A and I = 100 μm .

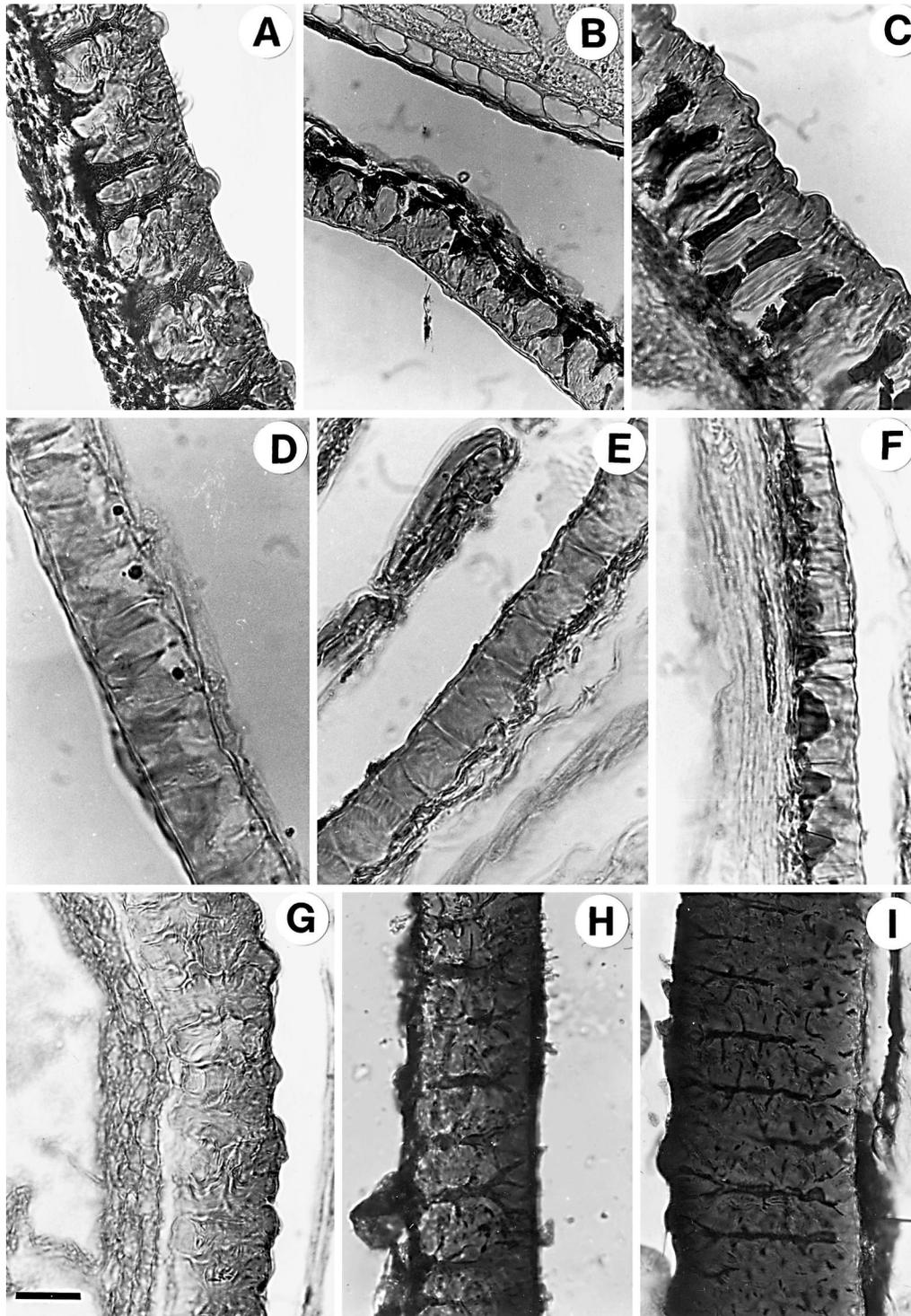


Figure 9. LM micrographs of transverse and longisections of pericarps of *Polygonum* and *Polygonella*. —A. *Polygonum ramosissimum* (Puissant s.n.), TS. Bar = 35 μm . —B. *Polygonum oxyspermum* subsp. *raii*. (Corbière 5306), TS. Bar = 70 μm . —C. *Polygonum bellardii* (Heldreich 877), TS. Bar = 30 μm . —D. *Polygonum shastense* (Carpenter s.n.), LS. Bar = 20 μm . —E. *Polygonella polygama* (Curtiss s.n.), LS. Bar = 15 μm . —F. *Polygonum molliaeforme* (Kotschy 778), LS. Bar = 10 μm . —G. *Polygonum afromontanum* (Hedberg 377), TS. Bar = 40 μm . —H. *Polygonella americana* (Fischer 10), TS. Bar = 20 μm . —I. *Polygonum tenue* (Greene s.n.), LS. Bar = 20 μm .

mum subsp. *raii*: Fig. 9B). More or less similar wall structures were observed in species of section *Duravia* (e.g., *Polygonum douglasii*, *Polygonum tenue*: Fig. 9I), section *Tephis* (although the convolution is more important and it lacks the dendritical branching: Fig. 9G), and only rarely in *Polygonella* (e.g., *Polygonella americana*: Fig. 9H). Almost straight radial walls (< 40 μm wide) with narrow lumina occur in other species of section *Duravia* (e.g., *Polygonum coarctatum*, *Polygonum shastense*, *Polygonum californicum*: Fig. 9D), most *Polygonella* (e.g., *Polygonella articulata*, *Polygonella polygama*: Fig. 9E), and in section *Pseudomollia* (Fig. 9F). Here the lumen appears narrowly rectangular, x-shaped to triangular with the broad base on the inner tangential wall. Dendritical canals are not observed. As emphasized elsewhere (Ronse De Craene et al., 2000), there is no link between the shape of the exocarp cells and the outer surface of the fruit.

CLADISTIC ANALYSIS

The cladistic analysis resulted in 108 trees of length 179 (consistency index (CI) 0.402, retention index (RI) 0.640). The consensus tree is shown in Figure 10 and the 50% majority-rule consensus tree with bootstrap and jackknife values in Figure 11. As is evident from Figures 10 and 11, the trees obtained are relatively well supported (given that all characters used were morphological). Two major clades can be recognized, one containing all species of section *Duravia* and the genus *Polygonella* with a bootstrap-jackknife support of 67%/70%, and another weakly supported clade (BS 64/59%) containing sections *Polygonum* and *Tephis*. In preliminary analyses *Polygonum molliaeforme* consistently fell within section *Duravia*, probably because of convergences in morphological characters, and was consecutively removed from the analysis. The greatest internal support is for the group of species recognized as *Polygonum polygaloides* and allied species (cf. Hickman, 1984, BS 92%). Two clades remain strongly supported within the *Polygonum* clade (sect. *Tephis*) and a clade of three species (*Polygonum arenastrum*, *Polygonum maritimum*, *Polygonum oxyspermum*). The 50% majority-rule consensus tree shows the collapse of internal branches in both clades. Species of *Polygonella* form three paraphyletic clades with species of *Polygonum* sect. *Duravia*, although two of the clades are well supported. Synapomorphies can be recognized for both clades, such as the presence of spines and ochrea morphology in the *Polygonum*

clade, and the *Duravia*-type of pollen and P/E index (except for one species) in the *Duravia* clade.

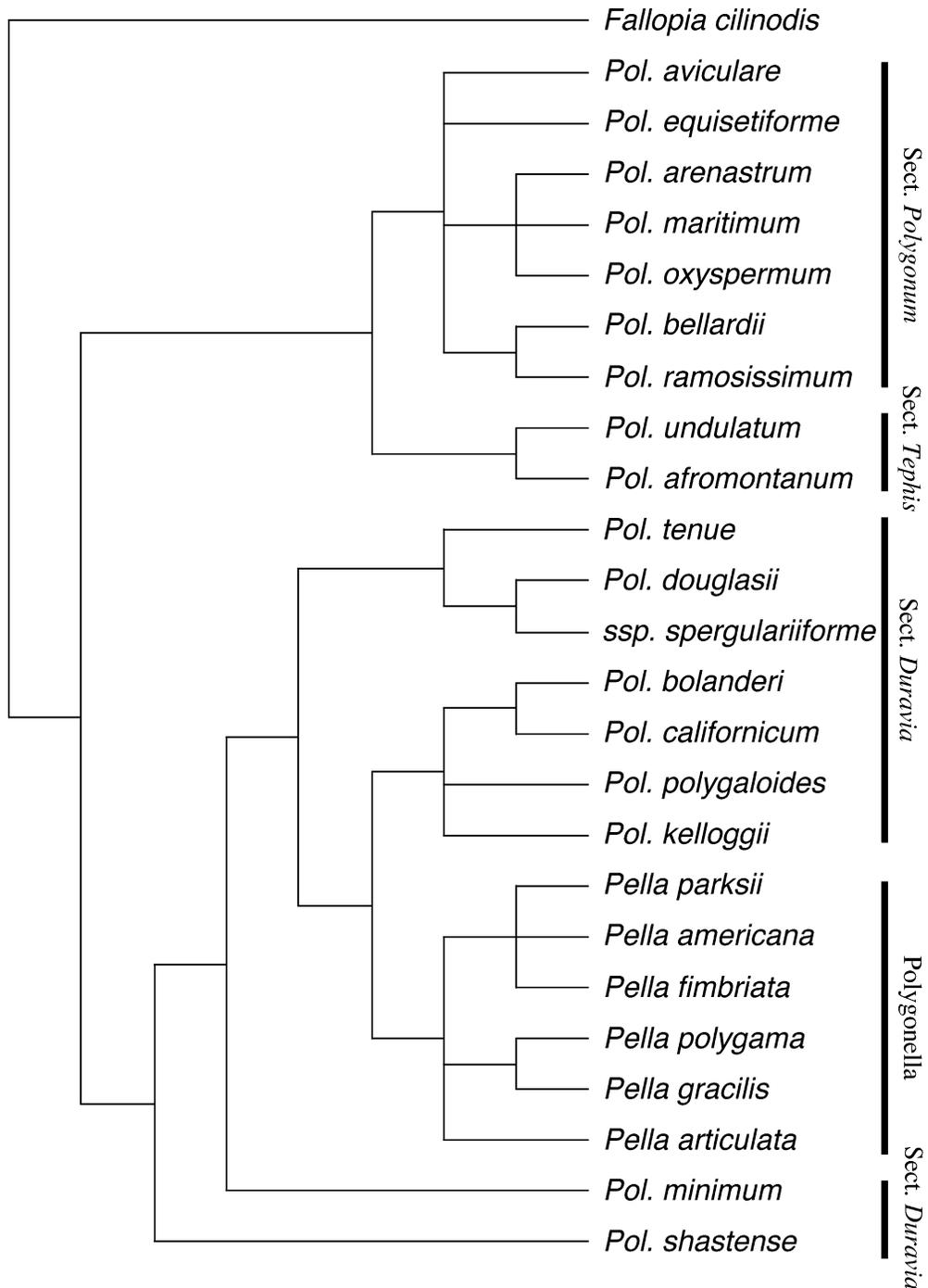
DISCUSSION

We found little unambiguous evidence to support a full segregation of the genus *Polygonella*, because several features known to be distinctive of the taxon appear regularly in *Polygonum*, especially in section *Duravia*. If the genus *Polygonella* is considered as sufficiently distinct, a number of species from *Polygonum* sect. *Duravia* would have to be transferred to *Polygonella*. This would considerably reduce the number of characters necessary to distinguish *Polygonella* as a genus, unless other evidence is found. Typical *Polygonella* species show the following features: a single flower per node arising from the axil of a short scaly bract, a tendency for unisexuality in some species, flowers often pendulous with the abscission zone in the middle of the pedicel, perianth mostly unequal with shorter often reflexed outer tepals, and inner tepal lobes mostly larger, accrescent, and not appressed to the fruit. Tepal venation is reduced to a single midvein. The number of stamens is usually not reduced, and the inner filaments are abruptly widened. The pollen has a well-marked dimorphism of the ectexine. Fruits are slender-stipitate and are often beaked; the surface is smooth, mostly with striae, and pericarp cells have a narrow lumen without dendritical branching and straight radial walls. However, as shown in Table 2 and Appendix 4, the differences between *Polygonella* and the other tribes are not straightforward. There are a few general characteristics for the species of *Polygonella*, although these are not shared by all, except for the scarious bracts, internodal branches, and the pedicel abscission zone. The cladistic analysis based on morphological characters does not permit the identification of a well supported *Polygonella* clade with these characters (Figs. 10, 11). Therefore, we cannot ascertain that these are synapomorphies.

Vautier (1949) and Horton (1963) interpreted the presence of a single unbranched vein as a reductive feature. Flowers of *Polygonella* (with tepals having an average length of 3 mm, even becoming accrescent in fruit) are not necessarily smaller than those of *Polygonum* s. str. It can be speculated that the reduction in tepal vein may be an adaptation to an arid environment necessitating less water transport. Some *Polygonum* growing in similar dry habitats also have a single unbranched vein (e.g., *Polygonum molliaeforme*: Fig. 1E).

The exine of pollen of section *Duravia* and *Po-*

Strict consensus of 108 trees

Figure 10. Strict consensus of 108 trees (length 179, CI 0.402, RI 0.640). Pol. = *Polygonum*; Pella = *Polygonella*.

Jackknife 50% majority-rule consensus tree

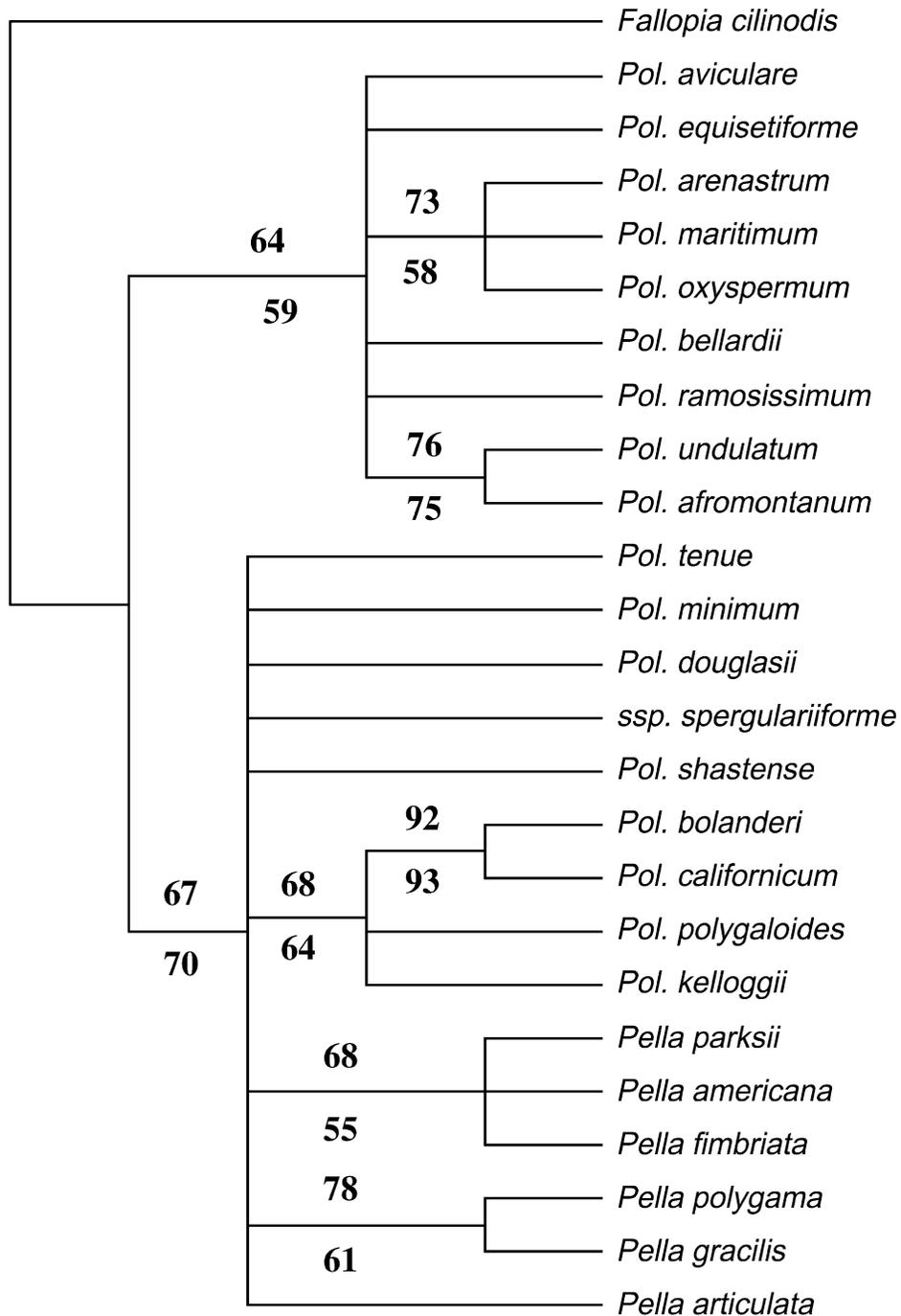


Figure 11. Bootstrap and jackknife 50% majority-rule consensus tree. Bootstrap values shown above branches, jackknife values below. Pol. = *Polygonum*; Pella = *Polygonella*.

lygonella appears to have a mixture of the pattern in *Persicaria* (an alveolate reticulum) and section *Polygonum* (a finely granular surface surrounding the furrows; see also Hedberg, 1946; Nowicke & Skvarla, 1977; Hong & Oh, unpublished). Hedberg (1946) argued that the similarities in pollen of *Polygonella* and section *Duravia* are the result of convergent evolution, because of differences in habit, a disjunct geographical distribution, and the repetition of the transition between the *Duravia*-type and *Avicularia*-type within the *Polygonella* group. Pollen of section *Polygonum* is invariably smooth with scattered microspinules, and there is little or no variation in this pattern. The *Avicularia*-type of pollen can be readily recognized and differs from the reticulate pollen found in some species of section *Duravia* and *Polygonella*, a fact not recognized by Hedberg. There are strong indications that the similarity in pollen morphology of section *Duravia* and *Polygonella* reflects a synapomorphy for both taxa. Regarding the structure of the exine one has a clear continuum of variation in the pollen of section *Duravia* and *Polygonella*. On one extreme, the pollen of *Polygonella polygama* and some *Polygonum douglasii* is reticulate-alveolate without dimorphism (Fig. 3I). A slight differentiation of the size of the reticulate pattern between the mesocolpium/poles and ectoapertures is found in *Polygonum tenue* (Fig. 3F) and *Polygonum douglasii* (var. *latifolium*; Fig. 3C). This difference is more pronounced in pollen of *Polygonum minimum* (Figs. 3H, 4C), *Polygonum douglasii* subsp. *spargulariiforme*, *Polygonum shastense*, *Polygonella parksii*, *Polygonella articulata*, and *Polygonella fimbriata* with a reticulate-rugulate pattern. A change in the pattern of sculpturing around the ectopores occurs in *Polygonum californicum* by the presence of microspinules above the reticulation (Figs. 3B, 4B). The area around the ectoapertures can also become psilate to foveolate without traces of a reticulation (Fig. 3E).

However, no clear link can be made between the smooth exine with microspinules of *Polygonum* sect. *Polygonum* (Fig. 3A), and the reticulate-alveolate pattern of *Polygonella* and *Polygonum* sect. *Duravia* (Fig. 3B, C, E, F, H, I). This distinction supports the recognition of section *Duravia* separate from section *Polygonum*. The pollen differences between *Polygonella* and section *Duravia* are almost inexistent, and the two are clearly interrelated.

Interestingly, the pollen of *Polygonum molliaeforme* of section *Pseudomollia* appears as intermediate between the *Avicularia*- and the *Duravia*-type (Hong & Oh, unpublished). Given the disjunct geographical distribution of section *Pseudomollia* in

Iran and section *Duravia* in North America, it is probable that a dimorphic exine has arisen independently and more than once. Moreover, some species of *Fallopia*, another genus of tribe Polygonaceae (e.g., *F. convolvulus*, *F. scandens*, *F. dumetorum*; Ronse De Craene, unpublished), also show a dimorphic exine (viz. a smooth mesocolpium but punctate in the region of the colpi), as rightly pointed out by Nowicke and Skvarla (1977). Indeed, we found that two pollen types occur side by side between different species of *Fallopia* (Hong et al., unpublished), viz. with a dimorphic exine or a more uniform one.

By observing fruit surface patterns with the SEM we could distinguish three main types: (1) smooth, possibly with small pits; (2) with globular protuberances (tubercles), lined along the anticlinal walls of the cells, or aggregate in rows; (3) with interconnected ridges separated by depressions (reticulate). In addition, longitudinal striae may be present and may be weakly or strongly developed. Wolf and McNeill (1986) recognized four surface patterns for species of section *Polygonum* occurring in Canada: smooth, roughened, papillose, and striate-papillose. A distinction between smooth and roughened achenes appears to be related to the collapse of the anticlinal cell walls. The papillose and striate-papillose types correspond with the types we described as tubercled. The value of surface patterns appears to be mostly restricted to the specific level in section *Polygonum*, with the occasional presence of smooth achenes and achenes having tubercles (e.g., *Polygonum arenastrum*, *Polygonum douglasii*, *Polygonum tenue*, *Polygonum ramosissimum*).

While we found highly distinctive surface patterns in some species, the different sections could not be delimited solely on the basis of the fruit surface, as different types overlap between the sections. There is also an intergradation between different patterns, with a smooth surface at one extreme, and the highly distinctive tubercled surface at the other. Stages in between are a rough surface with shallow to deep pits, and with widely spaced to aggregated tubercles.

There is strong overlap between some species of section *Duravia* and section *Polygonum* on the one hand, and between section *Duravia* and *Polygonella* on the other. Similar smooth fruit surfaces (possibly with pits lining the anticlinal cell walls) are found in *Polygonum* sect. *Duravia* (e.g., *Polygonum californicum*, *Polygonum minimum*) and section *Polygonum* (e.g., *Polygonum maritimum*). The slender stipitate fruits of typical species of *Polygonella* with smooth-striate surface (Fig. 7D, F) can be often recognized in species of section *Duravia*

(Fig. 7B, C). In contrast, other species of section *Duravia* have a pattern more similar to *Polygonum* sect. *Polygonum* (*Polygonum douglasii*: Fig. 8B, *Polygonum tenue*: Fig. 8E). The reticulate pattern of *Polygonum polygaloides* and allies (Fig. 8F) appears as a completely divergent type, possibly derived from a pitted surface as in *Polygonum tenue*. Smooth and tubercled surfaces can occur side by side in closely related species, or even within the same species. *Polygonella fimbriata* has its fruit partly covered with tubercles (Fig. 8H).

Sections of exocarps revealed two main patterns, which were not necessarily linked with the external fruit surface: (1) broadly square to cylindrical cells (> 50 μm) with strongly convolute radial walls, broad lumen and dendritical branching toward the periphery; (2) narrowly rectangular cells (< 40 μm) with straight radial walls, narrow lumen, and absence of dendritical branching.

The internal fruit wall in *Polygonum* sect. *Pseudomollia* resembles that of *Polygonella* to a great extent in lacking dendritical canals, and with straight radial walls and narrow lumen (Fig. 9F). This pattern also occurs in species of section *Duravia* centered around *Polygonum californicum*.

The presence of strongly convolute radial walls correlates with a tubercled surface (rarely smooth) and an absence of striae. All studied species of sections *Polygonum* (Fig. 9A–C) and *Tephis* (Fig. 9G) show this characteristic pattern, as well as some species of section *Duravia* (*Polygonum douglasii*, *Polygonum tenue*: Fig. 9I). *Polygonella americana* is an obvious exception for the genus with its convolute radial walls (Fig. 9H).

CAN *POLYGONELLA* BE MAINTAINED AS A GENUS SEPARATE FROM *POLYGONUM*?

Polygonum s.l. has always been difficult from a taxonomic point of view, and several attempts have been made in the past to improve the infrageneric limits (see Ronse De Craene & Akeroyd, 1988, for an overview). In contrast, *Polygonella* has always been considered as distinct, first close to *Atraphaxis*, then in the vicinity of *Polygonum* s. str. (Table 1). This study, however, has demonstrated that *Polygonum* s. str. and *Polygonella* share several characters that were thought to be distinctive, and that a strict taxonomic separation at the generic level is not tenable.

Based on the present study the following conclusions are significant:

(1) Strict delimitation between *Polygonella* and *Polygonum* s. str. is not supported. Characters of several species of *Polygonum* sect. *Duravia* overlap

with those of *Polygonella*. *Polygonum* sect. *Duravia* appears paraphyletic relative to *Polygonella*, with a basal position for the polymorphic *Polygonum douglasii*.

Especially on the basis of pollen (the distinctive *Duravia*-type of pollen and the reticulate exine), as well as fruit anatomy (rectangular cells with straight radial walls and more or less triangular lumen), a separation of section *Duravia* from section *Polygonum*, and including *Polygonella*, is best maintained. Polymorphic species, such as *Polygonum douglasii*, can have different characters spread over different populations. For example, *Howell* s.n. (ex *Wibbe* 7841), *Carpenter* s.n., and *Porter & Porter* 9722 have a tubercled fruit surface and a thick pericarp; *Howell* s.n. (ex *Wibbe* 7842) has a smooth surface with a thin pericarp. Similarly, pollen of *Polygonum douglasii* subsp. *spergulariiforme* strongly resembles the *Duravia*-type, while the other samples of *Polygonum douglasii* studied are intermediate with little differentiation between mesocolpium and colpi regions. However, more research in these polymorphic groups is clearly needed. Also, the sampling for this study is too limited to draw definite conclusions about the interspecific relationships of section *Duravia*.

(2) *Polygonum* sect. *Tephis* cannot be well separated from section *Polygonum*. Both sections share similar pollen morphology, fruit surface patterns, and fruit anatomy. Distinctive features are the afro-montane distribution and dimerous flowers of section *Tephis*.

The pollen with rough exine with microspinules and the roughly pitted fruit surface of *Polygonum afromontanum* (Figs. 3G, 4A, 6D) is found in several species of section *Polygonum*. Similarities with *Polygonum undulatum* are even greater. Ronse De Craene and Akeroyd (1988), however, maintained the section, mainly because of dimerous flowers with keeled outer tepals, and the development of two lateral veins on the tepals. Stamen number is also six in *Polygonum afromontanum* (with 5 tepals) and *Polygonum undulatum* (with 4 tepals), the two outer not being “duplicated,” as in *Polygonum molliaeforme* (numbers may vary between 6 and 8). In *Polygonum undulatum*, the perianth is dimerous, apparently by the loss of an outer tepal with two stamens. The dilated inner filaments and tepal epidermis (Hong et al., 1998) match those of section *Polygonum*. However, the inclusion of anatomical characters may support a subsectional rank. Given the limited geographical distribution, this could also be justified.

(3) *Polygonum* sect. *Pseudomollia* is distinctive in external fruit characters (winged lenticular achenes),

but shows overlap in characters of pollen and fruit anatomy with *Polygonella*. These are probably the result of convergences. The different phytogeography (the former occurs in Persia, while the latter is restricted to North America) supports this.

Section *Pseudomollia* Boiss. was originally erected on the basis of the lenticular achene with two-parted style, solitary flowers, and overlapping ochreae. Material investigated by Ronse De Craene and Akeroyd (1988) had only five stamens, as the outer were not “duplicated”; another specimen missed one outer pair altogether. Haraldson (1978) mentioned the presence of five stamens and two or three staminodes; these probably represent the outer stamens. Rechinger and Schiman-Czeika (1968) mentioned 5 to 8 stamens and suggested that anthers drop off easily, which might give the false impression of staminodes. The reduction of outer stamens and the inflated filament bases, coupled with one unbranched vein per tepal, as well as the tepal epidermal cells (Hong et al., 1998) fit within section *Polygonum*. Haraldson (1978) did not find the anatomical differences important enough to merit sectional rank. However, the fruit morphology (Fig. 6C) with lateral winglets along the beak is quite distinctive, as well as the pitted reticulate fruit surface. Also, the pollen with dimorphic exine and distinctive sculpturing is not matched in section *Polygonum*. The absence of secondary ramifications of the tepal veins is another distinctive feature, also found in *Polygonella* and some species of section *Duravia*. Given the extended proposal in this paper for delimiting the genus *Polygonum* s. str., *Pseudomollia* is best maintained as a section of *Polygonum*.

SECTIONAL AND SUBSECTIONAL DELIMITATION

Polygonella appears nested within a well-defined genus *Polygonum*. Characters shared by species of *Polygonum* have been listed in Ronse De Craene and Akeroyd (1988) and include the dilated inner filaments with occasional replacement of the outer stamen pair by single stamens, or their reduction, the absence of structural nectaries, similar tepal epidermal cells, the single vein per tepal, and the difference between outer and inner tepals. To reflect more natural monophyletic groupings, the merging of *Polygonella* within *Polygonum* is indicated and given below. Alternatively, the genus *Polygonella* could be maintained and expanded as to include all species of section *Duravia*. However, this shift is not advisable, as one cannot find sufficient diagnostic evidence to identify *Polygonella* as distinct from *Polygonum*, besides the pollen. In-

deed, the maintenance of a generic status is exaggerated, compared to other genera such as *Fallopia*, *Persicaria*, and *Fagopyrum*. For example, the inclusion of the genus *Reynoutria* Houtt. as a section of *Fallopia* by Ronse De Craene and Akeroyd (1988) has been supported by cytological studies (e.g., Bailey & Stace, 1992). A similar logic is applied here for *Polygonella*. *Polygonella* may be viewed as an extreme evolutionary line within section *Duravia*.

Hickman (1984) proposed the rank of subgenus *Duravia* for the North American species of *Polygonum* (see introduction). We do not support this subdivision on the basis of a range of characters (the variation of *Polygonum polygaloides* falls within *Polygonella*). Two distinctive features characterize *Polygonella*: the abscission zone is situated in the middle of the pedicel, and the branches appear internodal by fusion with the main stem. *Polygonella* is best included within section *Duravia* of *Polygonum* s. str. The characters shared by this section are obvious: *Duravia*-type pollen (with all possible intermediates), a reduced number of flowers per inflorescence, a smooth fruit surface with narrow pericarp of rectangular cells (*P. polygaloides* has a distinctive outer surface), and a tendency for the outer tepals to become strongly dimorphic from the inner, with a single unsplit vein. A subdivision of a subsection *Thysanella* separate from *Polygonella* (as was done by Horton, 1963) appears superfluous as the differences enumerated for *Thysanella* are made irrelevant by the inclusion of species from section *Duravia* within *Polygonella*.

We propose the following sectional division for *Polygonum* sensu stricto:

Polygonum L. sect. **Polygonum**

Subsection **Polygonum** (L.) Ronse De Craene & S.-P. Hong, stat. nov. TYPE: *Polygonum aviculare* L.

Subsection **Tephis** (Adans.) Ronse De Craene & S.-P. Hong, stat. nov. TYPE: *Polygonum undulatum* (L.) Bergius = *Atraphaxis undulatum* L.

Polygonum sect. **Pseudomollia** Boiss. TYPE: *Polygonum molliaeforme* Boiss.

Polygonum sect. **Duravia** S. Watson

Subsection **Duravia** (S. Watson) Ronse De Craene & S.-P. Hong, stat. nov. TYPE: *Polygonum californicum* S. Watson

Subsection **Polygonella** (Michx.) Ronse De Craene & S.-P. Hong, stat. nov. TYPE: *Polygonum articulatum* L.

A key to the sections and subsections is presented in Appendix 2.

We have shown that the notion of *Polygonella* as an independent genus should be abandoned. The results of this study reflect the need for a renewed investigation of the North American species of *Polygonum*. With a few exceptions no substantial molecular studies have been performed in the Polygonaceae, especially in the genus *Polygonum*. This would be a helpful addition to our morphological investigations. The understanding of the internal relationships of *Polygonella* to section *Duravia* could be highly improved, as our study does not clarify the internal relationship of the clade optimally.

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APPENDIX 1. Origin of species studied, with their synonymy. Species used in the cladistic analysis are marked with *.

● **Polygonum** sect. **Polygonum**

- Polygonum aviculare* L.*
SOUTH AFRICA. **Kimberley region**: Kalkdrift, *Brueckner 771* (UPS). BELGIUM. Bruges, subsp. *aequale*; pickled: *Ronse De Craene 25 Lb* (LV). SPAIN. **Malaga Prov.**: Fuengiola, *Nanfaldt 15203* (UPS) (pollen).
- Polygonum achoreum* Blake
U.S.A. **Wyoming**: Crook Co., Sundance, *Porter & Porter 8384* (UPS).
- Polygonum maritimum* L.*
FRANCE. **Bouches-du-Rhône**: Camargue, étang d'Iland, *Nordin 102* (UPS). GREECE. **Kos**: W of Tingakion, *Davis 67953* (E).
- Polygonum erectum* L.
U.S.A. **Illinois**: Fountaindale, *Bebb s.n.* (UPS). **Pennsylvania**: Delaware Co., 1 mi. NE of Broomall, *Wheeler 5660* (E).
- Polygonum bellardii* All.*
GREECE. **Thessaliae**: Pharsalum, *Heldreich 877*, ex Herb. *Bullefont 8369* (LV). HUNGARY: *Herb. De Dieu-donné* (BR).
- Polygonum equisetiforme* Sibth. & Sm.*
TUNISIA. **Jerba**: near hotel Toumana, *Ronse De Craene 975* (spirit 309 Lt) (LV).
- Polygonum arenastrum* Boreau*
U.K. **Devon**: Prawle Point, E. Prawle, *Ronse De Craene 1157* (spirit 405 Le) (LV).
- Polygonum oxyspermum* Meyer & Bunge ex Ledeb. subsp. *raii* (Bab.) D. A. Webb & Chater*
FRANCE. **Manche**: Vauville et Denneville, *L. Corbière 5306*, ex Herb. *Bullefont 8443* (LV).
- Polygonum ramosissimum* Michx.*
U.S.A. **Kansas**: St. Mary's, *P. A. Puissant s.n.* (LV).

● **Polygonum** sect. **Tephis**

- Polygonum afromontanum* Greenway*
KENYA. **Nanyuki Distr.**: Mt. Kenya, NW slope along Sirimon, *Hedberg 4320* (UPS). ETHIOPIA. **Kaffa Prov.**: *Danish-Ethiopian Botanical Expedition 1972–1973 1622* (K). **S Bale Prov.**: Ririka, *Hedberg 377* (UPS).
- Polygonum undulatum* (L.) Bergius*
SOUTH AFRICA. **Humansdorp Distr.**: 2.6 mi. from Assegai Bosch, *Fourcade 5962* (BOL). **Knysna**: in aperitis Zitzikamma, *Schlechter 5974* (E).

● **Polygonum** sect. **Pseudomollia**

- Polygonum molliaeforme* Boiss.
IRAN. Kuh-Daena, *Kotschy 778* (UPS); Denawand, *Bornmüller 8181* (K); Kuh-Daena, *Kotschy s.n.* (type) (E).

● **Polygonum** sect. **Duravia**

- Polygonum californicum* Meisn.*
U.S.A. **California**: Butler Co., N of Oroville, *Heller 11763* (NY); Eal River, *Jepson s.n.* ex Herb. *Wibbe 92-7830* (LV); Eal River, viii 1892, *Jepson s.n.* (UPS) (pollen); Glen Co., 8 mi. E of Newville, *A. A. Heller 11553* (E).
- Polygonum polygaloides* Meisn.*
U.S.A. **Oregon**: *Howell s.n.* (LV); ex Herb. J. Wibbe,

T. Howell s.n. (BR). **Wyoming:** Uinta Co., Snake River, *Nelson & Nelson 6463* (UPS). **California:** Nez Perce Co., Lake Waha, A. A. & E. G. Heller 3394 (E).

Subsp. *kelloggii** (E. Greene) Hickman [= *Polygonum kelloggii* Greene]: U.S.A. **Wyoming:** Johnson Co., Big Horn Range, W of Buffalo, Circle Park, *Porter & Porter 7555* (UPS).

Subsp. *confertiflorum** (Nutt. ex Piper) Hickman [= *Polygonum confertiflorum* Nutt. ex Piper]: U.S.A. **California:** Modoc Co., 9 mi. NW of Camby, *Bacigalupi & Smith 5982* (UPS). CANADA. **Saskatchewan:** Battle Creek, *Herb. Geological Survey of Canada 12890* (E).

3. *Polygonum shastense* Brewer*

U.S.A. **California:** E North Peak, *Nygsten s.n.* (UPS). **California?** Placer Co., A. M. Carpenter *s.n.* ex Herb. *Wibbe 92-7880* (LV); N slopes above Coldsham, Sierra Nevada, C. F. Sonne *s.n.* ex Herb. *Wibbe 92-7879* (LV).

4. *Polygonum tenue* Michx.*

U.S.A. **Massachusetts:** Milten Blue Hills, *Forbers 1346* (UPS); Baltic Co., P. A. Puissant *s.n.* (LV), *Greene s.n.* (UPS). **North Carolina:** Asha Co., bluff Mt., *Leonard et al. 2038* (E).

5. *Polygonum douglasii* E. Greene*

U.S.A. Placer Co., Sierra Nevada Mts., A. M. Carpenter *s.n.* ex Herb. *Wibbe 92-7840* (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 92-7841* (LV).

As var. *latifolium* E. Greene. U.S.A. **Oregon:** Siskiyou Mountains, *Howell s.n.*, ex Herb. *Wibbe 92-7842* (LV).

As *P. douglasii* greene var. *montanum* Small: U.S.A. **Montana:** Small, *Rydberg & Bessey 5364* (K). **Nevada:** Washol Co., Mt. Rose, Nevada agricultural Experiment Station Herbarium, C. L. Brown *s.n.* (E).

Subsp. *spergulariiforme** (Meisn. ex Small) Hickman [= *Polygonum coarctatum* Dougl. ex Meisn.]: U.S.A. **Oregon:** Grant's Pass, *Howell s.n.* ex Herb. *Wibbe 92-7881* (LV), *Lyal 1858* (K), *Lemmon 1210* (UPS). **California:** University of California Jepson Herb. (lectotype of *P. coarctatum*) (E); Trinity Co., Hettenshaw Valley, S. K. Harris *et al.* 942 (E); Trinity Co., Van Duren River, 3 mi. below Hettenshaw valley, S. K. Harris *et al. s.n.* (E).

6. *Polygonum bolanderi* Brewer ex A. Gray*

U.S.A. **California:** Napa Hills, C. G. Pringle *s.n.*, ex Herb. *Wibbe 92-7829* (LV).

7. *Polygonum paronychia* Cham. & Schlecht.

U.S.A. **California:** San Francisco, Golden Gate Heights, *Rose 47103* (UPS).

8. *Polygonum minimum* S. Watson*

U.S.A. **Washington:** Cascades, Stevens Pass, *Sandberg & Leiberg 799* (BR, UPS). **Montana:** on trail to Sperry Glacier, L. M. Umbach 823 (E).

• *Polygonella*

1. *Polygonella americana* (Fisch. & Mey.) Small*

U.S.A. **Texas:** Cat. Springs, *Fischer 10* (UPS). **Arkansas:** Hot Springs Co., Malvern, *Palmer 8473* (K). **Alabama:** Blount Co., Blackwarrior Creek, *Meisner 1845* (BR).

2. *Polygonella articulata* (L.) Meisn.*

U.S.A. **Massachusetts:** *Oakes? s.n.* (UPS). **New Jersey:** Woodbury, *Henry S. Conard s.n.* (LV); Middlesex Co., South Amboy, *Bodin s.n.* (UPS).

3. *Polygonella polygama* (Vent.) Engelm. & Gray [= *Polygonella parvifolia* Michx.]*

U.S.A. **North Carolina:** Brunswick Co., Orton Plantation Garden, *Godfrey 1046* (K). **California:** *Curtiss s.n.*

(UPS). **Florida:** Indian River, *Curtiss 2433* (LV), *Curtiss 5525* (K); Palm Beach, *Curtiss 5525* (E).

4. *Polygonella parksii* Cory*

U.S.A. **Texas:** Leon Co., Normangle, Hilltop lakes resort, *Correll & Correll 36649* (K).

5. *Polygonella fimbriata* (Elliott) Horton*

U.S.A. **Florida:** Tampa, *Blanton 6825* (S).

6. *Polygonella gracilis* Meisn.*

U.S.A. **Mississippi:** Sandy barrens, Pass Christian, A. B. Langlois 177, ex Herb. *Wibbe 92-7817* (LV). **Florida:** Orange Co., Killarney, *O. Vestlund s.n.* (UPS).

APPENDIX 2. Key to (sub)sections of *Polygonum* sensu stricto.

- 1a. Flowers dimerous, fruits usually lenticular.
 - 2a. Small annual herbs, pollen dimorphic, fruit surface tubercled with lateral wings -----
----- sect. *Pseudomollia*
 - 2b. Small to large shrubs, pollen monomorphic (*Avicularia*-type), fruit surface smooth to pitted -----
----- subsect. *Tephis*
- 1b. Flowers pentamerous, fruits usually trigonous.
 - 3a. Flowers borne in clusters of 2 to 4(6) per node, rarely with single flower per node, outer stamens occasionally reduced, pollen *Avicularia*-type, tepal vasculature dendritical -----
----- subsect. *Polygonum*
 - 3b. Flowers borne singly on each node (rarely 2 or more), always with 8 stamens and three carpels, pollen *Duravia*-type or derived within, tepal vasculature dendritical or reduced to a single vein.
 - 4a. Bracts subtending individual flowers or flower clusters leaf-like with papery ochreolae, abscission zone when present just below flower -----
----- subsect. *Duravia*
 - 4b. Bracts subtending individual flower scarious, abscission zone in the middle of the pedicel -----
----- subsect. *Polygonella*

APPENDIX 3. Characters used in the cladistic analysis (based on pers. obs.; Meisner, 1826, 1857; Haraldson, 1978; Horton, 1963; Lousley & Kent, 1981; Mitchell & Dean, 1978; Ronse De Craene, 1986; Ronse De Craene & Akeroyd, 1988; Ross-Craig, 1979; Small, 1897; Watson, 1873; Webb & Chater, 1964; Wheeler, 1938; Wolf & McNeill, 1986)..

1. Habit: erect to ascending herbs, rarely shrubs (0), prostrate to creeping herbs (1), climbing herbs (2).
2. Leaf shape: ovate-cordate (0), ovate to lanceolate (1), narrowly lanceolate-linear (2).
3. Ochrea morphology: entire (0), two-cleft (1), lacerate (2).
4. Ochrea at maturity: entire (0), lacerate (1).
5. Leaf base: jointed with ochrea (0), not or obscurely so (1).
6. Awns on top of ochrea: absent (0), present (1).
7. Heterophylly: absent (0), present (1).
8. Internodal fusion of branches: absent (0), present (1).
9. Inflorescence: with numerous flowers/node (0), with 2 to 4(6) flowers/node (1), with 1(2) flowers/node (2).
10. Bracts of flowers: leaflike with pellucid ochreolae (0), scarious (1), scarious with awns (2).

11. Flowers exerted from ochreola: not (0), barely so (1), entirely (2).
12. Pedicel orientation at fruiting: erect (0), curved (1).
13. Abscission zone of flower: absent (0), against the base of the flower (1), in the middle of the pedicel (2).
14. Gender distribution: bisexual (0), unisexual—gynodioecious or dioecious (1).
15. Differentiation of outer and inner tepals at fruiting (shape): subequal (0), slightly dimorphic (1), highly dimorphic (2).
16. Differentiation of outer and inner tepals at fruiting (size): subequal (0), outer smaller (1), inner smaller (2).
17. Division of perianth parts: below the middle (0), up to the middle (1).
18. Tepal venation: trifid (0), dendritical (1), only midvein (2).
19. Outer tepals at maturity: flattened (0), angular-cuculate (1), with a prominent keel (2).
20. Outer tepal orientation at fruiting: erect (0), reflexed (1).
21. Lateral walls of tepal epidermal cells: \pm straight (0), strongly undulating (1).
22. Cuticular striations on tepal epidermal cells: random (0), in rows (1).
23. Stamen number: eight (0), occasionally less than eight (1), always less than eight (2).
24. Stamen reductions: eight stamens present (0), outer stamen pairs replaced by single stamen (1), outer stamen pairs partly incomplete (2), outer stamen pairs with sterile anthers or lost (3), inner stamens missing (4).
25. Filament shape of three inner stamens: not dilated or only at the base (0), gradually dilated toward the base (1), abruptly dilated in the middle (2).
26. Trichomes at the base of the filaments: present (0), absent (1).
27. Pollen size (polar axis length): small to medium, $< 25 \mu\text{m}$ (0), large, $\geq 25 \mu\text{m}$ (1).
28. P/E ratio (pollen size): 1.1–1.4 (0), 1.5–1.8 (1).
29. Apertural margins: absent (0), similar texture to the rest of the grain (1), different texture from the rest of the grain (2).
30. Ektexine differentiation: none (0), two distinct zones (1).
31. Mesocolpial ridges: not differentiated (0), strongly developed (1).
32. Pollen ektexine sculpturing pattern: smooth to rough perforate-punctate (0), foveolate to reticulate (1), baculate (2).
33. Pollen ektexine microspinules: absent (0), smooth (1).
34. Pollen type sensu Hedberg (1946): *Avicularia*-type (0), *Duravia*-type (1), other (2).
35. Presence of glandular rim around gynoeceium: absent (0), present (1).
36. Merosity of flowers: trimerous (0), pentamerous (1), dimerous (2).
37. Number of carpels: three (0), two (1).
38. Occurrence of fruit dimorphism: absent (0), present at the same time (1), with a distinction between early- and late-season fruits (2).
39. Achene shape: broadly ovate ($L < 1.5W$) (0), intermediate ($L = 1.5-2W$) (1), lanceolate ($L > 2W$) (2).
40. Achene apex: without beak or with very short beak (0), with conspicuous to very long beak (1).
41. Stylar development: very short and equal in size to stigmatic lobes (0), two times as long as stigmatic lobes (1), $> 2\times$ stigmatic lobes (2).
42. Achene base: not stipitate or with very short stipe (0), conspicuously stipitate (1).
43. Achene shape in transection: subangular (0), with two convex and one concave side (1).
44. Achene covering by tepals: included (0), shortly exerted to 1/4 (1), strongly exerted above 1/4 (2).
45. Primary sculpturing pattern: smooth to inconspicuously pitted (0), with interrupted longitudinal ridges (1), with reticulate pattern (2).
46. Secondary sculpturing pattern: tubercles absent (0), present (1).
47. Longitudinal striations on achene: absent (0), present (1).
48. Radial walls of pericarp in longitudinal section: straight (0), convolute (1).
49. Thickness of pericarp in longitudinal section: $< 40 \mu\text{m}$ (0), $> 40 \mu\text{m}$ (1).
50. Shape of lumen of pericarp cells: broadly rectangular (0), narrowly rectangular (1).
51. Presence of dendritical canals in pericarp walls: absent (0), present (1).

Appendix 4. Data matrix for cladistic analysis. *Pol.* = *Polygonum*; *Pella* = *Polygonella*. [Exported from MacClade file]

	0	0	1	1	2	2	3	3	4	4	5
	1	5	0	5	0	5	0	5	0	5	0
<i>Fallopia_cilinodis</i>	2	0	0	0	0	0	0	0	0	1	0
<i>Pol._aviculare</i>	1	1	1	0	0	0	1	1	1	0	0
<i>Pol._equisetiforme</i>	1	1	0	0	0	0	0	1	1	0	0
<i>Pol._arenastrum</i>	1	1	1	0	0	0	0	0	0	1	0
<i>Pol._maritimum</i>	1	1	1	0	0	0	0	0	0	1	0
<i>Pol._oxyspermum</i>	1	1	1	0	0	0	0	0	0	1	0
<i>Pol._bellardii</i>	0	1	1	0	0	0	0	0	0	1	0
<i>Pol._ramosissimum</i>	0	1	1	0	0	0	0	0	0	1	0
<i>Pol._undulatum</i>	0	1	1	0	0	0	0	0	0	1	0
<i>Pol._afromontanum</i>	0	1	1	0	0	0	0	0	0	1	0
<i>Pol._tenue</i>	0	1	1	0	0	0	0	0	0	1	0
<i>Pol._minimum</i>	?	1	0	0	0	0	0	0	0	1	0
<i>Pol._douglasii</i>	0	?	0	0	0	0	0	0	0	1	0
<i>Pol._douglasii</i> subsp. <i>spergulariiforme</i>	0	2	0	0	0	0	1	1	0	1	0
<i>Pol._shastense</i>	?	1	0	0	0	0	0	0	0	1	0
<i>Pol._bolanderi</i>	0	2	0	1	0	0	1	1	0	1	0
<i>Pol._californicum</i>	0	2	0	1	0	0	1	1	0	1	0
<i>Pol._polygaloides</i>	0	?	0	0	0	0	0	0	0	1	0
<i>Pol._kelloggii</i>	0	2	0	0	0	0	0	0	0	1	0
<i>Pella_parksii</i>	0	2	0	0	0	0	0	0	0	1	0
<i>Pella_polygama</i>	0	1	0	0	0	0	0	0	0	1	0
<i>Pella_americana</i>	0	2	0	0	0	0	0	0	0	1	0
<i>Pella_articulata</i>	0	2	0	0	0	0	0	0	0	1	0
<i>Pella_gracilis</i>	0	1	0	0	0	0	0	0	0	1	0
<i>Pella_fimbriata</i>	0	2	0	0	0	0	0	0	0	1	0

[Note that some polymorphic entries were converted to missing data, represented by ?]