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WHAT IS THE TAXONOMIC STATUS OF POLYGONELLA? EVIDENCE OF FLORAL MORPHOLOGY

L. P. Ronse De Craene,² S.-P. Hong,³ and E. F. Smets³

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. Duraria, sect. Pseudomollia, sect. Tephis) has been carried out with light microscopy (LM) and scanning electron microscopy (SEM). Flowers were investigated for macroscopic characters, tepal epidermal characters, pollen, and fruit morphology and anatomy. Results demonstrate that the limits between both genera become blurred through section Duraria of Polygonum, especially in characters of pollen and fruit morphology. Polygonum sect. Duraria 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 Duraria including subsections Duraria and Polygonella. A cladistic analysis of morphological characters supports two distinct clades, section Polygonum with subsections Polygonum and Tephis, and section Duraria with subsections Duraria and Polygonella.

Key words: cladistic analysis, Duraria, 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 Fischer. & 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), Phyllepidium Rafin. (1808: 356), Lyonnaia Rafin. (1818: 266), Phyllepidium Rafin. (1836: 51), and Stopinacea Rafin. (1837: 11). Gray (1845: 232) recognized the genus Thysanella with one species (T. limbriata) originally placed in Polygonum. Nieuwlant (1914: 171) created the genus Psammogonum 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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² Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh EH3 5LR, Scotland, U.K.

³ RonsedeCraene@rbge.org.uk.

⁴ Laboratory of Plant Systematics, Department of Biology & Institute of Basic Sciences, Kyung Hee University, Seoul 130-701, Korea, spjong@khu.ac.kr.

⁵ Laboratory of Plant Systematics, Institute of Botany and Microbiology, Katholieke Universiteit Leuven, Kasteelpark Areenberg 31, B-3001 Leuven, Belgium, erik.smets@bio.kuleuven.ac.be.

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 Atriplex L. in a separate subtribe. Only later did authors consider it as related to Polygonum sensu lato (Bentham & Hooker, 1833; 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, 1919).

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 ocreole, 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 ocreole, 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 Koénigia L. (e.g., Haraldson, 1978; Ronse De Craene & Akeroyd, 1983; Brandlyge, 1993). Four sections are currently accepted within Polygonum s. str. (e.g., Dammer, 1893; Hedberg, 1946; Haraldson, 1978), viz. sections Pseudomollia, Tephis, Polygonum (= Ariculata), 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 achenes structure (with a membranaceous pericarp). Small (1895) included four other species in his subgenus Durava (Polygonum bolanderi, P. greenei, P. parvifolius, P. bidwillii) on the basis of lacerate ochraceae 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. bidwillii, 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 (1983) tried to solve this problem by accepting two polymorphic species, Polygonum polygalaoides 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 Ariculata (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 anatom-
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).

<table>
<thead>
<tr>
<th>Sections of Polygonum and Polygonella</th>
<th>Bentham &amp; Hooker (1883), Dammer (1893)</th>
<th>Small (1895, 1933)</th>
<th>Gross (1913)</th>
<th>Jaretzky (1925)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Polygonella</td>
<td>Polygonella</td>
<td>Polygonella, Dentoceras, Delopyrum Thysanella</td>
<td>Polygonella</td>
<td>Polygonella</td>
</tr>
</tbody>
</table>

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; Jaretzky, 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 fimbriatum 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 tepals (Ronse De Craene & Akeroyd, 1988; Hong et al., 1993);
- 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 (Wheel, 1938), and section Polygonum (Trail, 1895; Ronse De Craene & Akeroyd, 1986). 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-
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 sulfoseuccinic 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 safranin 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 (Gersterberger & 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 micromorphological 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).

*Fallotia cilinodis* (Michx.) Holub was used as outgroup, and characters were unordered and all had equal weight. *Polygonum mottleiforme* 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).

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

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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 polygonama) 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 trid (e.g., Polygonum afromontanum; Fig. 1A). In most cases it consists of a single dendratically 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 mollitaeforme, 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 pentamerosous Polygonacea 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 mollitaeforme instead of the usual stamen pair (Fig. 1A, E). Anthers are occasionally sterile, as in Polygonum ramosissimum (see also Ronse De Craene & Akervold, 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 funbrata, and its outer filaments are rarely inflated and are sometimes reduced (Horton, 1963). Nectar tissue is confined to the base of the inner filaments and extends onto the hypaethrium 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, 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 mollitaeforme 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 exine 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 Duraria: Polygonum douglasii (Rydberg & Bessey 5364).—C. Polygonella polygama (Godfrey 1046).—D. Section Polygonum: Polygonum ariculare (Rouge De Caeve 25 Lb).—E. Section Pseudomollia: Polygonum mollicforme (Boriamüller 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 36599). —B. Polygonum californicum: flower spread open (Jepson s.n.). —C. Polygonum tenue: flower spread open (Paussant s.n.). —D. Polygonum undulatum: flower spread open (Fourcade 5962). —E. Polygonum aviculare: flower spread open (Ronse De Craene 25 Lt). —F. Polygonum aviculare; transverse section of flower (Ronse De Craene 25 Lt). (F, embryo; I, inner stamen; O, outer stamen; P, pericarp; T, transitional stamen). Bars = 100 μm, except C, D = 1 mm.
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
poles, and rugulate/reticulate or sometimes foveolate with microspinules around the ecpoapertures. 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 ecpoapertures 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 Daravia-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 Daravia-type with strict boundaries between the mesocolpal area and the ecpoapertural 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 Polygonaceae and Persicariaceae (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 orthotropic 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
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. Durantia (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 oxysepermum 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 Duraviea (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
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 Daravia 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 articulare, 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 Daravia 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-
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 (20–30 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 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 oxyseptum subsp. rani (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 (Cartiss 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 Duraria (e.g., Polygonum douglasii, Polygonum tenue: Fig. 9J), section Tephis (although the convoluted 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 Duraria (e.g., Polygonum courcatum, Polygonum shastense, Polygonum californicum: Fig. 9D), most Polygonella (e.g., Polygonella articulata, Polygonella polygama: Fig. 9E), and in section Pseudomollis (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 (Ronce 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 Duraria and the genus Polygonella with a bootstrap-jackknife support of 67%/70%/6% and another weakly supported clade (BS 63/39%) containing sections Polygonum and Tephis. In preliminary analyses Polygonum molliaeformae consistently fell within section Duraria, 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 arenenum, Polygonum maritimum, Polygonum oxypermum). 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. Duraria, although two of the clades are well supported. Synapomorphies can be recognized for both clades, such as the presence of spinules and ochrea morphology in the Polygonum clade, and the Duraria-type of pollen and P/E index (except for one species) in the Duraria 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 Duraria. If the genus Polygonella is considered as sufficiently distinct, a number of species from Polygonum sect. Duraria 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, ascrescent, and not appressed to the fruit. Tepal venation is reduced to a single mid-vein. The number of stamens is usually not reduced, and the inner filaments are abruptly widened. The pollen has a well-marked dimorphism of the ektene. 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 scariosus bracts, intermodal 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 ascrescent 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 molliaeformae: Fig. 1E).

The exine of pollen of section Duraria and Po-
Figure 10. Strict consensus of 108 trees (length 179, CI 0.402, RI 0.640). Pol. = Polygonum; Pella = Polygonella.
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 disjoint geographical distribution, and the repetition of the transition between the Duravia-type and Articularea-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 Articularea-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 exoapertures 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. spargulariforme, Polygonum shastense, Polygonella paritkii, Polygonella articulata, and Polygonella fimbriata with a reticulate-rugulate pattern. A change in the pattern of sculpturing around the ectoapertures occurs in Polygonum californicum by the presence of microspinules above the reticulation (Figs. 3B, 4B). The area around the exoapertures 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 inextinct, and the two are clearly interrelated.

Interestingly, the pollen of Polygonum molliae-forme of section Pseudomollia appears as intermediate between the Articularia- and the Duravia-type (Hong & Oh, unpublished). Given the disjoint 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 delimitated 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 fruticata* 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 dendritic branching toward the periphery; (2) narrowly rectangular cells (< 40 μm) with straight radial walls, narrow lumen, and absence of dendritic branching.

The internal fruit wall in *Polygonum* sect. *Pseudomollisia* 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, 1983, for an overview). In contrast, *Polygonella* has always been considered as distinct, first close to *Atrophaxia*, 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 paraphylectic 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 fruit surface with a thin pericarp. Similarly, pollen of *Polygonum douglasii* subsp. *spergulariforme* strongly resembles the *Duravia*-type, while the other samples of *Polygonum douglasii* studied are intermediate with little differentiation between megascolpium 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 afroamontane 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 (1983), 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. *Pseudomollisia* 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 twoparted style, solitary flowers, and overlapping obovate. 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 Schimani-Czeika (1968) mentioned 5 to 8 stamens and suggested that another drops 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 *Duraria*. 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 *Duraria*. 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 strico:

**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 = *Atripaxis 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 Polygonacae, 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 Duratia could be highly improved, as our study does not clarify the internal relationship of the clade optimally.

Literature Cited


3. Polygonum sashense Brewer.*


6. Polygonum bolanderi Brewer ex A. Gray.*


7. Polygonum parvynchla Cham. & Schlecht.

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

8. Polygonum minimum Watson. *


**Polygonella**

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


2. Polygonella articulata (L.) Meisn.*


3. Polygonella polygonoides (Vent.) Engelmi. & Gray = Polygonella parviflora Michx.*

U.S.A. North Carolina: Brunswick Co., Otton 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 parksi Cory.*


5. Polygonella fulva fulva Hickman & Horton.*

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

6. Polygonella gracilis Meisn.*


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

1a. Flowers dimerous, fruits usually lenticular.

1b. Small annual herbs, pollen dimorphic, fruit surface tubercled with lateral wings. sect. Pseudomollisia

2a. Small to large shrubs, pollen monomorphic (Aeciculariae-type), fruit surface smooth to pitted subsect. Tephis

2b. Flowers pentamers, 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 Aeciculariae-type, tepal vasculature dendritic subsect. Polygonella

3b. Flowers borne singly on each node (rarely 2 or more), always with 3 stamens and 3 carpels, pollen Durioza-type or derived within, tepal vasculature dendritic or reduced to a single vein.

4a. Bracts subtending individual flowers or flower clusters leaf-like with papery oochaelic abscission zone when present just below flower subsect. Darioha

4b. Bracts subtending individual flower scarious, abscission zone in the middle of the pedicel subsect. Polygonella

**Appendix 3. Characters used in the cladistic analysis**


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: joined with ochrea (0), not or obscurely so (1).

6. Awns on top of ochrea: absent (0), present (1).

7. Heterophyll: 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: leaf-like with pellucid oochaelae (0), scarious (1), scarious with awns (2).
11. Flowers exserted from ochreola; not (0), barely so (1), entirely (2).
12. Pedicel orientation at fruiting: erect (0), curved (1).
13. Abscession 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—gyno-monocious 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), denticrinal (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: ± straight (0), strongly undulating (1).
22. Cuticular striations on tepal epidermal cells: random (0), in rows (1).
23. Stamens number: eight (0), occasionally less than eight (1), always less than eight (2).
24. Stamens reductions: eight stamens present (0), outer stamens pairs replaced by single stamen (1), outer stamens pairs partly incomplete (2), outer stamens 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 μm (0), large, ≥ 25 μm (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. Mesocarpial ridges: not differentiated (0), strongly developed (1).
32. Pollen ektexine sculpturing pattern: smooth to rough perforate-punctate (0), foveolate to reticulate (1), baccate (2).
33. Pollen ektexine microspinules: absent (0), smooth (1).
34. Pollen type sensu Hedberg (1946): Arcularia-type (0), Duraria-type (1), other (2).
35. Presence of glandular rim around gynocoeicum: absent (0), present (1).
36. Merosity of flowers: trimeros (0), pentameros (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 bead or with very short bead (0), with conspicuous to very long bead (1).
41. Soral development: very short and equal in size to stigmatic lobes (0), twice as long as stigmatic lobes (1), > 2 × stigmatic lobes (2).
42. Achene base: not stipitate or with very short stipe (0), conspicuously stipitate (1).
43. Achene shape in transsection: subangular (0), with two convex and one concave side (1).
44. Achene covering by tepals: included (0), sharply 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: tubercules 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 μm (0), ≥ 40 μm (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).

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- *Fallopa.citinodis*: 20000000001210000000000102010000110000001
- *Pol.aviculare*: 1111001000100010010001011100001000100100101110011
- *Pol.quissetiforme*: 1110000100010000000000010000100010010000001
- *Pol.arenastrum*: 1111000000000100010000010000100010010000000
- *Pol.maritimum*: 1111000010000000000000010000100010010000000
- *Pol.oxytropum*: 1111000010000000000000010000100010010000000
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- *Pol.donglasi subsp. spergulariforme*: 0111000000000100000000010000100010010000000
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- *Pella.fimbriata*: 0111000000000100000000010000100010010000000

[Note that some polymorphic entries were converted to missing data, represented by ?]
WHAT IS THE TAXONOMIC STATUS OF POLYGONELLA?
EVIDENCE OF FLORAL MORPHOLOGY

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. Duraria, sect. Pseudomollia, sect. Tephis) has been carried out with light microscopy (IM) 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. Duraria 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 Duraria 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, Duraria, floral morphology, fruit, pollen, Polygonaceae, Polygonella, Polygonum, sectional classification.
genera in the Polygonaceae, which were eventually transferred into Polygonella, such as Lyonia Rafin. (1808: 352), Phylepidum Rafin. (1808: 356), Ly- onella Rafin. (1818: 266). Phylepidum Rafin. (1836: 51), and Stopinaca Rafin. (1837: 11). (ray (1845: 232) recognized the genus Thysanella with one species (T. fimbriata) originally placed in Po- lygonum. Nieuwland (1914: 171) created the genus

Psammogonum for two species, P. articulatum Nieuwl. and P. anmericanum Nieuwl. Small (1896, 1909, 1913, 1924) described five new species in Polygonella and erected two additional genera (De- lopyrum 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 seg- regate 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

We thank I. C. Oh (Kyung Hee University, Seoul) for kindly putting part of his photographie material from his unpublished MSc. thesis at our disposal. We thank Peter Linder for sending herbarium material of Polygonum undu- latum. Technical assistance by Anja Vandenperre for material studied at Leuven (Katholieke Universiteit Leuven) is acknowledged. This research was supported by research grants (project n0 2. (M)38.91; scanning electron microscope and project n G.0143.95; general research project from the EW.O.) a grant from the Research Council of the KUL (OT/97/23) to I., Ronse )e Craene, and by research grants (Non-Directed Research Fund: Project n 1997-001- 1)00332 from the Korea Research Foundation and a 20()/3 Professor Sahhatical Year' from Kyung Hee University) to S.-P. Hong.

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i.ronedecaene@rlge.org.uk.
: laboratory of Plant Systematics, I)epartment of Biology & Institute of Basic Sciences, Kyung Hlee University, Seoul 130-701, Korea. sphong@khu.ae.kr.
SLaboratory of Plant Systematics, Institute of Botany and Microbiology, Katholieke Universiteit leuven, Kasteelpark Arenberg 31. B-3(0)1 I.uven. Belgium. erik.smets@abio.kuleuven.ac.be.

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; )ammer, 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 biaracts (Watson. 1873: Small. 1897; Rydberg. 1932; ;raham & Wood. 1965: sec Table 2). Horton (1963) added a few anatomical features, such as tie very short vessel elements and a strongly reduced vascularization of the flower (as was observed by Vau

Horton recognized two subgenera in Polygonella, viz. subgenus polygonella comprising the great majority of the species, and subgenus Thysanella with only one species (Polygonella fimбриata (Ell.) Horton) consisting of two varieties. Subgenus Polygonella was described as having two outer aids 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, aid the filaments all alike and without teeth. Nesomi and Bates (1984) considered the two varieties of Polygonella fimбриata as two valid species, P. fimбриata and Polygonella robulsta. In a cladistic analysis. Lewis (1991. cited in Lewis & Crawford. 1995) found that P. fimбриata and P. robusta appear as a
basal clade within Polygonella.

The circumscription of the genus Polygonum Il.
lias changed considerably since its much broader
circumscription in earlier authors. In recent ap-
proaches to the family Polygoniaceae, the genus is
currently segregated in the genera Polygonum s.
str., Fanloplia Adans., Persicaria Mill., with segre-
gates Aconogonon (Meisn.) IRlb. and Historia
Mill., and Koenigia Il. (e.g., Haraldson, 1978;
Ronse l)e Craene & Akeroyd. 1988; Brandblige.

1993). Four sections are currently accepted within
Polygonum s. str. (e.g., lami er, 1893; Hedberg.
1946: Haraldson. 1978). viz. sections Pseudomoll-
ia, Tephis, Polygonum (= Aricularia), and Duraria
(see Table 1). Ronse l)e Craene and Akeroyd
(1988) recognized two sections only (Polygonum.
7Tphis), as they believed the distinctive characters
to be unimportant in commonison to the inherent
variability of section Polygonum. U 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 Duraria. Watson (1873) and HHar-
alson (1978) pointed out that section Tephis is
more similar to section Duraria than to section Po-
lygonum.

Section Duravia was erected by Watson (1873)
for a single species, Polygonum californicuni, on
the basis of its supposedly distinctive achene struc-
ture (with a membranaceous pericarp). Small
(1895) included four other species in his subgeius
Duraria (Polygonum bolanderi, PI greenei, P. par-
ryi, P. bidueilliae) on the basis of lacerate ochrea
and spicate inflorescences. (Geene (1904) elevated
l)uravia to generic rank on the basis of three dis-
tinctive characters (viz. solitary flowers, persistent
styles, and absence of articulation at the base of
the leaf blade). He accepted three other species (l).
bidwelliae, 1). greenei, and D. bolanderi) besides 1).
ca<li/orrica.

The taxonomni of North American lPolygonum.
sections Polygonum and Duravia alike. remains
confused, as different populations tend to show
wide gene flow at a high level of interbreeding
(e.g., Mertens & Raven. 1965: W'ilieeler. 1938).
lickman (1984) tried to solve this problem by ac-
cepting two polymorphic species, IPolygonum po-
lgaloides and Polygoninun dourglasii. each with a
nublirler of subspecies that hladlb)e previously de-
scribed under various species. He elevated section
Duravia to the rank of subgenus with no sections.
section Duraria with five species and section Monti-
cola with the two heterogeneous species.

Hettberg (1946) described a distinct pollen type.
hle Duravlia-type, for 18 species of Polygonum sen-
su lato. deviating from the other species of the gen-
us, and including members of Polygonella. How-
ever, several species possessing the Duravia-type
of pollen were placed by Small (1895) in his sub-
genus 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 polliole anal-

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).

<table>
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<th>Author</th>
<th>Section</th>
<th>Subgenus</th>
<th>Subsection</th>
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<tr>
<td>Meisner (1857)</td>
<td>Sect. Avicularia</td>
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<td>Sect. Avicularia</td>
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<tr>
<td>Small (1895, 1933)</td>
<td>Sect. Pseudomollia</td>
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<td>Avicularia sect. Avicularia</td>
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<tr>
<td>Jaretzky (1925)</td>
<td>Sect. Tephis</td>
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<td>Avicularia sect. Tephis</td>
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<td>Polygonella</td>
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<td>Polygonella</td>
<td>Dento-</td>
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<tr>
<td></td>
<td>Delopyrum</td>
<td>-</td>
<td>Thysanella</td>
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</table>

Haraldson (1978) 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 Du-
riveria and section Polygonum (see Dammer, 1893;
Cross, 1913; Jaretzky, 1925; Graham & Wood,
1965; Ronse De Craene & Akeroyd, 1988; Table
1). Several North American species were retained
in section Polygonum (Watson, 1873; Small, 1895).
Since no difference was made at the sectional level
(Rydberg, 1932, 1954; Small, 1903, 1933; Kaul.
1986). Indeed, the taxonomy of section Duravia ap-
ppears confusing and it is difficult to draw a sharp
line between section Polygonum and section Du-
ravia, 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 firmriata filaments are basally inflated as in Polygonum sect. Polygonum and section Duravia; the inner filaments of Polygonella macrophylla are intermediate (Horion, 1963);

* The similar epidermal (ell morphology of the tepals (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 parn'iifolia (= 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 poly'gama) 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-

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Ronse De Craene et al.
Taxonomic Status of Polygonella

Table 1. Extended.

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<tr>
<td>Sect. Polygonum</td>
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<td>Sect. Polygonum</td>
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<tr>
<td>Sect. Duravia</td>
<td>Sect. Polygonum</td>
<td>Sect. Duravia</td>
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<tr>
<td>Sect. Tephis</td>
<td>-Sect. Tephis</td>
<td>Sect. Tephis</td>
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<tr>
<td>Polygonella, Gono-</td>
<td>Polygonella</td>
<td>Polygonella</td>
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<tr>
<td>Polygonella subg. pyrum</td>
<td>Polygonella</td>
<td>Polygonella subg.</td>
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</table>
| Thysanella               | Polygonella subg. | Sect. Duravia sub-
| Thysanella               | Thysanella        | sect. Polygonella |

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

MATERIAL. ANIMOLUS

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., 2(00)), 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 sulfo succinic 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 safranin 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., 20(X)).

For SEM observations herbarium material was treated with aerosol-(O' stored in 70% alcohol (Erbar, 1995), and dissected before treatment i with di-methoxy nitrate (Gerstherger & 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 PAII version 4.0 (Swofford, 1998).

Fallopia cilinodis (Michx.) Holubi was used as outgroup, and characters were unordered and all had equal weight. Polygonum molliaciforme 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 swap-
ping and the steepest descent option. Relative support for clades was assessed with a 50% majority-rule bootstrap and jackknife analysis.

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[Begin Page: Page 324]

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ON O 1 e O O e
Ail tepals are similar in size and shape (Figs. 11, 2C, I). 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, Duriaud, and Tephis (Figs. A, E, 21)). In section Polygonum the fruit tends to outgrow the perianth in size as to become increasingly exserted, and the tepals become appressed to the fruit. In sections Tephis, Duriaud, 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. u1C).

The vasculature of the tepals is only rarely trifid (e.g., Polygonum a'fromonluanuim; 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).
ii Polygonella, Polygonum mollissimum, and some species of section Duravia there is only a single non-branching vein or ramifications are few (Fig. SC, E).

The most common arrangement of the stamens in the pentamierous Polygonaceae is of four equal stamens ii 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. 1 H. C; see, e.g., Laubengayer. 1937; Vautier. 1949; Ronse De Craene & Smets, 1991). Flowers are occasionally trimerous with six tepals (Fig. 1I). The transitional tepals have an intermediate shape and size (Figs. IA, B, 2C, E) or are sometimes abnormally shaped (Fig. 1I)). A single stamen is often found in sections Tephis and Polygonum mollissimm instead of the usual stamen pair (Fig. IA, E). Anthers are occasionally sterile, as in Polygonium ramosissimum (see also Ronse De Craene & Akerovd. 1988). In all taxa studied the filaments of the inner stamens are inflated toward the base (Figs. IA-E, 2A-E). In most species, the inflation is basipetally progressive from the middle of the filament, but in most species of Polygoniell 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 reduced (Horton. 1963). Nectar tissue is confined to the base of the inner filaments and extends onto the hypantherium 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, Iolygonella riliculata, did we observe an apparently glandular nectary (nectary?) of tissue surrounding the base of the gynoeceum (see also Horton, 1063). 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 lentilinar (two carpels), and the fruit develops as an achene or nut. A condition, with two carpels is consistently found in sections Pseudomollia (Fig. oC) and Tephis. rarely in section Polygonum, and is almost absent in section Duraria and Polygonella. This may correspond with the loss of the intermediate tepal with accompanying stamens (Fig. 21)). Other differences between individual species exist in the presence (Figs. 6A, 7C) 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. ). 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 transsection, as two ribs are more prolonged compared to the third (Fig. 61R). or the opposite occurs (Fig. 2F).

OILLEN MORIOLOGY (FIS. 3. 4)

In all genera and sections investigated the pollen is prolate to spheroidal and tricolporate (Polar axis/Equatorial diameter = 1.1-1.68). The ektexine is the most variable feature, and is either reticulate (Fig. 3B-FI1, ), teetate (smooth and spinulose: Fig. 3A), or rough (Fig. 31). 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 (Aricularia-type sensu Hedberg, 1946) consistently have tricolporate, rarely hexa-pantocolporate (= hexarugate), prolate-spheroidal grains with the exine surfaces smooth with spinules (Figs.

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Figure 2. Flowers of Polygonum and Polygonella, SEM micrographs-A. Polygonella parksii: stamens and gynoe- 

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3A, 4A). In Polygonum afroamontanum the exine surface is more or less roughened although comparable with section Polygonum (Figs. 31, 4A).

Pollen of section Pseudomollia is tricolporate. prolate, and nearly triangular in polar view (Figs. 31, 41). II differs strongly from section Polygonum in its (dimorphic exine, verrucose on both poles and mesocolpium, but mostly psilate around the ectoap- 

erture (Figs. 31, 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 mesocolpiuni and the

dimorphic exine (Duravia-type sensu Hedberg, 1946). The exine is semitectate-reticulate at the mesocolpiuni and the

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poles, and rugulate/reticulate or sometimes foveolate with microspinules around the ectoapertures. For some (e.g., Polygonella polygarnii, Polygonell(i articulait, Polygonuim 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. 31). Homogeneously distributed lumina are found in some Polygonella (Fig. 31). As this difference increases, more typical Duraria-types occur (e.g., Polygonum californicum, Polygonella parksii, Polygonelli cameronica: Fig. 3H, 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 Durari-type with strict boundaries between third mesocolal area and the ectoapertural area and strictly reliculate pollen with only a slight difference between these zones.
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. 5A), 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 Polygonoeae 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 orthotropic 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...
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, 1). Very often small canals branch from the lumen into the surrounding sclerenchymatous tissue (Fig. 9A, B, H, 1). Due to space constraints the anticlinal walls can become variously convoluted or bent in cross or longitudinal sections (Fig. 9A, G, 1). 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. 81). Longitudinal cuticular striae are often present (Fig. 81), but not in Polygonella fimbriata (Figs. 71). 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. 81), Polygonum coarctatum, and Polygonum tenue: Fig. 8E). The fruit surface of Polygonum polygaloides s.l. (including subspecies
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*kelloggii*: Fig. 8F: subspecies confertiflorum: Fig. 7C) is unique ani shows a scalariform-reticulate pattern with longitdiinally running ridges bridged at regular intervals wth varialions dpcn(eling on the samples or subspecies studtid. 'h'ies ridges do not necessarily correspond with lhc anticlinal walls of the cells.

Several species of section *Polygonum* and a few of section *Duraria* have a distinct surface pattern covered lb tubiercles. 'Tubercles mny be equidistant and sparsely covering the fruit along the anticlinal walls of the cells (c.g., *Polygonum bellardii*: Figs. 6B, 8A). crowded on ridges fornmedl y the anticlinal cell walls (e.g., *'olygonum nechoreum*. *Polgo- 

*equisetiformm*: Fig. 8C), or in longitudinal rows or clusters wiltotit connection 1t lthe anticlinal walls of the cells (e.g., *Polygonumn t renasrrttum*. Polgt-o- num aviculare., *Pol'gonum douglusii*: Figs. 73, 8B). Tubiercles imay be associated with pits. but never witi superficial striae. *Polygonumn douglasii* and *Polygonum tenue* differ markedly from most otter species of section *Duravia* in lie presence of tu- 

bercles arranged in short longitudinaly placed rows (Fig. 8B). In some cases fruits with smooth-pitted surfaces and with globular energerences occur side by side in the same species (e.g., *Polygonum arenastrum*. *Polygonrum douglasii*. *Polygonm nspe r- 

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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 neck of the fruit (Fig. 6C); the reticulation is more compact and is covered with tuberules 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, 71, 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) in Polygonum oxysper-
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Figure 9. IM micrographs of transverse and longisections of pericarps of Polygonum and Polygonella. -A. Po-lygonum rumosissimum (Puissant s.n.), TS. Bar = 35 pm. -B. Polygonum oxyspermum subsp. rii. (Corbire 5306), 'S. Bar = 70 pm. -C. Polygonum bellardi (Heldreich 877), TS. Bar = 30 <,m. -l). Polygonumi shastense (Carpenter s.n.), IS. Bar = 20 pi. -E. Pollygonella polygania (Curtiss s.n.), IS. Bar = 15 pm. -F. Polygonum molliaeforim (Kotschy 778), IS. Bar = 10 JxmL. -t. Polygonum afmontanum (Hedberg 377), TS. Bar = 40 pm. -H. Polygonella americana (Fischer 10), TS. Bar = 20 pm. -l. Polygonum tenue (Greene s.n.), IS. Bar = 20 Lm.
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. 91), 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 ani 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 polygamma: 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.

Cl. IISTIC AN MI.Ysis

Thie cladistic analysis resulted in 108 trees of length 179 (consistency index (Cl) 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 miorphological 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 arenasirum, Polygonum marimuim, Polygonum oxysperml m). 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 spinules 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 uncial 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 mid-vein. The number of stamens is usually not reduced, and the inner filaments are abruptly widened. The pollen has a well-marked dimorphism of the ektexine. Fruits are slender-stipitate and are often beaked; the surface is smooth, mostly with striae. and pericarp cells have a narrow lumen without diendritical 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 synapo-
morphies.

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 molliae/forme: Fig. I E).

The exine of pollen of section Duravia and Pol-

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Strict consensus of 108 trees

Fallopia cilinodis
Pol. aviculare
Pol. equisetiforme
Pol. arenastrum
Pol. maritimum
Pol. oxyspermum
Pol. bellardii
Pol. ramosissimum
Pol. undulatum
Pol. afromontanum
Pol. tenue
Pol. douglasii
ssp. spergulariiforme
Pol. bolanderi
Pol. californicum
Pol. polygaloides
Pol. kelloggii
Pella parksii
Pella americana
Pella fimbriata
Pella polygama
Pella graciiis
Pella articulata
Figure 10. Strict consensus of 108 trees (length 17, CI 0.402, RI 0.40). Pol. = Polygonum; Pella = Polygonella.

Jackknife 50% majority-rule consensus tree

Falloppia cilinodis
Pol. aviculare
Pol. equisetiforme
73 Pol. arenastrum
58 Pol. maritimum
59 Pol. oxyspermum
76 Pol. undulatum
75 Pol. afromontanum
Pol. tenue
Pol. minimum
Pol. douglasii
ssp. spargariiforme
Pol. shastense
92 Pol. bolanderi
67 68 93 Pol. californicum
0 64 Pol. polygaloides
70

Pol. kelloggii

68 Pella parksii
Pella americana
55 Pella fimbriata
78 Pella polygama

61 Pella gracilis
Pella articulata

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 Avicula-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 Avicula-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. 31). 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. spargariiforme, Polygonum shastense, Polygonella parksii, Polygonella articulata, and Polygonella fimbriata with a reticulate-rugulate pattern. A change in the pattern of sculpturing around the ectoapertures 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
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 molliae-forme 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 Polygononeae (e.g., E 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. 71, F) can be often recognized in species of section Duravia

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(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 Lm) with strongly convolute radial walls, broad lumen and dendritical branching toward the periphery; (2) narrowly rectangular cells (< 40 pxm) 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 POLYGONUM 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 Polygonum, 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. spargariiforme 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 af-romontane 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 lepal 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 Polygononella 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 Polygononum 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. Indeed, 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 remote 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 undulatiun L.

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 Duraria could be highly improved, as our study does not clarify the internal relationship of the clade optimally.

Literature cited


Marek, S. 1954. Morphological and anatomical features of the fruits of genera Polygonum ... Rumex L. and keys for their determination. Monogr. lot. 2: 77-161. [In Polish with English summary.]


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APIreNIOIX 1. Origin of species studied, with their synonymy. Species used in the cladistic analysis are marked with *.
* Polygonum sect. Polygonum
1. Polygonum aviculare L.*
2. Polygonum achooreum Blake
3. Polygonum maritirnmum L.*
4. Polygonum erectum L.
5. Polygonum bellardii Ail.*
6. Polygonum equisetiforme Sibth. & Sm.*
   TUNISIA. Jerba: near hotel Toumana, Ronse De Craene 975 (spirit 309 Lt) (LV).
7. Polygonum arenastrum Boreau*
   U.K. Devon: Prawle Point, E. Prawle, Ronse De Craene 1157 (spirit 405 Le) (LV).
8. Polygonum oxyspermum Meyer & Bunge ex Ledeh. subsp. raii (Bab.) D. A. Webb & Chater *
   FRANCE. Manche: Vauville et Denneville, L Corbire 5306, ex Herb. Bullemont 8443 (LV).
9. Polygonum ramosissimum Michx.*
   U.S.A. Kansas: St. Mary's, P A. Puissant s.n. (LV).

* Polygonum sect. Tethis
1. Polygonum afromontanum Greenway*
2. Polygonum undulatum (L.) Bergius*
   SOUTH AFRICA. Humansdorp Distr.: 2.6 mi. from Assegai Bosch, Fourcade 5962 (BOL). KNYSNA: in aper-tis Zitzikamma, Schlechter 5974 (E).

* Polygonum sect. Pseudomollia
1. Polygonum molliaeforme Boiss.
   IRAN. Kuh-Daena, Kotschy 778 (UPS); Denawand, Bornmiiller 8181 (K); Kuh-Daena, Kotschy s.n. (type) (E).
* Polygonum sect. Duravia
I. 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 (IV); Eal River, viii 1892, Jepson s.n. (UPS) (pollen); Glen Co., 8 mi. E of Newville, A. A. Heller 11553 (E).
2. Polygonum tpolgaloides Meisn.*
U.S.A. Oregon: Howell s.n. (IV); ex Herb. J. Wibbe,

3. Polygonum shastense Brewer*
4. Polygonum tenue Michx.*
5. Polygonum douglasii E. Greene*
As var. latifoliuim E. Greene. U.S.A. Oregon: Siskiyou Mountains, Howell s.n., ex Herb. Wibbe 92-7842 (IN).
6. Polygonum bolanderi Brewer ex A. Grav*
7. Polygonum paronrichia Chami. & Schlecht.
8. Polygonum miniminum S. Watson*

* Polygonella
1. Polygonella americana (Fisch. & Mey.) Small*
2. Polygonella articulata (L.) Meisn.*
3. Polygonella polygama (Vent.) Engelm. & Gray [ = Polygonella panvifolia Michx.]*

(UPS). Florida: Indian River, Curtiss 2433 (IN). Curtiss 5525 (K); Palm Beach, Curtiss 5525 (E).
4. Polygonella parksi Cory*
5. Polygonella fimbriata (Elliott) Horton*
U.S.A. Florida: Tampa, Blanton 6825 (S).
6. Polygonella gracilis Meisn.*

At*PENI)IX 2. Key to (siu)sections of Polygonumr sensu stricto.

la. Flowers dimerous. fruits usually lenticular.
2a. Small annual herbs, pollen dimorphic. fruit surface tubercled with lateral wings .... sect. Pseudomollia
21. Small to large shrubs, pollen monomorphic (Aricaria-type), fruit surface smooth to pitted .................. subsect. Tephis
lb. Flowers lentaierous. 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 Aricaria-type, tepal vasculature dendritical ..........S----- sect. Polygonum
3b. Flowers borne singly on each node (rarely 2 or more), always with 8 stamens and three carpels. pollen Duravia-i type or derived within. tepal vasculature dentiritieal or reduced to a single vein.
la. Bracts subtending individual flowers or flower clusters leaf-like with papyry ochreolae, abscission zone when present just below flower
.... --............ --... -- subsect. D)uraria
4lb. Bracts subtending individual flower scarious, abscission zone in the middle of the pedicel
- ---- -- subsect. Polygonella


1. Habit: erect to ascending herbs, rarely shrubs (0). prostrate to creeping herbs (1), climbing herbs (2).
2. Leaf shape: ovate-cordate (0), ovale 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 exserted 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. (ender distribution: bisexual (0), unisexual-gyno-monoecious 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: 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 μm (0), large, > 25 μm (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), bacculate (2).
33. Pollen ektexine microspinules: absent (0), smooth (1).
34. IPollen type sensu Itedberg (1946): Avicularia-type (0), Duravia-type (1), other (2).
35. Presence of glandular rim around gynoecium: absent (0), present (1).
36. Mérosity 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), > 2X 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 exserted to 1/4 (1), strongly exserted 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: tubercules absent (0), present (1).
47. Longitudinal striations on achene: absent (0), present ( ).
48. Radial walls of pericarp in longitudinal section: straight (0), convolute (1).
49. Thickness of pericarp in longitudinal section: < 40 pm (0), > 40 lm (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).

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Taxonomic Status of Polygonella


Fallopiacilinodis
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Pol..renastrum
Pol..maritirum
Pol..oxyspermum
Pol..bellardii
Pol..ramosissiimum
Pol..undulatum
Pol..fromon tanum
Pol..enue
Pol.Jninimum
Pol.d.douglasii
Pol..douglasii subsp.
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Pol..shastense
Pol.Jbolanderi
Pol..californicumi
Pol..polvgaloides
Pol..kelloggii
Pella.parksii
Pella-polygama
Pella.zamericana
Pellauzticulata
Pella.gracilis
Pella-finmbriata

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