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Chromosome number, morphology, pairing, and DNA values of species and hybrids in the genus *Fallopia* (*Polygonaceae*)

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Key words: Angiosperms, *Polygonaceae, Fallopia, Reynoutria.* – Chromosome number, microdensitometry, meiosis, hybridisation, dioecism, alien plants.

Abstract: The taxa in this study have in the past been treated together in sect. *Tiniaria* Meissner of *Polygonum* L. s.l., and more recently the large erect rhizomatous herbaceous perennials have been separated from the twining annuals and perennials as the genera *Reynoutria* and *Fallopia* respectively. These taxa range in ploidy level from diploid to octoploid, with base numbers of both 10 and 11 present. The plants are primarily Asiatic in distribution, although many of the large erect perennials are now naturalized in many parts of Europe. Cytological examination has revealed the presence of a number of previously unknown hybrid taxa in the British Isles. The readiness with which hybridisation occurs between taxa of differing base number and ploidy level, and similarities revealed in chromosome morphology, meiotic pairing and in DNA C-value, suggest to the authors that these two genera are best amalgamated under *Fallopia.*

The genus *Fallopia* Adanson sensu Holub (1971) contains those annual and perennial, herbaceous and woody, climbing taxa that had been designated by Meissner (1826) as sect. *Tiniaria* of the genus *Polygonum* L. Earlier, they had also been separated generically from *Polygonum* by Webb & Chater (1963) under *Bilderdykia* Dumort., over which *Fallopia* has priority.

They are represented in Europe by *F. dumetorum* (L.) Holub and *F. convolvulus* (L.) Löve, both natives, while *F. baldschuanica* (Regel) Holub [incl. *F. aubertii* (L. Henry) Holub] and *F. multiflora* (Thunb.) Haraldson, both from Asia, occur there as garden plants. In our work we have also used material of *F. cilinodis* (Michaux) Holub, from North America, but we were not able to obtain material of the American *F. scandens* (L.) Holub, which is very close to *F. dumetorum*, nor of the Chinese *F. cynanchoides* (Hemsl.) Haraldson, which is close to *F. cilinodis.*

The precise relationships between these climbers and the erect, herbaceous, rhizomatous perennials of the genus *Reynoutria* Houtt. has long been debated. *Reynoutria* contains two eastern Asian species, *R. japonica* Houtt. (*Polygonum cuspidatum* Siebold & Zucc.) and *R. sachalinensis* (F. Schmidt ex Maxim.) Nakai, which have both become problematical garden escapes in Europe, as they are very

vigorous and successfully compete with native vegetation. They were retained in the genus *Reynoutria* by WEBB & CHATER (1963) and HARALDSON (1978), but united with *Fallopia* by HEDBERG (1946) [under *Tiniaria* (MEISSNER) REICHB.], by SHINNERS (1967) (under *Reynoutria*) and by RONSE DECRAENE & AKEROYD (1988) (under *Fallopia*). Many other authors have preferred to include the species of *Reynoutria* and *Fallopia* under *Polygonum*.

In our opinion the genera *Fallopia* and *Reynoutria* should be united under the former name as a genus separated from *Polygonum*. We consider that the species of *Fallopia* mentioned above should be segregated into four sections: *Fallopia*, to include the annual climbers *F. convolvulus, F. dumetorum*, and *F. scandens; Parogonum* HARALDSON, to include the perennial climbers *F. cilinodis* and *F. cynanchoides; Sarmentosae* (GRINTZ.) HOLUB [= *Pleuropterus* (TURCZ.) HARALDSON] to include the woody climbers *F. multiflora* and *F. baldschuanica*; and *Reynoutria* (HOUTT.) RONSE DECRAENE, to include the robust rhizomatous herbaceous perennials *F. japonica* (HOUTT.) RONSE DECRAENE and *F. sachalinensis* (F. SCHMIDT ex MAXIM.) RONSE DECRAENE. This classification is adopted in this paper, and support for it is outlined in the discussion. We are thus in close agreement with the conclusions of RONSE DECRAENE & AKEROYD (1988).

Chromosome counts from the literature (Table 1) reveal the climbing taxa (sections *Fallopia, Parogonum*, and *Sarmentosae*) to be diploids, with the exception of the tetraploid *F. convolvulus*, and the non-climbing herbaceous perennials (sect. *Reynoutria*) to be tetraploids and octoploids. In all cases the base number is either 10 or 11 (ignoring the aberrant counts of 34, 52, and 102), with one taxon, *F. cilinodis*, reported with both $2n = 20$ and 22.

In the present paper seven species of the genus *Fallopia* plus three extra varieties of *F. japonica* and numerous intra- and inter-sectional hybrids, both artificial and found wild in the British Isles, have been studied using the techniques of karyotyping, meiotic analysis, microdensitometry, and fluorescent and Giemsa C-banding. This is the first systematic cytological study of the group since that of JARETZKY (1928), and was carried out in the hopes of understanding taxonomic patterns and evolutionary relationships within the genus *Fallopia*.

Material and methods

Seed provenances and localities of the material used are listed in Table 2.

Mitotic preparations. Actively growing roots were collected between 1000 and 1130 a.m. and pre-treated at 4 °C for 20 h in 0.002 M 8-hydroxyquinoline. They were then fixed in 3 : 1 ethanol : ethanoic acid and stored in fixative at 4 °C until required. The root-tips were next hydrolysed in 5N HCl for 8–10 min at 10 °C. The HCl was replaced by 70% alcohol, and the meristematic regions dissected out in a drop of 45% ethanoic acid. The meristems were then macerated using tungsten needles in a drop of 2% aceto-orcein. Wet preparations were tapped out, squashed, and examined on a Zeiss universal microscope. Photographs were taken using Kodak Technical Pan film which was developed with Kodak HC 110 developer diluted to 1 in 60.

Meiotic preparations. Flower buds at the appropriate stage of development were fixed between 1030 and 1130 a.m. in freshly made 3 : 1 fixative and stored in this at 4 °C until required. Anther contents were teased out using fine tungsten needles in a drop of 2% aceto-orcein. By using a combination of gentle tapping and heating with a spirit burner, the pollen mother cells could be separated from their callose cell walls. After squashing, wet preparations were examined as above.

Table 1. Previously published *Fallopia* chromosome counts

Species	Chr. no.	Reference
F. dumetorum	2n = 20	Numerous reports
F. baldschuanica	2n = 20	JARETZKY (1928)
		SCHNACK & FERNANDES (1946)
F. multiflora	n = 11	SUGIURA (1936)
	2n = 22	SUZUKA (1950, in BOLKHOVSKIKH & al. 1969)
		DOIDA (1960)
F. cilinodis	2n = 20	JARETZKY (1928)
		LÖVE & LÖVE (1964, in BOLKHOVSKIKH & al. 1969; 1982)
	2n = 22	KAPOOR & GERVAIS (1982)
F. scandens	2n = 34	SMITH (1963, in BOLKHOVSKIKH & al. 1969)
	2n = 20	LÖVE & LÖVE (1982)
F. cynanchoides	Cytologically unknown	
F. convolvulus	2n = 20	Numerous reports
	2n = 40	Numerous reports
F. sachalinensis	2n = 44	SINOTÔ (1929)
		SOKOLOVSKAYA (1960, 1965, both in BOLKHOVSKIKH & al. 1969)
		WCISLO (1977)
	2n = c.44	JARETZKY (1928)
	2n = c.66	MENSHIKOVA (1964, in BOLKHOVSKIKH & al. 1969)
	2n = 102	LEE (1972)
F. japonica var. *compacta*	2n = 44	JARETZKY (1928)
F. japonica	n = 22	SUGIURA (1931, 1936)
	2n = 44	DOIDA (1960)
		MAJOVSKY & al. (1974)
		MURIN (1974)
	2n = 52	LIU, Y., fide PING-SHENG (1985)
	2n = > 60	ZHUKOVA (1967; in BOLKHOVSKIKH & al. 1969)
	2n = c.88	JARETZKY (1928)
	2n = 88	LEE (1972)
		WCISLO (1977)

Feulgen microdensitometry. Actively growing roots were collected at midday to ensure a high mitotic index. They were fixed in 4% neutral methanal (formaldehyde) for 2 h at 20 °C, then washed well in several changes of distilled water, before being re-fixed in 3 : 1 fixative and stored at 4 °C. Batches (including an *Allium cepa* control) were hydrolysed in 5N HCl for 60 min at 20 °C. They were then rinsed in distilled water and stained in Feulgen reagent for 2 h in the dark. The roots were then rinsed well in SO_2 water and squashes made (as previously described) on an unsubbed slide in 45% ethanoic acid. Coverslips were removed using the dry-ice method and slides were taken through two changes of 100% ethanol before mounting in Euparal. Colourimetric measurements were made using a Vickers M 85 scanning microdensitometer.

Giemsa C-banding. Air dried preparations were made using the technique of JAMIESON

Table 2. New *Fallopia* chromosome counts. All localities in the British Isles unless otherwise stated

Coll. no.	Origin	Ordnance Survey National Grid Ref.	2n
F. dumetorum			
P 149	Seed ex Lund No 184, Sweden	–	20
P 177	Seed ex Rogate, W. Sussex	–	20
F. baldschuanica			
P 151	Cutting ex Cambridge, Cambs.		20
P 152	Cutting ex Cambridge, Cambs.		20
P 153	Seed ex P 152 Cambridge, Cambs.	–	20
P 163	Sichuan, China	–	20
P 175	Seedling ex P 98, Leicester, Leics.	–	20
F. multiflora			
P 100	Not known	–	22
P 162	Seed ex Peking, China	–	22
F. cilinodis			
P 148	Seed ex Warsaw, Poland	–	22
P 156	Seed ex Montreal, Canada	–	22
P 167	Seed ex Quebec, Canada (granite outcrop)	–	22
P 168	Seed ex Quebec, Canada (shade form)	–	22
F. convolvulus			
P 150	Seed ex Italy No. 224	–	40
P 154	Sileby, Leics.	43/602.153	40
P 178	Leicester, Leics.	43/5.0	n = 20
F. japonica var. *japonica*			
P 114	Seed ex Tokyo, Japan	–	44
P 172	Tochigi Pref., Japan	–	44
P 5	Brithdir, Merioneth. (Garden)	23/761.177	88
P 6	Stoughton, Leics.	43/644.026	88
P 8	Criccieth, Caerns.	23/492.381	88
P 9	Boston Lodge, Merioneth.	23/589.382	88
P 10	Pentre'r-felin, Caerns.	23/526.396	88
P 11	Llangwnadl, Caerns.	23/218.335	c 88
P 12	Race Course, Leicester, Leics.	43/617.013	88
P 14	Southmead House, Leicester, Leics.	43/617.015	88
P 15	Stroud, S. Hants.	41/720.234	88
P 18	Petersfield, S. Hants.	41/744.234	88
P 19	Pwllheli, Caerns.	23/374.350	88
P 20	Dunton Basset, Leics.	42/549.892	88
P 21	Hindhead, Surrey	41/886.356	88
P 22	Chilworth, Surrey	51/012.466	88
P 23	Heckfield, Surrey	41/726.612	88
P 24	Aberystwyth, Cards.	22/601.820	88
P 25	Sileby, Leics.	43/602.153	88

Table 2 (continued)

Coll. no.	Origin	Ordnance Survey National Grid Ref.	2n
P 26	Itchen Abbas, N. Hants.	41/541.329	88
P 27	Ynys, Merioneth.	23/597.353	88
P 34	Ammanford, Carms.	22/61.11	88
P 35	Tyn Coed, Merioneth.	23/67.18	88
P 36	Fowey Turn, E. Cornwall	20/052.532	c 88
P 37	Doublebois Turn, E. Cornwall	20/188.643	88
P 39	Toxteth, S. Lancs.	33/3.8	88
P 42	Cardingmill Valley, Salop.	32/4.9	88
P 46	Llandrindrod Wells, Rads.	32/058.612	88
P 48	Llanstephan, Carms.	23/354.112	88
P 96	Milngavie, Stirlings.	26/5.7	88
P 97	Gomshall, Surrey	51/09.48	88
P 110	Sligo, Co. Sligo	–	88
P 112	Lisdoonvarna, Co. Clare	–	88
P 113	Seed ex Peking, China	–	88
P 122	Whitchurch, Glam.	31/14.80	88
P 123	Bolton, S. Lancs.	34/693.082	88
P 135	Mynytho, Caerns.	23/30.31	88
P 169	Salem, USA, male-fertile	–	88
F. japonica var. *compacta*			
P 2a	Bracken Hill, Sevenoaks, W. Kent (Garden)	51/616.572	44
P 2b	Bracken Hill, Sevenoaks, W. Kent (Garden)	51/616.572	44
P 7	Broughton Astley, Leics. (Garden)	42/525.927	44
P 99	North Ledaig, Main Argyll	17/908.368	44
F. japonica var. "*uzenensis*"			
P 105	Seed ex Tokyo, Japan	–	66, 88
F. japonica var. "*terminalis*"			
P 134	Hachijo Islands, Tokyo, Japan	–	44
F. sachalinensis			
P 53	Ballyconneely, W. Galway	02/620.446	c 44
P 54	Brithdir, Merioneth.	23/761.177	44
P 55	Nant-Y-Frith, Flints.	32/265.542	c 44
P 56	Errislannen, W. Galway	02/620.495	44
P 57	Howey, Rads.	32/051.587	44
P 58	Howey N. 1984, Rads.	32/051.591	44
P 59	Howey Village, Rads.	32/051.588	44
P 60	Elstead, Surrey	41/98.41	44
P 61	Godalming, Surrey	41/9.4	44
P 63	Falcondale, Cards.	22/569.500	44
P 64	Cirencester, E. Gloucs.	42/025.023	44
P 65	Llandewi, Rads.	32/102.680	44
P 66	Aber, Cards.	22/477.483	44

Table 2 (continued)

Coll. no.	Origin	Ordnance Survey National Grid Ref.	2n
P 67	Amroth, Pembs.	22/171.071	44
P 68	Amroth beach, Pembs.	22/166.071	44
P 71	Cwm Ystwth, Cards.	22/79.74	44
P 72	Ironbridge 1984, Salop.	33/670.033	44
P 73	Bryn Eithyn, Cards.	22/582.782	44
P 74	Cwrt Newydd, Cards.	22/493.477	44
P 115	Seed ex Tokyo No 376, Japan	–	44
P 127	Cheshunt, Herts.	52/368.028	44
P 155	Llanisloe House, Carms.	22/253.087	44
P 171	Tochigi Pref., Japan	–	44
(*F. japonica* var. *compacta* × *F. sachalinensis*) × *F. baldschuanica*			
P 102	Seed from P 33, Surrey	51/09.48	32
P 146	Seed from Cheshunt hybrid A, P 125, Herts.	52/368.028	32
P 147	Seed from Cheshunt hybrid B, P 126, Herts.	52/368.028	32
F. japonica var. *compacta* × *F. baldschuanica*			
P 69	Artificial hybrid	–	32
F. sachalinensis × *F. baldschuanica*			
P 101	Artificial hybrids	–	32
P 139	Seed from P 58, Rads.	32/052.591	32
P 140	Seed from P 160, Glam.	31/187.813	32
P 145	Seed ex P 127, Herts.	52/368.028	32
F. japonica var. *compacta* × *F. sachalinensis*			
P 13	South Wylam, Co. Durham	45/124.646	44
P 16	A 429, Cirencester, E. Gloucs.	42/039.033	44
P 33	Gomshall, Surrey	51/09.48	44
P 78	Artificial hybrid	–	44
P 79	Artificial hybrids	–	44
P 116	Tottenham Marshes, Middlesex	52/352.909	44
P 125	Cheshunt A, Herts.	52/368.028	44
P 126	Cheshunt B, Herts.	52/368.028	44
F. japonica var. *japonica* × *F. baldschuanica*			
P 77	Seed from P 12, Leics.	43/617.013	54
P 80	Seed from P 8, Caerns.	23/492.381	54
P 81	Seed from Loughborough, Leics.	43/544.204	54
P 82	Seed from P 9, Merioneth.	23/589.382	54
P 83	Seed from P 19, Caerns.	23/374.350	54
P 86	Seed from P 26, N. Hants.	41/541.329	54
P 87	Seed from P 5, Merioneth.	23/761.177	54
P 88	Seed from P 35, Merioneth.	23/67.18	54
P 89	Seed from P 3, Salop.	33/671.033	54
P 90	Seed from P 18, S. Hants.	41/744.234	54
P 91	Seed from P 10, Caerns.	23/526.396	54

Table 2 (continued)

Coll. no.	Origin	Ordnance Survey National Grid Ref.	2n
P92	Seed from P25, Leics.	43/602.153	54
P93	Seed from P27, Merioneth.	23/597.353	54
P94	Artificial hybrids	–	54
P157	Merlewood, Cumberland	35/25.17	54
P164	Railway Fields, Haringay Middlesex.	51/317.882	54
F. japonica var. *japonica* × *F. sachalinensis*			
P51b	Dolgellau 1982, Merioneth.	23/711.183	88
P1	Roundstone, W. Galway	02/726.424	66
P4	Brithdir, Merioneth. (Garden)	23/763.177	66
P17	A 429 Cirencester, E. Gloucs.	42/039.033	c 66
P28	Loughborough, Leics.	43/544.204	66
P29	Preston, S. Lancs.	34/510.298	c 66
P30	Pont Rhyd Sarn, Merioneth.	23/859.287	c 66
P31	Maam, W. Galway	02/963.533	66
P32	Lye Green, E. Sussex	51/511.336	c 66
P40	Cirencester, E. Gloucs.	42/025.023	66
P41	Small Wood End, Cheshire	33/806.602	66
P43	Ironbridge middle, Salop.	33/67.03	66
P44	Amroth ditch, Pembs.	22/167.071	66
P45	Amroth male, Pembs.	22/167.071	66
P47	Llandrindrod Wells, Rads.	32/058.612	66
P49	Dolgellau 1984, Merioneth.	23/711.183	66
P52	Dolgellau 1982, Merioneth.	23/711.183	66
P75	Artificial hybrids	–	66
P109	Polperro, E. Cornwall	20/226.516	66
P119	Brithdir male, Merioneth.	23/761.177	66
P121	Whitchurch, Glam.	31/14.80	66
P128	Cirencester Abbey Grounds 1985, E. Gloucs.	42/025.023	66
P130	Cirencester Abbey Plant 2, E. Gloucs.	42/025.023	c 66
P136	Honor Oak Cemetery, W. Kent	51/354.744	66
P158	Bristol, W. Gloucs.	31/531.777	66
P159	Bristol, W. Gloucs.	31/531.777	66
P165	Southport, S. Lancs.	34/332.178	c 66
P50	Dolgellau 1984, Merioneth.	23/711.183	88
P51a	Dolgellau 1984, Merioneth.	23/711.183	88
F. japonica var. *japonica* × *F. japonica* var. *compacta*			
P76	Artificial hybrid	–	66

& al. (1986) on unsubbed slides using material fixed with in 3 : 1 or 4% neutral methanal. The banding techniques of SCHWARZACHER & al. (1980), NEWTON (1985), and TEOH & HUTCHINSON (1983) were employed.

Results

Chromosome numbers. Table 2 shows the counts produced in this study. The earlier literature counts (Table 1) are largely confirmed, except that no "aberrant" numbers (e.g., 2n = 34, 52, 102) were encountered; *F. cilinodis* was found only with a base number x = 11 and *F. convolvulus* only as a tetraploid. Hence taxa with x = 10 are either diploids or tetraploids and all climbers, and taxa with x = 11 are diploids, tetraploids or octoploids and all rhizomatous except *F. cilinodis* (*F. multiflora*, in sect. *Sarmentosae*, is a woody rhizomatous climber; *F. japonica* and *F. sachalinensis*, in sect. *Reynoutria*, are herbaceous but strongly rhizomatous).

Attempts to map the native distribution of the tetraploid and octoploid *F. japonica* cytotypes have been handicapped by the difficulty in obtaining viable wild collected seed from China. Pooling our own and published results gives one octoploid and 5 tetraploids from Japan, and a single octoploid from each of China and Korea.

An examination of a number of clones of plants of sect. *Reynoutria* naturalised in the British Isles has revealed some interesting points. Only the octoploid cytotype of *F. japonica* var. *japonica* was found to be naturalised in the British Isles and, further, all these plants were found to be male-sterile.

The presence of a number of hybrids was also detected. The production and examination of a series of artificial hybrids fully supports the putative origins assigned to these wild hybrids. The hybrids fall into two categories, interspecific hybrids within sect. *Reynoutria*, and intersectional hybrids between taxa in sect. *Reynoutria* and sect. *Sarmentosae*. Two different intrasectional *Reynoutria* hybrids were found (Table 2). First *F. japonica* × *F. sachalinensis* = *Fallopia* × *bohemica* (CHRTEK & CHRTKOVÁ) J. BAILEY. This was found at 22 localities; of these 21 were hexaploid and one (presumably due to an unreduced gamete) octoploid. These results probably explain MENSHIKOVA's 2n = 66 count for *F. sachalinensis* (BOLKHOVSKIKH & al. 1969) since these hybrids are closer morphologically to the *F. sachalinensis* parent. ZHUKOVA's count of more than 60 for *F. japonica* (BOLKHOVSKIKH & al. 1969) may also be of this origin, though one cannot rule out the cross between *F. japonica* and *F. japonica* var. *compacta* (2n = 66). This cross has been made at Leicester and the mature plants are morphologically virtually indistinguishable from octoploid *F. japonica*. The second type of hybrid found was that between *F. sachalinensis* and *F. japonica* var. *compacta*. This was very difficult to distinguish on morphological grounds from the *F. japonica* var. *japonica* × *F. sachalinensis* hybrids described above, but cytologically it differed in being tetraploid (2n = 44).

The routine collection and germination of open pollinated seed from male-sterile *F. japonica* and *F. sachalinensis* plants led to the discovery of the second class of hybrids (BAILEY 1988). Examination of seed from the octoploid *F. japonica* plants usually revealed a chromosome complement of 2n = 54 (Fig. 10) and a karyotype notably less symmetrical than that of the female parent. It was suspected that such seedlings were the result of cross-fertilisation by the commonly grown garden plant

Fallopia baldschuanica ("Russian Vine"). Artificial cross-pollinations revealed that plants with the same unusual karyotype and distinctive morphology could readily be obtained. An examination of seed from male-sterile plants of *F. sachalinensis* and of *F. japonica* var. *compacta* × *F. sachalinensis* revealed that that seed too had been produced by cross-pollination with *F. baldschuanica*. These hybrids also had a markedly asymmetrical karyotype (Figs. 8, 9) and a complement of 2n = 32. Artificial hybrids between *F. sachalinensis* and *F. baldschuanica* have subsequently been made.

Meiotic behaviour. The diploid and tetraploid species (Table 3) examined all proved to be regular bivalent formers, albeit with a rather low chiasma frequency (1.16–1.38 per bivalent). Occasional cells with one or two quadrivalents were found in some of the tetraploid accessions of *F. convolvulus*, *F. japonica* var. *compacta*, and *F. sachalinensis*. As we had access to only male-sterile octoploid *F. japonica* we were unable to obtain any data on this cytotype (female meiosis being out of the question for cytologically difficult polyploids with only one ovule per flower). There is, however, indirect evidence for regular meiosis, in that all the hybrids between male-sterile octoploid *R. japonica* and other species gave rise to strictly euploid hybrids.

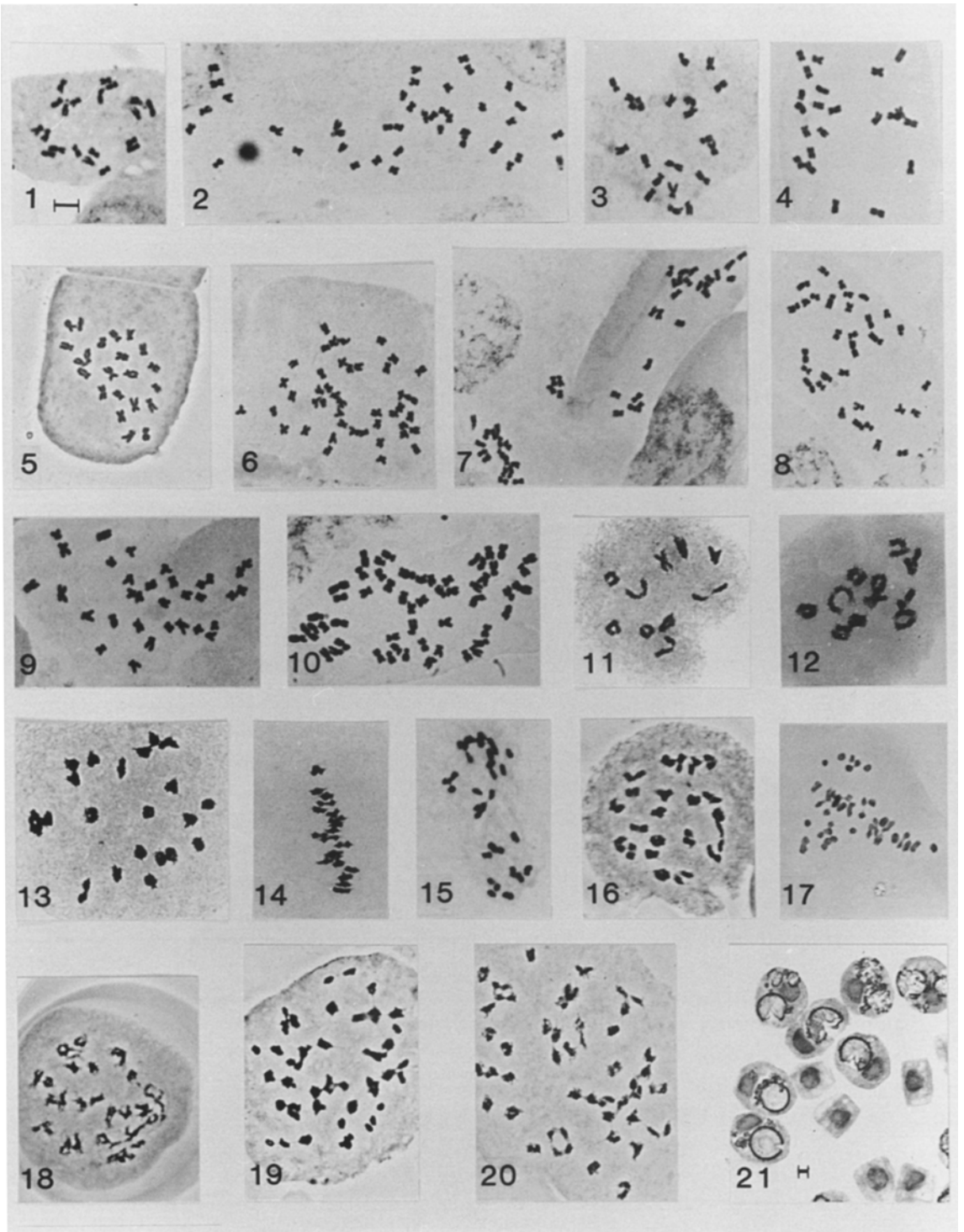
The analysis of meiosis in some of these hybrids was extremely difficult, owing to the large numbers of chromosomes, poor staining, stickiness and the fact that, even in well separated preparations, recognisable meiotic figures were rarely, if ever, to be seen in the 6x hybrids (Fig. 19).

The regularity of meiosis in intra-sectional *Reynoutria* hybrids appeared to be determined more by the ploidy level of the hybrid than by the combinations of taxa involved. Hence hybrids between *F. japonica* and *F. sachalinensis* at both tetraploid (P 13, P 78a, P 79c) and octoploid levels (P 51b) had very much more regular meiosis than hybrids between the same species at the hexaploid level. Indeed, in terms of chiasmata frequency (1.07–1.35), regularity of meiosis and pollen fertility, the three tetraploid hybrids listed above were little inferior to the parental species. Meiosis was remarkably regular in the octoploid *F. japonica* × *F. sachalinensis* (P 51b), with mostly bivalents and only 2 or 3 quadrivalents produced per cell.

On the other hand the hexaploid *F. japonica* × *F. sachalinensis* plants (P 29, P 75d, P 119, and P 32) and the 6x *F. japonica* × *F. japonica* var. *compacta* plant (P 76d) had extremely irregular meiosis, with large numbers of univalents and significant numbers of multivalents up to quadrivalents. This often led to the occurrence of micronuclei in the pollen tetrads, and was adequately reflected in the low pollen fertilities obtained.

In hybrids between the tetraploid taxa of sect. *Reynoutria* and *F. baldschuanica* (2n = 32) meiosis was again most irregular (Fig. 15). Indeed spindle formation seemed to be affected, with the stages from diakinesis to anaphase I being more or less indistinguishable. Restitution dyads and micronuclei were frequently found at the tetrad stage.

Meiosis in the pentaploid (2n = 54) *F. japonica* × *F. baldschuanica* hybrids (Figs. 17, 18) was much more interesting. The 5 cells that could be examined on a univalent/bivalent basis revealed regular formation of 10 univalents and 22 bivalents. This is interpreted as regular homoeologous pairing of the haploid *F. japonica*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set, the 10 *F. baldschuanica* chromosomes remaining unpaired. Further weight was added to this interpretation with the examination of 16 cells with polar views of metaphase I, where 32 chromosome bodies were almost invariably seen.

Microdensitometry. Results are shown in Table 4 and Fig. 22. DNA 2C-values ranging between 0.68 pg for *F. dumetorum* (2n = 20) to 6.48 for *F. japonica* (2n = 88) were found. In terms of DNA 2C-values per 2x genome, these results fall into three groups. Firstly, a low C-value group comprising the annual climbing taxa *F. dumetorum* (0.68 pg) and *F. convolvulus* (0.72 pg). Secondly, a middle value group encompassing the erect rhizomatous perennials of sect. *Reynoutria* and the rhizomatous climbing perennial *F. multiflora*, where the range was 1.29–1.62 pg per 2x genome (1.23–1.59 pg in the intra-section *Reynoutria* hybrids). The third group contained the woody climber *F. baldschuanica* and the scrambling *F. cilinodis* with a range between 1.96 and 2.22 pg DNA.

Hybrids between sect. *Reynoutria* and *F. baldschuanica* showed a somewhat higher 2C-value per 2x genome than hybrids within sect. *Reynoutria*. This was due to the higher relative proportion contributed by *F. baldschuanica*. It will be noted that the standard deviations for the microdensitometry results are somewhat high; this was in part due to the need to use only cells at metaphase for the DNA estimation work, which will be commented on more fully in the discussion.

Karyotyping. Selected karyotypes are shown in Figs. 23 and 24 and a summary of the karyotype measurements in Table 5. In well condensed cells (essential for the polyploid taxa) chromosome length varied between 2 and 3 μm. The chromosomes were mainly metacentric to sub-metacentric. The most asymmetrical chromosome of sect. *Reynoutria* was categorised nsm(−) according to the system of ABRAHAM & PRASAD (1983), and in the whole genus the most asymmetrical chromosome with an arm ratio of 3.3 was well within the nsm(+) category. This combination of small numerous chromosomes with little asymmetry does really restrict the inferences that can be drawn from them, especially as there is a base number difference present too. The total karyotype lengths were as to be expected roughly in proportion to the DNA C-values reported earlier.

Figs. 1–21. Mitotic and meiotic preparations of *Fallopia*. Mitotic preparations: Fig. 1. *F. dumetorum*, 2n = 20, P 177. – Fig. 2. *F. convolvulus*, 2n = 40, P 150b. – Fig. 3. *F. baldschuanica*, 2n = 20, P 163. – Fig. 4. *F. cilinodis*, 2n = 22, P 148. – Fig. 5. *F. multiflora*, 2n = 22, P 162. – Fig. 6. *F. japonica*, 2n = 44, P 134b. – Fig. 7. *F. sachalinensis*, 2n = 44, P 155. – Fig. 8. *F. sachalinensis* × *F. baldschuanica*, artificial hybrid 2n = 32, P 101b. – Fig. 9. (*F. japonica* var. *compacta* × *F. sachalinensis*) × *F. baldschuanica*, 2n = 32, P 146c. – Fig. 10. *F. japonica* × *F. baldschuanica*, 2n = 54, P 91b. – Meiotic preparations: Fig. 11. *F. baldschuanica*, 10 II, P 174. – Fig. 12. *F. cilinodis*, 11 II, P 148. – Fig. 13. *F. sachalinensis*, 20 II, 1 IV, P 68. – Fig. 14. *F. convolvulus*, 20 II, P 178. – Fig. 15. (*F. japonica* var. *compacta* × *F. sachalinensis*) × *F. baldschuanica*, 22 I, 5 II, P 101. – Fig. 16. *F. japonica* var. *compacta* × *F. sachalinensis*, 22 II, P 13. – Fig. 17. *F. japonica* × *F. baldschuanica*, 10 I, 22 II, P 83. – Fig. 18. *F. japonica* × *F. baldschuanica*, P 83. – Fig. 19. *F. japonica* × *F. sachalinensis*, 21 I, 22 II, P 32. – Fig. 20. *F. japonica* × *F. sachalinensis*, unique 8x form 2n = 88, 40 II, 2 IV, P 50. – Fig. 21. *Fallopia* root-tip cells fixed in formalin showing large tannin vesicles. Bar in Fig. 1 applies to Figs. 1–20, bars: 5 μm

Table 3. Meiotic analysis data of the *Fallopia* spp. investigated

Taxon	Acc. no.	2n	No. cells[1] examined	Meiotic configurations[2]							Mean xta per cell	Mean xta per biv.
				I	IIs[3]		IIIs	IVs			VIs	
					Rod	Ring		3xta	4xta	5xta		
F. dumetorum	P 177	20	3 (3)		19	11						13.67	1.37
F. baldschuanica	P 174	20	19 (19)		150	40						12.11	1.21
F. multiflora	P 162	22	15 (15)	4	129	34						13.1	1.19
F. cilinodis	P 148	22	5 (5)	1	32	21	1					15.2	1.38
F. convolvulus	P 178	40	7 (7)		92	36		6				26.0	1.30
F. japonica var. *compacta*	P 2	44	23 (23)	4	416	79	2	3				25.2	1.16
F. japonica var. *japonica*	P 114b	44	7 (7)		125	29						26.14	1.18
F. sachalinensis	P 68	44	13 (13)		208	70		2	2			27.69	1.26
4x "Reynoutria" × *F. baldschuanica*	P 102a	32	10 (0)	189	(61)		2	1					
4x "Reynoutria" × *F. baldschuanica*	P 102b	32	5 (0)	46	(28)		17	2					
F. sachalinensis × *F. baldschuanica*	P 101b	32	7 (0)	141	(34)		5						
F. japonica var. *compacta* × *F. sachalinensis*	P 13	44	10 (10)		163	40		5	1	1		26.7	1.21
F. japonica var. *compacta* × *F. sachalinensis*	P 78a	44	3 (2)		41	3						23.5	1.07
F. sachalinensis × *F. japonica* var. *compacta*	P 79c	44	34 (26)	5	422	96	1	19	5	1	1	29.8	1.35
F. japonica var. *japonica* × *F. baldschuanica*	P 80d P 83b	54	16 (0)	50	(110)								
F. japonica var. *japonica* × *F. japonica* var. *compacta*	P 76b	66	3 (0)	40	(39)		11	4					
F. japonica var. *japonica* × *F. sachalinensis*	P 75d	66	7 (0)	52	(62)		7						
F. japonica var. *japonica* × *F. sachlinensis*	P 32	66	11 (0)	153	(169)		23	6					
F. japonica × *F. sachalinensis* (8x)	P 51b	88	12 (3)	4	92	20		22	5		1	53.3	1.21

[1] Numbers in parentheses refer to number of cells in which chiasmata were counted.

[2] Columns under "Meiotic configurations" do not contain unspecifiable configurations, so that their accumulated chromosome numbers do not necessarily sum up to the number expected from the number of cells examined.

[3] Numbers in parentheses refer to bivalents that could not be distinguished as rod or ring.

Table 4. DNA C-values of *Fallopia* taxa

Taxon	Accession	No. cells	2C DNA pg	S.D.	pg DNA per 2x genome	2n
F. dumetorum	P 177	35	0.68	0.12	0.68	20
F. baldschuanica	P 163	84	1.96	0.32	1.96	20
F. multiflora	P 162	46	1.41	0.22	1.41	22
F. cilinodis	P 148	59	2.14	0.26	2.14	22
F. cilinodis	P 156b	130	2.21	0.27	2.21	22
F. convolvulus	P 150	32	1.44	0.25	0.72	40
F. sachalinensis	P 171	58	2.65	0.29	1.33	44
F. japonica var. *compacta*	P 2A	56	2.57	0.33	1.29	44
F. japonica	P 114b	50	2.59	0.35	1.30	44
F. japonica	P 172	133	3.06	0.38	1.53	44
F. japonica var. *japonica*	P 169	65	6.48	0.65	1.62	88

Chromosome banding. Where traditional cytological staining techniques fail in the elucidation of karyotypes, various banding techniques such as Giemsa C-banding and the use of various combinations of fluorochromes can often be of service. Much time was spent employing these techniques but without any conspicuous success. Certain preparations appeared to have the propensity for banding, as revealed by darker regions found in some orcein squashes, but this was not revealed in C-bands, or fluorescent bands with chromomycin, distamycin or DAPI.

Discussion

Microdensitometry and tannins. Very few C-values have been published for the *Polygonaceae*, so it is rather difficult to make meaningful comparisons. Bennett & al. (1982) gave 2C-values of 3.4 pg and 8.8 pg respectively for the tetraploid *Rumex acetosella* and the octoploid *R. crispus*, both of which are rather higher than our results. Leeman & Ruch (1983) gave a 2C-value of 7.0 pg for a male plant of *R. acetosa* (2n = 12 AXYY). Grime & al. (1988) reported a 2C-value of 3.4 pg for *Fallopia japonica*, but they did not count the chromosome number of their material and their fixation method involved 3 : 1 (see below), so that the significance of their results is unclear.

Whilst we are reasonably satisfied with the accuracy of our comparative DNA data, we are less so with the absolute DNA values obtained. Much of the blame for this must go on the use of metaphase cells for measurement, but it is not impossible that real differences were also involved since there is some regional variation amongst plants. Price (1988) listed several well-documented cases of intra-specific variation in DNA content. In the case of *Allium* (unpublished) we demonstrated that the use of late prophase and metaphase rather than early prophase resulted in a 22% underestimate of C-value. It was necessary to use metaphase and late prophase in *Fallopia* since unless the DNA was highly concentrated the nuclei did not take up the stain properly. Initial attempts at using early prophase cells led to readings that ranged between 10% and 60% of the metaphase readings,

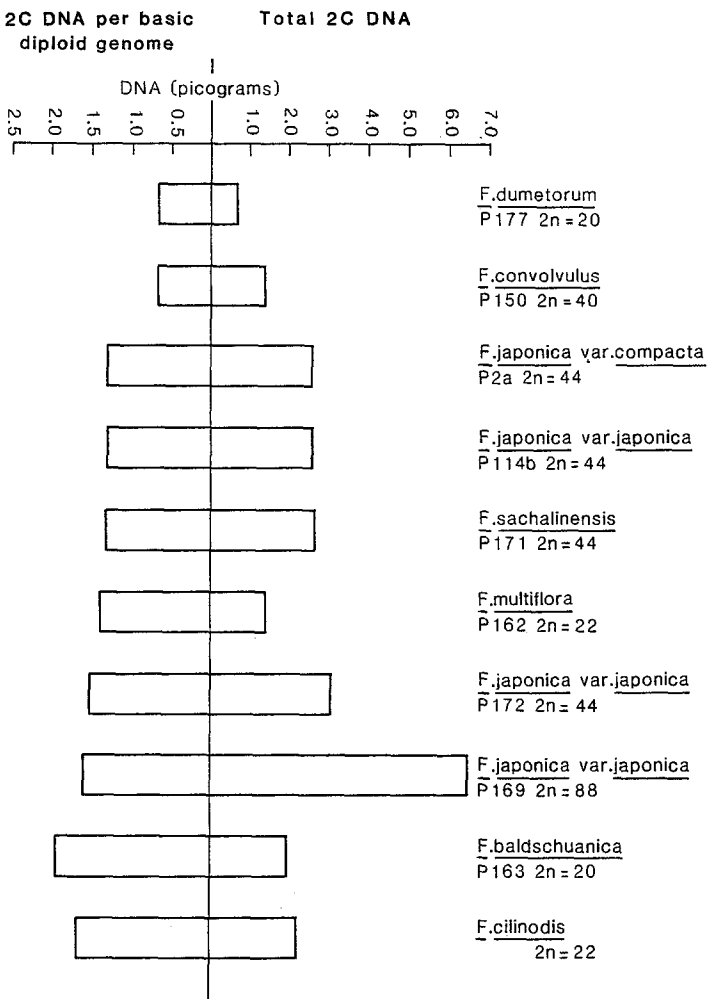

Fig. 22. DNA C-value expressed graphically as total amount and amount per diploid genome

with several orders of magnitude of difference between the highest and lowest value, clearly of little use for DNA estimation purposes.

What conclusions, if any, can be drawn about the pattern of DNA variation in this group with its range of ploidy level, life-form, and growth habit? In terms of 2x 2C-values the annual diploids have the lowest, the sect. *Reynoutria* taxa and *F. multiflora* occupy the middle range, and the climbing herbaceous *F. cilinodis* and the woody climber *F. baldschuanica* have the highest amounts. From these data it is not really possible to say with certainty whether amongst the herbaceous perennial taxa there is an increase or decrease in genome size with increasing ploidy level. Since the diploid *F. multiflora* falls amongst the tetraploids and the variation of the octoploids is high, it appears that no such differences exist. The annual taxa *F. dumetorum* and *F. convolvulus* clearly have the lowest DNA contents and it might be argued that this is linked to the annual habit. If, as BENNETT & al. (1982) suggested, the minimum generation time is linked to the nuclear DNA content, a low C-value and fast minimum generation time is obviously advantageous to annual

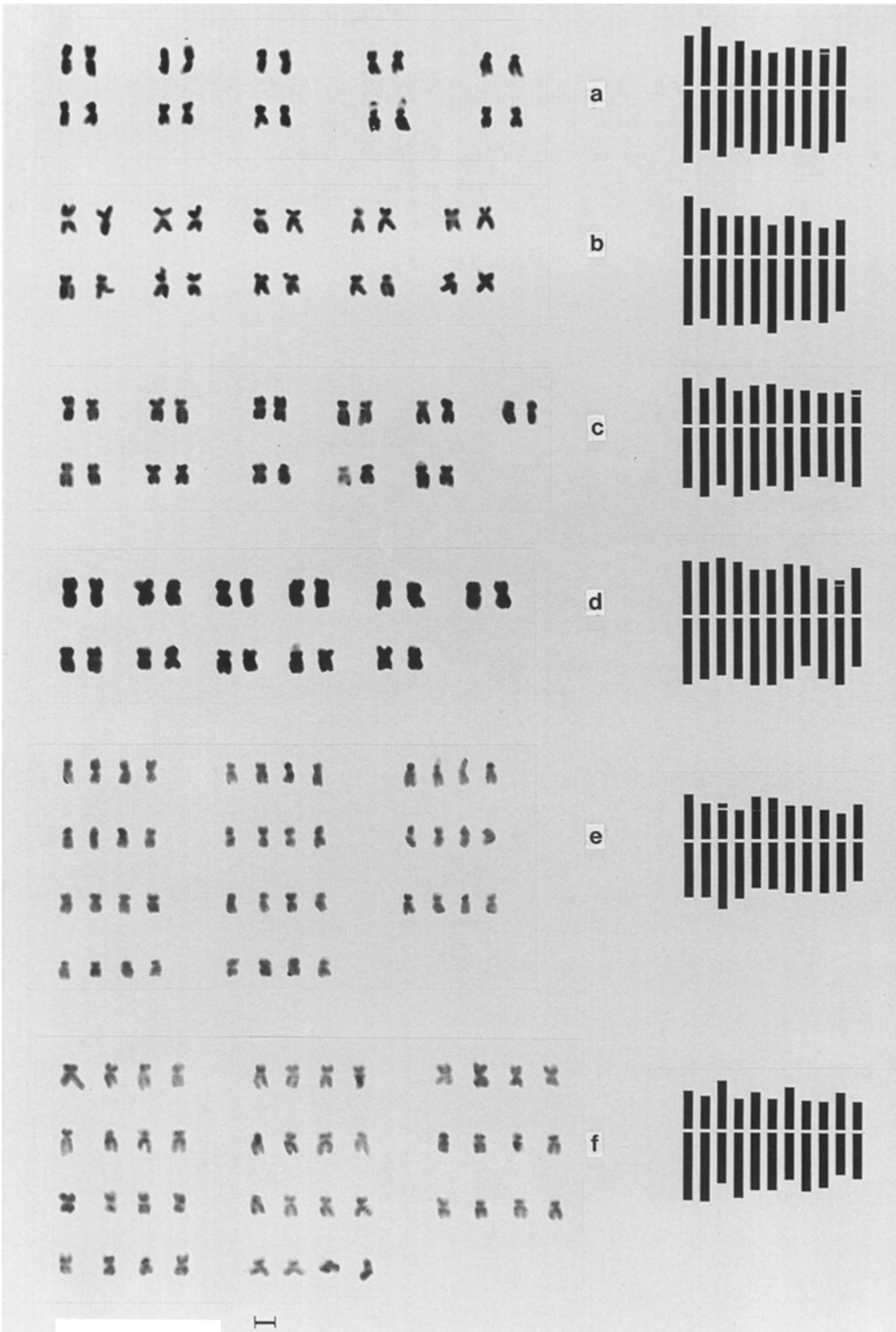

Fig. 23. Karyotypes of *Fallopia* spp. *a F. dumetorum* 2n = 20 (P 177); *b F. baldschuanica* 2n = 20 (P 163); *c F. multiflora* 2n = 22 (P 162); *d F. cilinodis* 2n = 22 (P 148); *e F. sachalinensis* 2n = 44 (P 155); *f F. japonica* var. *compacta* 2n = 44 (P 99a). Bar: 2 µm

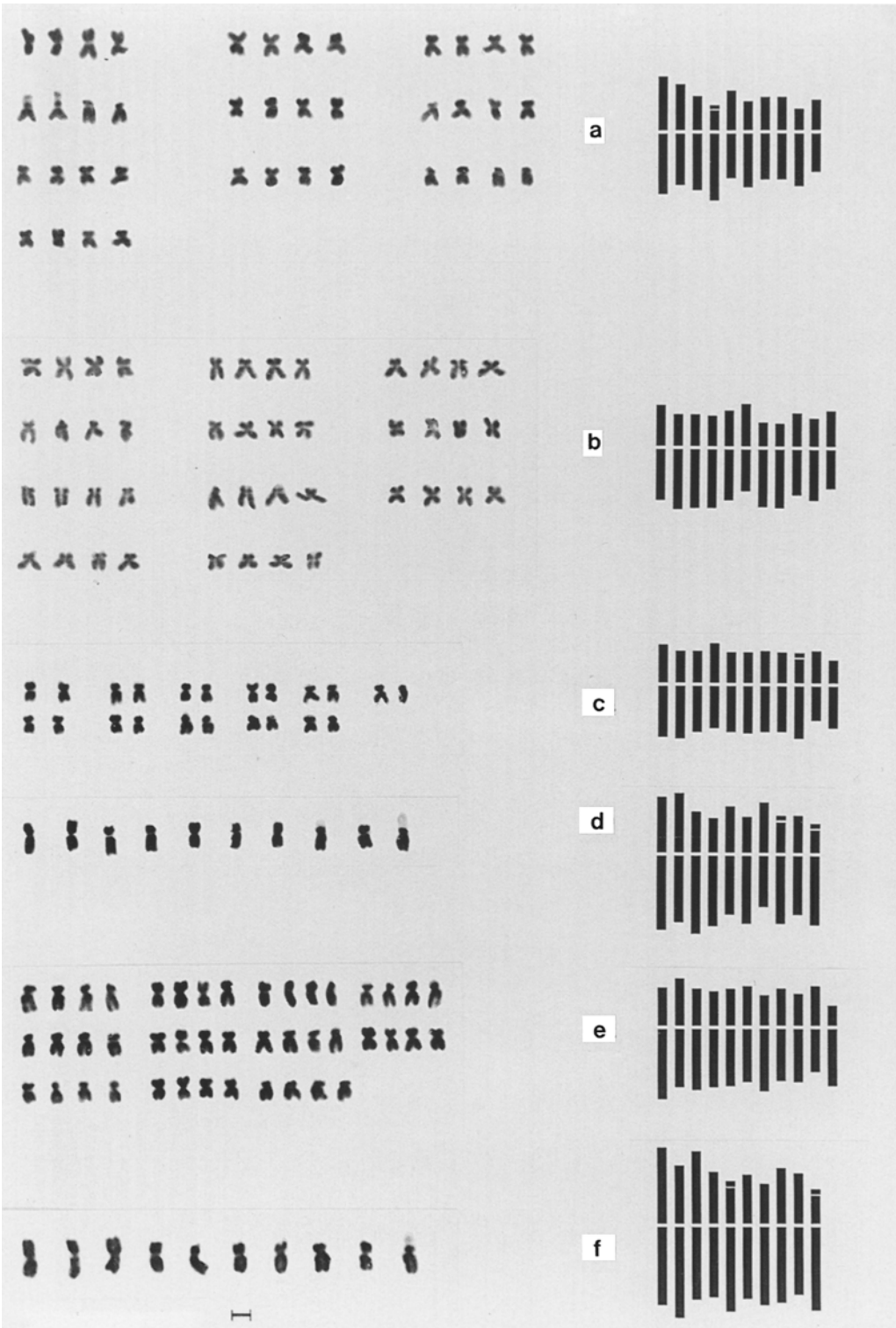

Fig. 24. Karyotypes of *Fallopia* spp. *a F. convolvulus* 2n = 40 (P 150); *b F. japonica* var. *japonica* 2n = 44 (P 134 b); *c, d F. sachalinensis* × *F. baldschuanica* 2n = 32 (P 101b); *c F. sachalinensis* complement, *d F. baldschuanica* complement; *e, f F. japonica* var. *japonica* × *F. baldschuanica* 2n = 54 (P 91), *e F. japonica* complement, *f F. baldschuanica* complement. Bar: 2 µm

Table 5. Summary of principal *Fallopia* karyotype data

Taxon	Acc. no.	2n	No. cells	Mean karyotype length μm	Arm ratio least sym. chromosome	Mean arm ratio
F. dumetorum	P 177	20	2	40.73	2.19	1.47
F. baldschuanica	P 163	20	2	60.9	3.14	1.83
F. baldschuanica	P 151	20	2	54.7	3.19	1.87
F. baldschuanica	P 175	20	4	49.72	2.66	1.6
F. multiflora	P 162	22	4	52.79	3.13	1.8
F. cilinodis	P 148	22	2	54.8	2.45	1.34
F. convolvulus	P 150	40	2	86.5	3.32	1.43
F. sachalinensis	P 155	44	1	95.8	2.29	1.58
F. japonica var. *compacta*	P 99a	44	1	101.4	2.15	1.69
F. japonica	P 134b	44	1	93.8	2.62	1.7

and ephemeral taxa. The notion that small DNA values are more advantageous for annuals than perennials must of course be balanced against the need to maintain genetic heterozygosity, which might argue the need for a larger DNA amount for annual taxa.

Data published by BENNETT & SMITH (1976) lend support to both possibilities, as well as a third, that there need be no difference in C-value between them. In the genus *Hordeum*, for example, the 2x C-values show no significant difference between annual and perennial taxa, though it should be noted that there is little variation in 2x C-value amongst the taxa listed. On the other hand the diploid (2n = 14) species of *Lathyrus* show a definite tendency for the perennials to have a higher C-value than the annuals. But in the 2n = 8 species of *Crepis* the annuals have the highest and lowest C-values with the perennials having the medium values.

The finding of tetraploids with less DNA than related diploids is not an uncommon one, as SEAL (1983) found in *Festuca* and JONES & REES (1968) in *Allium*. In the case of *Festuca* there was also a decreasing 2x C-value with increasing ploidy level.

Much of the study of the cytology of this group has been hampered by the presence of tannins in the cytoplasm. Even following the recommendations of GREILHUBER (1986) in the use of methanal rather than 3 : 1 fixation has not entirely resolved this. Figure 21 shows the tannin vacuoles present in a methanal-fixed squash of *Reynoutria* cells. LEEMAN & RUCH's (1983) fluorescent studies on the related *Rumex acetosa* encountered similar problems. They concluded that even with methanal fixation the "UV absorbing substance" was still capable of affecting the fluorescent staining abilities of the cells. This presence of tannins we hold partly responsible for the lack of results in both our Giemsa and fluorescent banding studies.

Meiosis. Generally speaking, sect. *Reynoutria* bivalents appear somewhat diffuse. This diffuseness is probably analogous to that found in the majority of sect. *Reynoutria* mitotic preparations, where it generally obscures the precise position of the

centromere. Chiasmata were similarly obscure, and scoring of them was done at pro-metaphase rather than at pachytene or diplotene.

Taking the average chiasmata frequency per bivalent it may be seen that the range of values for diploids and tetraploids is not very different. The range of chiasma frequencies per bivalent of 1.16 to 1.38 is rather low, but this is not unusual in the case of small chromosomes. JOHN & LEWIS (1965) reported that in the grasshopper *Chorthippus brunneus* the number of chiasmata per bivalent was related to the length of the chromosome, the longest chromosome in the complement having 2 or 3 chiasma, medium sized chromosomes 1 or 2, and the smaller (3–6 μm) ones only 1.

The potentially in-breeding taxa *F. convolvulus, F. dumetorum*, and *F. cilinodis* have the highest chiasma frequency, which is in agreement with results presented by STEBBINS (1971) in tribe *Hordeeae* (*Triticeae*) of the *Poaceae*, where there is an inverse relationship between degree of out-crossing and chiasma frequency. STEBBINS (1971) suggested that low recombination frequencies and predominant self-fertilisation are alternative strategies for maintaining adaptive gene combinations in situations where this has a high selective value.

Finally, if JACKSON (1982) is correct and the first chiasma is not randomly distributed but allocated one per bivalent, it is possible that taxa with low chiasmata frequency are to a certain extent preadapted to successful (i.e. fertile) polyploidy, in that the number of multivalents in a newly created autoploid or segmental alloploid would be reduced simply by a lack of the chiasmata needed to form them. A rod bivalent requires 0.5 chiasma per chromosome whilst a rod trivalent needs 0.67 chiasma per chromosome. This aside, lack of a significant number of multivalents in the polyploid taxa points to some means of multivalent suppression, unless, of course, these taxa arose as strict allopolyploids in which case multivalent suppression would not be necessary.

Chromosome number and ploidy level. In the genus *Fallopia* as a whole we are confronted by a range of chromosome numbers from 20 to 88 containing base numbers of both 10 and 11. Polyploidy is, however, restricted to the herbaceous erect rhizomatous perennials of sect. *Reynoutria* and to the annual climber *F. convolvulus*. This latter is something of a special case in that not only is it the most widely distributed taxon in the group (in recent times circumpolar according to HULTÉN & FRIES 1986) but, throughout its range, it is found only as a weed of arable land. It is as a weed of cereal crops that it is perhaps best adapted, the loss of the winged persistent perianth as present in the closely related *F. dumetorum* allowing it to mimic the harvested cereal grains more closely and ensuring its incorporation into the seed corn. This is perhaps yet another case of man unwittingly selecting simultaneously for better cereals and better weeds. Tetraploid annual weeds are not very common, and we can suggest that the weedy habit was adopted after the occurrence of polyploidy or that the burden of producing twice the amount of DNA was more than balanced by the increased heterozygosity and a greater tolerance of inbreeding. Alternatively, the introduction of the polyploid wheats with their larger grain size would have preferentially favoured the incorporation of the larger seeds from the occasional spontaneous tetraploid individuals of *F. convolvulus*.

Polyploidy in sect. *Reynoutria* is, in all but the mountain forms, associated with

gigantism, which reaches its peak in *F. sachalinensis* which may attain a height of 3 metres with leaves up to 40 cm in length – quite remarkable growth for a herbaceous plant. Polyploidy is also associated with asexual reproduction in these taxa, production of new plants from rhizome fragments being the chief means of spread of these plants in Europe. A correlation between high polyploidy and vegetative reproduction is not uncommon in the plant kingdom, though in this case it is not an escape from infertility since plants at all ploidy levels are fertile (providing both sexes are available).

The other point of interest is the fact that the genus comprises two different base numbers, x = 10 and 11. In order to see whether this is significant in the context of the *Polygonaceae* we examined the recorded base numbers and ploidy levels in the related genera and sections which make up the taxonomic group *Polygonum* s.l. This proved to be quite informative since, apart from *Koenigia* which has a base number of x = 7 and *Fagopyrum* which has a base number of x = 8, all the other taxonomic groupings have mixed base numbers of x = 10 and 11, with some having in addition x = 12 and 13. They also exhibited a similar pattern to *Fallopia* regarding polyploidy, taxa being mainly represented at the diploid and tetraploid level, but all having a scattering of taxa up to the octoploid level.

Genome homologies. Summaries of the hybrid combinations and of the parental and hybrid meiotic behaviour are given in Figs. 25 and 26. Starting with the male-sterile octoploid *F. japonica* var. *japonica* it will be noted that, although we have not studied female meiosis in this variety, we have examined the male meiosis of an octoploid *F. japonica* var. *japonica* × *F. sachalinensis* cross. This clearly shows that regular meiosis is possible at the octoploid level and if a hybrid can produce regular meiosis the octoploid species would be expected to do no worse. The regular meiotic segregation of *F. japonica* var. *japonica* is also vouched for indirectly by the examination of seed produced by it, which has in all cases been exactly euploid. The meiotic behaviour of the pentaploid *F. japonica* var. *japonica* × *F. baldschuanica*

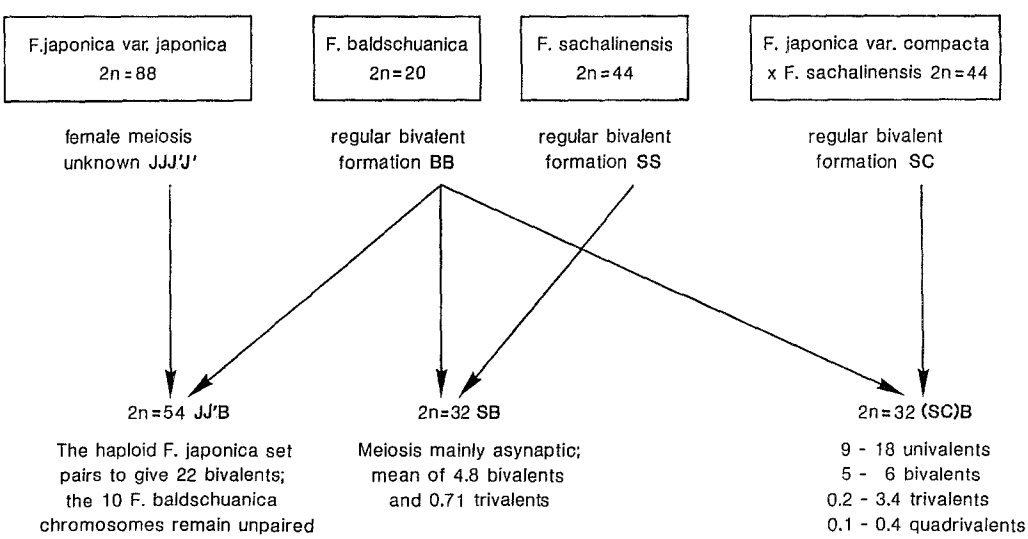

Fig. 25. Genome homologies in the inter-sectional hybrids in *Fallopia* sect. *Reynoutria* × sect. *Fallopia*

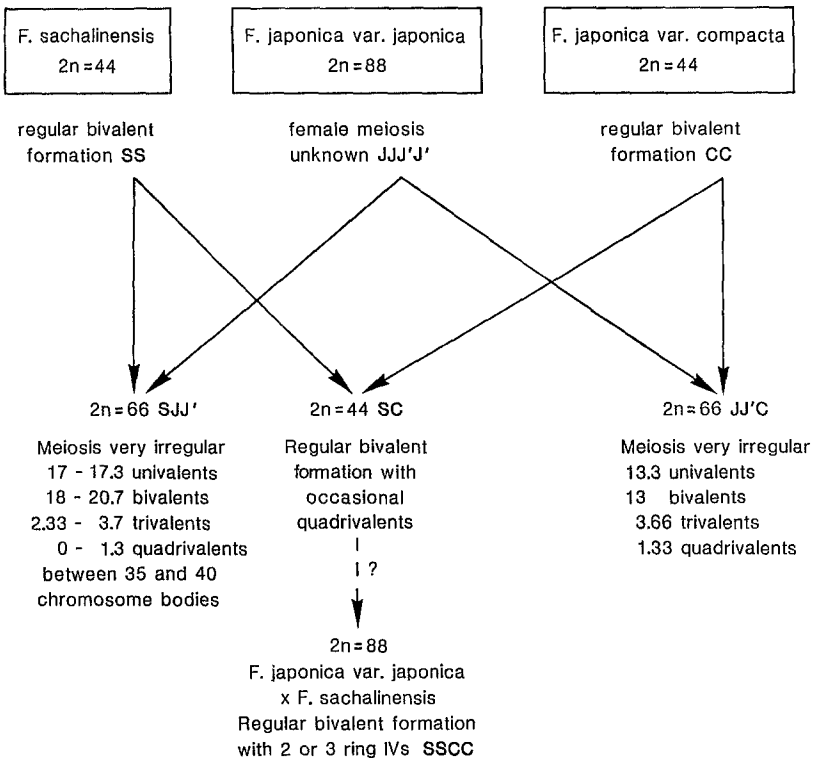

Fig. 26. Genome homologies in the intra-sectional hybrids in *Fallopia* sect. *Reynoutria*

hybrid is not only most clear-cut (Fig. 25), but holds the key to what is occurring amongst these hybrids. Meiosis in these plants regularly gives 22 bivalents and 10 univalents, which we interpret as pairing within the tetra-haploid *F. japonica* genome, leaving the 10 *F. baldschuanica* chromosomes unpaired (Fig. 17). This is an extremely interesting result since it is an example of good homogenetic pairing and is indicative of the existence of some method of multivalent suppression in the octoploid parent. Observation of the meiotic behaviour of the di-haploid sets of *F. sachalinensis* and *F. japonica* var. *compacta* × *F. sachalinensis* in their hybrids with *F. baldschuanica* shows that in the case of *F. sachalinensis* hybrids very little pairing occurs (Fig. 25). In contrast the meiosis of some plants of (*F. japonica* var. *compacta* × *F. sachalinensis*) × *F. baldschuanica* reveals as many as 10 bivalent equivalents, including up to 3.8 multivalents. These multivalents suggest that some degree of homology still exists between sect. *Reynoutria* and *F. baldschuanica* genomes. It must be borne in mind that these figures were rather difficult to interpret, and the possibility of error should not be ignored.

In the intra-sectional *Reynoutria* hybrids (Fig. 26), regular meiosis (apart from the occasional ring multivalent) is found in *F. japonica* var. *compacta* × *F. sachalinensis* and in the octoploid *F. japonica* × *F. sachalinensis* hybrids. The position is quite different with the hexaploid hybrids formed by crosses between octoploid *F. japonica* var. *japonica* and the tetraploid sect. *Reynoutria* taxa. In these meiosis is most irregular, although, particularly in *F. japonica* var. *japonica* × *F. sachalinensis*

and to a lesser extent in *F. japonica* var. *japonica* × *F. japonica* var. *compacta*, there appears to be a core of about 22 bivalents and multivalents.

Whilst the tetra-haploid genome of *F. japonica* var. *japonica* is capable of forming bivalents, the di-haploid genome of *F. sachalinensis* is not. This suggests that the tetraploid is considerably more ancient than the octoploid and that in the course of time it has been effectively diploidised with a number of 22 in terms of homology. The octoploid on the other hand has probably not been around long enough for full diploidisation to occur. On the basis of this one can assign letters to the different genomes (x = 22 in sect. *Reynoutria* and 10 in *F. baldschuanica*) as shown in Figs. 25 and 26. Octoploid *F. japonica* has the genomic formula JJJ'J', *F. japonica* var. *compacta* CC, *F. sachalinensis* SS and *F. baldschuanica* BB. Viewed from this angle the fertility of the *F. japonica* var. *compacta* × *F. sachalinensis* hybrid results from the homology between the S and C genomes, whilst the infertility of the hexaploids is caused by there being an unpaired S or C in the presence of two J genomes, explaining the more or less 22 bivalents plus multivalents found. Thus, in the triploid hybrids, the one involving *F. sachalinensis* has a genomic formula of SB. With two heterologous genomes one would expect little pairing, as observed. The position in the double hybrid (*F. japonica* var. *compacta* × *F. sachlinensis*) × *F. baldschuanica* is a little more complex, since if the assumption that the S genome is pairing with the C genome is correct, any offspring in this hybrid with *F. baldschuanica* would, due to random segregation of bivalents, be a random mixture of chromosomes from the S and C genomes. The presence of the occasional quadrivalent in the SC parent reinforces the idea that there is some homology between the S and C genomes and this might explain the greater degree of pairing found in some plants of this combination.

In assigning the species and hybrids a genomic formula we have deliberately chosen letters based on the specific names rather than ones which imply degrees of genomic homology. Classical techniques of the genome analysis of species and hybrids seek to assign genome homologies and auto- or allo-ploid origin to polyploids. Such techniques fail when confronted with multivalent suppressors, which are clearly indicated in the case of *F. japonica* var. *japonica*.

The case for *Fallopia*. In order to put our cytological and hybridisation data in context, it is necessary first to review briefly the recent history of the classification of this group and the reasons for and against amalgamation of the genera *Fallopia* and *Reynoutria*. Löve & Löve (1956), whilst allowing that palynological data and some morphological similarities indicated a generic association of *Reynoutria* and *Bilderdykia* (= *Fallopia*), claimed that this was "strongly contradicted by the available cytological data". No details of this cytological evidence were presented. Webb & Chater (1963) pointed out that the twining woody perennial *Polygonum baldschuanicum* provided a link between the two genera, but that, as it shared stigmatal morphology and a chromosome base number of 10 with *Bilderdykia*, it was best assigned to that group. Holub (1971) acknowledged that *Reynoutria* and *Fallopia* make a single distinct group in the context of a segregate of *Polygonum* s.l. with a pollen type, chemical constituents and keeled or winged outer perianth segments in common. However, he considered that differences in chromosome base number, stigma characters and growth habit warranted generic separation. Whilst mentioning *Polygonum multiflorum*, his lack of first hand knowledge of it caused him

to list it as only possibly belonging to the genus *Fallopia*. HARALDSON (1978) rectified this default and made the combination *F. multiflora*. Whilst she found similarities in trichome types, she found differences in petiole and stem anatomy, and chose to maintain the taxa as two genera. It is, of course, a moot point whether these differences in vasculature are more a reflection of the relative size and life form of the plants under consideration than an indicator of some more fundamental evolutionary divergence.

At the sectional level, these taxa have often been considered as one group ever since 1826 when MEISSNER added the newly described *Polygonum cuspidatum* to his sect. *Tiniaria*. This was also followed by STEWARD (1930), HEDBERG (1946), who proposed that sect. *Tiniaria* be accorded generic rank, and GRAHAM & WOOD (1965). SHINNERS (1967) amalgamated the two groups under the generic name *Reynoutria* – then the oldest name known for these taxa. In 1988 RONSE DECRAENE & AKEROYD amalgamated *Reynoutria* with *Fallopia*, adding new data on the similarities in stamen type and tepal vasculature, and remarking that "the anatomical heterogeneity of *Fallopia* breaks down any clear distinction from *Reynoutria*".

An important factor in the history of the classification of this group is that of its distribution pattern. The important taxon *F. multiflora* is usually overlooked in the context of the European flora, whilst the American *F. cilinodis* is missed in the context of a study of Asiatic taxa. Indeed most authors opting for segration of the two groups whether at sectional or generic level have been unaware of, or have understood poorly the nature of, the herbaceous climber *F. multiflora*. In fact it is this taxon which is the key link between the two groups of species. Diploid with a base number of 11 and a 2C-value clearly within the range of sect. *Reynoutria* (Table 4, Fig. 22), it also shares with this group the possession of a rhizome and some aspects of stigma morphology. It closely resembles a climbing version of a sect. *Reynoutria* taxon, and STEWARD (1930) described a variety of it which resembles sect. *Reynoutria* even more closely in being more erect and with less tendency to climb. We have unfortunately been unable to attempt hybridisations using *F. multiflora*, since our material has only flowered once, and then in November, after the sect. *Reynoutria* plants had finished flowering. This is indeed unfortunate, for we consider on morphological and cytological grounds that, if this is not the actual progenitor of the erect herbaceous plants of sect. *Reynoutria*, it and they certainly sprang from a common ancestor; hybridisation data would have been most illuminating in this context.

The hybridisation data that we have regarding *F. baldschuanica* and sect. *Reynoutria* certainly support amalgamation of the two groups. The scale of the hybridisation phenomenon, the extremely high fertility of the hybrid seed, and the vigour of the F_1 plants all point to a close taxonomic relationship, as do the similarities in the karyotypes and the evidence of multivalent formation in the triploid *F. baldschuanica* × tetraploid sect. *Reynoutria* hybrids. Differences in chromosome base number (*Fallopia* x = 10, *Reynoutria* x = 11) have traditionally been given as grounds for segregation, but, when the full range of taxa is considered, with *F. multiflora* (2n = 22) and *F. cilinodis* (2n = 20 and 22), any such distinction breaks down. In any case, chromosome base number in other segregates of *Polygonum* s.l. is a notoriously unreliable predictor of taxonomic grouping, with most segregates possessing two or more different base numbers. In view of all this steadily

accumulating evidence, there can be little doubt that these taxa are best treated as a single genus, the proper name for that genus being *Fallopia*.

Note added in proof:

Further *Polygonaceae* 2C DNA amounts recently published (BENNETT, M. D., SMITH, J. B., 1991: Phil. Trans. Roy. Soc. London Ser. B **334**: 309–345) are:

Polygonum lapathifolium 1.4 pg; *P. persicaria* 0.9 pg; *Rumex acetosa* 3.3 pg; *R. obtusifolius* 3.1 pg. The figures for *Rumex* confirm the levels previously reported. The figures for *Polygonum* are the first reported for sect. *Persicaria* (= genus *Persicaria* of many authors); the values are in the same range as those reported in this paper for the herbaceous twining species of *Fallopia*.

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