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Chromosome numbers and karyotypes of South American species and populations of *Hypochaeris* (Asteraceae)

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One hundred and thirty-seven new chromosome counts are reported from 104 populations of 26 native South American taxa of *Hypochaeris* (Asteraceae, Lactuceae), together with two invasive Mediterranean species: *H. glabra* and *H. radicata*. First reports are provided for seven taxa (*H. alba*, *H.* cf. *eremophila*, *H. caespitosa*, *H. hookeri*, *H. parodii*, *H. patagonica* and *H. pinnatifida*) and one new ploidy level is reported (diploid for *H. incana*, so far known only as a tetraploid). Including the results of this study, the chromosomes of 39 of the *c.* 50 *Hypochaeris* species known from the New World have now been counted. Most species are diploid with $2n = 2x = 8$ and have bimodal, asymmetrical karyotypes. Tetraploidy ($2n = 4x = 16$) is reported here for the first time in *H. caespitosa*. Infra-specific polyploidy (probably autopolyploidy) is reported in *H. incana* and *H. taraxacoides*, both cases including infra-populational cytotype mixtures ($2x$ and $4x$). Polyploidy is now known from eight South American *Hypochaeris* species (*c.* 16%). Basic karyotype analyses allow the placement of the newly counted taxa into previously proposed but slightly modified groupings and provide the framework for further molecular cytogenetic analyses. The reported findings suggest that chromosomal change in South American *Hypochaeris*, in contrast to Old World species, has not involved aneuploidy, but polyploidy and/or more subtle changes in chromosome length, perhaps via satellite DNA amplification/deletion or activity of retroelements, and rDNA reorganization. © 2007 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2007, **153**, 49–60.

ADDITIONAL KEYWORDS: cytotype mixture – evolution – polyploidy – speciation.

INTRODUCTION

Hypochaeris (Asteraceae, Lactuceae) is a genus of more than 15 species occurring in Eurasia and north-west Africa (DeFillips, 1976; Oberprieler, 2002) and about 50 taxa confined to South America, many of which are localized in the Southern Cone (Bortiri, 1999). The apparently rapid recent speciation of the genus in South America (Tremetsberger *et al*., 2005), combined with the relatively large size and small number of chromosomes, offers a system in which the role of chromosomal rearrangements during speciation can be examined (Stebbins, 1971; Cerbah, Coulaud & Siljak-Yakovlev, 1998; Weiss *et al*., 2003; Weiss-Schneeweiss *et al*., 2003).

Earlier studies have provided detailed information about chromosome numbers and karyotypes of European species of *Hypochaeris* (Parker, 1976; Mugnier & Siljak-Yakovlev, 1987; Barghi, Mugnier & Siljak-Yakovlev, 1989; Siljak-Yakovlev *et al*., 1994; Cerbah *et al*., 1995, 1998). These taxa have symmetrical karyotypes and different basic chromosome numbers

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($x = 3$, 4, 5, 6), which have been used in conjunction with morphology (Hoffmann, 1893) for sectional classification within the genus. Molecular phylogenetic studies using ITS and chloroplast genes (*trnL* intron and *trnL*/*trnF* spacer and *matK*) have confirmed these as monophyletic groups (Samuel *et al*., 2003).

South American taxa of *Hypochaeris* are poorly studied karyologically. Most chromosome numbers for South American *Hypochaeris* that have been documented so far (see review in Weiss *et al*., 2003; Baeza, Vosyka & Stuessy, 2004) are diploids with $2n = 8$, with a few cases of intraspecific and/or intrapopulational tetraploidy (all based on $x = 4$). Only *H. caespitosa* appears to be uniformly tetraploid (this study), with the caution that only one population has been examined so far. Recent karyological analyses of South American species of *Hypochaeris* have extended the survey of chromosome numbers to 32 species (Weiss *et al*., 2003), with detailed karyotypic analysis of 14 species including 5S and 18S-25S rDNA sequence localization by FISH (Cerbah *et al*., 1998; Weiss-Schneeweiss *et al*., 2003; Ruas *et al*., 2005). These data, together with the positions of secondary constrictions (SCs) and satellites, have allowed the grouping of taxa into several karyotypic classes. Detailed analyses of the presence/absence and chromosomal localization of 5S and 18S-25S rRNA genes have also permitted hypotheses to be made regarding relationships among South American taxa as well as with Eurasian relatives (Weiss-Schneeweiss *et al*., 2003; Tremetsberger *et al*., 2005).

The main objectives of this paper are: (1) to report new counts for 104 populations of 26 taxa of *Hypochaeris* collected in Chile, Argentina, Bolivia, Ecuador, Peru and Venezuela; (2) to analyse in detail the karyotypes of 14 South American species; (3) to analyse karyotypic variation in tetraploid cytotypes in comparison with their diploid relatives. The karyotypic information presented in this paper will lay foundations for the study of karyotype evolution in *Hypochaeris* using molecular cytogenetic methods (Weiss-Schneeweiss, unpubl. data).

MATERIAL AND METHODS

Bud and seed material was collected in South America in 2002 and 2003 (Table 1). In all instances, collections were of populational samples. Vouchers have been deposited at CONC, LP, LPB, QUSF and WU.

For mitotic chromosome counts, root meristems were obtained from surface-sterilized seeds germinated for a few days on wet filter paper. Root tips were pretreated with 0.1% colchicine for 2 h at room temperature in darkness, and 2 h at 4 °C, fixed in 3:1 ethanol: acetic acid for 24 h and stored at –20 °C until use. For meiotic chromosome counts, flower buds were fixed in modified Carnoy's solution (4 chloroform: 3 absolute ethanol: 1 glacial acetic acid), transferred to 70% ethanol, and stored at 4 °C until used.

Chromosome preparations were made using Feulgen staining with Schiff's reagent (Merck, Vienna, Austria) following standard methods (Weiss *et al*., 2003). Root tips and flower buds were washed in distilled water to remove the fixative, hydrolysed in 5N HCl (Merck, Vienna) for 30 min at 20 °C and washed and stained with Schiff's reagent in darkness for 1–2 h. Squash preparations were made in a drop of 45% acetic acid. After removal of the coverslip on dry ice, preparations were dried for 24 h at 37 °C and mounted in DPX. Chromosome numbers were determined from at least 20 cells of at least two florets for meiotic counts, and of at least three seedlings for mitotic observations. Measurements (chromosome arm length) were made from five randomly selected chromosomal spreads. Microphotographs were taken on monochrome Kodak film, scanned and processed in Corel Photo-Paint v.10.0 using only those functions that apply equally to all pixels in the image. Idiograms were prepared using the program Autoidiogram (courtesy of Dr W. Harand, University of Vienna, Austria).

RESULTS AND DISCUSSION

CHROMOSOME NUMBERS

One hundred and thirty-seven new chromosome counts are presented from 104 populations of 26 species of *Hypochaeris* from South America (Table 1), including first reports for seven taxa: *H. alba*, *H.* cf. *eremophila*, *H. caespitosa*, *H. hookeri*, *H. parodii*, *H. patagonica* and *H. pinnatifida*. *Hypochaeris radicata* and *H. glabra* from the Mediterranean occur in South America as nonindigenous weeds and have been included for completeness of the survey. This study brings the total number of counts for the genus in South America to more than 230 populations and 39 species, plus a few counts for putative hybrids (Weiss *et al*., 2003: table 1; Ruas *et al*., 2005; this study).

All chromosome counts in South American *Hypochaeris* are based on $x = 4$, with mostly diploids ($2n = 8$) being found. Among the native South American *Hypochaeris* species investigated so far, 25 are uniformly diploid ($2n = 8$), seven exhibit both diploid and tetraploid cytotypes (*H. chondrilloides*, *H. incana*, *H. meyeniana*, *H. scorzonerae*, *H. sessiliflora*, *H. taraxacoides*, *H. tenuifolia*) and one is tetraploid ($2n = 16$; *H. caespitosa*), although the latter observation is based on counts from one population only.

Polyploidy (all tetraploids; $2n = 4x = 16$) has been reported previously in seven South American *Hypochaeris* species: *H. chondrilloides* (Wulff, 1998), *H. incana* (Moore, 1981), *H. meyeniana*, *H. scorzonerae*

Table 1. New chromosome counts of *Hypochaeris* from South America. Counts are mostly from (1) mitotic preparations obtained from root tips of germinated seedlings, and/or (2) mitotic (asterisk) and (3) meiotic divisions in field-fixed flower buds. Abbreviations of collectors: AJ, A. Jiménez; AT, A. Tribsch; CB, C. Baeza; EU, E. Urtubey; FE, F. Essl; HV, H. Valdebenito; JR, J. Robayo; KT, K. Tremetsberger; MS, M. Staudinger; PL, P. López; PS, P. Schönswetter; PSI, P. Simón; RH, R. Hössinger; SG, S. Gómez; TS, T. Stuessy., ++, first report(s) for taxon; +, new ploidy level

Taxon	2*n*	Location (voucher number)
++*H. alba* Cabrera	8, 8*	Argentina, Prov. Corrientes, Mburucuyá, near Estancia Santa Teresa in National Park (*EU, KT 156*). Figs 1, 16; Table 2
	8, 8*	Argentina, Prov. Corrientes, Bella Vista, Parque Cruz de los Milagros (*EU, KT 159*)
H. albiflora (O.K.) Azevêdo-Gonçalves & Matzenbacher	8, 8*	Argentina, Prov. Buenos Aires, Diagonal 74 from Punta Lara to La Plata, before highway (*EU, KT 116*)
	8*	Argentina, Prov. Buenos Aires, Sierra de la Ventana, Abra de la Ventana (*EU, KT 129*)
	8	Argentina, Prov. Chaco, Resistencia, Balneario Paranacito (*EU, KT 155*)
H. cf. *albiflora*	8	Argentina, Prov. Jujuy, 1.3 km south of Arroyo Horquetas, down from Laguna Yala area (*TS, EU, KT 18059*)
H. apargioides Hook. & Arn.	8*	Argentina, Prov. Río Negro, 3 km down from 1st refuge on Cerro Buitrero (*TS, EU, KT 18023*)
	8	Chile, Región IX, 3 km east of junction on road to Lonquimay (*TS, CB, KT 18099*)
	8*	Chile, Región X, Volcán Villarrica, near refuge (*KT, SG 1083*)
	8	Chile, Región VIII, Yumbel, from railway station Yumbel to Puente Perales (*KT, CB 1013*)
	8	Chile, Región VIII, Yungay (*KT, CB 1014*)
	8	Chile, Región VIII, on road between Cabrero and Cerro Negro (*KT, CB 1015*)
	8*	Chile, Región IX, Volcán Lonquimay, near refuge (*KT, AJ, SG 1056*)
++*H. caespitosa* Cabrera	16	Argentina, Prov. Córdoba, Cerro Los Gigantes (*EU, KT 148*). Figs 12, 16; Table 2
H. chillensis (Kunth) Hieron.	8, 8*	Argentina, Prov. Jujuy, 6.8 km north of Yala on route 9 (*TS, EU, KT 18060*)
	8	Argentina, Prov. Córdoba, Cerro Los Gigantes (*EU, KT 149*)
	8*; 4II	Argentina, Prov. Córdoba, road from Yacanto de Calamuchita to Champaquí (*EU, KT 137*)
H. chondrilloides (A. Gray) Cabrera	8, 8*	Argentina, Prov. Jujuy, *c*. 40 km south of Humahuaca along route 9 (*TS, EU, KT 18067*)
	8; 4II	Argentina, Prov. Jujuy, Iturbe, flood-plain of the Río Grande (*TS, EU, KT 18072*). Figs 2, 16; Table 2
	8	Argentina, Prov. Río Negro, General Roca, Villa Manzano (*PSI 1057*)
H. elata (Wedd.) Griseb.	8; 4II	Bolivia, Depto. La Paz, *c*. 3 km on dirt road toward Peñas from main motorway La Paz-Huarina (*TS, KT, RH 18506*). Figs 3, 16; Table 2
	8*	Argentina, Prov. Jujuy, 1.9 km north-east of route 9 on road to Iruya (*TS, EU, KT 18070*)
	8*	Argentina, Prov. Jujuy, 0.8 km north-west of Chaupi Rodeo on road to Iruya (*TS, EU, KT 18073*)
	8*	Argentina, Prov. Jujuy, 16.4 km west of Humahuaca on road toward El Aguilar (*TS, EU, KT 18077*)
	8*	Argentina, Prov. Jujuy, 22.6 km west of Humahuaca on route 14 toward El Aguilar (*TS, EU, KT 18080*)
	8*	Peru, Prov. Cusco, Inca ruins Tipón on road 3south from Cusco to Oropesa (*KT, RH 1094*)
	8*	Bolivia, La Paz, Cota-Cota, Universidad Mayor de San Andrés, Botanical Garden (*TS, KT, RH 18500*)
++*H.* cf. *eremophila* Cabrera	8*	Chile, Región I, cliffs along route II between Socoroma and Putre (*TS, KT 18097*)
H. glabra L.	10	Argentina, Prov. Buenos Aires, Sierra de la Ventana, path to La Blanqueada (*EU, KT 123*)

Table 1. *Continued*

Taxon	2*n*	Location (voucher number)
++*H. hookeri* Phil.	8; 4II	Argentina, Prov. Río Negro, *c*. 6 km south of Bariloche airport (*TS, EU, KT 18019*)
	8	Argentina, Prov. Río Negro, 29 km east of junction between routes 23 and237, on dirt road toward Pichileufu (*TS, EU, KT 18040*). Table 2
	8, 8*	Argentina, Prov. Río Negro, Estancia Rayhuao *c*. 29 km south of Pilcaniyeu (*TS, EU, KT 18044*). Figs 4, 16; Table 2
+*H. incana* (Hook. & Arn.) Macloskie	8, 16	Argentina, Prov. Río Negro, 19 km south of Río Ñirihuao near top of Cerro Buitrero (*TS, EU, KT 18022*). Figs 13, 16; Table 2
	8	Chile, Región XII, Punta Arenas, in front of the airport (*PS, MS, AT 5640*). Figs 5, 16; Table 2
H. megapotamica Cabrera	8, 8*	Argentina, Prov. Buenos Aires, Sierra de Tandil, entrance to La Cascada near parking (*KT, PSI 1000*)
	8*	Argentina, Prov. Buenos Aires, Sierra de Tandil, left slope of La Cascada (*KT, PSI 1004*)
H. meyeniana (Walp.) Grieseb.	8*	Argentina, Prov. Jujuy, 24.1 km west of Purmamarca (*TS, EU*, *KT 18063*)
	4II	Argentina, Prov. Jujuy, 1.9 km north-east of route 9 on road to Iruya (*TS, EU, KT 18071*)
	4II	Argentina, Prov. Jujuy, 4.7 km north-west of Chaupi Rodeo on road to Iruya (*TS, EU, KT 18076*)
	8II	Bolivia, Depto. La Paz, 10 km north-east of La Paz, above dam Incachaca (*TS, KT, RH 18504*)
	16*	Bolivia, Depto. La Paz, 15 km west of La Huarina on road to Achacachi (*TS, KT, RH 18510*)
	8II	Bolivia, La Paz, 12.2 km north of Huilacala (*TS, KT, RH 18513*)
H. meyeniana × *H. echegarayi*	16*	Bolivia, Depto. La Paz, 10 km north-east of La Paz, above dam Incachaca (*TS, KT, RH 18502*)
H. microcephala (Sch. Bip.) Cabrera	8	Argentina, Prov. La Plata, La Plata, Museo de Historia Natural, Paseo del Bosque (*TS, EU, KT 18001*)
	8, 8*	Argentina, Prov. Buenos Aires, La Plata airport, *c*. 5 km south-east of city (*TS, EU, KT 18007*)
	8	Argentina, Prov. Buenos Aires, La Plata airport, *c*. 5 km south-east of city (*TS, EU, KT 18008*)
	8	Argentina, Prov. Buenos Aires, La Plata airport, *c*. 5 km south-east of city (*TS, EU, KT 18009*)
	8; 4II	Argentina, Prov. Buenos Aires, Magdalena, Reserva Parque Costero del Sur (*EU, KT 113*)
	8, 8*	Argentina, Prov. Buenos Aires, between Villa Elisa and Boca Cerrada close to Reserva Natural Punta Lara (*EU, KT 115*)
	8*	Argentina, Prov. Buenos Aires, Sierra de la Ventana, ascending to Abra de la Ventana (*EU, KT 130*)
	8*	Argentina, Prov. Corrientes, Bella Vista, Calle Sarmiento and Buenos Aires (*EU, KT 158*)
	8; 4II	Argentina, Prov. Corrientes, Bella Vista, Parque Cruz de los Milagros (*EU, KT 160*)
	8*	Argentina, Prov. Buenos Aires, Sierra de Tandil, resting area on the way to La Cascada (*KT, PSI 1002*)
	8	Bolivia, La Paz, Cota-Cota, Universidad Mayor de San Andrés, Botanical Garden (*TS, KT, RH 18522*)
H. cf. *microcephala*	8*	Argentina, Prov. Chaco, Roque Saenz Peña, road 16 (*EU, KT 154*)
H. palustris (Phil.) De Wild.	8	Argentina, Prov. Río Negro, Cerro López (*TS, EU, KT 18029*)
	8	Argentina, Prov. Río Negro, Cerro López (*TS, EU, KT 18030*)
	8, 8*	Argentina, Prov. Río Negro, El Tronador, Parque Nacional Nahual Huapi, La Garganta del Diablo waterfall (*TS, EU, KT 18048*)
	4II	Chile, Región IX, road from Las Mellizas to Cerros de Lanco (*KT, AJ, SG 1060*)

Table 1. *Continued*

Taxon	2*n*	Location (voucher number)
H. pampasica Cabrera	8, 8*	Argentina, Prov. Buenos Aires, Magdalena, Reserva Parque Costero del Sur (*EU, KT 112*)
	8; 4II	Argentina, Prov. Buenos Aires, Sierra de la Ventana (*EU, KT 121*)
	8, 8*	Argentina, Prov. Buenos Aires, Sierra de la Ventana, Reserva Natural, path to La Blanqueada (*EU, KT 124*)
++*H. parodii* Cabrera	8; 4II	Argentina, Prov. Jujuy, Laguna Yala, c. 2 km down from main laguna (*TS, EU, KT 18057*). Figs 6, 16; Table 2
	8*	Ecuador, Prov. Cotopaxi, 5.5 km east of Pujilí (*TS, KT, HV, RH 18551*)
	8*	Ecuador, Prov. Cotopaxi, Pujilí, fuel station on east side of town (*TS, KT, HV, RH 18555*)
++*H. patagonica* Cabrera	8	Argentina, Prov. Santa Cruz, Patagonia, Río Pintura, *c*. 3 km north-west of Cueva de las Manos (*FE, PS 6202*). Figs 7, 16; Table 2
H. petiolaris (Hook. & Arn.) Griseb.	8	Argentina, Prov. Buenos Aires, Sierra de la Ventana (*EU, KT 122*). Figs 8, 16; Table 2
++*H. pinnatifida* (Speg.) Azevêdo-Gonçalves & Matzenbacher	8*	Argentina, Prov. Buenos Aires, Sierra de la Ventana, Reserva Natural, passing Palo Alto along path to Blanqueada (*EU, KT 125*)
	8, 8*	Argentina, Prov. Buenos Aires, Sierra de Tandil, left slope of La Cascada (*KT, PSI 1003*). Figs 9, 16; Table 2
	8, 8*	Argentina, Prov. Buenos Aires, Sierra de Tandil, ridge on the right side of La Cascada (*KT, PSI 1006*)
H. radicata L.	8*	Argentina, Prov. Buenos Aires, route II, between La Plata and La Balandra (*TS, EU, KT 18004*)
	8*	Argentina, Prov. Buenos Aires, Villa Elisa (*TS, EU, KT 18016*)
	8*	Argentina, Prov. Río Negro, 5 km east of junction between routes 23 and 237, on dirt road toward Pichileufu (*TS, EU, KT 18037*)
	8*	Argentina, Prov. Río Negro, E edge of Bariloche, *c*. 1 km from town (*TS, EU, KT 18017*)
	8	Argentina, Prov. Río Negro, *c*. 6 km south of Bariloche airport (*TS, EU, KT 18020*)
	8	Argentina, Prov. Río Negro, 23 km north-west of Villa Mascardi on road to El Tronador (*TS, EU, KT 18047*)
	4II	Argentina, Prov. Jujuy, 9.7 km west of Yala on road to Laguna Yala (*TS, EU, KT 18056*)
	8	Chile, Región VIII, Talcahuano, Caleta Lenga (*TS, KT 18093*)
	8; 4II	Chile, Región IX, 9 km east of Río Cautin and road to Lonquimay, on road to Río Blanco (*TS, CB, KT 18098*)
	8*	Argentina, Prov. Córdoba, Cerro Los Gigantes, in the garden of the family Bazan (*EU, KT 150*)
	4II	Argentina, Prov. Córdoba, Cerro Los Gigantes (*EU, KT 151*)
	4II	Ecuador, Prov. Pichincha, 12 km south of San Juan on road to Volcán Atacazo (*TS, KT, HV, RH 18537*)
	8*	Ecuador, Prov. Cotopaxi, road from park recreo entrance to Volcán Cotopaxi (*TS, KT, HV, RH, JR 18542*)
	8*	Ecuador, Prov. Cotopaxi, 1.5 km south-west of Chaupi on road to Illinizas (*TS, KT, HV, RH, JR 18546*)
	8	Bolivia, La Paz, Cota-Cota, Universidad Mayor de San Andrés, Botanical Garden (*KT, TS, RH 18523*)
	8, 8*	Ecuador, Prov. Pichincha, old road from Quito to Santo Domingo de los Colorados (*TS, KT, HV, RH 18532*)
	8	Ecuador, Prov. Cotopaxi, 5.5 km east of Pujilí (*TS, KT, HV, RH 18550*)
H. sessiliflora Kunth.	8	Ecuador, Prov. Cotopaxi, 5.5 km east of Pujilí (*TS, KT, HV, RH 18549*). Figs 10, 16; Table 2
	8	Ecuador, Prov. Pichincha, 9.5 km south of San Juan on road to Volcán Atacazo, near the antennas (*TS, KT, HV, RH 18536*)

Table 1. *Continued*

Taxon	2*n*	Location (voucher number)
	8; 4II	Ecuador, Prov. Pichincha, 12.5 km south of San Juan on road to Volcán Atacazo (*TS, KT, HV, RH 18538*)
	8*	Ecuador, Prov. Cotopaxi, *c*. 20 km south of Aloag, then *c*. 5 km east towards Volcán Cotopaxi, NASA tracking station (*TS, KT, HV, RH, JR 18541*)
	8*	Ecuador, Prov. Cotopaxi, along road toward Volcán Cotopaxi (*TS, KT, HV, RH, JR 18543*)
	8*	Ecuador, Prov. Cotopaxi, 0.3 km west of Zumbahua (*TS, KT, HV, RH 18554*)
H. spathulata (J. Rémy) Reiche	8	Chile, Región VIII, Provincia de Arauco, Caleta Rumena (*CB, PL 2764*). Fig. 16; Table 2
+*H. taraxacoides* (Walp.) Benth. & Hook. f.	16, 16*	Argentina, Prov. Jujuy, 0.8 km north-west of Chaupi Rodeo on road to Iruya (*TS, EU, KT 18074*)
	8, 16	Argentina, Prov. Jujuy, 31.4 km west of Humahuaca on road to El Aguilar (*TS, EU, KT 18089*). Figs 15, 16; Table 2
	16	Bolivia, Depto. La Paz, *c*. 47 km west-north-west of La Paz on road to Huarina (*c*. 26 km south-east of Huarina) (*TS, KT, RH 18508*). Figs 14, 16; Table 2
H. thrincioides (J. Rémy) Reiche	8	Chile, Región VIII, Talcahuano, Caleta Lenga (*TS, KT 18092*)
H. variegata (Lam.) Baker	8	Argentina, Prov. Buenos Aires, Sierra de la Ventana, at the base of Cerro de la Ventana near the refuge (*EU, KT 117*)
	8*	Argentina, Prov. Buenos Aires, Sierra de la Ventana, Reserva Natural, path to La Blanqueada, passing Palo Alto (*EU, KT 126*)
	8, 8*	Argentina, Prov. Buenos Aires, Sierra de la Ventana, Reserva Natural, path to La Blanqueada (*EU, KT 127*). Figs 11, 16; Table 2
	8, 8*; 4II	Argentina, Prov. Buenos Aires, Sierra de la Ventana, ascending to Abra de la Ventana, 600 m (*EU, KT 131*)
	8; 4II	Argentina, Prov. Buenos Aires, Sierra de la Ventana, ascending to Abra de la Ventana, 670 m (*EU, KT 133*)
	8, 8*	Argentina, Prov. Buenos Aires, Sierra de Tandil, path to La Cascada (*KT, PSI 1001*)

(both Weiss *et al*., 2003), *H. sessiliflora* (Olsen, 1980), *H. taraxacoides*, which was reported as *H. stenocephala* (Stebbins, Jenkins & Walters, 1953; Diers, 1961) and *H. tenuifolia* (Weiss *et al*., 2003). We also add *H. caespitosa* (Fig. 12) to this list. *H. taraxacoides* (Bortiri, 1999) has been reported to possess diploid cytotypes (Parker, 1971) and we confirm that this species contains both diploids and tetraploids (*18089*, a mixed population of 2*x* and 4*x*; *18508*, a uniformly tetraploid population). In *H. incana*, previously known only as a tetraploid (Moore, 1981), a diploid population (*5640*) and a mixed diploid/tetraploid population (*18022*) have now been found. Four new tetraploid populations have also been detected in *H. meyeniana*, a species that has been reported previously at both diploid (Diers, 1961; Weiss *et al*., 2003) and tetraploid levels (Weiss *et al*., 2003).

Although the aim of this paper is to report new cytological data for native South American species of *Hypochaeris*, additional counts for the introduced *H. radicata* and *H. glabra* are included. *Hypochaeris radicata* is abundant in Chile and Argentina (Matthei, 1995; T.F. Stuessy, pers. observ.), and is often intermixed with native species. Because of the possibility of hybridization between *H. radicata* (also $2n = 2x = 8$) and native congeners, sampling of this taxon is important. The other weedy species, *H. glabra*, is much less common in South America. Chromosome numbers from this study agree with previous results for *H. radicata* ($2n = 8$) and *H. glabra* ($2n = 10$; Tremetsberger *et al*., 2004). The karyotypes of both species are symmetrical, while these of native South American *Hypochaeris* are asymmetrical. No karyological evidence (symmetry vs. asymmetry of karyotype) has been found so far to indicate ongoing hybridization between *H. radicata* and native *Hypochaeris* species.

KARYOTYPES

Microphotographs and idiograms for 12 taxa (*H. alba*, *H. caespitosa*, *H. chondrilloides*, *H. elata*, *H. hookeri*, *H. incana*, *H. parodii*, *H. patagonica*, *H. petiolaris*, *H. pinnatifida*, *H. sessiliflora*, and *H. taraxacoides*) are presented here for the first time (Figs 1–15, 16). Additionally, we present idiograms for two other diploid species, *H. spathulata* (Chile, population *2764*) and *H. variegata* (Argentina, population *127*) (Fig. 16), that have been observed previously as variable concerning karyotype (*H. spathulata*), or were reported from different localities (*H. variegata*, Brazil).

Karyotype groups of diploid cytotypes

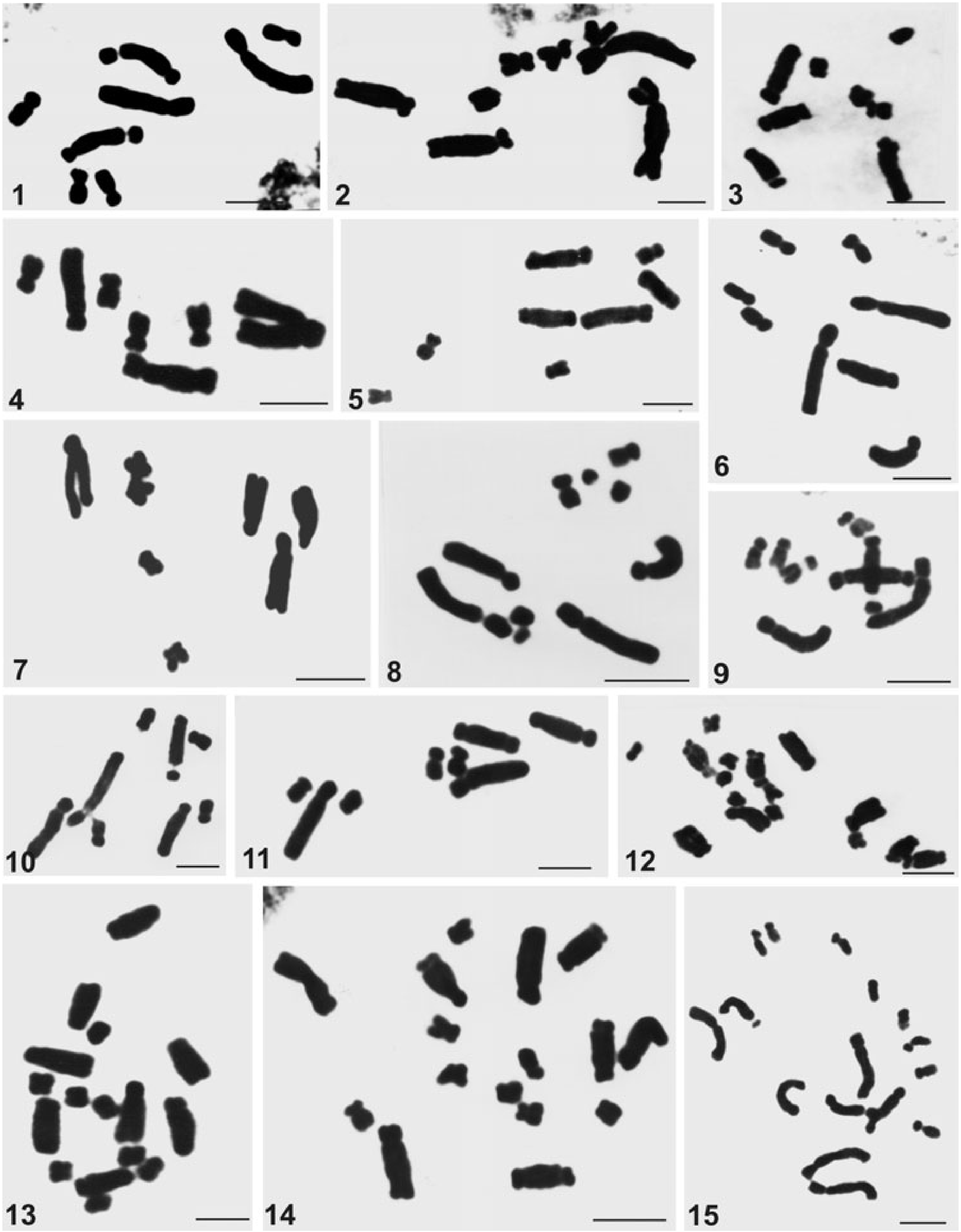
Newly analysed karyotypes of South American species of *Hypochaeris* are all bimodal and asymmetrical (Figs 1–15, 16), similar in overall morphology among themselves and also similar to karyotypes of species analysed previously (Weiss *et al*., 2003). The diploid karyotypes consist of two large and two small chromosome pairs. In most of the species, a satellite or secondary constriction (SC) is present on the long arm of chromosome pair number 2 and the short arm of chromosome pair number 3 (Fig. 16; Weiss-Schneeweiss *et al*., 2003). Despite this general uniformity of chromosome pair morphology, some karyotype differentiation can be seen in individual chromosome pair length and the presence of satellites (Figs 1–15, 16).

In earlier studies we have proposed four karyotype groups (A–D), based on the presence or absence of satellite/SC in chromosomes 2 and 3 and localization of 5S and 18S-25S rDNA sequences (Weiss *et al*., 2003; Weiss-Schneeweiss *et al*., 2003; Table 3). Karyotypes of most of the diploid cytotypes/species reported here also fall into these four groups (Weiss-Schneeweiss *et al*., 2003; Table 3). The karyotype of group A (= *patagonica*-group) possesses a secondary constriction on the long arm of chromosome 2 and a satellite on the short arm of chromosome 3. So far it has contained only one species, *H. lutea* (syn. *H. rosengurttii* var. *rosengurttii*; Ruas *et al*., 1995; Freitas de Azevêdo-Gonçalves, 2004), but now also includes *H. patagonica* (Figs 7, 16). Group B (= *apargioides*-group), comprising ten previously reported taxa (Weiss-Schneeweiss *et al*., 2003), additionally includes seven newly reported diploid taxa, among them *H. alba* (Fig. 1), *H. elata* (Fig. 3), *H. hookeri* (Fig. 4), *H. incana* (Fig. 5), *H. parodii* (Fig. 6), *H. pinnatifida* (Fig. 9), and *H. taraxacoides* (not shown). This group is characterized by the presence of secondary constrictions on the long arm of chromosome 2 and the short arm of chromosome 3. Group C (= *tenuifolia*-group) possesses only one SC on chromosome pair 3, but two 35S rDNA loci (inactive locus in chromosome 2; active locus in chromosome 3 forming a SC) and comprises two previously reported species: *H. chillensis* and *H. tenuifolia*. Group D (= *acaulis*-group) possesses only one locus of 18S-25S rDNA on chromosome 3 (Weiss-Schneeweiss *et al*., 2003). Additionally to four taxa reported earlier (Table 3), it now also includes *H. grisebachii* (Ruas *et al*., 2005) and *H. petiolaris* (Fig. 8; Weiss-Schneeweiss, unpubl. FISH data). *Hypochaeris sessiliflora* (Figs 10, 16) has a distinct karyotype, which was proposed as hypothetical (Weiss-Schneeweiss *et al*., 2003) and basal to the whole South American group (Tremetsberger *et al*., 2005). A previously published photograph of *H. sessiliflora* (Weiss *et al*., 2003) suggested that it belongs to group C, but detailed analysis of new accessions indicates its independent position (in *sessiliflora*-group). The karyotype of *H. chondrilloides* (Fig. 2) belongs to yet another previously unknown group (= *chondrilloides*-group) having a large deletion of the short arm of chromosome pair 3 (possibly including the SC), which makes this chromosome almost telocentric (Figs 2, 16). An updated hypothesis of chromosomal evolution based on these new data is in preparation.

All newly analysed species have strong karyotype asymmetry (71.88–80.69%; Table 2). The ratio of the longest to the shortest chromosome ranges from 2.56 in tetraploid *H. taraxacoides* to 4.55 in *H. chondrilloides*. The karyotype length (calculated as haploid chromosome complement length) varies from 13.63 to 24.75 μm (Table 2). Chromosome size correlates in general with the karyotype groups, e.g. most of the 17 species of group B have relatively long karyotypes (18.17–22.75 μm), although *H. elata* (13.63 μm) and *H. thrincioides* (15.26 μm; Weiss-Schneeweiss *et al*., 2003) have significantly shorter chromosomes (Table 2).

Karyotypes of tetraploid cytotypes

The 4*x* cytotypes in *H. caespitosa*, *H. tenuifolia* and in one population of *H. taraxacoides* possess karyotypes consisting of four equal-sized sets of chromosomes, which may indicate that these polyploids are of autopolyploid origin (Figs 12, 14; Weiss *et al*., 2003). The co-occurrence of diploids and polyploids within two of these species (*H. tenuifolia* and *H. taraxacoides*), and particularly within populations (Weiss *et al*., 2003; present study), further strengthens the hypothesis of autopolyploidy and suggests recurrent polyploid formation, perhaps via unreduced gametes (Ramsey & Schemske, 1998; Weiss *et al*., 2002). Differences observed between homologous chromosomes (rDNA elimination) in some tetraploids (*H. incana*) that coexist with diploids in the same populations may reflect either changes in the polyploids' genomes after autopolyploidization or may suggest an allopolyploid origin of these tetraploids, after hybridization with an as yet undetermined species. The karyotypes of the tetraploid cytotypes of *H. incana* and *H. taraxacoides* belong to group B (= *apargioides* group) with minor modifications, while the distinct karyotype of *H. caespitosa* merits its recognition as a separate group (= *caespitosa*-group; Figs 12, 16).



Figures 1–15. Mitotic chromosomes of diploid (Figs 1–11) and tetraploid (Figs 12–15) South American cytotypes of *Hypochaeris,* all based on $x = 4$. Fig. 1. *H. alba* (*156*). Fig. 2. *H. chondrilloides* (*18072*). Fig. 3. *H. elata* (*18506*). Fig. 4. *H. hookeri* (*18044*). Fig. 5. *H. incana* (5640). Fig. 6. *H. parodii* (*18057*). Fig. 7. *H. patagonica* (*6202*). Fig. 8. *H. petiolaris* (*122*). Fig. 9. *H. pinnatifida* (*1003*). Fig. 10. *H. sessiliflora* (*18549*). Fig. 11. *H. variegata* (*127*). Fig. 12. *H. caespitosa* (*148*). Fig. 13. *H. incana* (*18022*). Fig. 14. *H. taraxacoides* (*18508*). Fig. 15. *H. taraxacoides* (*18089*). Scale bar = 5 μm.

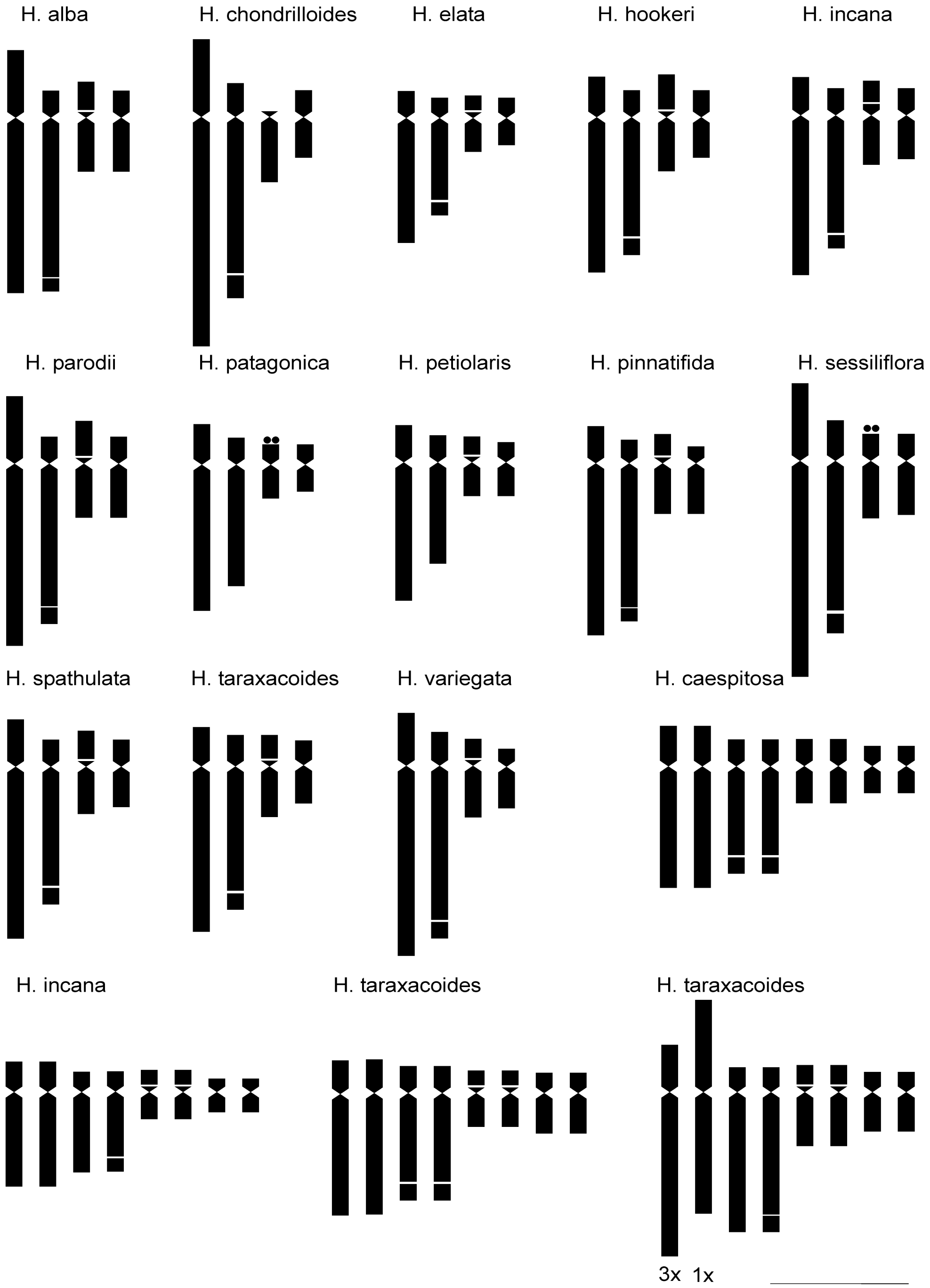


Figure 16. Idiograms of diploid and tetraploid South American *Hypochaeris* species ($x = 4$). $3x$ and $1x$ three homologous chromosomes 1 of one type and one homologous chromosome 1 of the other type (rearrangement). For vouchers see Table 1. Scale bar = 5 µm.

Haploid chromosome complement lengths of some tetraploids (*H. incana* and *H. taraxacoides*) are lower than the expected doubled value of karyotype length of closely related diploid cytotypes, e.g. the karyotype length of diploid *H. incana* (accession *5640*) is 18.83 µm, whereas the tetraploid cytotype of this species is only 22.26 µm (accession *18022*; Table 2). Reduction of chromosome length may be connected to elimination or inactivation of some types of repetitive DNA sequences such as rDNA, which might be gradually occurring in two out of four homologous chromosomes number 2 in tetraploid *H. incana* (*18022*) and,

Table 2. Chromosome statistics for species of *Hypochaeris* from South America. AsI (asymmetry index in percentage) expresses the proportion of all long arms to the total haploid set of chromosome lengths; RI (ratio index) compares the longest/shortest chromosome; HCL is the total haploid chromosome length (± SD)

			Relative chromosome length (%)				
Species/population	AsI	RI	Chr. 1	Chr. 2	Chr. 3	Chr. 4	HCL (μm)
H. alba	74.73	3.00	39.56	32.97**	14.29*	13.19	22.75 ± 1.80
H. caespitosa (4*x*)	76.80	3.43	42.82	34.84**	16.98	12.50	14.01 ± 1.30
H. chondrilloides	77.91	4.55	46.81	31.88**	11.07	10.28	24.31 ± 2.79
H. elata	76.16	3.22	41.31	31.18**	14.67*	12.84	13.63 ± 1.33
H. hookeri[1]	73.80	2.83	38.97	31.65**	15.58*	13.76	18.17 ± 1.53
H. hookeri[2]	73.93	2.92	37.71	31.25**	18.11*	12.93	19.33 ± 1.58
H. incana[3]	75.20	2.78	39.19	30.43**	16.36*	14.07	18.83 ± 1.78
H. incana[4] (4*x*)	71.88	3.70	41.60	31.44**	15.72*	11.24	22.26 ± 2.08
H. parodii	73.33	3.08	41.11	30.00**	15.56*	13.33	22.50 ± 1.89
H. patagonica	75.29	3.97	42.87	33.97	12.35***	10.81	16.19 ± 1.79
H. petiolaris	73.84	3.46	42.69	31.15	13.97*	12.33	15.25 ± 1.54
H. pinnatifida	80.69	3.09	38.92	34.25**	14.44*	12.59	19.94 ± 1.88
H. sessiliflora	74.26	3.63	43.96	31.31**	12.65***	12.12	24.75 ± 2.33
H. spathulata	74.53	3.25	41.42	30.57**	15.28*	12.74	19.63 ± 1.79
H. taraxacoides[5]	75.65	3.19	39.52	32.66**	15.44*	12.38	19.23 ± 1.43
H. taraxacoides[5] (4*x*)	75.07	3.57	30.93 × 3 10.35 × 1[7]	31.74**	15.48*	11.56	38.26 ± 3.13
H. taraxacoides[6] (4*x*)	75.00	2.56	38.34	33.34**	13.34*	15.00	30.00 ± 2.50
H. variegata	77.89	4.02	41.64	34.91**	13.08*	10.36	21.71 ± 2.08

*SC on short arm; **SC on long arm; ***satellite on short arm.

Population numbers: [1]*18040*; [2]*18044*; [3]*5640*; [4]*18022*; [5]*18089*; [6]*18508*.

[7] three homologous chromosomes of one type and one with rearrangement (see Fig. 16).

to a lesser degree, in *H. taraxacoides* (*18508*; Weiss-Schneeweiss, unpubl. data), as shown in other species groups such as *Nicotiana* (Clarkson *et al*., 2005). Such genomic changes (sequence elimination and amplification) accompanying polyploid formation have been studied mostly in allopolyploids (*Brassica*, Song *et al*., 1995; wheat group, Ozkan, Levy & Feldman, 2001). Similar patterns might be expected in autopolyploids, but these are karyologically less studied. Preliminary results of more detailed studies of such changes in *Hypochaeris* indicate that autopolyploids may also undergo rather rapid rearrangements that involve repetitive DNA (Weiss-Schneeweiss *et al.* unpubl. data).

In one population of *H. taraxacoides* (*18089*), however, which contains both 2*x* and 4*x* cytotypes, the karyotype length of the tetraploid cytotype is almost the expected double value of the diploid cytotype (Table 2). This is to be expected if the tetraploids originated recently within a diploid population. Interestingly, the karyotype of this tetraploid race of *H. taraxacoides* (Fig. 15) differs from the diploid cytotype by the absence of SCs in two out of four homologous chromosomes number 2 and a rearrangement within chromosome 1 (Figs 15, 16). This suggests relatively rapid genomic changes after polyploidization, assuming that the polyploids are of recent origin.

The karyotype of *H. caespitosa* differs from all other karyotypes (Fig. 12), both diploid and tetraploid, in the absence of the SC on the short arm of chromosome 3. Yet, the overall short arm length is relatively similar to that observed in other species, with the exception of *H. chondrilloides*. The absence of the SC in *H. caespitosa* is therefore associated with the loss of the 18S-25S rDNA locus only (Weiss-Schneeweiss, unpublished), while *H. chondrilloides* lacks almost the entire short arm, suggesting a larger deletion.

The presence of 2*x* and 4*x* cytotypes in almost all polyploid taxa, either in different populations or within one (cytotype mixture), indicates the autopolyploid origin of the tetraploid cytotypes and suggests recurrent origins of tetraploid cytotypes. Newly arisen polyploids often have a broader spectrum of ecological tolerance (Levin, 1983, 2002), thus opening up new evolutionary potentials. Although Stebbins (1971) considered autopolyploid formation to be a dead-end,

Table 3. Karyotype groups, including all known karyotypes/idiograms for diploid and tetraploid cytotypes/taxa

Group	Taxon	References
Group A	*H. lutea* (2*x*)	Ruas *et al.* (1995, 2005)[1]
patagonica group	*H. patagonica* (2*x*)	Present study
Group B	*H. alba* (2*x*)	Present study
apargioides group	*H. albiflora* (2*x*)	Cerbah *et al.* (1998)[2]; Ruas *et al.* (1995, 2005)[2]
	H. apargioides (2*x*)	Weiss *et al.* (2003)
	H. brasiliensis (2*x*)	Ruas *et al.* (1995), 2005)
	H. clarionoides (2*x*)	Weiss *et al.* (2003)
	H. elata (2*x*)	Present study
	H. hookeri (2*x*)	Present study
	H. incana (2*x*)	Present study
	H. incana (4*x*)	Present study
	H. meyeniana (2*x*)	Weiss *et al.* (2003)
	H. parodii (2*x*)	Present study
	H. pinnatifida (2*x*)	Present study
	H. sessiliflora (2*x*)*	Weiss *et al.* (2003)
	H. spathulata (2*x*)	Weiss *et al.* (2003), present study
	H. stenocephala (4*x*)	Stebbins *et al.* (1953)
	H. taraxacoides (2*x*)	Present study
	H. taraxacoides (4*x*)	Present study
	H. thrincioides (2*x*)	Weiss *et al.* (2003)
	H. variegata (2*x*)	Ruas *et al.* (1995); present study
Group C	*H. chillensis* (2*x*)	Cerbah *et al.* (1998)
tenuifolia group	*H. tenuifolia* (2*x*; 4*x*)	Weiss *et al.* (2003)
Group D	*H. acaulis* (2*x*)	Weiss *et al.* (2003)
acaulis group	*H. megapotamica* (2*x*)	Cerbah *et al.* (1998); Ruas *et al.* (1995, 2005)
	H. palustris (2*x*)	Weiss *et al.* (2003)
	H. pampasica (2*x*)	Cerbah *et al.* (1998); Ruas *et al.* (1995, 2005)
	H. petiolaris (2*x*)**	Present study
	H. grisebachii (2*x*)	Ruas *et al.* (2005)
sessiliflora group	*H. sessiliflora* (2*x*)**	Present study
chondrilloides group	*H. chondrilloides* (2*x*)	Present study
caespitosa group	*H. caespitosa* (4*x*)	Present study

*based on chromosome morphology only; **based on chromosome morphology and FISH data (Weiss-Schneeweiss, unpubl. data).

[1] published as *H. rosengurttii* var. *rosengurttii.*

[2] published as *H. microcephala* var. *albiflora.*

recent investigations have shown that autopolyploidy can be advantageous and may play an important role in plant evolution (Ramsey & Schemske, 1998, 2002; Wendel, 2000).

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