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CHROMOSOME NUMBERS AND POLYPLOIDY IN POLISH ANGIOSPERMS

PAULINA GACEK, GRZEGORZ GÓRALSKI AND ANDRZEJ J. JOACHIMIAK*

Department of Plant Cytology and Embryology, Jagiellonian University, Grodzka 52, 31-044 Cracow, Poland

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Our survey of data collected in the Chromosome Number Database for Polish angiosperms indicated that the 1,498 species with chromosome counts represent 40% of the total angiosperms (3,719) occurring in Poland, including 1,205 native species (53% of native species) and 194 anthropophytes (56% of anthropophytes). The chromosome numbers are known for all native species occurring in Poland within 298 genera and 46 families, and for all anthropophytes from 79 genera and 11 families. The remaining angiosperm groups are less explored: chromosome counts from Poland are known for 9% of cultivated species and 5% of ephemerophytes. According to generic basic chromosome numbers, 46.44% of Polish angiosperms have been classified as polyploid. By three different threshold methods, the contribution of polyploid plants to the Polish flora is 64.64%, 50.89% or 42.89%. Polyploidy is more common among indigenous than non-indigenous plants, and the ploidy distribution among plants from the Polish Tatras does not differ significantly from that observed in the rest of native Polish plants.

Key words: Chromosome numbers, Polish flora, polyploidy, threshold method, mountain plants.

INTRODUCTION

Somatic chromosome number is one of the most basic and useful pieces of information in many areas of plant research. Significant progress in our knowledge of it has greatly facilitated the resolution of issues such as the origin, relationships, relative age and peculiar distribution of plant species. Chromosomes are not just part of the plant phenotype but also the hereditary elements and units of mutation and transmission. As a remarkably dynamic feature, chromosome numbers are particularly suited for tracking plant diversification and evolution. They may be successfully used, in combination with other features (e.g., habit, nuclear DNA amount, molecular markers), to construct phylogenetic trees, particularly in taxa with extensive variation in chromosome number (Cerbah et al., 1999; Watanabe et al., 1999; Ito et al., 2000; Lysak et al., 2005; Navajas-Perez et al., 2005; Hansen et al., 2006).

Karyological studies in Poland began in the 1940s under the guidance of Professor Maria Skalińska, and in the following decades were continued by a team in the Department of Plant Cytology and Embryology of the Jagiellonian University. The results obtained by this team and other Polish researchers have been reported in many co-written and individual papers and summarized in three publications (Skalińska and Pogan, 1973; Pogan and Wcisło, 1983, 1990). A synthetic review of the karyology of Polish angiosperms was made only once, by Eugenia Pogan in 1972. At that time the Polish flora was estimated at about 2,300 species, of which only 19% had chromosome counts (438 species). Narrower karyological syntheses were made for the flora of the Tatra Mts. (110 species, Skalińska, 1963) and Polish grasses (55 species, Frey, 1973; 313 species, Mizianty, 2003).

Many new chromosome records have been published since the last publication summarizing chromosome counts of Polish angiosperms (Pogan and Wcisło, 1990). For many plants the taxonomic and/or nomenclatural treatments have changed. This stimulated work on a new summary of chromosome numbers of Polish angiosperms, published in the form of the freely available Chromosome Number Database (Góralski et al., 2009, http://www.chromosomes.binoz.uj.edu.pl). This form of publication is easily searchable and open for additions as new data are received. The survey gives the taxonomic and nomenclatural treatments

*e-mail: a.joachimiak@uj.edu.pl

recommended in the critical checklist of vascular plants in Poland (Mirek et al., 2002) without removing the original names used by particular authors.

The breadth of research examining the karyology of Polish angiosperms has allowed us to summarize certain karyological aspects of Polish flora, to list taxa not tested so far, and to recommend the main directions of future research. We also used the collected data to estimate the share of polyploids in the Polish flora and in particular groups of species. We hope that this summary will encourage researchers to complete the data on the chromosome numbers of Polish angiosperms at a time when chromosome counting is not as popular as it once was in this country.

MATERIALS AND METHODS

Data collected in the Chromosome Number Database were used to assess the ploidy level of Polish plants, with particular emphasis on native and permanently established species. In most cases it was possible to use information on the lowest somatic chromosome numbers (LSCN) reported within genera (Appendix 1 in electronic version). The data of this subject were obtained primarily from the Index to Plant Chromosome Numbers available at http://www.tropicos.org/Project/IPCN. The LSCNs that do not match the other chromosome numbers within the genus have been omitted in the ploidy estimates, such as 2n=10 recorded in *Phleum echinatum* (which in all other *Phleum* species is x=7), or 2n=18 in *Sagittaria* (x=11 for all other *Sagittaria* specimens analyzed so far).

The data on somatic chromosome number(s) allowed us to specify basic chromosome number(s) within genera and to calculate the exact ploidy levels (2x, 3x, 4x, and so on) of the majority of analyzed species. The basic numbers were additionally consulted with syntheses (Wanscher, 1934; Darlington and Janaki Ammal, 1945; Darlington and Wylie, 1955; Raven, 1975) and taxon-specific literature. For two records the chromosome numbers could not be clearly classified as polyploid or aneuploid on a particular ploidy level (*Scopolia carniolica* 2n=46, *Stachys silvatica* 2n=66), making it difficult to estimate ploidy precisely; these species were analyzed only by the threshold methods described below.

Chromosome number data were further used to assess ploidy level by the threshold methods developed by Grant (1963), Goldblatt (1980) and Wood et al. (2009). The threshold value was set at n=14 or more (Grant 1963) or n=11 or more (Goldblatt 1980). According to Wood et al. (2009), species with a somatic chromosome number greater than or equal to 3.5 times the lowest haploid count of the host genus should be considered polyploid. We removed taxa known to possess holocentric chromosomes (Cyperaceae, *Cuscuta*, *Luzula*) from the analysis due to extensive chromosome changes which may lead to simultaneous fusion or fragmentation of individual chromosomes or even whole chromosome sets (Kuta et al., 2004; Hipp et al., 2009). Mutations of this kind have nothing to do with true ploidy changes and make it difficult to determine the original basic chromosome number within a genus.

Differences in the proportions of diploid and polyploid plants, or the proportions of diploid, polyploid and diploid/polyploid species in the compared datasets, were cross-tabulated (2×2 and 2×3 contingency tables) and analyzed with Pearson's chi-square test.

RESULTS AND DISCUSSION

The present Chromosome Number Database comprises 3,387 records on the chromosome numbers of 1,498 species (records relating to the 17 taxa excluded from the actualized checklist were censored). This means that we have knowledge of the chromosome numbers of about 40% of Poland's angiosperms. This is the estimate for all 3,719 species listed by Mirek et al. (2002) from Poland, including ephemerophytes, cultivated plants, and 6 species classified "doubtful". The proportion of native and permanently established species with known chromosome numbers is higher (see below). As for the higher taxa, we have karyological data on 60.9% of the genera (26.7% in full and 34.2% in part) and 78% of the families (15.7% in full and 61.9% in part) (Tab. 1, Appendices 2, 3 in electronic version). There is little evidence of intraspecific karyological differentiation of Polish plants between areas of occurrence. Of the 344 taxa analyzed from the north (N) and south (S) of Poland, only two showed such variation: *Cirsium arvense* var. *horridum* (N – 2n=34,68; S – 2n=34) and *Caltha* f. *radicans* ssp. *cornuta* (N – 2n=32,56; S – 2n=32,48).

CHROMOSOME COUNTS OF NATIVE AND PERMANENTLY ESTABLISHED TAXA

From the standpoint of research on the structure and history of the Polish flora, the most important data concern the karyology of native species and permanently established anthropophytes (hereinafter, "anthropophytes"). This group of species determines the distinctiveness of our flora and hence deserve special attention. According to the checklist (Mirek et al., 2002), the Polish flora includes 2,256 native species and 344 anthropophytes. Chromosome counts were reported for 1,205 native species (53%) and 194 anthropophytes (56%). It can therefore be assumed that the sample size of our study provides a good taxonomic and ecological representation of these elements of the Polish flora.

The biggest challenge for the future will be to make chromosome counts of representatives of large apomictic genera. So far there has been significant progress in this respect only for *Rubus*, in which only 24% of the species (20 of 85) remain to investigate. A significant group among the 1,201 species without chromosome counts (1,051 native species and 150 anthropophytes; Appendix 4 in electronic version) are representatives of *Alchemilla* (46 species, 79%), *Hieracium* (86 species, 83%) and *Taraxacum* (259 species, 91%). Almost all of these species have been classified as native to the Polish flora.

In the most numerous and least-explored apomictic genus, *Taraxacum*, with the well defined basic chromosome number x=8 and dominated by triploid and tetraploid microspecies, attempts are being made to develop indirect methods of assessing ploidy level (Marciniuk et al., 2010a,b). Together with nuclear 2C DNA measurements they may provide an alternative to time-consuming chromosome counting. DNA estimations can also be helpful in determining ploidy in other agamospermous species (Trávníèek et al., 2011) and in plants showing huge chromosome variation in root-tip tissues (Joachimiak et al. 2001).

It may be quite problematic to make an exhaustive examination of apomictic genera possessing many hardly recognizable microspecies. After

TABLE 1. Families and genera presented in the checklist (Mirek et al., 2002) and Chromosome Number Database (Góralski et al., 2009, onwards); NG Checklist – number of genera in checklist, NG ChND – number of genera in Chromosome Number Database (April 2011)

Family	NG Checklist	Genus	NG ChND	Genus
Aceraceae	1	*Acer*	1	*Acer*
Adoxaceae	1	*Adoxa*	1	*Adoxa*
Agavaceae	1	*Yucca*	0	
Aizoaceae	1	*Tetragonia*	0	
Alismataceae	5	*Alisma Baldellia Caldesia Luronium Sagittaria*	2	*Alisma Sagittaria*
Amaranthaceae	1	*Amaranthus*	1	*Amaranthus*
Amaryllidaceae	2	*Galanthus Leucoium*	2	*Galanthus Leucoium*
Anacardiaceae	2	*Cotinus Rhus*	1	*Rhus*
Apiaceae	52	*Aegopodium Aethusa Ammi Anethum Angelica Anthriscus Apium Astrantia Berula Bifora Bunium Bupleurum Carum Caucalis Chaerophyllum Cicuta Cnidium Conioselinum Conium Conopodium Coriandrum Daucus Echinophora Eryngium Falcaria Foeniculum Hacquetia Heracleum Laserpitium Levisticum Libanotis Meum Mutellina Myrrhis Oenanthe Orlaya Ostericum Pachypleurum Pastinaca Petroselinum Peucedanum Pimpinella Pleurospermum Pseudorlaya Sanicula Scandix Selinum Seseli Silaum Sium Torilis Turgenia*	33	*Aegopodium Anethum Angelica Anthriscus Apium Astrantia Berula Bupleurum Carum Chaerophyllum Cicuta Cnidium Daucus Eryngium Falcaria Hacquetia Heracleum Laserpitium Levisticum Libanotis Mutellina Myrrhis Oenanthe Pachypleurum Pastinaca Petroselinum Peucedanum Pimpinella Sanicula Selinum Seseli Sium Torilis*
Apocynaceae	1	*Vinca*	1	*Vinca*
Aquifoliaceae	1	*Ilex*	0	
Araceae	3	*Acorus Arum Calla*	3	*Acorus Arum Calla*
Araliaceae	2	*Aralia Hedera*	1	*Hedera*
Arecaceae	1	*Phoenix*	0	
Aristolochiaceae	2	*Aristolochia Asarum*	2	*Aristolochia Asarum*
Asclepiadaceae	2	*Asclepias Vincetoxicum*	2	*Asclepias Vincetoxicum*

TABLE 1. *Cont.*

Family	NG Checklist	Genus	NG ChND	Genus
Asteraceae	110	*Achillea Acroptilon Adenostyles Ageratum Ambrosia Ammobium Anacyclus Anaphalis Andryala Antennaria Anthemis Aposeris Arctium Arnica Arnoseris Artemisia Aster Asteriscus Bellidiastrum Bellis Bidens Calendula Callistephus Carduus Carlina Carthamus Centaurea Chamaemelum Chamomilla Chondrilla Chrysanthemum Cicerbita Cichorium Cirsium Cnicus Coleostephanus Conyza Coreopsis Cosmos Crepis Crupina Dahlia Dendranthema Dimorphotheca Doronicum Echinacea Echinops Erechtites Erigeron Eupatorium Filago Gaillardia Galinsoga Gazania Gnaphalium Guizotia Hedypnois Helenium Helianthus Helichrysum Heliopsis Helipterum Hieracium Homogyne Hypochoeris Inula Iva Lactuca Lapsana Leontodon Leontopodium Leucanthemum Liatris Ligularia Linosyris Matricaria Mycelis Onopordum Parthenium Petasites Picris Podospermum Prenanthes Pulicaria Pyrethrum Rhagodiolus Rudbeckia Santolina Saussurea Scolymus Scorzonera Senecio Serratula Silphium Silybum Solidago Sonchus Spilanthes Stokesia Tagetes Tanacetum Taraxacum Telekia Tragopogon Tussilago Verbesina Volutaria Xanthium Xeranthemum Zinnia*	67	*Achillea Adenostyles Antennaria Anthemis Aposeris Arctium Arnica Arnoseris Artemisia Aster Bellidiastrum Bellis Bidens Calendula Carduus Carlina Centaurea Chamomilla Chondrilla Chrysanthemum Cicerbita Cichorium Cirsium Conyza Crepis Dendranthema Doronicum Echinacea Echinops Erigeron Eupatorium Filago Galinsoga Gnaphalium Helianthus Helichrysum Hieracium Homogyne Hypochoeris Inula Iva Lactuca Lapsana Leontodon Leontopodium Leucanthemum Ligularia Matricaria Mycelis Onopordum Petasites Picris Prenanthes Pulicaria Rudbeckia Scorzonera Senecio Serratula Silybum Solidago Sonchus Tanacetum Taraxacum Telekia Tragopogon Tussilago Xanthium*
Balsaminaceae	1	*Impatiens*	1	*Impatiens*
Begoniaceae	1	*Begonia*	0	
Berberidaceae	3	*Berberis Epimedium Mahonia*	1	*Berberis*
Betulaceae	2	*Alnus Betula*	2	*Alnus Betula*
Bignoniaceae	2	*Campsis Catalpa*	0	
Boraginaceae	16	*Alkanna Amsinckia Anchusa Asperugo Borago Cerinthe Cynoglossum Echium Heliotropium Lappula Lithospermum Myosotis Nonea Omphalodes Pulmonaria Symphytum*	10	*Anchusa Borago Cerinthe Cynoglossum Echium Lithospermum Myosotis Omphalodes Pulmonaria Symphytum*
Brassicaceae	55	*Alliaria Alyssum Arabidopsis Arabis Armoracia Aubrieta Barbarea Berteroa Biscutella Brassica Bunias Cakile Camelina Capsella Cardamine Cardaminopsis Cardaria Cheiranthus Chorispora Cochlearia Coincya Conringia Coronopus Crambe Dentaria Descurainia Diplotaxis Draba Erophila Eruca Erucastrum Erysimum Euclidium Hesperis Hirschfeldia Hutchinsia Iberis Isatis Kernera Lepidium Lobularia Lunaria Malcolmia Matthiola Myagrum Nasturtium Neslia Raphanus Rapistrum Rhynchosinapis Rorippa Sinapis Sisymbrium Teesdalea Thlaspi*	33	*Alliaria Alyssum Arabis Armoracia Barbarea Berteroa Biscutella Brassica Bunias Cakile Camelina Capsella Cardamine Cardaminopsis Cochlearia Dentaria Descurainia Diplotaxis Draba Eruca Erysimum Hesperis Hutchinsia Kernera Lepidium Lunaria Nasturtium Raphanus Rorippa Sinapis Sisymbrium Teesdalea Thlaspi*

TABLE 1. *Cont.*

Families	NG Checklist	Genus	NG ChND	Genus
Buddlejaceae	1	*Buddleia*	0	
Butomaceae	1	*Butomus*	1	*Butomus*
Buxaceae	2	*Buxus Pachysandra*	0	
Caesalpiniaceae	1	*Gleditsia*	1	*Gleditsia*
Callitrichaceae	1	*Callitriche*	1	*Callitriche*
Calycanthaceae	1	*Calycanthus*	0	
Campanulaceae	6	*Adenophora Campanula Jasione Legousia Phyteuma Platycodon*	4	*Adenophora Campanula Jasione Phyteuma*
Cannabaceae	2	*Cannabis Humulus*	2	*Cannabis Humulus*
Cannaceae	1	*Canna*	0	
Capparaceae	1	*Cleome*	0	
Caprifoliaceae	7	*Kolkwitzia Linnaea Lonicera Sambucus Symphoricarpos Viburnum Weigela*	5	*Linnaea Lonicera Sambucus Symphoricarpos Viburnum*
Caryophyllaceae	30	*Agrostemma Arenaria Celosia Cerastium Corrigiola Cucubalus Dianthus Gypsophila Heliosperma Herniaria Holosteum Honckenya Illecebrum Lychnis Melandrium Minuartia Moehringia Moenchia Myosoton Petrorhagia Polycarpon Sagina Saponaria Scleranthus Silene Spergula Spergularia Stellaria Vaccaria Viscaria*	21	*Agrostemma Arenaria Cerastium Cucubalus Dianthus Gypsophila Heliosperma Herniaria Honckenya Illecebrum Lychnis Melandrium Myosoton Petrorhagia Saponaria Scleranthus Silene Spergula Spergularia Stellaria Viscaria*
Celastraceae	2	*Celastrus Euonymus*	1	*Euonymus*
Ceratophyllaceae	1	*Ceratophyllum*	1	*Ceratophyllum*
Cercidiphyllaceae	1	*Cercidiphyllum*	0	
Chenopodiaceae	13	*Atriplex Axyris Bassia Beta Chenopodium Corispermum Halimione Kochia Polycnemum Salicornia Salsola Spinacia Suaeda*	5	*Atriplex Chenopodium Corispermum Kochia Salicornia*
Cistaceae	1	*Helianthemum*	1	*Helianthemum*
Commelinaceae	2	*Commelina Tradescantia*	0	
Convolvulaceae	4	*Calystegia Convolvulus Ipomoea Merremia*	2	*Calystegia Convolvulus*
Cornaceae	1	*Cornus*	1	*Cornus*
Corylaceae	2	*Carpinus Corylus*	2	*Carpinus Corylus*
Crassulaceae	5	*Crassula Jovibarba Rhodiola Sedum Sempervivum*	1	*Sedum*
Cucurbitaceae	6	*Bryonia Cucumis Cucurbita Echinocystis Sicyos Thladiantha*	4	*Bryonia Echinocystis Sicyos Thladiantha*
Cuscutaceae	1	*Cuscuta*	1	*Cuscuta*
Cyperaceae	16	*Baeothryon Blysmus Bulboschoenus Carex Cladium Cyperus Dichostylis Eleocharis Eleogiton Eriophorum Isolepis Rhynchospora Schoenoplectus Schoenus Scirpoides Scirpus*	9	*Blysmus Bulboschoenus Carex Eleocharis Eriophorum Isolepis Rhynchospora Schoenoplectus Scirpus*
Dipsacaceae	7	*Cephalaria Dipsacus Knautia Scabiosa Succisa Succisella Virga*	4	*Dipsacus Knautia Scabiosa Succisa*

TABLE 1. *Cont.*

Family	NG Checklist	Genus	NG ChND	Genus
Droseraceae	2	*Aldrovanda Drosera*	2	*Aldrovanda Drosera*
Elaeagnaceae	2	*Elaeagnus Hippophaë*	2	*Elaeagnus Hippophaë*
Elatinaceae	1	*Elatine*	1	*Elatine*
Empetraceae	1	*Empetrum*	0	
Ericaceae	10	*Andromeda Arctostaphylos Calluna Chamaedaphne Erica Kalmia Ledum Oxycoccus Rhododendron Vaccinium*	3	*Calluna Oxycoccus Rhododendron*
Euphorbiaceae	2	*Euphorbia Mercurialis*	2	*Euphorbia Mercurialis*
Fabaceae	40	*Amorpha Anthyllis Arachis Astragalus Caragana Ceratonia Chamaecytisus Cicer Colutea Coronilla Dorycnium Galega Genista Genistella Glycine Gymnocladus Hedysarum Hippocrepis Laburnum Lathyrus Lembotropis Lens Lotus Lupinus Medicago Melilotus Onobrychis Ononis Ornithopus Oxytropis Phaseolus Pisum Robinia Sarothamnus Tetragonolobus Trifolium Trigonella Ulex Vicia Wisteria*	24	*Anthyllis Astragalus Caragana Chamaecytisus Coronilla Dorycnium Galega Genista Hedysarum Lathyrus Lotus Lupinus Medicago Melilotus Onobrychis Ononis Ornithopus Oxytropis Robinia Sarothamnus Tetragonolobus Trifolium Trigonella Vicia*
Fagaceae	3	*Castanea Fagus Quercus*	2	*Fagus Quercus*
Fumariaceae	3	*Corydalis Dicentra Fumaria*	1	*Corydalis*
Gentianaceae	4	*Centaurium Gentiana Gentianella Swertia*	4	*Centaurium Gentiana Gentianella Swertia*
Geraniaceae	3	*Erodium Geranium Pelargonium*	2	*Erodium Geranium*
Grossulariaceae	1	*Ribes*	1	*Ribes*
Haloragaceae	1	*Myriophyllum*	1	*Myriophyllum*
Hamamelidaceae	1	*Hamamelis*	0	
Hippocastanaceae	1	*Aesculus*	1	*Aesculus*
Hippuridaceae	1	*Hippuris*	1	*Hippuris*
Hydrangeaceae	1	*Hydrangea*	0	
Hydrocharitaceae	4	*Elodea Hydrilla Hydrocharis Stratiotes*	3	*Elodea Hydrilla Hydrocharis*
Hydrocotylaceae	3	*Hydrocotyle Hydrophyllum Nemophila*	1	*Hydrocotyle*
Hydrophyllaceae	1	*Phacelia*	0	
Hypericaceae	1	*Hypericum*	1	*Hypericum*
Iridaceae	6	*Crocosmia Crocus Gladiolus Iris Narcissus Sisyrynchium*	3	*Crocus Gladiolus Iris*
Juglandaceae	3	*Carya Juglans Pterocarya*	1	*Juglans*
Juncaceae	2	*Juncus Luzula*	2	*Juncus Luzula*
Juncaginaceae	1	*Triglochin*	1	*Triglochin*
Lamiaceae	34	*Acinos Ajuga Amethystea Ballota Betonica Calamintha Chaiturus Clinopodium Dracocephalum Elsholtzia Galeobdolon Galeopsis Glechoma Hyssopus Lamium Lavandula Leonurus Lycopus Marrubium Melissa Melittis Mentha Monarda Nepeta Ocimum Origanum Physostegia Prunella Salvia Scutellaria Sideritis Stachys Teucrium Thymus*	22	*Acinos Ajuga Ballota Betonica Elsholtzia Galeobdolon Galeopsis Glechoma Lamium Leonurus Lycopus Marrubium Melittis Mentha Nepeta Origanum Prunella Salvia Scutellaria Stachys Teucrium Thymus*

TABLE 1. *Cont.*

Family	NG Checklist	Genus	NG ChND	Genus
Lemnaceae	3	*Lemna Spirodela Wolffia*	3	*Lemna Spirodela Wolffia*
Lentibulariaceae	2	*Pinguicula Utricularia*	2	*Pinguicula Utricularia*
Liliaceae	26	*Allium Anthericum Asparagus Bulbine Colchicum Convallaria Eremurus Erythronium Fritillaria Gagea Hemerocallis Hosta Hyacinthoides Hyacinthus Kniphofia Lilium Lloydia Maianthemum Muscari Ornithogalum Polygonatum Scilla Streptopus Tofieldia Tulipa Veratrum*	15	*Allium Anthericum Asparagus Colchicum Convallaria Fritillaria Gagea Lilium Lloydia Maianthemum Ornithogalum Polygonatum Scilla Tofieldia Veratrum*
Linaceae	2	*Linum Radiola*	1	*Linum*
Lobeliaceae	1	*Lobelia*	1	*Lobelia*
Loranthaceae	1	*Viscum*	1	*Viscum*
Lythraceae	2	*Lythrum Peplis*	2	*Lythrum Peplis*
Magnoliaceae	2	*Liriodendron Magnolia*	0	
Malvaceae	9	*Abutilon Alcea Althaea Anoda Hibiscus Lavatera Malope Malva Malvastrum*	4	*Althaea Lavatera Malope Malva*
Martyniaceae	1	*Martynia*	0	
Menyanthaceae	2	*Menyanthes Nymphoides*	2	*Menyanthes Nymphoides*
Monotropaceae	1	*Monotropa*	0	
Moraceae	2	*Ficus Morus*	1	*Morus*
Myricaceae	1	*Myrica*	0	
Najadaceae	1	*Najas*	1	*Najas*
Nyctaginaceae	2	*Mirabilis Oxybaphus*	0	
Nymphaeaceae	2	*Nuphar Nymphaea*	2	*Nuphar Nymphaea*
Oleaceae	4	*Forsythia Fraxinus Ligustrum Syringa*	3	*Fraxinus Ligustrum Syringa*
Onagraceae	6	*Chamaenerion Circaea Epilobium Godetia Ludwigia Oenothera*	4	*Chamaenerion Circaea Epilobium Oenothera*
Orchidaceae	24	*Anacamptis Cephalanthera Chamorchis Coeloglossum Corallorhiza Cypripedium Dactylorhiza Epipactis Epipogium Goodyera Gymnadenia Hammarbya Herminium Leucorchis Liparis Listera Malaxis Neottia Neottianthe Ophrys Orchis Platanthera Spiranthes Traunsteinera*	14	*Cephalanthera Coeloglossum Cypripedium Dactylorhiza Epipactis Goodyera Gymnadenia Leucorchis Listera Neottia Ophrys Orchis Platanthera Traunsteinera*
Orobanchaceae	1	*Orobanche*	1	*Orobanche*
Oxalidaceae	1	*Oxalis*	1	*Oxalis*
Paeoniaceae	1	*Paeonia*	0	
Papaveraceae	5	*Argemone Chelidonium Eschscholtzia Glaucium Papaver*	3	*Chelidonium Glaucium Papaver*
Parnassiaceae	1	*Parnassia*	1	*Parnassia*
Philadelphaceae	2	*Deutzia Philadelphus*	0	
Plantaginaceae	2	*Littorella Plantago*	2	*Littorella Plantago*
Platanaceae	1	*Platanus*	0	
Plumbaginaceae	2	*Armeria Limonium*	1	*Armeria*

TABLE 1. *Cont.*

Family	NG Checklist	Genus	NG ChND	Genus
Poaceae	86	*Aegilops Agropyron Agrostis Aira Alopecurus Ammophila Anthoxanthum Apera Arrhenatherum Avena Avenula Beckmannia Bellardiochloa Bothriochloa Brachypodium Briza Bromus Calamagrostis Catabrosa Chloris Coix Cortaderia Corynephorus Cynodon Cynosurus Dactylis Dactyloctenium Danthonia Dasypyrum Deschampsia Desmazeria Digitaria Dinebra Echinochloa Eleusine Elymus Elytrigia Eragrostis Eriochloa Festuca Gastridium Gaudinia Glyceria Hainardia Helictotrichon Hierochloë Holcus Hordelymus Hordeum Koeleria Lagurus Leersia Lolium Lophochloa Melica Milium Miscanthus Molinia Nardus Oreochloa Panicum Parapholis Paspalum Pennisetum Phalaris Phleum Pholiurus Phragmites Poa Polypogon Puccinellia Schismus Sclerochloa Scolochloa Secale Sesleria Setaria Sorghum Stipa Trisetum Triticum Ventenata Vulpia xCalammophila xFestulolium Zea*	51	*Agropyron Agrostis Aira Alopecurus Ammophila Anthoxanthum Apera Arrhenatherum Avena Avenula Bellardiochloa Bothriochloa Brachypodium Briza Bromus Calamagrostis Catabrosa Corynephorus Cynosurus Dactylis Danthonia Deschampsia Digitaria Echinochloa Elymus Festuca Glyceria Hierochloë Holcus Hordelymus Hordeum Koeleria Lolium Melica Milium Molinia Nardus Oreochloa Panicum Phalaris Phleum Phragmites Poa Puccinellia Scolochloa Sesleria Setaria Stipa Trisetum Vulpia xCalammophila*
Polemoniaceae	5	*Cobaea Collomia Gilia Phlox Polemonium*	1	*Polemonium*
Polygalaceae	1	*Polygala*	1	*Polygala*
Polygonaceae	7	*Fagopyrum Fallopia Oxyria Polygonum Reynoutria Rheum Rumex*	6	*Fagopyrum Fallopia Oxyria Polygonum Reynoutria Rumex*
Portulacaceae	3	*Calandrinia Montia Portulaca*	0	
Potamogetonaceae	2	*Groenlandia Potamogeton*	1	*Potamogeton*
Primulaceae	13	*Anagallis Androsace Centunculus Cortusa Cyclamen Dodecatheon Glaux Hottonia Lysimachia Primula Samolus Soldanella Trientalis*	10	*Anagallis Androsace Centunculus Cortusa Glaux Hottonia Lysimachia Primula Samolus Soldanella*
Proteaceae	1	*Simsia*	0	
Pyrolaceae	4	*Chimaphila Moneses Orthilia Pyrola*	4	*Chimaphila Moneses Orthilia Pyrola*
Ranunculaceae	24	*Aconitum Actaea Adonis Anemone Aquilegia Batrachium Callianthemum Caltha Ceratocephala Cimicifuga Clematis Consolida Delphinium Eranthis Ficaria Helleborus Hepatica Isopyrum Myosurus Nigella Pulsatilla Ranunculus Thalictrum Trollius*	19	*Aconitum Actaea Adonis Anemone Aquilegia Batrachium Callianthemum Caltha Clematis Consolida Delphinium Ficaria Helleborus Hepatica Isopyrum Nigella Ranunculus Thalictrum Trollius*
Resedaceae	1	*Reseda*	1	*Reseda*
Rhamnaceae	3	*Ceanothus Frangula Rhamnus*	2	*Frangula Rhamnus*
Rosaceae	39	*Acaena Agrimonia Alchemilla Amelanchier Amygdalus Aphanes Armeniaca Aruncus Cerasus Chaenomeles Comarum Cotoneaster Crataegus Cydonia Dryas Exochorda Filipendula Fragaria Geum Holodiscus Kerria Laurocerasus Malus Mespilus Padus Persica Physocarpus Potentilla Prunus Pyracantha Pyrus Rosa Rubus Sanguisorba Sibbaldia Sorbaria Sorbus Spiraea Waldsteinia*	22	*Agrimonia Alchemilla Aphanes Aruncus Comarum Crataegus Dryas Filipendula Fragaria Geum Malus Padus Physocarpus Potentilla Prunus Pyrus Rosa Rubus Sanguisorba Sibbaldia Sorbus Waldsteinia*

TABLE 1. *Cont.*

Family	NG Checklist	Genus	NG ChND	Genus
Rubiaceae	5	*Asperula Cruciata Galium Rubia Sherardia*	4	*Asperula Cruciata Galium Sherardia*
Ruppiaceae	1	*Ruppia*	0	
Rutaceae	5	*Citrus Dictamnus Phellodendron Ptelea Ruta*	1	*Ruta*
Salicaceae	2	*Populus Salix*	2	*Populus Salix*
Santalaceae	1	*Thesium*	1	*Thesium*
Saururaceae	1	*Houttuynia*	0	
Saxifragaceae	5	*Astilbe Bergenia Chrysosplenium Heuchera Saxifraga*	2	*Chrysosplenium Saxifraga*
Scheuchzeriaceae	1	*Scheuchzeria*	0	
Scrophulariaceae	25	*Antirrhinum Bartsia Chaenorhinum Cymbalaria Digitalis Euphrasia Gratiola Kickxia Lathraea Limosella Linaria Lindernia Melampyrum Mimulus Misopates Nemesia Odontites Orthantha Pedicularis Penstemon Rhinanthus Scrophularia Tozzia Verbascum Veronica*	17	*Bartsia Chaenorhinum Cymbalaria Digitalis Limosella Linaria Lindernia Melampyrum Mimulus Misopates Odontites Orthanta Pedicularis Rhinanthus Scrophularia Verbascum Veronica*
Simaroubaceae	1	*Ailanthus*	0	
Solanaceae	12	*Atropa Capsicum Datura Hyoscyamus Lycium Lycopersicon Nicandra Nicotiana Physalis Salpiglossis Scopolia Solanum*	6	*Datura Hyoscyamus Lycium Physalis Scopolia Solanum*
Sparganiaceae	1	*Sparganium*	1	*Sparganium*
Staphyleaceae	1	*Staphylea*	1	*Staphylea*
Tamaricaceae	1	*Myricaria*	1	*Myricaria*
Thymelaeaceae	2	*Daphne Thymelaea*	1	*Daphne*
Tiliaceae	1	*Tilia*	1	*Tilia*
Trapaceae	1	*Trapa*	1	*Trapa*
Trilliaceae	1	*Paris*	1	*Paris*
Tropaeolaceae	1	*Tropaeolum*	0	
Typhaceae	1	*Typha*	1	*Typha*
Ulmaceae	1	*Ulmus*	1	*Ulmus*
Urticaceae	2	*Parietaria Urtica*	2	*Parietaria Urtica*
Valerianaceae	2	*Valeriana Valerianella*	1	*Valeriana*
Verbenaceae	1	*Verbena*	1	*Verbena*
Violaceae	1	*Viola*	1	*Viola*
Vitaceae	2	*Parthenocissus Vitis*	2	*Parthenocissus Vitis*
Zannichelliaceae	1	*Zannichellia*	1	*Zannichellia*
Zosteraceae	1	*Zostera*	1	*Zostera*
Zygophyllaceae	2	*Tribulus Zygophyllum*	0	

excluding these genera (*Alchemilla, Hieracium, Taraxacum*), 1,812 native species remain, of which 1,150 (63%) have established chromosome numbers. Among the large non-apomictic genera poorly researched so far, *Carex*, with 76 species lacking chromosome counts, deserves special attention.

Poland's native flora is represented by 533 genera and 111 families; anthropophytes are listed among 176 genera and 46 families. The karyological data include chromosome numbers of native species from 448 genera and 104 families, and anthropophytes from 117 genera and 34 families.

Chromosome numbers are known for all native species listed in 298 genera and 46 families, and all anthropophytes from 79 genera and 11 families. We have no information on the chromosome numbers of any of the native species in 85 genera and 7 families, nor for the anthropophytes listed in 59 genera and 12 families. Most of the genera not examined on this respect contain 1–2(3) species, with the exception of *Euphrasia* (11 native species), *Pulsatilla* (6 native species), *Minuartia* (5 native species), *Sagina* (5 native species) and *Vaccinium* (4 native species). The same applies to unexplored families, with the exception of Fumariaceae (4 anthropophytes). Although plants belonging to karyologically unexplored genera/families in Poland represent a small share (9%) of native and permanently established anthropophyte species, they form a significant share (17%) of the plants without established chromosome numbers.

The data on chromosome numbers of native and permanently established taxa should be supplemented by direct chromosome counting in the Polish plants not studied so far. Only then will they be fully reliable and of use for summarizing the karyology and distinctiveness of the Polish flora. When possible, the data on taxa already in the Chromosome Number Database should be broadened to include plants collected from different localities in Poland. Currently the data on plants from the south (1,337 species) far outweigh the data from other areas (Fig. 1). This can be only partially explained by the higher species richness of southern Poland.

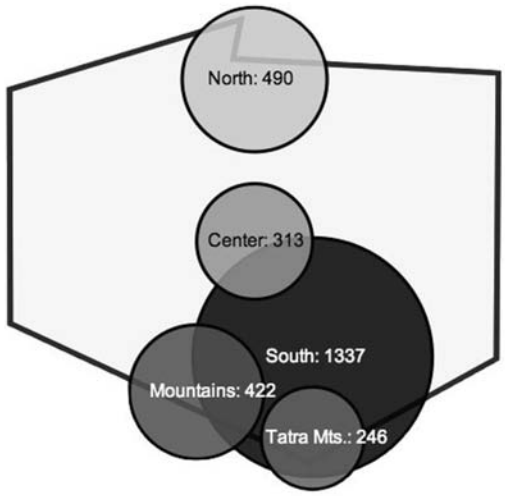

Fig. 1. Chromosome number data for plants from different areas of Poland.

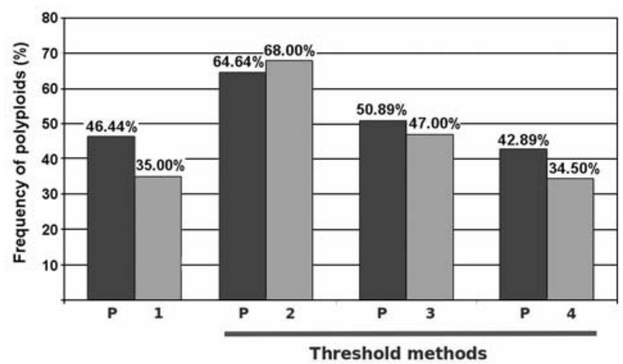

Fig. 2. Frequency of polyploid species according to four different estimation methods. P – Polish plants; 1, 2, 3, 4 – polyploidy estimated for flowering plants by Stebbins (1950), Goldblatt (1980), Grant (1963), and Wood et al. (2009), respectively.

OTHER TAXA

The remaining angiosperms recorded from Poland are classified as cultivated species (534; "frequently cultivated and having the potential to establish permanently in the wild"), ephemerophytes (511), and extinct or probably extinct (40) (Mirek et al., (2002). The status of 33 species in Polish flora remains to be clarified, and 6 previously reported species are doubtful.

Almost all of those groups are insufficiently researched in Poland. Of the taxa with recognized statuses, the Chromosome Number Database contains only 9% (45) of the cultivated plants, 5% (25) of the ephemerophytes, and 8% (3) of the extinct or probably extinct species. Besides those, chromosome numbers are known for 64% (21) of the species with uncertain status. Among the doubtful species, only *Arum maculatum* has a record in the database.

Much remains to be done in terms of direct examination of Polish plants, but reliable data on the two largest poorly investigated groups of species (cultivated species and ephemerophytes) may be obtained from existing databases and the scientific literature. These species come from different, often remote areas, and presumably their chromosome numbers are unaffected by the fact of their presence in Poland. The data obtained indirectly will be a valuable supplement to the Chromosome Number Database. For chromosome counting, attention should focus on cultivated plants and ephemerophytes with completely unknown chromosome numbers and species showing diverse chromosome numbers, to determine which cytotype(s) occur in Poland. The species of interest are listed in Appendix 5 (in electronic version).

FREQUENCY OF POLYPLOID PLANTS

Polyploidy is the most common karyotype variation and a key factor in the formation of new vascular plant species (Stebbins, 1950, 1971; Levin, 2002). Polyploidization probably was also critical to the

TABLE 2. Ploidy distribution among Polish native species and anthropophytes (%)

	Diploids (2x)	Lower polyploids (3x, 4x)	Higher polyploids (5x-22x)	Diploid/ polyploid	Mixed polyploids*
Native species (N=1167)	45.59	29.21	15.89	4.71	4.60
Anthropophytes (N=194)	64.95	21.56	10.26	2.13	1.10

* – lower and higher polyploids (e.g. 4× and 6×)

evolution of bryophytes (Przywara and Kuta, 1995; Kuta and Przywara, 1997). Despite the fundamental role of polyploidy in plant diversification, the frequency of polyploid speciation in angiosperms is still a debated issue (Otto and Whitton, 2000; Wood et al., 2009; Mayrose et al., 2011).

Polyploidy commonly is inferred when somatic chromosome numbers among related species follow a polyploid series (Stebbins, 1950), but this approach is questionable in the case of ancient polyploids (Otto and Whitton, 2000). For this reason, various indirect methods have been proposed, largely based on analysis of haploid chromosome numbers (Grant, 1963; Stebbins, 1971; Goldblatt, 1980; Masterson, 1994), guard cell size (Masterson, 1994) or molecular traces of ancient genome duplication (Lysak et al., 2005; Cui et al., 2006). Depending on the estimation method, the inferred proportion of polyploid taxa among angiosperms ranges from 30% to 80% (Bennett, 2004). A recent in-depth phylogenetic analysis indicates that almost all angiosperms underwent at least one polyploidization event in their evolutionary history (Soltis et al., 2009).

When polyploidy was calculated according to generic basic chromosome numbers, 46.44% of Polish angiosperm species with chromosome counts were inferred to be polyploid (possessing three or more basic chromosome sets). The rest of the plants showed diploid (49.45%) or diploid/polyploid chromosome numbers (4.11%). That estimate of polyploid frequency in the Polish flora is substantially higher than the 35% which Stebbins (1950) estimated for flowering plants by the same method.

According to two of the three threshold methods, the contribution of polyploid plants to the Polish flora is even higher. The obtained scores (64.64%, 50.89%, 42.89%) are more consistent with the results for flowering plants from Goldblatt (1980), Grant (1963) and Wood et al. (2009) (Fig. 2).

On the grounds of basic chromosome numbers, 47.32% of the native species and anthropophytes are polyploid, 48.35% diploid, and 4.33% diploid or polyploid. There is a considerable difference between native plants (45.59% diploid species) and anthropophytes (64.95% diploid species). Poly-ploidy is more common among indigenous than among non-indigenous plants. The distribution of ploidy levels in the compared groups is shown in Table 2.

The difference in the shares of diploids and polyploids between native plants and anthropophytes is highly significant (χ^2=22.16, P<0.0001, N=1302). On the other hand, anthropophytes do not differ in this respect from the rest of the non-indigenous Polish plants with established chromosome numbers (χ^2=0.03, P>0.8, N=288). The differences do not change after diploid/polyploid species are included in the diploids or polyploids (data not shown).

The relatively high frequency of polyploid species presumably is a specific feature of Poland's indigenous flora. The frequencies obtained by the three threshold methods for native plants (67.58%, 53.46%, 47.22%) and anthropophytes (48.45%, 37.63% and 25.77%) confirmed the substantial difference between them. The higher share of polyploids in native plants may be related to the Quaternary history of Polish flora. The majority of them were recruited from nearby regions after the last deglaciation, whereas the anthropophytes arrived relatively recently. Arguing that polyploids were more successful than diploids in colonizing deglaciated areas, Brochman et al. (2004) demonstrated that in arctic plants the frequency of diploids is much higher among taxa restricted to the Atlantic (glaciated) than to the Beringian (non-glaciated) region.

Some authors have suggested that polyploids are better adapted for harsher environmental conditions than diploids are (Flovik, 1940; Brochmann et al., 2004; Nie et al., 2005, and references therein). Skalińska (1963), however, reported a relatively low proportion of polyploids (43.6%) in the Polish Tatras, based on chromosome counts of 110 taxa. Our estimates using the basic numbers for 228 species from that area showed 115 (50.44%) diploid, 107 (46.93%) polyploid and 6 (2.63%) diploid/polyploid species. A comparison with the rest of the native Polish plants with chromosome counts (417, 473 and 49 species, respectively) showed a nonsignificant difference between the Tatras and the rest of Poland (χ^2=4.51, P>0.1, N=1167). This counterintuitive outcome is in accord with results Hadac (1989) gave for plants from two mountain valleys in the Slovak Tatras (51% and 53% diploids). Hadac suggested that high mountains could provide a favorable habitat for native diploids because ".. high mountain plants could well survive [glaciation] in the mountain complex or in the adjacent tundra, and come back without losing contact with their original home. So the natural selection of less adapted forms was very slight and even diploids with a relatively narrow scale of adaptation could survive."

A study of the alpine flora of the Hengduan Mts. (Nie et al., 2005) based on 522 taxa belonging to 152 genera and 44 families showed a great prevalence of diploid taxa (78%). Moreover, the endemic species from this area (considered one of the world's richest centers of endemism) were characterized by the lowest known share of polyploids (only 16%). In this context it is interesting to examine the frequency of polyploids among the endemic plants inhabiting Tatra Mts.

The Tatras are the northernmost center of endemism in Europe; there are 34 endemic and subendemic species (ESS) occurring in the Polish Tatras (Piękoś-Mirkowa et al., 1996). All of them except *Melampyrum herbichii* have chromosome records in Polish and/or Slovak chromosome number databases (http://www.binoz.uj.edu.pl:8080/chromosomes/, Marhold et al., 2007 and http://www.chromosomes.sav.sk/). According to basic chromosome number, 11 of them are diploid, 21 polyploid, and 1 diploid/polyploid. Thus, in contrast to all Tatra plants, the share of polyploids within this group (63.64%) is extremely high. This value also differs radically from the proportion calculated by Nie et al. (2005) for endemic species of the Hengduan Mts. On the other hand, the ploidy distribution (diploid – polyploid – diploid/polyploid) in ESS from the Polish Tatras does not differ significantly from that observed in all arctic plants analyzed by Brochman et al. (2004) (χ^2=2.78, P>0.2, N=1752). In terms of the 5 zonal groups distinguished by Brochman and coworkers, ESS from the Tatra Mts. showed the greatest similarity to group 4, representing mainly arctic taxa with infrequent occurrence in boreal and/or temperate alpine areas (χ^2=0.56, P>0.7, N=177). The difference in the proportion of polyploids between ESS (63.64%) and the rest of the plants from the Tatra Mts. (44.62%) probably is not conditioned environmentally. The lack of a direct link between polyploidy and habitat has been stressed by a number of authors (e.g., Ehrendorfer, 1980; Nie et al., 2005; Brochman et al. 2004).

This statistical survey showed a significant difference in the proportion of polyploids between indigenous and non-indigenous plants and between ESS and the rest of the plants inhabiting the Tatra Mts. Further studies on chromosome numbers and polyploidy in the different taxonomic, geographical and ecological elements of the Polish flora should yield more comprehensive data on the extent of karyological diversification among Polish angiosperms – and its possible causes.

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