CYTOTAXONOMY OF SPANISH PLANTS. I. INTRODUCTION. PTERIDOPHYTA AND GYMNOSPERMAE

ASKELL LÖVE & EBBE KJELLQVIST

Department of Environmental, Population and Organismic Biology, University of Colorado, Boulder, Colorado 80302 & Agricultural Research and Introduction Centre, Izmír - Karsiyaka, Turkey

(Recibido el 9 de abril de 1972)

Resumen. Este es el primer artículo de una serie de trabajos sobre citotaxonomía de plantas españolas, procedentes principalmente de regiones montañosas del sur y centro del país. Se estudian los números cromosómicos de las siguientes Pteridophyta y Gymnospermae: Hippochaete ramosissima (Desf.) C. Börner, 2n = 216; Ophioglossum vulgatum L., 2n = 480; Pteridium herediae (Clemente ex Colmeiro) Löve & Kjellqvist, comb. nov., de suelos calizos, 2n = 52; Adiantum capillus-veneris L., 2n = 60; Asplenium adiantum-nigrum L., 2n = 144; Asplenium septentrionale (L.) Hoffm., 2n = 144; Asplenium melanocaulon Willd., 2n = 72; Ceterach officinarum DC., 2n = 144; Cystopteris fragilis (L.) Bernh., 2n = 168; Dryopteris filix-mas (L.) Schott, 2n = 164; Polypodium australe Fée, 2n = 74; Pinus halepensis L., 2n = 24; Juniperus communis L. subsp. hemispherica (J. & C. Presl.) Nyman, 2n = 22; Juniperus oxycedrus L. subsp. oxycedrus, 2n = 22; Sabina vulgaris Antoine var. humilis (Endl.) Antoine, 2n = 22. Se discute brevemente la taxonomía y ecología de algunos de estos taxa.

Summary. This is the first in a series of papers on the cytotaxonomy of Spanish plants, mainly from two mountain regions in the southern and central parts of the country. It reports the chromosome numbers for the following taxa of Pteridophyta and Gymnospermae: Hippochaete ramosissima (Desf.) C. Börner. 2n = 216; Ophioglossum vulgatum L., 2n = 480; Pteridium herediae (Clemente ex Colmeiro) Löve & Kjellqvist, comb. nov., from calcareous soil, 2n = 52; Adiantum capillus-veneris L., 2n = 60; Asplenium adiantum-nigrum L., 2n = 144; Asplenium septentrionale (L.) Hoffm., 2n = 144; Asplenium melanocaulon Willd., 2n = 72; Ceterach officinarum DC., 2n = 144; Cystopteris fragilis (L.) Bernh., 2n = 168; Dryopteris filix-mas (L.) Schott, 2n = 164; Polypodium australe Fée, 2n = 74; Pinus halepensis L., 2n = 24; Juniperus communis L. subsp. hemispherica (J. & C. Presl.) Nyman, 2n = 22; Juniperus oxycedrus L. subsp. oxycedrus, 2n = 22; Sabina vulgaris Antoine var. humilis (Endl.) Antoine, 2n = 22. The taxonomy and ecology of some of these taxa are summarily discussed.

Fourscore and ten years have elapsed since the initiation of studies of chromosome numbers of plants, by Guignard (1882) and Strasburger (1882), an approach that immediately resulted in the correct conclusion that each good species of living beings is characterized by a single chromosome number in its vital organs. It also led to the acknowledgement of the fact that differences in chromosome number between two populations of closely related biota are a strong indication of reproductive distinction of taxonomically separate gene pools. This recognition in turn resulted in the gradual emergence of the science of cytotaxonomy, which combines cytological and taxonomical methods as basis for a biological classification at and around the species level; since even the first observers of chromosome numbers realized their taxonomical and evolutionary significance, this approach may perhaps even be regarded as being older than genetics itself.

Cytotaxonomy was born in central and northern Europe, and its growth even there was slow during the first half a century. During the past generation, however, interest in this approach has increased considerably so that not only cytologists but, to a much higher degree, taxonomists presently expend considerable effort in collecting chromosome information from various taxa from different parts of the globe for use as basic material for studies on the very important evolutionary classification of plants. Although this has resulted in an almost complete knowledge of the chromosome numbers of the floras of northern and boreal lands, especially in Europe but also in parts of North America and eastern Asia, considerably less attention has been paid to the evolutionary classification and cytotaxonomy of more southern regions where evolution seems to be most active. Pioneer investigations in the Mediterranean region in recent years seem to promise that these rich and remarkable floras will soon become the main field of interest for those who study chromosomes as a basis for considerations of evolutionary processes, taxonomic and geographic.

This report is the first in a series on the cytotaxonomy of Spanish plants based on collections made mainly in mountainous areas in the Cazorla Sierras of the province of Jaén in southern Spain and in the Albarracín Sierras of the provinces Cuenca and Teruel in central Spain (cf. KJELLQVIST & LÖVE, 1963; LÖVE & KJELLQVIST, 1964). The root tips used in these studies were fixed in the field, but chromosome numbers were also determined from plants grown from seeds in a greenhouse at the Montreal Botanical Garden. The root tips were mainly fixed in the Svalöv modification of the Navashin-Karpechenko fluid, sectioned, and stained with crystal violet, but in some cases the squash technique and Feulgen staining were employed. Voucher

specimens and several duplicates were preserved for later reference; sets of these have been deposited in the herbarium of the University of Liverpool (LIVU) and in the herbarium of the University of Lund (LD), whereas duplicates will hopefully be given to a few leading herbaria in Spain, Canada and the United States when the study has been completed.

The investigations were made possible by NATO Science Grant No. 69, hereby gratefully acknowledged, when the senior author was at the Université de Montréal in Canada and the junior author at the University of Lund in Sweden. We also wish to thank for the able assistance in the field and laboratory given us by Mrs. Britt Kjellovist.

The taxonomy of the material was determined by aid of available floras and herbarium specimens, in Lund and Montreal, but considerable efforts in checking and correcting these determinations were made by Prof. V. H. Heywood and his students, then at Liverpool, now at Reading, England, and then especially by Dr. B. Valdés, now at Sevilla. We cannot express strongly enough our gratefulness for this invaluable help and also for the assistance in planning the work and constant advice during its progress by Prof. Heywood. Numerous other colleagues have also given us help in various ways; we hope they will accept our gratitude without names and observe that we have followed their recommendations without transferring our responsability to their names.

Although this study may ultimately be used for various more detailed discussions of taxonomic, geographic and historical problems concerning the flora of Spain, we will discuss only essential observations in this series of papers, and we will refrain from making taxonomical changes of status when this can be avoided. When such changes, however, are proposed, they will be based on morphological, geographical, and cytological considerations of the collections available to us and will be a result of our attempts, since 1942 (Löve & Löve, 1942), to apply the biological species concept to the historical study of floras. Therefore, we would like to emphasize at this stage, that we preferably accept as subspecies those taxonomically closely related populations which differ in part or as a whole in certain morphological characters and occupy relatively large areas which are partially or completely isolated geographically. Subspecies are at least potentially capable of interbreeding without reduction in fertility. It follows that they have the same chromosome number and usually also at least very similar karyotypes. In our opinion, subspecies of a well defined biological species are actually major geographical races corresponding to those of the human species (Hul-TÉN, 1967, 1968). As a consequence of this definition of the subspecies the

category of species is defined by its incapability of interbreeding with other such taxa, or by its lack of even potential miscibility (MAYR, 1942, 1963; Löve & Löve, 1942; van Steenis, 1957; Löve, 1964). Morphologically somewhat different populations occupying smaller areas are regarded as varieties (cf. Löve, 1970a), whereas clinal variations and demes (cf. MAYR, 1963; LANGLET, 1971) are not given taxonomic recognition. It is our opinion that when there is insecurity as to the occurrence of a reproductive barrier between two morphologically and geographically more or less distinct taxa, they ought to be preliminarily accepted as species and not as subspecies. It certainly is «a lesser evil to keep forms separated that are identical than to identify such as are distinct» (HALLE, 1913), and a biologically heterogenous taxon with a species name but including reproductively isolated gene pools is apt to lead those unaware of its illogical composition to fallacious conclusions (ROTHMALER, 1944). Since chromosome number differences are the most obvious indicators of reproductive isolation and barriers to miscibility, we regard them as a sufficient warning against including such populations in the same species, as sometimes is done even in the otherwise modern Flora Europaea and by authors who otherwise strictly adhere to the definitions above, which seem to correspond rather closely to the apparent intention of LINNAEUS and later taxonomists of central and northwestern Europe.

In the present paper only taxa studied of Spanish Pteridophyta and Gymnospermae are included, whereas families of monocotyledons and dicotyledons will be discussed in following reports. References to earlier reports, frequently too numerous to be cited, may be most easily consulted by aid of the chromosome atlases by Löve & Löve (1961) and Bolkhovskikh & al. (1969).

EQUISETACEAE

Hippochaete ramosissima (Desf.) C. Börner.

Equisetum ramosissimum Desf.

Voucher: Provincia de Jaén: Sierra de Cazorla, Laguna de Valdeazores, in a meadow near the lake; N. 0580. 2n = 216.

This family is rare in the Cazorla Sierras, and according to Galiano & Heywood (1960), it is represented only by this species, which is rare. Our chromosome count is a confirmation of earlier reports from Italy by Manton

(1950), from northern India by MEHRA & BIR (1959), and from Holland by BIR (1960).

OPHIOGLOSSACEAE

Ophioglossum vulgatum L.

Voucher: Provincia de Jaén: Sierra de Cazorla, Pantano del Tranco; N. 0588. 2n = 480.

This very rare species, which according to Galiano & Heywood (1960) was then known in southern Spain only from the Sierra de Segura which is not far from the locality where we collected a single plant, has been reported to have chromosome numbers varying from 2n = 480 to 1140, mainly from India (Verma, 1956, 1957, 1958; Ninan, 1958), whereas Manton (1950) reported about 500-520 chromosomes from English material. Our specimen belongs to the species in its strict sense as originally described from Sweden, and we could ascertain that its chromosome number is 2n = 480, plus or minus a few chromosomes in each plate.

HYPOLEPIDACEAE

Pteridium herediae (Clemente ex Colmeiro) Löve & Kjellqvist.

Voucher: Provincia de Jaén: Sierra de Cazorla, Arroyo Maillar, in calcareous soil in a dense *Pinus* forest; N. 042. 2n = 52.

Students of the genus Pteridium generally agree that the widely distributed taxon named as the species P. aquilinum (L.) Kuhn in flora manuals actually is a single species that includes some few well defined and geographically more or less disjunct subspecies. This is corroborated by the fact that all these races are ecologically rather similar and calciphobous, and also by that sixteen investigators from various parts of the globe have found all the races to be characterized by the octoploid chromosome number 2n = 104. There is no reason to believe that this is not true for almost all the Pteridium aquilinum of most parts of Spain.

Our material from the Arroyo Maillar is the first exception to this rule. The population dominated the forest floor in soils distinctly rich in lime in a dense forest, and its chromosome number was found to be 2n = 52, or

the tetraploid multiple only of the basic number x = 13 (cf. Molesworth Allen, 1968; Löve & Löve, 1969). The plants are also morphologically different from specimens of typical *P. aquilinum* from silicious areas in southern Spain, since they are definitely smaller, with more suberect, not horizontal, leaves which are tripinnate or nearly so with subbipinnatifid leaflets. The leaflets are clearly oblong and stiped, and both the leaf-stalks and the stipes of the pinnae are distinctly grooved and the stipes are slightly pilose or chaffy at the base.

We have made considerable efforts in searching the literature for names that may have been given to this plant in the past. Actually, there are numerous names that have been given to taxa split out of this complex at various levels though they are usually included in the collective species P. aquilinum without a special designation. Most of these names seem to belong to phenetic modifications, and almost all seem to be correctly grouped with the octoploid species. It is a matter of conjecture that the tetraploid taxon may be related to the recently described fma. congestum Pinto da Silva from Portuguese serpentine (PINTO DA SILVA, 1970). It is apparently identical to P. aquilinum var. gintlii (Rohlena) Kümm. which also has 2n = 52 chromosomes (Löve, unpubl.) and grows in calcareous areas in Crna Gora and Srbija in Yugoslavia (cf. ROHLENA 1941-42; VUKICEVIC 1970). However, our plant seems to be identical the species Pteris herediae, which was described by CLEMENTE, in COLMEIRO (1867) from Aznalcóllar, in the province of Sevilla. Although the description is short, it exactly fits our plant: «Foliis subtripinnatis, foliolis subbipinnatifidis, oblongis, stipite et petiolis canaliculatis, stipite basi tantum piloso paleaceo». In the genus Pteridium its name is Pteridium herediae (Clemente ex Colmeiro) Löve & Kjellqvist, comb. nov., based on Pteris herediae Clemente ex Colmeiro, Enum. Cript. Esp. y Port. 1: 16 (1867).

We have only seen this species in the voucher area, although it is certainly more widespread in southern Spain. According to Molesworth Allen (1968), it is met with in several other calcareous areas of the southern parts of the Iberian Peninsula, and may even reach Malaya. It also seems to be common in calcareous areas in the Balkan Peninsula. We would like to suggest that *P. herediae* may be a plant of Tethyan distribution, surviving in calcareous areas in southern Eurasia, although its possible occurrence outside southern Europe needs to be verified.

ADIANTHACEAE

Adiantum capillus-veneris L.

Vouchers: Provincia de Jaén: Sierra de Cazorla, Cueva de la Magdalena, on moist limestone cliffs; N. 036. Ibid., Pantano del Tranco; N. 0197.
2n = 60.

This is the twentieth report of the tetraploid number for this widespread species from various parts of its area in the temperate and southern regions of the northern hemisphere. It seems to be common in humid and calcareous soil in southern Spain.

ASPLENIACEAE

Asplenium adiantum-nigrum L.

Voucher: Provincia de Teruel: Sierra de Albarracín; N. 0507. 2n = 144.

This is an addition to a dozen reports from Britain, Central Europe, and India of the tetraploid number for this species in its strict sense.

Asplenium septentrionale (L.) Hoffm.

Voucher: Provincia de Teruel: Sierra de Albarracín, near Tragacete; N. 0404 and N. 0504. 2n = 144.

Fourteen previous reports of the tetraploid number for this species are here confirmed from two Spanish populations.

Asplenium melanocaulon Willd.

Voucher: Provincia de Jaén: Sierra de Cazorla, Laguna de Valdeazores, in a meadow close to the lake; N. 021. 2n. = 72.

It has long been known by ecologists that the species conventionally named A. trichomanes in flora manuals falls into two taxa, one of which is exclusively met with on calcareous soils, the other only on basic rocks. Already Willdenow (1809) was aware of that the collective species included two morphologically distinct taxa, but although he described the calciphilous one as the species A. melanocaulon, retaining the Linnaean name for the

basiphilous taxon, this was generally ignored. It was not until the discovery that the calciphilous plant is a diploid with 2n = 72 chromosomes, as contrasted to the calciphobous tetraploid with 2n = 144, that taxonomists again became aware of the morphological, geographical and ecological distinctions of these taxa.

In recent decades several attempts have been made to classify these taxa, but although the selection of categories in a biological system ought to have been simple when their distinct reproductive isolation is known, some timidity in biological logic has resulted in that they are accepted by some recently published manuals at the subspecific level only. This was proposed by MEY-ER (1961 who named them subsp. bivalens and subsp. quadrivalens respectively, thus indirectly but incorrectly indicating that their cytological characteristics were their most apparent attributes. This classification, with the required change of subsp. bivalens into subsp. trichomanes, is followed by Crabbe, Jermy & Lovis (in Tutin & al., 1964) in their treatment of the genus in Flora Europaea, despite of the fact that Lovis (1964) had correctly stated that the diploid plant, which reaches further north than the tetraploid taxon does (cf. Löve, 1970b), actually had been described from North America by WILLDENOW (1809) as the species A. melanocaulon, and that American and European material is identical. A species status for the two taxa had also been accepted by Fuchs (1963), who identified the tetraploid with A. trichomanes L. as emended by Hudson (1762), and named the diploid A. trichomaniforme, a preoccupied hybrid name replaced by Soó (in footnote to Fuchs, 1963) with the new name A. linnaei Soó. ROTHMALER (1963), apparently unaware of the new names just mentioned, called the diploid A. lovisii, without validating it with a description, and typified the Linnaean species with the tetraploid, as did Fuchs (1963), contrary to CRABBE, JERMY & LOVIS (in TUTIN & al., 1964).

Since the separation of the diploid as the species A. melanocaulon by WILLDENOW (1809) undoubtedly was correct, this automatically typifies the Linnaean species with the tetraploid. It is likely that both species occur in Spain, although our collection from the Sierra de Cazorla included only the diploid species, which is more northerly and more alpine than the tetraploid.

Ceterach officinarum DC.

Voucher: Provincia de Jaén: Sierra de Cazorla, Laguna de Valdeazores, in a meadow close to the lake; N. 022. 2n = 144.

This tetraploid submediterranean species reaches the Swedish island Gotland in the Baltic Sea (cf. Hylander, 1953), whereas in the eastern Mediterranean it is often replaced by the smaller and more thermophilous *C. javorkeanum* (Vida) Soó (cf. Vida, 1963; Sušnik & Lovka, 1970).

ATHYRIACEAE

Cystopteris fragilis (L.) Bernh.

Vouchers: Provincia de Jaén: Sierra de Cazorla, Laguna de Valdeazores;
N. 024. Provincia de Teruel: Sierra de Albarracín; N. 0521. 2n = 168.

Both our collections belong to the species in its strict sense, excluding the dodecaploid taxon *C. regia* (L.) Desv. which is identified with it by Crabbe (in Tutin & al., 1964). Both populations were found to be octoploid with 2n = 168 chromosomes, as previously reported by nineteen students of the genus in Eurasia and North America, from India in the south to Iceland in the north.

ASPIDIACEAE

Dryopteris filix-mas (L.) Schott.

Voucher: Provincia de Teruel: Sierra de Albarracín; Sierra Alta; N. 0506. 2n = 164.

Although other taxa of this complex may occur in Spain, whereas none was met with in the Cazorla Sierras (cf. Galiano & Heywood, 1960), our specimens belong to the typical species and are also characterized by the same chromosome number as previously reported from various European and North American regions.

POLYPODIACEAE

Polypodium australe Fée

Voucher: Provincia de Teruel: Sierra de Albarracín; N. 0520. 2n = 74.

This diploid mainly southern and western European species was the only taxon of the genus encountered by us in Spain, although both the tetraploid and hexaploid species also occur there, according to VALENTINE (in TUTIN & al., 1964). The chromosome number is a first report from this part of the distribution area of the taxon.

PINACEAE

Pinus halepensis L.

Voucher: Provincia de Jaén: Sierra de Cazorla, Nava de San Pedro; N. 0235.
2n = 24.

The chromosome number of this typically Mediterranean tree has been reported from cultivated material by Mehra & Khoshoo (1956), Saylor (1964), and Pederick (1967), who all counted 2n = 24 chromosomes. This is confirmed by this first study of a natural population.

CUPRESSACEAE

Juniperus communis L. subsp. hemispherica (J. & C. Presl) Nyman.

Vouchers: Provincia de Jaén: Sierra de Cazorla, Pico Cabañas; N. 0115. Provincia de Teruel: Sierra de Albarracín; N. 0539. 2n = 22.

This race of mountains in southern Europe has not been previously studied by cytologists. Its chromosome number is the same as reported by several authors for the subsp. *communis* and subsp. *alpina* (Neilr.) Celak. from other parts of Europe and North America.

Juniperus oxycedrus L. subsp. oxycedrus

Voucher: Provincia de Jaén: Sierra de Cazorla, Guadahornillos; N. 0302. 2n = 22.

This southern European species has been divided into three ecologically distinct races, the two widespread subsp. oxycedrus of dry hills and mountains and subsp. macrocarpa (Sibth. & Sm.) Ball of sands or rocky places near the sea, and the subsp. transtagana Franco of southwestern Portugal

(cf. Franco, in Tutin & al., 1964). No chromosome counts have previously been published for any of these races.

Sabina vulgaris Antoine var. humilis (Endl.) Antoine. Juniperus sabina L. var. humilis Endl.

Vouchers: Provincia de Jaén: Sierra de Cazorla, Pantano del Tranco; N. 0201.

Provincia de Teruel: Sierra de Albarracín; N. 0523. 2n = 22.

This alpine southern and central European and southwest Asiatic montane species is represented in our material by the variety *humilis*. The chromosome number 2n = 22 is a confirmation of previous counts from Germany by Seitz (1951) and Reese (1952), though the latter reported the inexact number 2n = 22 - 24.

BIBLIOGRAPHY

- BIR, S. S. (1960) Chromosome numbers of some Equisetum species from the Netherlands. Acta Bot. Neerland. 9: 224-234.
- BOLKHOVSKIKH, Z., GRIF, V., MATVEYEVA, T. & O. ZAKHARYEVA (1969) Chromosome numbers of flowering plants. Leningrad.
- Colmeiro, M. (1867) Enumeración de las criptógamas de España y Portugal 1. Madrid. Fuchs, H. P. (1963) Nomenklatorische Liste der in Ungarn vorkommenden Gefässkryptogamen. Acta Bot. Acad. Sci. Hung. 9: 11-20.
- Galiano, E. F. & V. H. Heywood (1960) Catálogo de plantas de la provincia de Jaén (Mitad oriental). Jaén.
- Guignard, L. (1882) Recherches sur le développement de l'antère et du pollen des Orchidées. Ann. Sci. Nat. Bot. (Paris), sér. 6, 13: 136-199.
- Halle, T. G. (1913) Some remarks on the classification of fossil plants. Geol. Fören. Förhandl. 35: 367-382.
- HUDSON, W. (1762) Flora anglica. London.
- Hultén, E. (1967) Comments on the flora of Alaska and Yukon. Arkiv Bot. (Stockholm) 2, 7: 1-147.
- (1968) Flora of Alaska and neighboring territories. Stanford.
- Hylander, N. (1953) Nordisk kärlväxtflora 1. Stockholm.
- KJELLQVIST, E. & A. LÖVE (1963) Chromosome numbers of some Carex species from Spain. Bot. Not. (Lund) 116: 241-248.
- LANGLET, O. (1971) Two hundred years genecology. Taxon 20: 653-722.
- Löve, A. (1964) The biological species concept and its evolutionary structure. Taxon 13: 33-45.
- (1970a) Emendations in the Icelandic flora. Taxon 19: 298-302.
- (1970b) İslenzk ferdaflóra. Reykjavík.

- Löve, A. & E. Kjellovist (1964) Chromosome numbers of some Iberian Cistaceae.

 Portugal. Acta Biol. (ser. A) 8: 69-80.
- Löve, A. & D. Löve (1942) Chromosome numbers of Scandinavian plant species. Bot. Not. (Lund) 1942: 19-59.
- ———— & D. Löve (1961) Chromosome numbers of Northwest and Central European plant species. Op. Bot. (Lund) 5: 1-581.
- & D. Löve (1969) Remarks on the cytotaxonomy of Mediterranean plants. V Simp. Fl. Eur. (Sevilla): 285-291.
- Lovis, J. D. (1964) The taxonomy of Asplenium trichomanes in Europe. Brit. Fern Gaz. 9: 147-160.
- Manton, I. (1950) Problems of cytology and evolution in the Pteridophyta. Cambridge.
- MAYR, E. (1942) Systematics and the origin of species. New York.
- ——— (1963) Animal species and evolution. Cambridge, Mass.
- MEHRA, P. N. & S. S. BIR (1959) A note on chromosome numbers in some Indian species of Equisetum. Amer. Fern. Journ. 49: 86-92.
- Менка, Р. N. & T. N. Кноsноо (1956) Cytology of conifers. I. Journ. of Genet. 54: 165-180.
- MEYER, D. E. (1961) Zur Zytologie der Asplenien Mitteleuropas. (XXIX. Abschluss). Ber. Deutsch. Bot. Ges. 74: 449-461.
- Molesworth Allen, B. (1968) Pteridium aquilinum on limestone. Brit. Fern Gaz. 10: 34-36.
- NINAN, C. A. (1958) Studies on the cytology and phylogeny of the Pteridophytes. VI. Observations on the Ophioglossaceae. Cytologia 23: 291-315.
- Pederick, L. A. (1967) The structure and identification of the chromosomes of *Pinus* radiata D. Don. Sil. Genet. 16: 69-77.
- PINTO DA SILVA, A. R. (1970) A flora e a vegetação das áreas ultrabásicas do nordeste transmontano. Subsídios para o seu estudo. Agron. Lusit. 30: 175-361.
- Reese, G. (1952) Ergänzende Mitteilungen über die Chromosomenzahlen mitteleuropäischer Gefässpflanzen. I. Ber. Deutsch. Bot. Ges. 64: 241-256.
- ROHLENA, J. (1941-42) Conspectus florae Montenegrinae. Preslia 20-21: 506 p.p.
- ROTHMALER, W. (1944) Systematische Einheiten in der Botanik. Feddes Repert. 54: 1-22.
- ———— (1963) Exkursionsflora von Deutschland. Kritischer Ergänzungsband Gefässpflanzen. Berlin.
- SAYLOR, L. C. (1964) Karyotype analysis of Pinus group Lariciones. Sil. Genet. 13: 165-169.
- Seitz, F. W. (1951) Chromosomenzahlenverhältnisse bei Holzpflanzen. Zeitschr. Forstgenet. Forstpflanzenzücht 1: 22-32.
- Steenis, C. G.G. J. van (1957) Specific and infraspecific delimitation. Fl. Males. Bull., Ser. I 5, 3: CLXVII-CCXXXIV.
- Strasburger, E. (1882) Über den Teilungsvorgang der Zellkernen und das Verhältnis der Kernteilung und Zellteilung. Arch. mikrosk. Anat. 21: 476-590.
- Sušnik, F. & M. Lovka (1970) Citološke in horološke razikave rodu Ceterach Gars. v Sloveniji. Biol. Vestn. (Ljubljana) 18: 19-25.

- Tutin, T. G. et al. (eds.) (1964) Flora Europaea, 1: Lycopodiaceae to Platanaceae. Cambridge.
- VERMA, S. C. (1956) Cytology of Ophioglossum. Curr. Sci. 25: 398-399.
- ———— (1957) Cytology of Ophioglossum coriaceum A. Cunn. Cytologia 22: 393-403.
- ——— (1958) Cytology of Ophioglossum vulgatum. Acta Bot. Neerland. 7: 629-634.
- VIDA, G. (1963) A new Asplenium (sectio Ceterach) species and the problem of the origin of Phyllitis hybrida (Milde) C. Christ. Acta Bot. Acad. Sci. Hung. 9: 197-215. Vukicevic, E. (1970) Pteridophyta. Flora S. R. Srbije 1: 59-121.
- WILLDENOW, K. L. (1809) Enumeratio plantarum horti regii botanici Berolinensis. Berolini.