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Cytological variation within the family of *Lemnaceae*

by

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Contents

1. Introduction

The duckweed family represents a group of world-wide distribution; this biological success is undoubtedly influenced by the predominant or exclusive vegetative propagation of the *Lemnaceae*, a spontaneous fragmentation of the clones forming part of their genetical make-up. The populations of duckweeds frequently have an enormous biomass, but their genetical variation is rather limited, a given genotype being expressed by countless, physiologically independent phenotype modules. The particular behaviour of the *Lemnaceae* makes them an interesting object for studies on variation, for the vegetative propagation may stabilize any random alteration appearing within clones.
As far as the cytological investigations are concerned, the duckweeds represent a very difficult material, the chromosomes of numerous taxa being exceedingly small and often tending to stick together in metaphase plates. In spite of these difficulties, cytological variation within the *Lemnaceae*

offers a challenging problem as changes in chromosome numbers, their possible transmission to next cell generations as well as bearing upon the population structure and the whole differentiation pattern call for a special attention.

The present paper deals with 30 taxa out of the 35 that form the duckweed family, all the four genera viz. *Spirodela* Schleiden, *Lemna* L., *Wolffiella* Hegelm. and *Wolffia* Horkel being represented. On the whole, material from 1500 localities was studied; this number is obviously not related to the actually examinated units and/or fronds. The study was carried out during fifteen years (1966-1980).

Acknowledgements

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Generous help of very numerous contributors who collected samples for our collection was acknowledged in the foreword of this volume; the author wishes to express here her cordial thanks to Ms. Ruth Mason, Canterbury, New Zealand, who arranged a most interesting field trip during our visit to New Zealand in 1979.
Last, but not least, very special thanks are addressed to our colleague and friend Prof. Dr. E. Landolt, who stimulated us to undertake this study, precisely determined the whole studied material, translated the Summary into German, provided a cheerful assistance in numerous field trips and, on many occasions, offered not only useful information but also constructive critism.

2. Material and methods

The material from the present study was taken for the most part from sterile clonal cultures kept at the Geobotanical Institute, Swiss Federal Institute of Technology (SFIT), in Zürich. Some of those clones were repeatedly examined at a certain time interval; in addition, cultures independently obtained from various laboratories in the world but representing various parts of the same original clone, were sometimes studied. Only about 20% of the material comprised population samples from Europe, North America and New Zealand; 10-15 units were then taken at random in various parts of a given population.

The material was fixed in acetic alcohol (1:3) with a small addition of ferric acetate and stored at about -20°C. As the staining solution, lacto-propionic orcein diluted 1:1 with distilled water from the original stock prepared according to DYER (1963) was used. Whenever possible, young parts of the fronds were separated from old tissues for the squashes. Only mitotic chromosomes were studied. Drawings were made with a Leitz camera lucida using a supplementary magnifying tubus. The magnification of the drawings is about 4000X. The material proved unsuitable for microphotography, too many chromosomes staying out of the focus at a given time.

3. Results

The presentation of the results follows the sequence of taxa corresponding to the structure of the family of *Lemnaceae*, the current nomenclature proposals of LANDOLT (1980, 1980a, see the preceeding papers in this volume) being applied.

Prior to describing our results in detail, we should like to precise the meaning of the terms used in the present paper when cytological variation is being commented upon.

a) the term "intra-individual variation" refers obviously to variation observed within a single frond or clone. It should be noted that cultures issued from the same original clone and kept in various laboratories were sometimes independently obtained from several sources or studied repeatedly at some time interval; be as it may, the term is applied to cases when the genetic value of the material as an individual was definite.

b) the term "intra-populational variation" was used in cases when numerous units sampled in the wild within a given population represented differences as to their respective chromosome numbers, but most frequently were cytologically uniform. The term is arbitrarily chosen and may not correspond to actual differences between individuals in the genetic sense, distinction between genets and ramets being practically impossible in the duckweeds.

c) the term "cytological differentiation" or "racial variation" used as well in the author's previous paper on the *Lemna* L. (URBANSKA-WORYTKIEWICZ 1975)

applies to cases when clones and/or population samples from given localities were cytologically uniform but differed from each other as to the level of polyploidy or aneuploid vs. euploid rank.

3.1. *Spirodela* Schleiden

The genus *Spirodela* comprises *S. intermedia*, *S. biperforata*, *S. polyrrhiza*, and *S. punctata*; all these taxa were studied in the course of the present work. The chromosomes of *Spirodela* are the smallest of the family and certainly belong to the smallest in the plant world (0.1μ - 0.5μ); for this reason, we do not offer any remarks concerning their morphology. Save for *S. punctata*, chromosomes in *Spirodela* do not show pronounced size differences.

Three levels of cytological variation observed in *Spirodela* correspond to a) intra-individual variation, b) variation within populations and c) cytological differentiation indicated by samples of various origin that were cytologically uniform yet represented different cytotypes. It should be noted, however, that cytologically heterogenous samples were rare representing only 4.7% of the studied material of *Spirodela* (Tables 1, 2).

On the whole, intra-individual variation within *Spirodela* was represented by rare cases of both aneusomaty and mixoploidy. However, only aneuploid individuals occurring side by side with euploid ones were observed within the mixed populations. Chromosome numbers found within *Spirodela* form a series consisting of 2n=20, 30, 40, 50, the pentaploids representing the highest

Table 1. Cytological variation within the genus *Spirodela*

Taxon	Intra-individual variation		Variation within populations		Racial variation		N of the studied samples
	Aneu-somaty	Mixo-ploidy	Aneu-ploidy	Poly-ploidy	Aneu-ploidy	Poly-ploidy	
S. intermedia	-	-	-	-	-	+	16
S. biperforata	+	-	-	-	-	+	7
S. polyrrhiza	+	+	+	-	-	+	187
S. punctata	+	-	+	-	+	+	83

level of polyploidy so far observed. The euploid differentiation seems to follow a certain trend related to particular taxa (Table 3). It is possible, however, that more extensive studied might reveal quite comparable patterns in all four species.

Table 2. Cytologically uniform and heterogenous samples found in the studied material of the genus *Spirodela*

Taxon	Uniform samples	Heterogenous samples			Total
		Aneusomaty	Mixoploidy	Mixed populations	
S. intermedia	16	-	-	-	16
S. biperforata	6	1	-	-	7
S. polyrrhiza	183	1	2	1	187
S. punctata	81	2	-	-	83

Table 3. Chromosome numbers found in cytologically uniform samples of the genus *Spirodela*

Taxon	Number of samples							Total
	2n=20	2n=30	2n=40	2n=50	2n=60	2n=70	2n=80	
S. intermedia	2	14	-	-	-	-	-	16
S. biperforata	1	5	-	-	-	-	-	6
S. polyrrhiza	-	11	171	1	-	-	-	183
S. punctata	-	-	58*	22	-	-	-	81

* + a single aneuploid sample with 2n=43-44

3.1.1. *Spirodela intermedia* W. Koch

2n=20, 30 (Figs 1-2)

Out of the 16 studied clones, two were diploid with 2n=20, the remainder being 30chromosomic. Except for the euploid differentiation, no cytological variation was observed. The chromosome numbers of *S. intermedia* are published

Figs 1-2. *Spirodela intermedia*; somatic metaphases. Collection numbers are given in parentheses. 1. 2n=20; South America, Peru (7747). 2. 2n=30; South America, Argentina (7201).

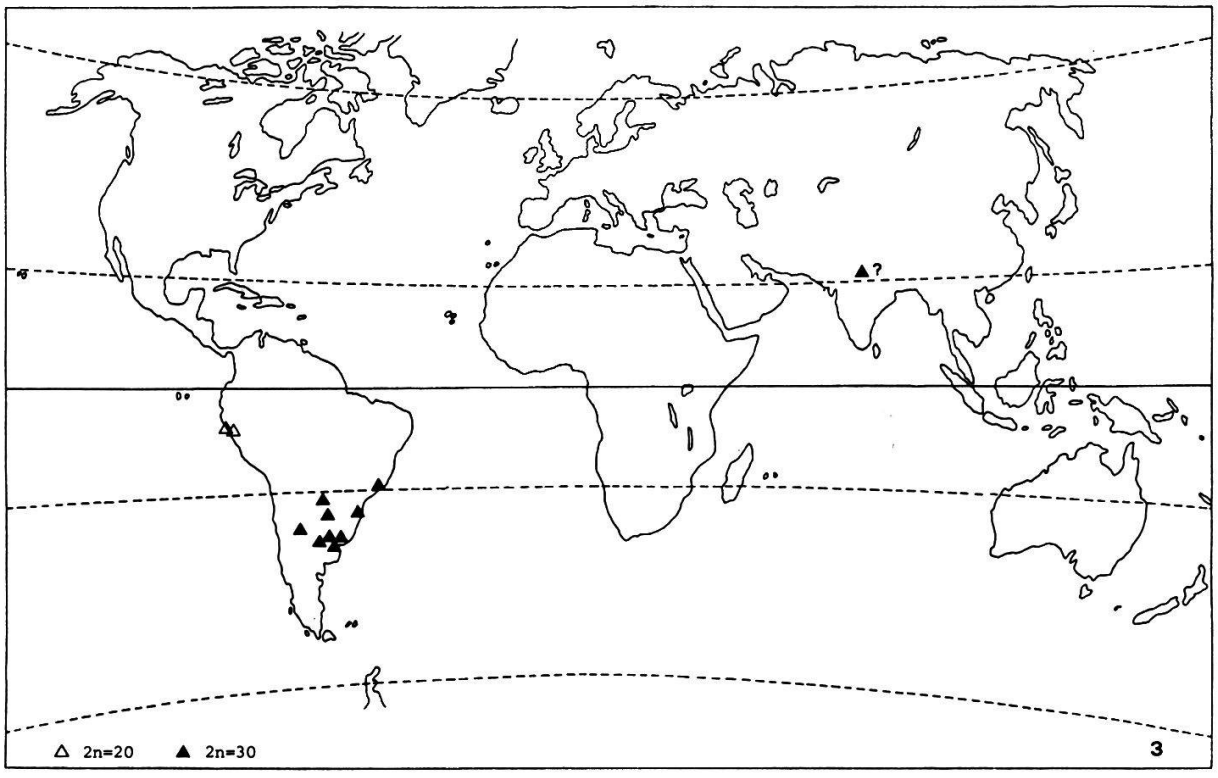


Fig. 3. *Spirodela intermedia*. Geographical distribution of the studied material. Some stations in South America are not indicated.

here for the first time; it is interesting to note that they correspond to the lowest level of polyploidy within the family of the *Lemnaceae*.

3.1.2. *Spirodela biperforata* W. Koch

2n=20, 30 (Figs 5-6)

Only 7 clones were studied; one of them proved to be 20chromosomic, whereas the others invariably had 2n=30. In a single 30chromosomic clone several aneusomic cells (2n=32) were observed. *S. biperforata* has not been hitherto studied cytologically.

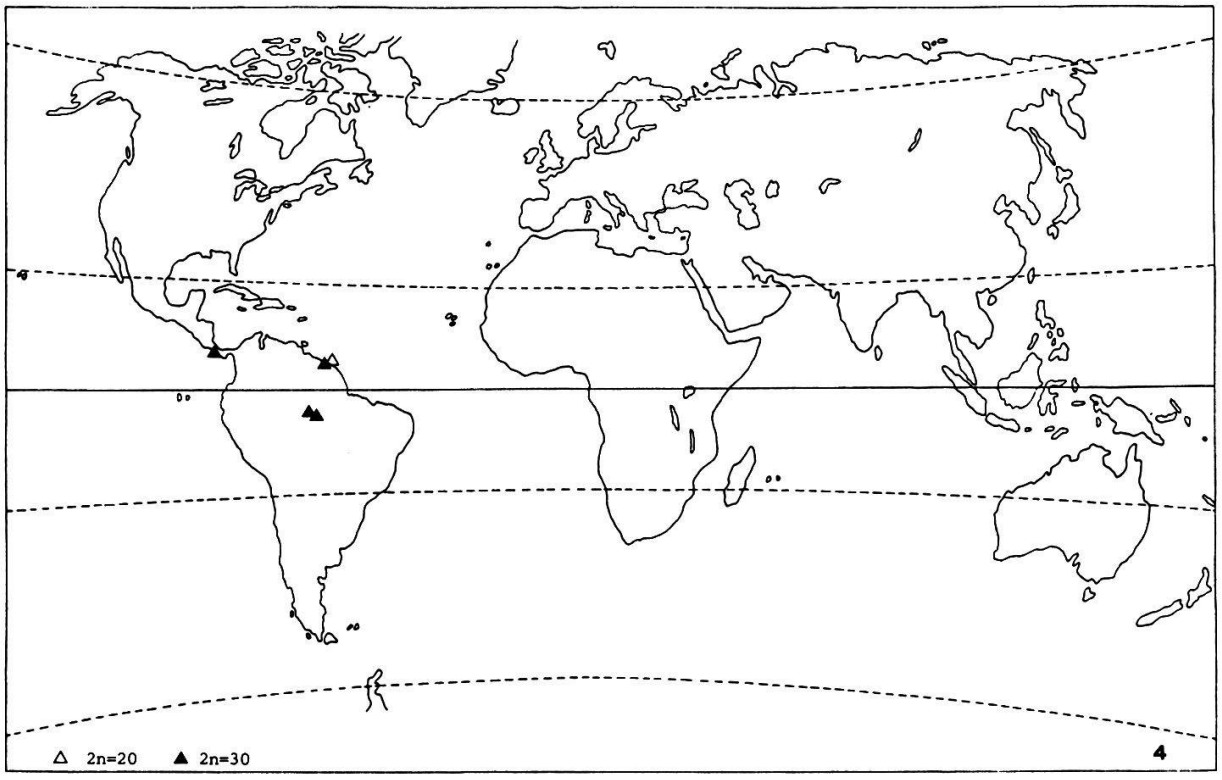
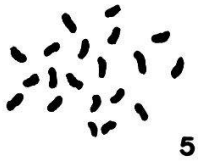


Fig. 4. *Spirodela biperforata*. Geographical distribution of the studied material. Two 30 chromosomic stations in South America are not indicated.



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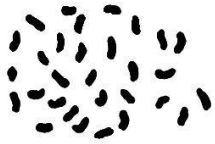

6

Figs 5-6. *Spirodela biperforata*: somatic metaphases. Collection numbers are given in parantheses. 5. 2n=20; South America, Surinam (8528). 6. 2n=30; Central America, Panama (8410).

3.1.3. *Spirodela polyrrhiza* (L.) Schleid.

2n=30, 40, 50 (Figs 7-9)

Spirodela polyrrhiza was well represented in the studied material of the genus; on the whole, 187 samples originating from various parts of the large distribution area of this taxon were examined. Population samples, however, represented only a minor part of the investigated material (49).

Intra-individual variation was observed only three times. One clonal sample proved to be aneusomatic, hypotetraploid cells with 2n=34 being occasionally found among tetraploid ones; another clone was mixoploid with the respective chromosome numbers 2n=40 and 2n=80. The third case corresponded in fact both to mixoploidy and aneusomaty, three cells with 2n=62 being observed in otherwise pentaploid (2n=50) clone. Intra-populational variation was found only once in a sample from North America consisting of tetraploid and hypotetraploid units (2n=40, 38).

Cytological differentiation occurring within *Spirodela polyrrhiza* comprised three euploid cytotype viz. triploids, tetraploid and pentaploids. 175 samples were 40chromosomic, whereas the triploid chromosome number 2n=30 was found in the material from eleven localities. In a single sample, 2n=50 was revealed as a prevailing chromosome number.

The tetraploid chromosome number 2n=40 was reportes in *Spirodela polyrrhiza* for the first time by BLACKBURN (1933) and later confirmed by other authors

Figs 7-9. *Spirodela polurrhiza:* somatic metaphases. Collection numbers are given in parentheses. 7. 2n=30; North America, Mexico (7652). 8. 2n=40; Europe, Italy (7621). 9. 2n=50; Central America, Puerto Rico (7110).

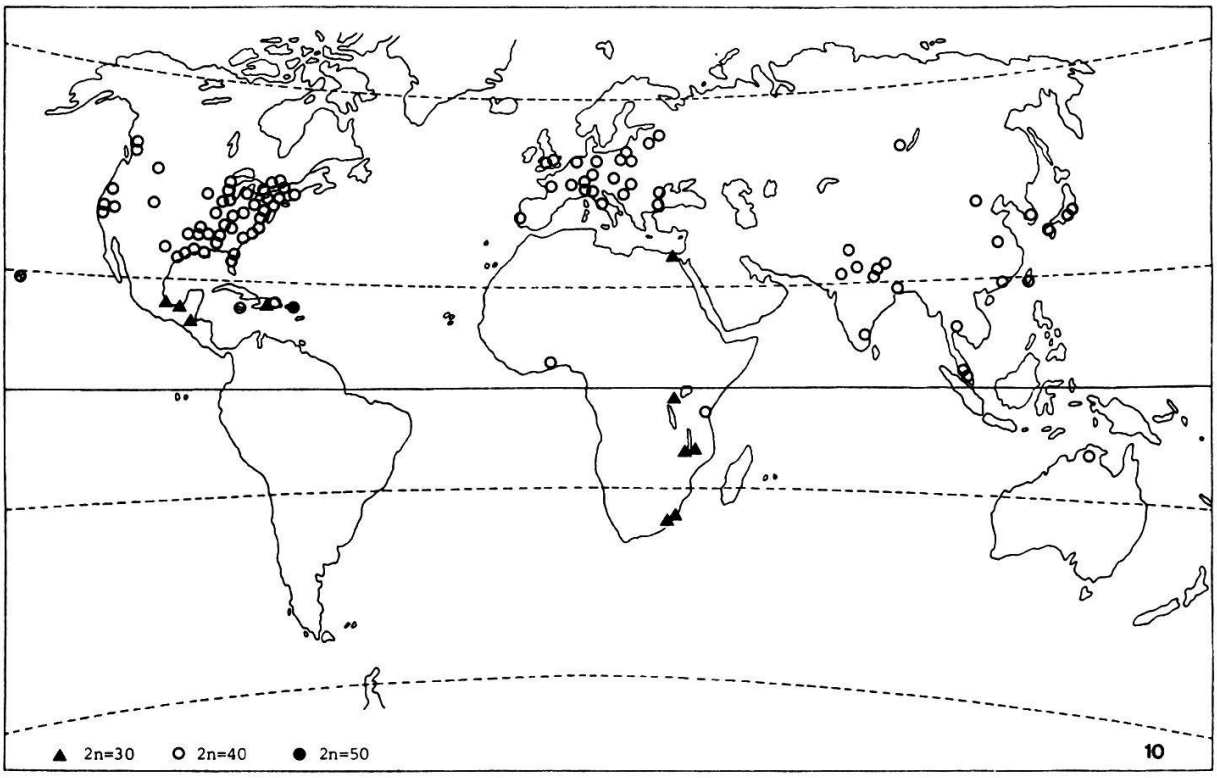

Fig. 10. *Spirodela polyrrhiza*: geographical distribution of the studied material. Numerous tetraploid stations are not included.

(TISCHLER 1935, ROHWEDER 1937, EHRENBERG 1945, WCISLO 1970). The present study corroborates these data and points out that 2n=40 is indeed prevailing within *S. polyrrhiza*. On the other hand, 2n=30 and 2n=50 as well as various forms of cytological variation are reported here for the first time.

3.1.4. *Spirodela punctata* (G.F.W. Meyer) Thompson

2n=40, 43-44, 50 (Figs 11-12)

Spirodela punctata was studied from 83 localities, population samples representing only 8.4% of the material.

Intra-individual variation was exceedingly rare; both observed cases represented aneusomaty, hypertetraploid cells occurring among the tetraploid ones. No intra-populational variation was found.

Cytological differentiation occurring within *Spirodela punctata* comprised most frequently two levels of polyploidy (2n=40, 50). Tetraploid samples prevailed in the studied material (59), whereas the pentaploid chromosome number 2n=50 was observed in the material from 22 localities. In addition to the euploid samples, a single aneuploid clone with hypertetraploid number (2n=43-44) was found.

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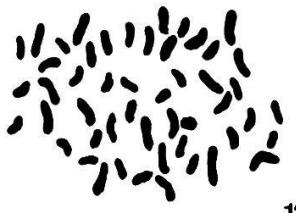

12

Figs 11-12. *Spirodela punctata*: somatic metaphases. Collection numbers are given in parentheses. 11. 2n=40; North America, Louisiana (8028). 12. 2n=50; Australia, Victoria (7479).

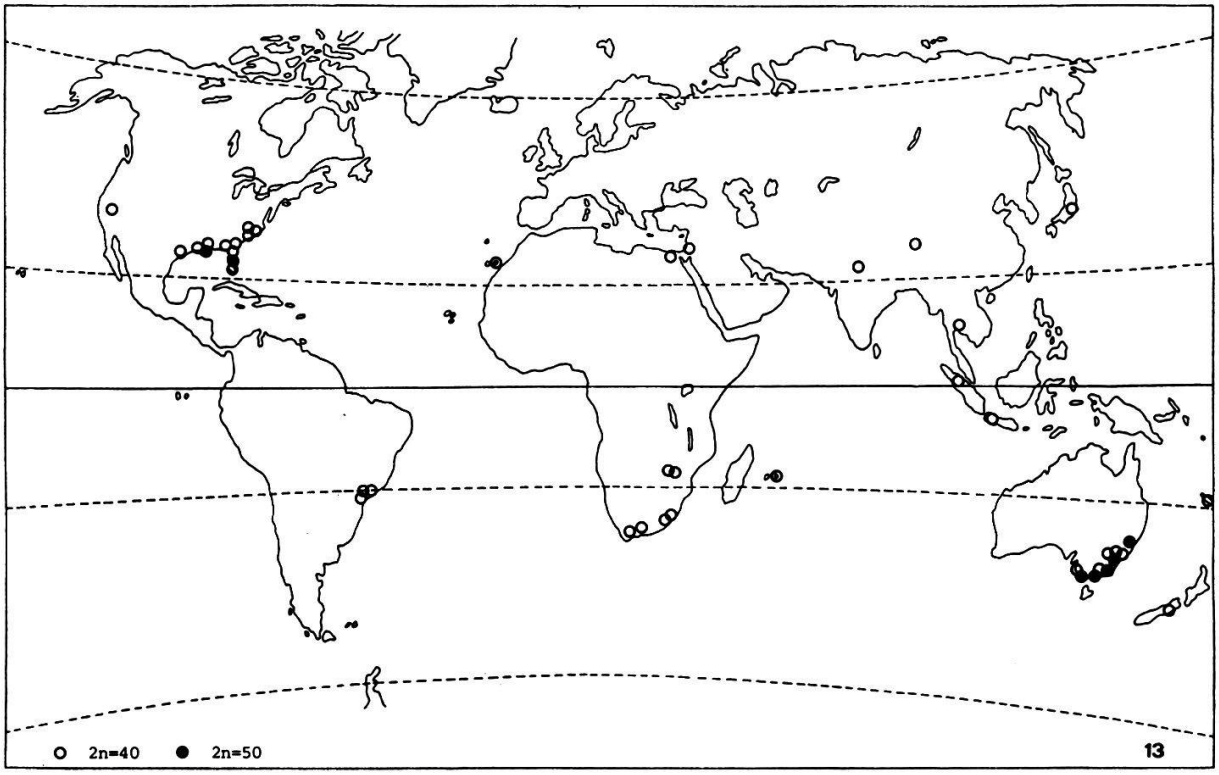

Fig. 13. *Spirodela punctata*: geographical distribution of the studied material. Numerous tetraploid stations as well as some pentaploid stations from Australia are not included.

3.2. *Lemna* L.

Out of thirteen taxa the genus *Lemna* consists of, eleven were studied in the course of the present work. Chromosomes in *Lemna* were most frequently longer and thicker than those occurring in most taxa of *Spirodela*, an average length being about 1.2μ. They were often metacentric; however, the centromere region was not always clearly defined and it seems that several heterochromatic segments might occur. Detailed studies on chromosome morphology in the genus *Lemna* should require a more precise analysis and perhaps different staining methods than those used in the present study.

Interspecific differences in chromosome length were not distinct, save for *Lemna gibba* that usually had longer and thicker chromosomes than other taxa

of the genus. In this respect, the present observations corroborate the previous reports of BLACKBURN (1933) and WCISLO (1970). Infraspecific variation in chromosome length was rather continuous; more pronounced differences were sometimes observed in *L. trisulca* (Fig. 15) as well as in some samples of *L. minor* (Figs 48-49).

Some part of our results concerning the genus *Lemna* was previously published (URBANSKA-WORYTKIEWICZ 1975). At that time, Dr. E. Landolt who determined the material, assigned it provisionally to five species groups viz. *L. trisulca* s.l., *L. perpusilla* s.l., *L. gibba* s.l., *L. minor* s.l. and *L. valdiviana* s.l. Landolt's taxonomical treatment of the family *Lemnaceae* has presently been concluded and the nomenclature revised (LANDOLT 1980, 1980a, see p. 17-19 of the present volume*); the re-examined material has been partly given an independent taxonomical rank and some samples were assigned to different taxa than in 1975. To avoid the inevitable confusion, we were obliged to re-assess our previous data; together with more recent results, they were thus included into the present paper which should accordingly be considered as the valid one as far as our report on cytological variation occurring within precisely determined taxa of the *Lemnaceae* is concerned.

Variation in chromosome number occurring in *Lemna* L. follows general patterns comparable to those described in *Spirodela*, an intra-individual variation, variation within populations as well as racial variation being found (Tables 4-6). It should be stressed, however, that all studied taxa of the genus *Lemna* were most frequently represented by a 40chromosomic cytotype, whereas in the examinated taxa of *Spirodela* various frequencies of 2n=30, 2n=40 and 2n=50 were observed. Heterogenous samples in *Lemna* represented exactly the same minor part of the studied material as in *Spirodela* viz. 4.7%, in spite of the fact that nearly three times as many samples were examined (888 vs. 292 in *Spirodela*). On the other hand, a racial variation within *Lemna* was more pronounced than that in *Spirodela*, a complete euploid series: 2n=20, 30, 40, 50, 60, 70, 80 being accompanied by the aneuploid differentiation on tetraploid level (Table 4).

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* a monography of the duckweed family is now being prepared and shall appear in the next volume of this review (i.e. Veröff. Geobot. Inst. ETH, Stiftung Rübel *71*).

Table 4. Cytological variation within the genus *Lemna* L.

Taxon	Intra-individual variation		Variation within population		Racial variation		N of the studied samples
	Aneu-somaty	Mixo-ploidy	Aneu-ploidy	Poly-ploidy	Aneu-ploidy	Poly-ploidy	
L. trisulca	+	-	-	-	-	+	65
L. perpusilla	-	-	-	-	-	-	9
L. aequinoctialis	+	+	-	-	-	+	174
L. turionifera	-	+	+	-	-	+	57
L. gibba	+	-	+	+	-	+	113
L. disperma	-	-	-	-	-	-	17
L. obscura	+	-	+	+	-	+	33
L. japonica	-	-	-	-	-	+	6
L. minor	+	+	+	-	+	+	305
L. minuscula	+	-	+	-	+	-	45
L. valdiviana	+	+	-	-	-	-	65

Table 5. Cytologically uniform and heterogenous samples found within the studied material of genus *Lemna*

Taxon	Uniform samples	Heterogenous samples			Total
		Aneusomaty	Mixoploidy	Mixed populations	
L. trisulca	64	1	-	-	65
L. perpusilla	9	-	-	-	9
L. aequinoctialis	165	5	4	-	174
L. turionifera	52	-	2	3	57
L. gibba	108	1	-	4	113
L. disperma	17	-	-	-	17
L. obscura	30	1	-	2	33
L. japonica	6	-	-	-	6
L. minor	291	8	2	4	305
L. minuscula	40	2	-	3	45
L. valdiviana	64	-	1	-	65

Table 6. Chromosome numbers found in cytologically uniform samples of the genus *Lemna*

Taxon	Number of samples									To-
	2n=20	2n=30	2n=36	2n=40	2n=42	2n=50	2n=60	2n=70	2n=80	tal
L. trisulca	1	-	-	52	-	-	6	-	5	64
L. perpusilla	-	-	-	9	-	-	-	-	-	9
L. aequinoctialis	1	-	-	149	-	7	4	-	4	165
L. turionifera	-	-	-	41	9	1	-	-	1	52
L. gibba	-	-	-	91	-	11	-	2	4	108
L. disperma	-	-	-	17	-	-	-	-	-	17
L. obscura	-	-	-	29	-	1	-	-	-	30
L. japonica	-	-	-	5	-	1	-	-	-	6
L. minor	1	3	-	258	24	5	-	-	-	291
L. minuscula	-	-	3	37	-	-	-	-	-	40
L. valdiviana	-	-	-	64	-	-	-	-	-	64

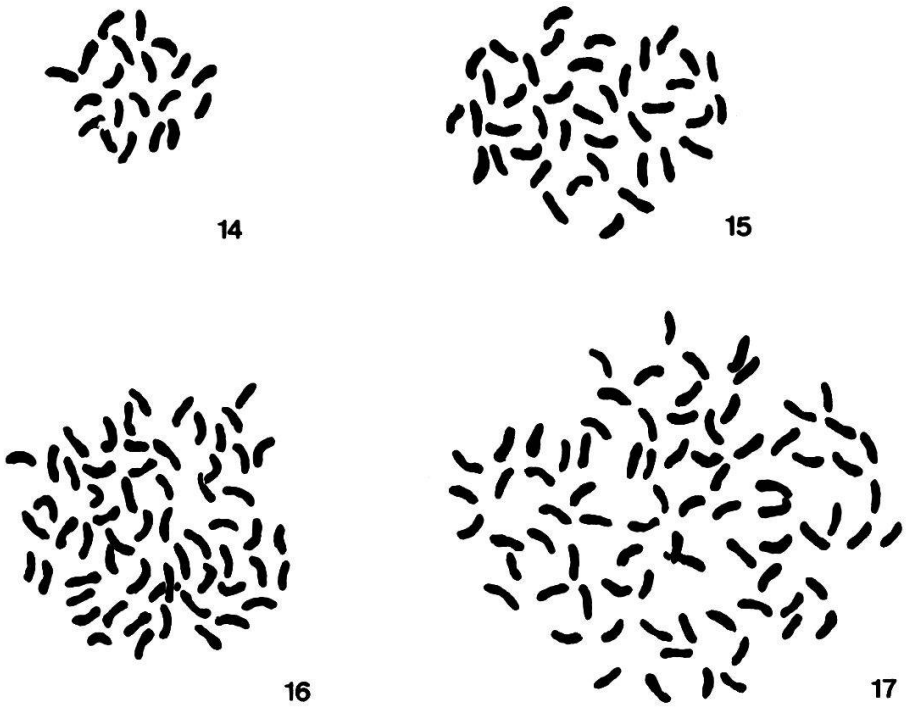
3.2.1. *Lemna trisulca* L.

2n=20, 40, 60, 80 (Figs 14-17)

64 samples of *Lemna trisulca* originating from various parts of the large distribution area of this taxon were mostly represented by clonal cultures, only 9 population samples being studied.
No intra-individual variation except for a single case of aneusomaty (2n=40, 42) was observed. Mixed populations were not found.

The studied material of *L. trisulca* was mostly represented by tetraploid samples. In addition, a single diploid clone as well as some high polyploid samples (2n=60, 2n=80) were found.
L. trisulca was studied cytologically for the first time by BLACKBURN (1933) who found a hypertetraploid chromosome number 2n=44. The same number was given a few years later by TISCHLER (1936) and ROHWEDER (1937). More recently, WCISLO (1970) reported an approximate chromosome number in *L. trisulca* 2n≈40.

The previous data correspond to some extent to the present results, for our European material of *L. trisulca* was invariably tetraploid; it is possible that the hypertetraploid number 2n=44 might indicate an aneuploid differentiation occasionally appearing within *L. trisulca*. On the other hand, euploid chromosome numbers representing diploid, hexaploid and octoploid level were observed in *L. trisulca* so far only by the present author (see also URBANSKA-WORYTKIEWICZ 1975).



Figs 14-17. *Lemna trisulca*: somatic metaphases.Collection numbers are given in parentheses. 14. 2n=20; Australia, Victoria (7258). 15. 2n=40; Europe, Switzerland (6624). 16. 2n=60; North America, Pennsylvania (7928). 17. 2n=80; Canada, Ontario (7583).

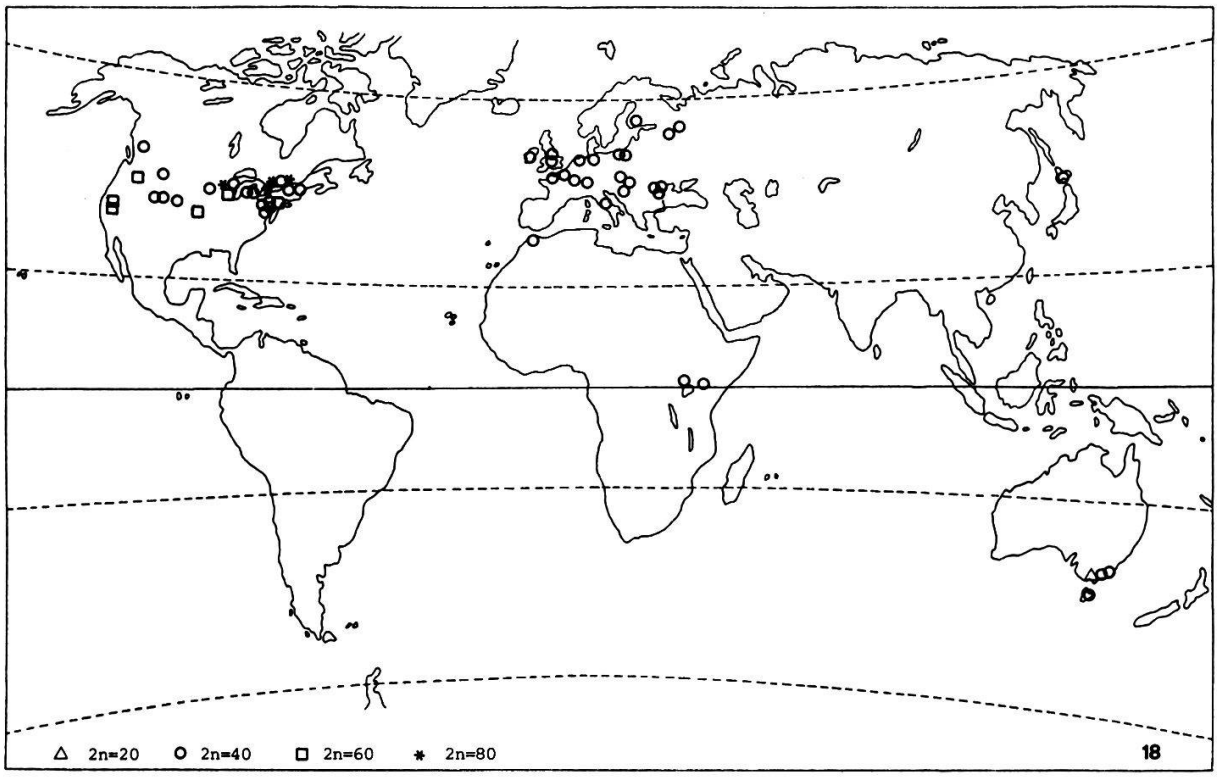


Fig. 18. *Lemna trisulca*. Geographic distribution of the studied material. Some tetraploid stations are not included.

3.2.2. *Lemna perpusilla* Torrey

2n=40 (Fig. 19)

Only 9 samples of *L. perpusilla*, all representing wild populations, were investigated. They proved to be invariably tetraploid; no cytological variation was found.

In the previous publication by the author (URBANSKA-WORYTKIEWICZ 1975), various chromosome numbers are given for *L. perpusilla*. Most of the samples being now assigned to the closely related *L. aequinoctialis* (LANDOLT 1980; see also LANDOLT and URBANSKA-WORYTKIEWICZ 1980), the chromosome numbers of *L. perpusilla* other than 2n=40 have to be annulled.

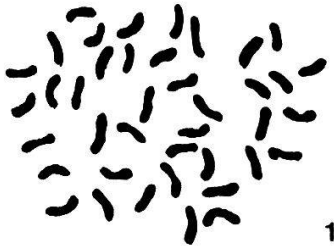


Fig. 19. *Lemna perpusilla*: somatic metaphase. Collection number is given in parentheses. 2n=40; North America, North Carolina (8507).

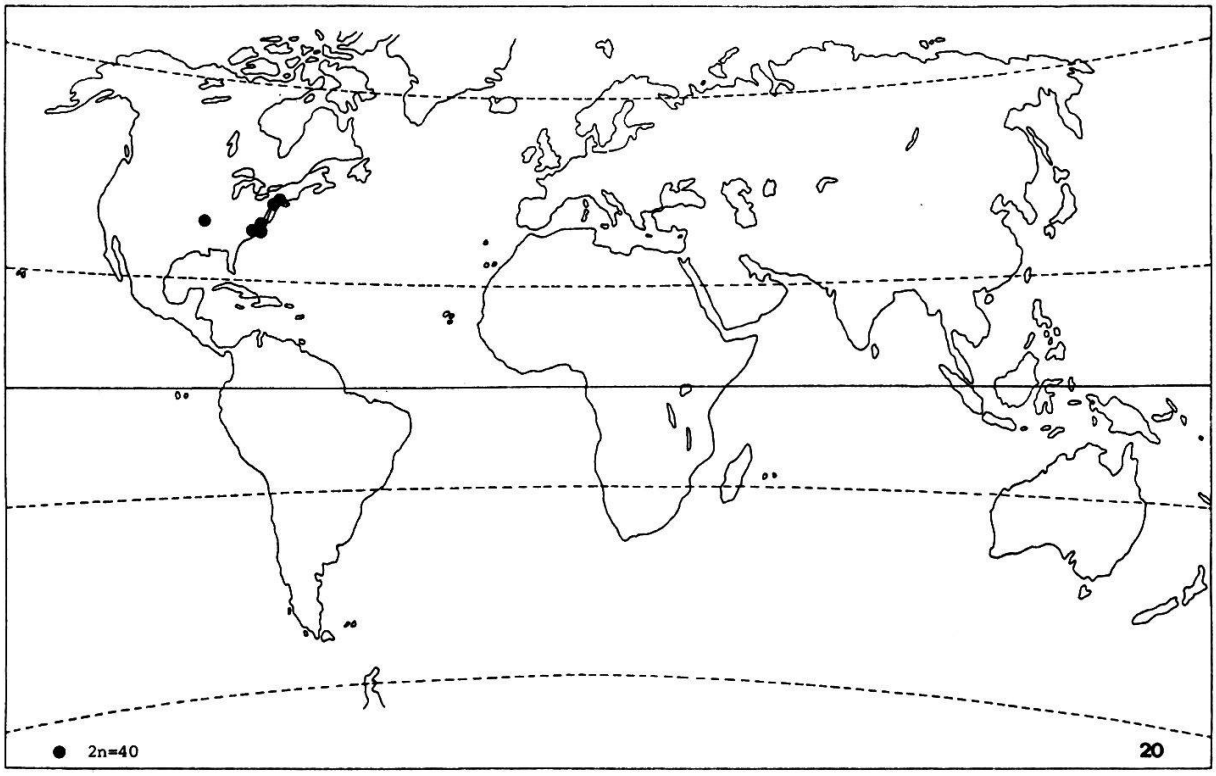


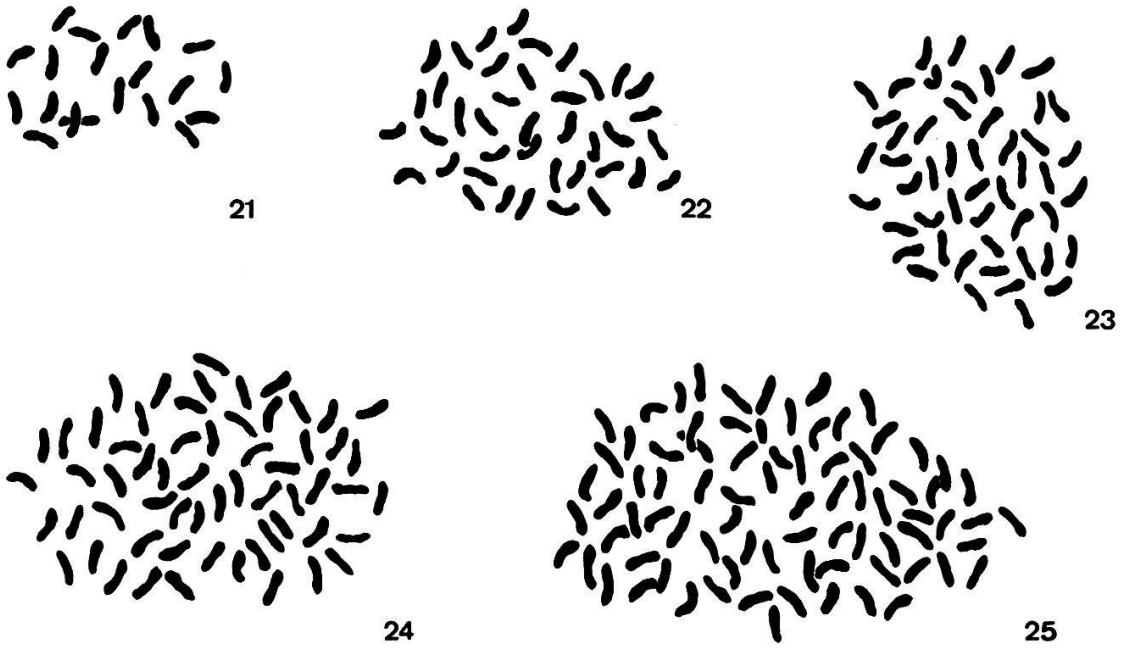
Fig. 20. *Lemna perpusilla*. Geographic distribution of the studied material. Some stations are not indicated.

3.2.3. *Lemna aequinoctialis* Welwitsch

2n=20, 40, 50, 60, 80 (Figs 21-25)

L. aequinoctialis was studied from 174 localities distributed all over the world. Most of this material represented clonal cultures, population samples being taken only in 49 habitats.

Intra-individual variation occurring within *L. aequinoctialis* comprised both aneusomaty as well as mixoploidy. Aneusomaty was observed in five samples; it appeared on tetra- and hexaploid levels, hyperploid cells being most frequent. Mixoploidy was rare; it deserves, however, a special mention, for the differences between cells of given individual apparently did not result from a doubling or a reduction by half of the prevailing chromosome number. In three



Figs 21-25. *Lemna aequinoctialis*: somatic metaphases. Collection numbers are given in parentheses. 21. 2n=20; Africa, Malawi (7382). 22. 2n=40; North America, Louisiana (8038). 23. 2n=50; Asia, Hongkong (7204). 24. 2n=60; North America, Texas (8079). 25. 2n=80; North America, California (6746).

samples, 40chromosomic cells represented the majority, but some pentaploid or nearly pentaploid ones occurred as well. A further interesting case of mixoploidy was found in an otherwise 50chromosomic sample where some cells comprised approximately 80 chromosomes. No intra-populational variation was observed.

Polyploid differentiation occurring within *Lemna aequinoctialis* was rather pronounced as far as particular cytotypes are concerned, five levels of polyploidy being found; it should be stressed, however, that the tetraploid samples were by and large the most frequent (158). A single sample was diploid, whereas higher levels of polyploidy were represented by pentaploids (7 samples), hexaploids (4 samples) and octoploids (4 samples).

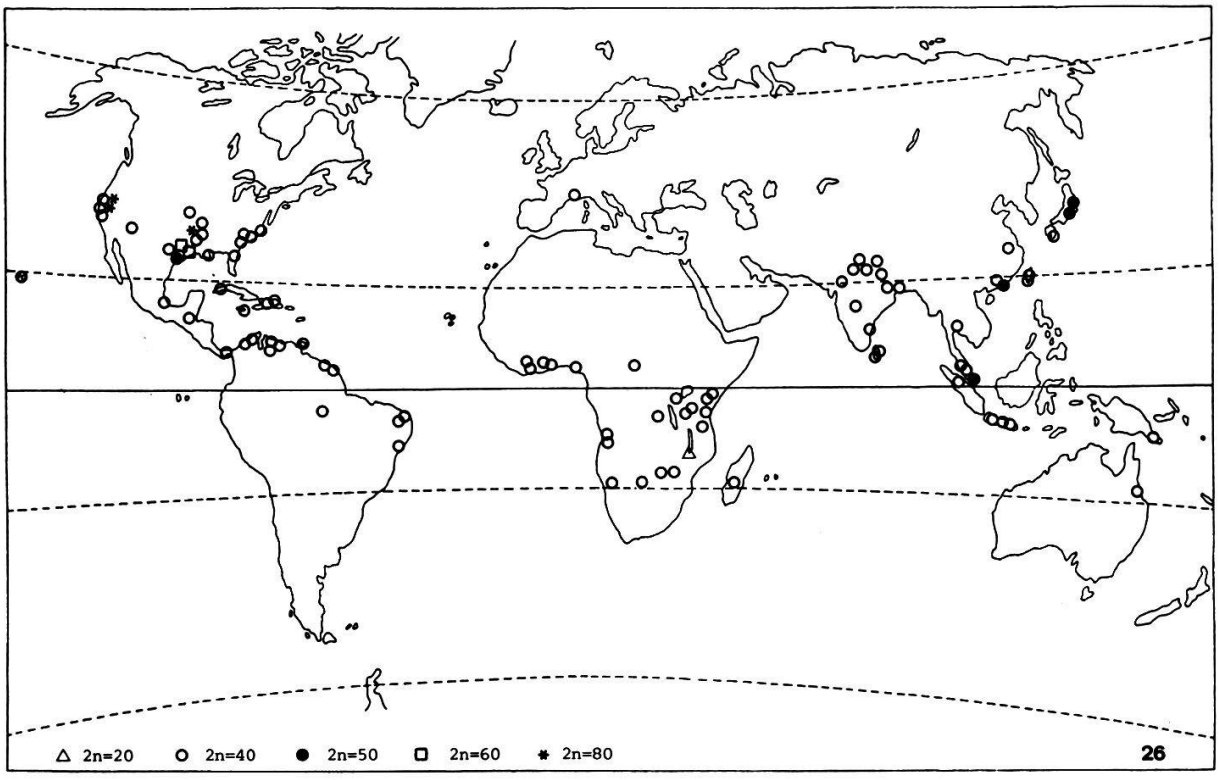


Fig. 26. *Lemna aequinoctialis*. Geographical distribution of the studied material. Some 40chromosomic stations are not included; two 50chromosomic stations from Japan were likewise not marked.

The present results were partly corroborated by Japanese colleagues who studied cultures issued from six clones examined some years ago by ourselves. Four of these clones were found tetraploid in accordance to our results; on the other hand, two samples previously observed as pentaploid (2n=50) revealed occurrence of aneuploid chromosome numbers representing higher levels of polyploidy viz. 78 and 81. In addition, further chromosome numbers representing various euploid and aneuploid cytotypes of the kind not found in the present investigagtions were observed in the material originating from various localities in Japan (2n=66, 70, 72, 84; TAKIMOTO, personal communication). It should be noted parenthetically that the Japanese scientists used the name of *Lemna paucicostata*.

Some of our results concerning *L. aequinoctialis* were previously published under the name *L. perpusilla* (URBANSKA-WORYTKIEWICZ 1975). The nomenclature of the group being now revised (LANDOLT 1980, see p. 17-18 of the present volume), we propose that the data on cytological variation reported here are the first contribution on *Lemna aequinoctialis*.

3.2.4. *Lemna turionifera* Landolt

2n=40, 42, 50, 80 (Figs 27-30)

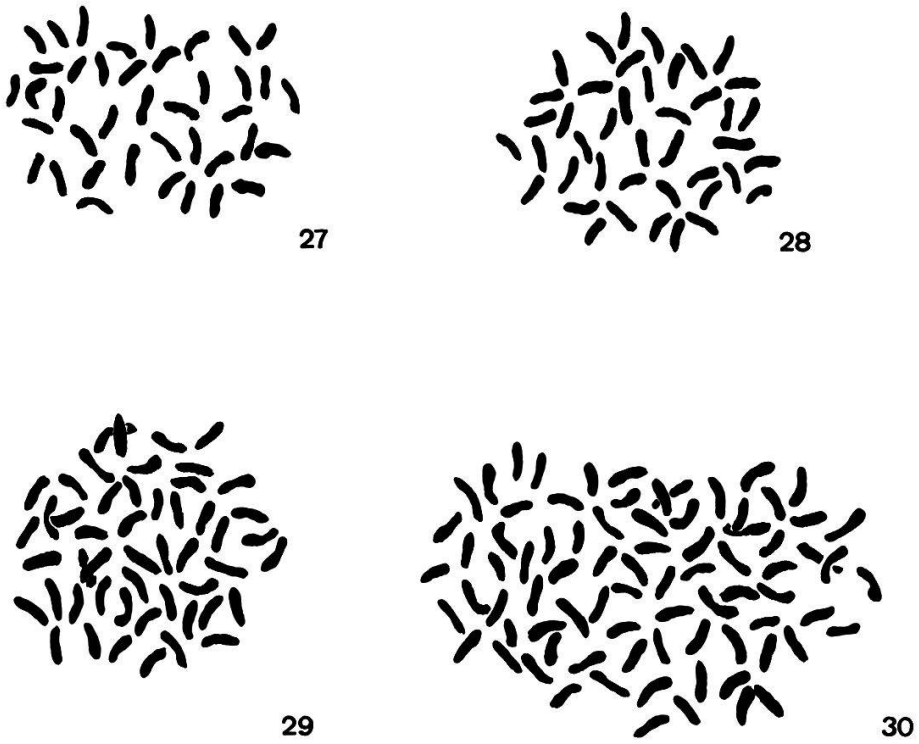
Lemna turionifera was studied from 57 localities, 26 population samples and 31 clonal cultures being examined.

Intra-individual variation occurring within *L. turionifera* was infrequent. Only mixoploid individuals were observed; the peculiar differentiation pattern was comparable to that described above in *L. aequinoctialis*, the particular cells in otherwise tetraploid individuals being nearly pentaploid or hexaploid. Intra-populational variation was found three times, tetraploid and hypotetraploid (2n=36, 38) units occurring side by side.

Cytological differentiation in *L. turionifera* was rather pronounced, four different cytotypes being observed (Figs 27-30). The tetraploid samples were largely prevailing in the studied material; in addition, nine hypertetraploid

samples with 2n=42 were found. Higher polyploids were observed only twice (2n=50, 2n=80, respectively).

Lemna turionifera was not studied cytologically hitherto.



Figs 27-30. *Lemna turionifera*: somatic metaphases. Collection numbers are given in parentheses. 27. 2n=40; Canada, Manitoba (6853). 28. 2n=42; North America, Iowa (7390). 29. 2n=50; North America, Texas (8098). 30. 2n=80; North America, Washington (6735).

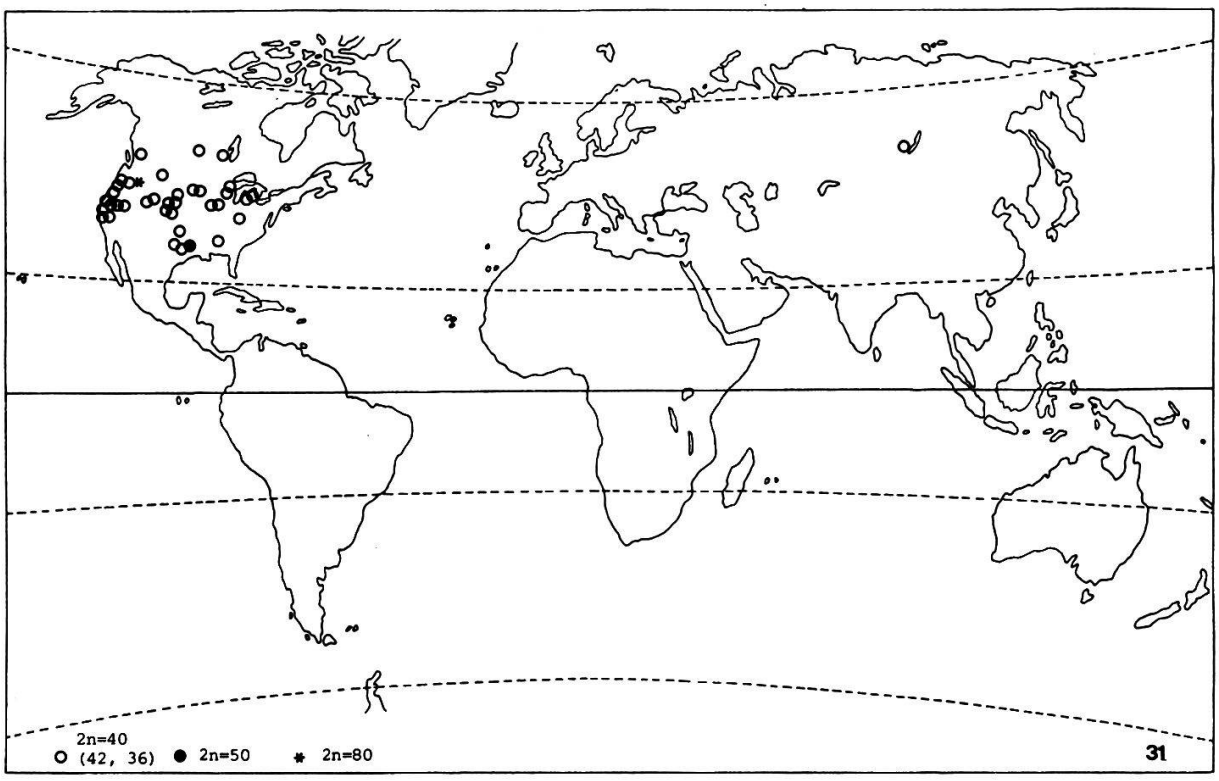


Fig. 31. *Lemna turionifera*. Geographical distribution of the studied material. Some 40chromosomic stations are not indicated.

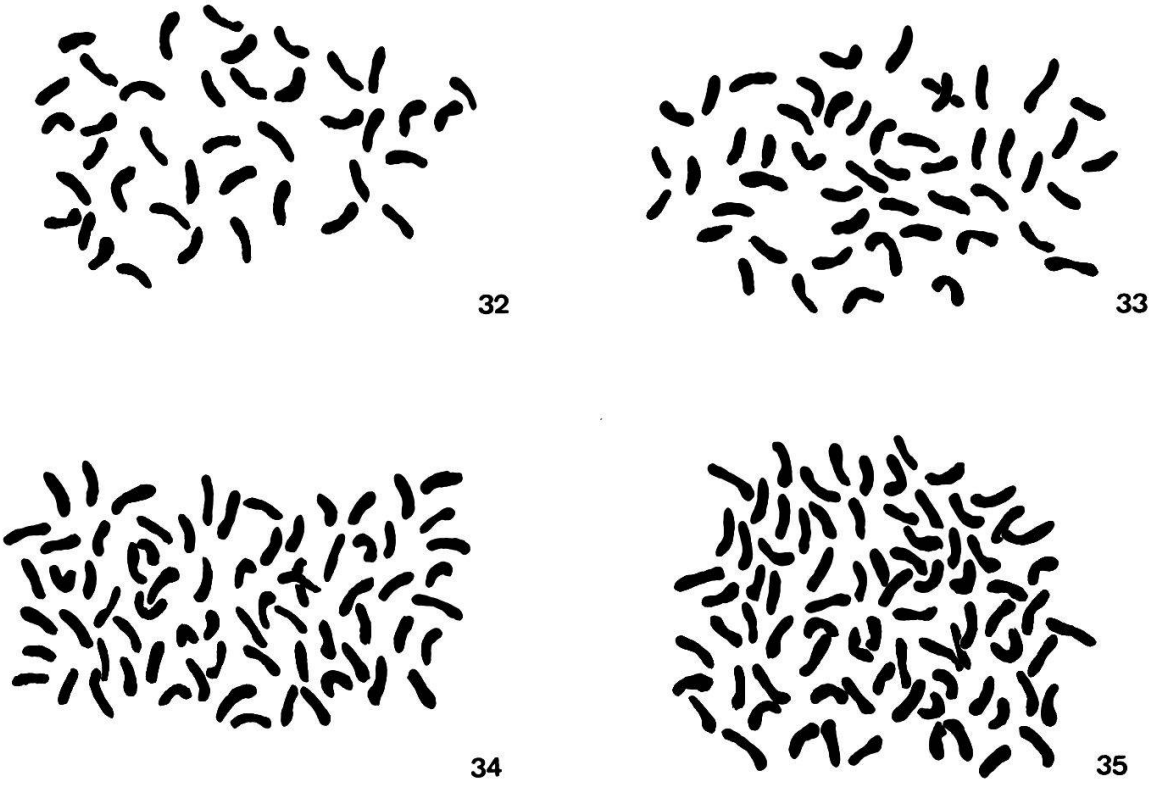
3.2.5. *Lemna gibba* L.

2n=40, 50, 70, 80 (Figs 32-35)

The studied material of *Lemna gibba* was rather ample, 113 localities being represented; however, only 19 population samples were investigated.
Intra-individual variation within *L. gibba* was found only once, the respective cells of an aneusomatic clone carrying 40 and about 45 chromosomes. Intra-populational variation was found in four samples, all of them consisting of tetra- and pentaploid or hypopentaploid units.
Polyploid differentiation observed within *Lemna gibba* comprised four cytotypes; 96 samples proved to be tetraploid, whereas the remainder corresponded to higher levels of polyploidy viz. pentaploid (11 samples), septaploid (two

samples) and octoploid (four samples).

The euploid chromosome numbers represented above were reported by the present author for the first time in 1975. It is interesting to note that all the other scientists studying *L. gibba* found hexaploid or nearly hexaploid chromosome numbers: BLACKBURN (1933), TISCHLER (1936) and ROHWEDER (1937) reported 2n=64, whereas WCISLO (1970) gave only an approximative count. The hexaploid chromosome numbers were not recorded in our material.



Figs 32-35. *Lemna gibba*: somatic metaphases. Collection numbers are given in parentheses. 32. 2n=40; North America, Mexico (7309). 33. 2n=50; South America, Argentina (7922). 34. 2n=70; South Africa (7249). 35. 2n=80; South Africa (7735). Partly from URBANSKA-WORYTKIEWICZ 1975.

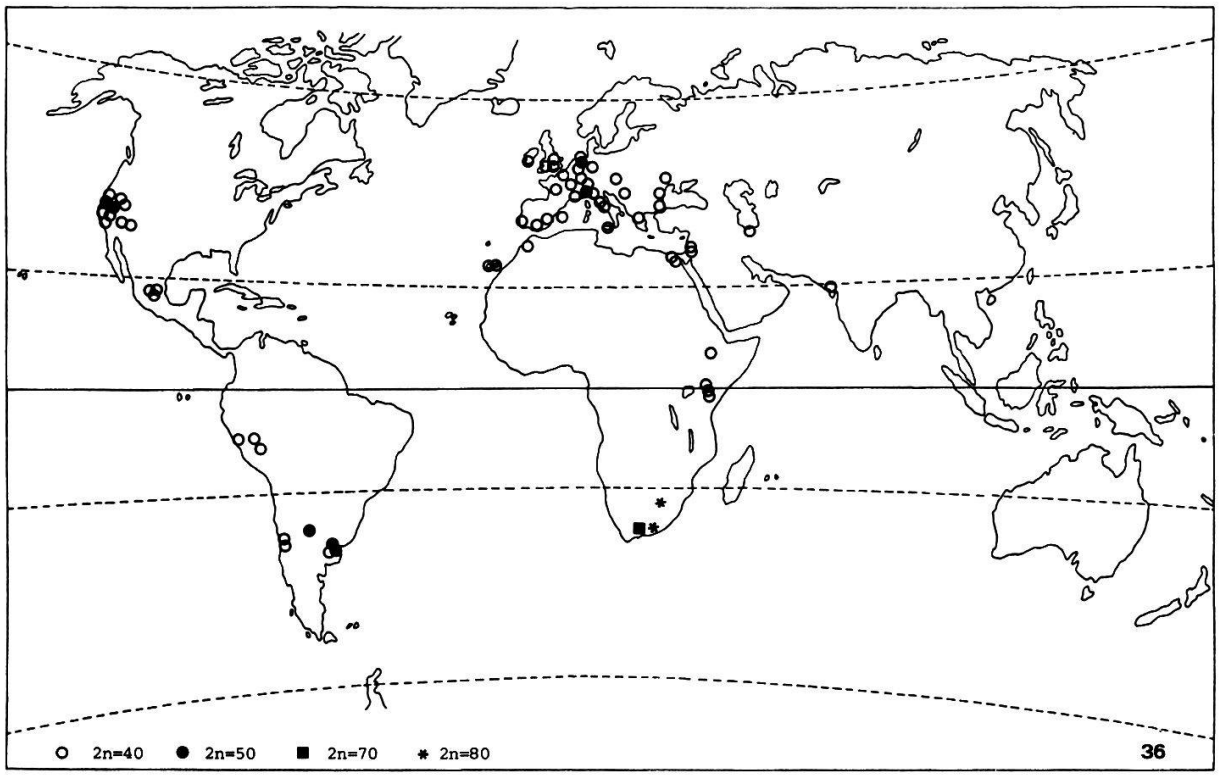


Fig. 36. *Lemna gibba*: geographical distribution of the studied material. Some tetraploid stations are not included.

3.2.6. *Lemna disperma* Hegelm.

2n=40 (Fig. 37)

The clonal material of *L. disperma* studied from 17 localities proved to be fairly uniform cytologically, only tetraploid chromosome numbers 2n=40 being found.

L. disperma has not been cytologically studied hitherto.

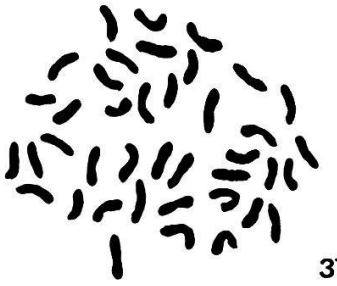


Fig. 37. *Lemna disperma*: somatic metaphase. Collection numbers are given in parentheses. 2n=40; South Australia, Glencoe West (7818).

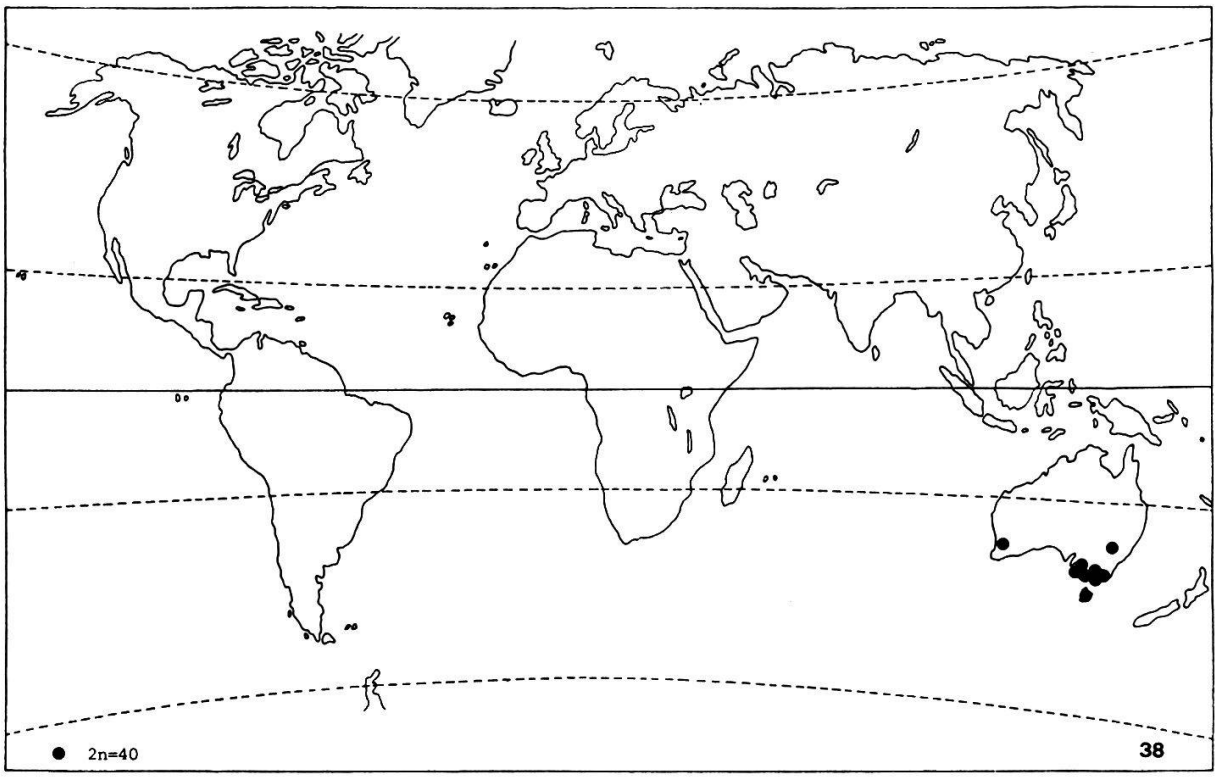


Fig. 38. *Lemna disperma*: geographical distribution of the studied material. Some 40chromosomic stations are not included.

3.2.7. *Lemna obscura* (Austin) Daubs

2n=40, 50 (Figs 40-41)

The studied material of *Lemna obscura* originated from 33 localities, population samples representing about 50 per cent.

Intra-individual variation was observed only once, an aneusomatic unit (2n=40, 42) being found within a tetraploid population sample from North Carolina. As far as intra-populational variation is concerned, each of the two mixed populations represented a different aspect of cytological variation: one sample consisted of tetraploid and hypotetraploid units, whereas the other comprised tetra- and pentaploids.

Data on *Lemna obscura* are presented here for the first time.

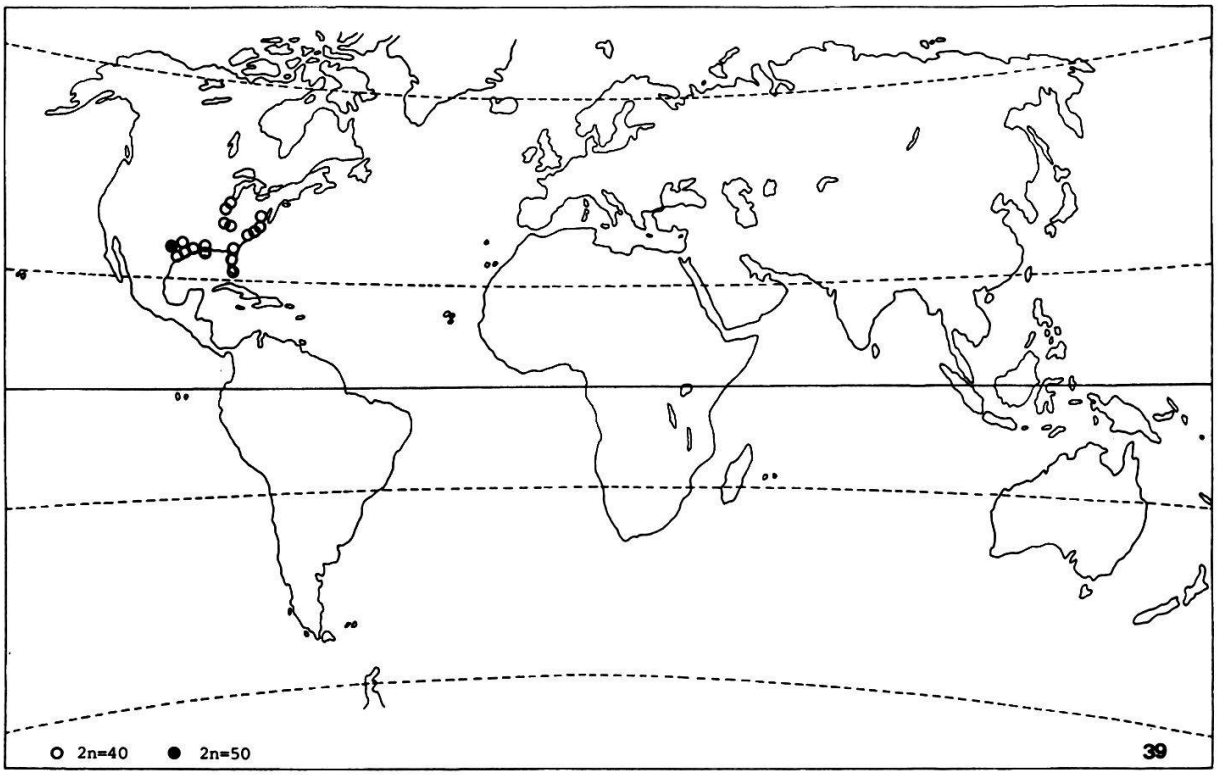
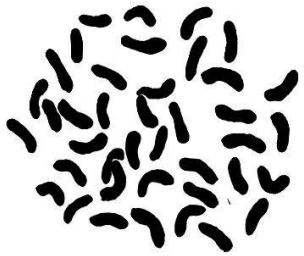


Fig. 39. *Lemna obscura*: geographical distribution of the studied samples. Some tetraploid stations are not included.



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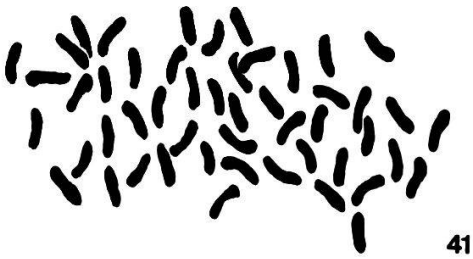


41

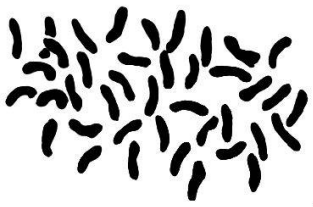
Fig. 40-41. *Lemna obscura*: somatic metaphases. Collection numbers are given in parentheses. 40. 2n=40; North America, Louisiana (8058). 41. 2n=50; North America, Texas (8076).

3.2.8. *Lemna japonica* Landolt

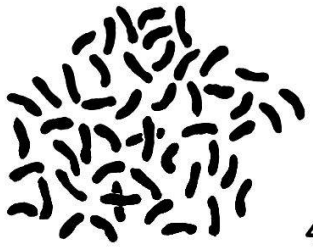
2n=40, 50 (Figs 42-43)

Lemna japonica was studied in 6 clonal cultures from various parts of its limited distribution area. 5 samples proved to be tetraploid, whereas a single clone had 2n=50. No other aspects of cytological variations were observed.

Lemna japonica was not studied cytologically so far.



42



43

Figs 42-43. *Lemna japonica*: somatic metaphases. Collection numbers are given in parentheses. 42. 2n=40; Asia, China (7951). 43. 2n=50; Asia, Japan (7182).

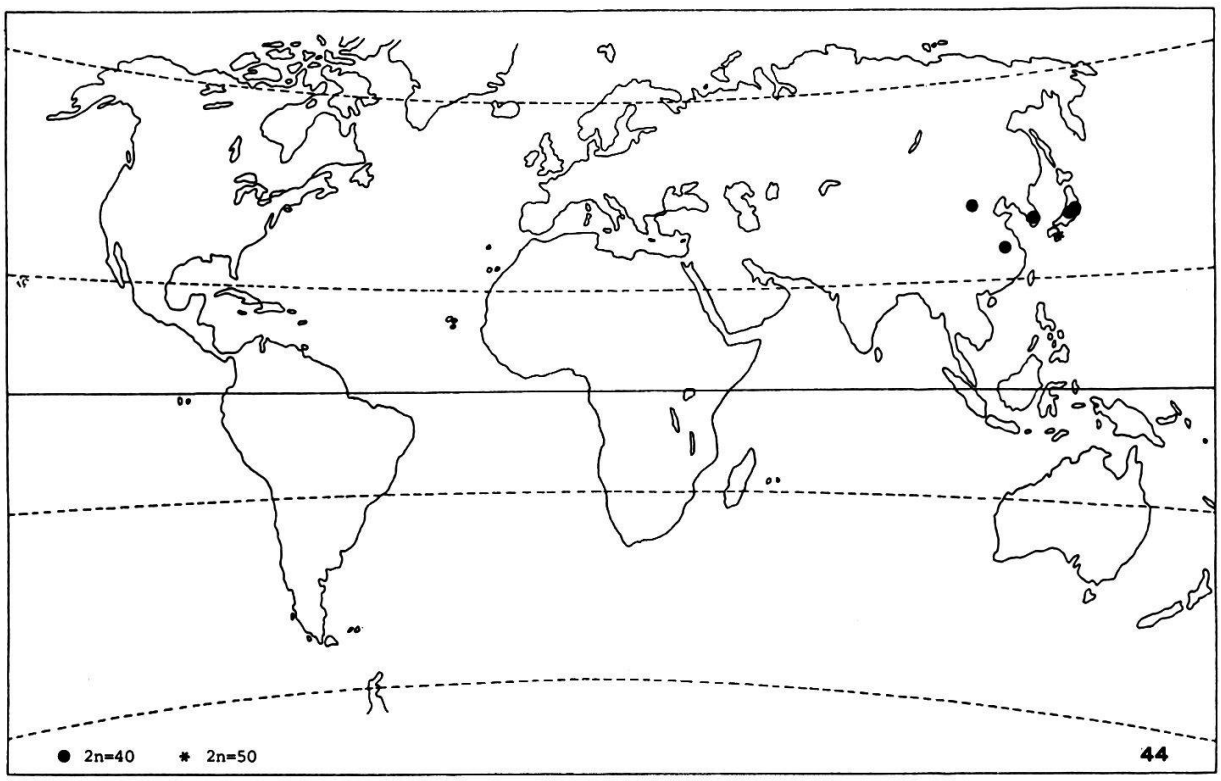


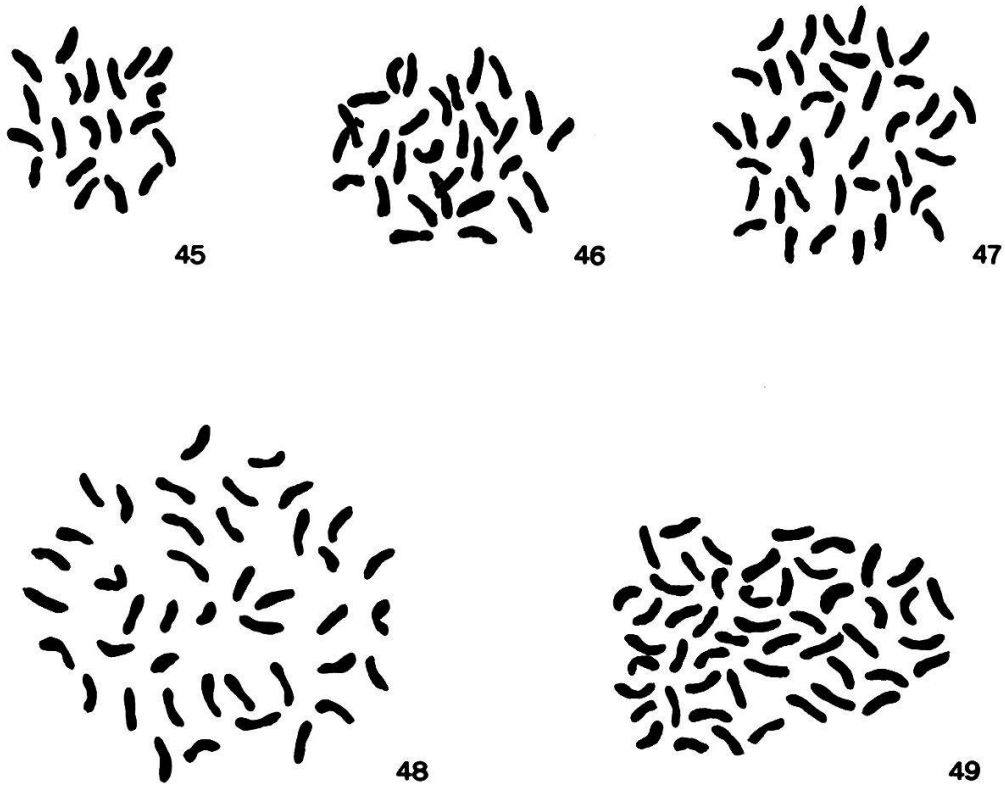
Fig. 44. *Lemna japonica*: geographical distribution of the studied material.

3.2.9. *Lemna minor* L.

2n=20, 30, 40, 42, 50 (Figs 45-49)

Lemna minor was the best represented taxon within the whole studied material of the family. Samples of 305 various origines were examined; however, they represented mostly clonal cultures, only 46 population samples being taken in the wild.

As far as intra-individual variation in *L. minor* is concerned, both aneusomaty as well as mixoploidy were observed. Out of 8 aneusomatic clones, seven were tetraploid; aneusomic cells found in this material carried either hypertetraploid chromosome numbers 2n=41, 42, 43 or hypotetraploid ones (2n=36, 38). A single aneusomatic clone manifested a more complex variation, both hypo- and hypertetraploid cells occurring in addition to normal tetraploid ones. Aneusomaty occurred as well within a triploid clone, hypertriploid



Figs 45-49. *Lemna minor*: somatic metaphases. Collection numbers are given in parentheses. 45. 2n=20; Africa, Natal (7789). 46. 2n=30; South Africa (7244). 47. 2n=40; Europe, Switzerland (6626). 48. 2n=42; Canada, Ontario (7572). 49. 2n=50; North America, Pennsylvania (6742). Partly from URBANSKA-WORYTKIEWICZ 1975.

cells being,however, infrequent. Mixoploidy in *L. minor* was found twice. A mixoploid unit comprising cells with 2n=40 and those with approximate pentaploid chromosome numbers was observed in otherwise tetraploid population samples from North America, Kansas. The second case of mixoploidy was rather unusual: in a clone from New Zealand kept in culture at our Institute and examined three times at certain time intervals, 2n=20 then 2n=40 and again 2n=20 were observed in the consecutive series. It should be noted that only tetraploid chromosome number 2n=40 was found in a large population sample taken by the author in the same station several years later.

Intra-populational variation occured only exceptionally in *L. minor*. Three mixed population samples comprised the prevailing tetraploid units as well as some aneuploid (hypertetraploid) ones.

Cytological differentiation found within *L. minor* comprised four euploid chromosome numbers (2n=20, 30, 40, 50) and a single aneuploid one (2n=42). The tetraploid chromosome number 2n=40 proved to be positively prevailing: it occurred in 271 samples. Twenty-four samples were hypertetraploid, 42 chromosomes invariably occurring in all studied cells. Other cytotypes were represented by pentaploids (five samples), triploids (three samples) and a single sample was diploid.

The present results obtained on *Lemna minor* are partly corroborated by the previous data. The tetraploid number 2n=40 was found by BLACKBURN (1933), TISCHLER (1936, 1937), ROHWEDER (1937), DELAY (1947) and WCISLO (1970), whereas BROOKS (1940) reported 2n=42. Recent data of MURIN and MAJOVSKY (in

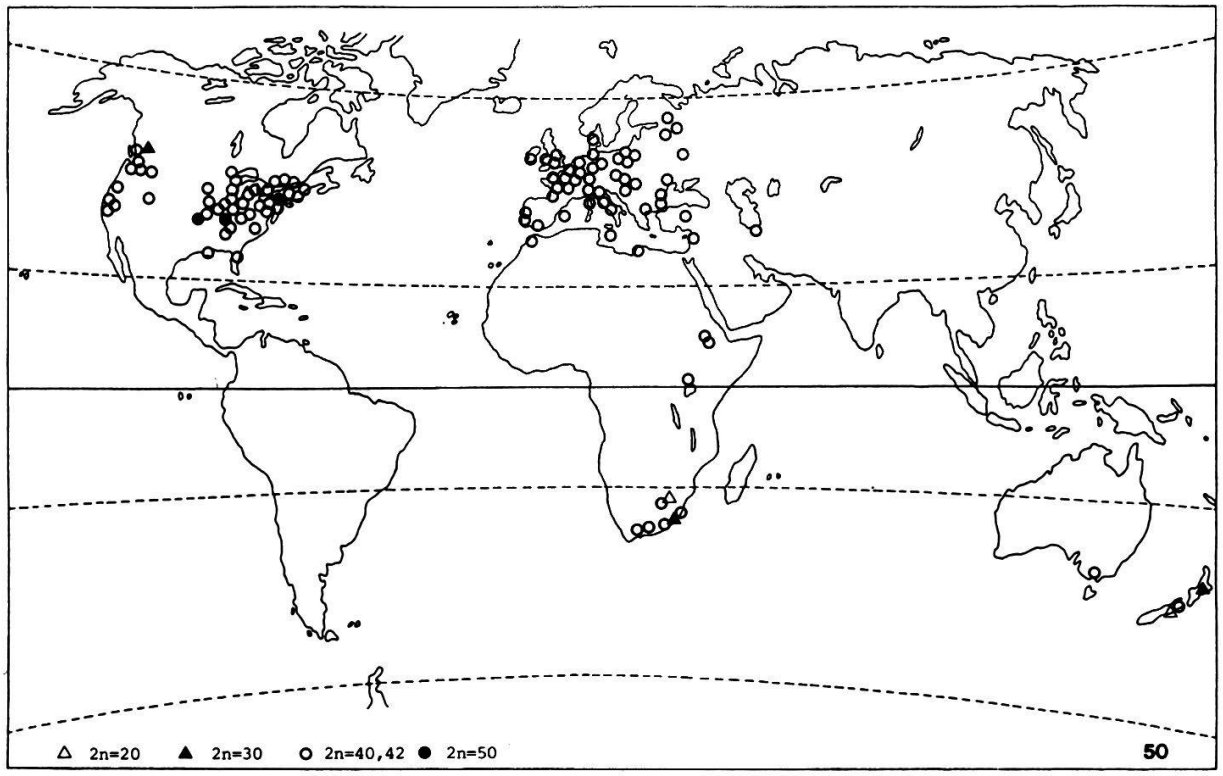


Fig. 50. *Lemna minor*: geographical distribution of the studied material. Numerous tetraploid and hypertetraploid stations are not included, in particular those from North America and Europe.

LOEVE 1978) further indicate the particular differentiation pattern occurring within *Lemna minor*. On the other hand, lower chromosome numbers viz. 2n=20 and 2n=30 as well as various aspects of intra-individual and intra-populational variation were not reported so far, except for the preliminary report by the present author (URBANSKA-WORYTKIEWICZ 1975).

3.2.10. *Lemna minuscula* Herter

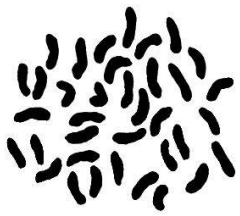
2n=36, 40 (Figs 51-52)

L. minuscula was studied in 45 samples; 10 population samples were taken in the wild, the remainder represented clonal cultures.

Intra-individual variation occurring within *L. minuscula* was found only twice; in both cases, tetraploid and hypotetraploid cells were observed. A comparable pattern was noted in intra-populational variation, tetraploid and hypotetraploid units occurring side by side.

Cytologically uniform samples of *L. minuscula* represented two cytotypes, the most frequent being the representative of the whole family 2n=40, whereas three clonal cultures proved to be invariably hypotetraploid (2n=36). It seems probable that occasionally appearing aneusomaty may result in plants and/or populations that represent various chromosome numbers.

In the previous publication by the author (URBANSKA-WORYTKIEWICZ 1975), *Lemna minuscula* was treated together with *L. valdiviana*, as suggested by



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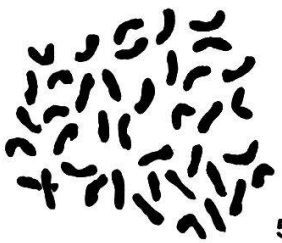


52

Figs 51-52. *Lemna minuscula*: somatic metaphases. Collection numbers are given in parentheses. 51. 2n=36; North America, California (6863). 52. 2n=40; South America, Argentina (7369).

E. LANDOLT who determined the material. The taxon has presently received a separate rank (LANDOLT 1980, see p. 19 of this volume). No data on cytology of *L. minuscula* other than the preliminary report of the present author are known.

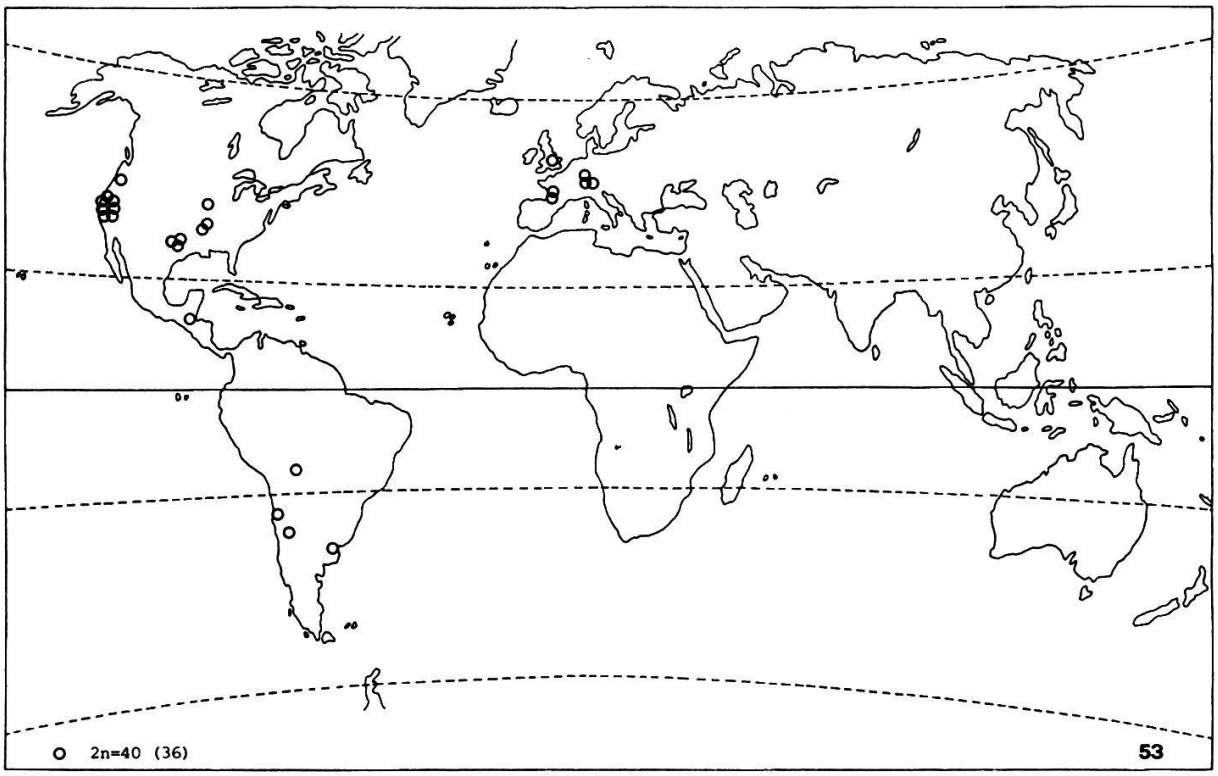


Fig. 53. *Lemna minuscula*: geographical distribution of the studied material. Some tetraploid stations are not included.

3.2.11. *Lemna valdiviana* Phil.

2n=40 (Fig. 54)

The studied material of *Lemna valdiviana* originated from 65 localities and comprised 12 population samples.

L. valdiviana proved to be fairly uniform cytologically, tetraploid chromosome number 2n=40 being observed in the whole examinated material. In a single

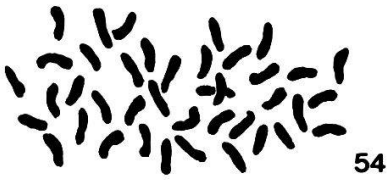


Fig. 54. *Lemna valdiviana*: somatic metaphase. Collection number is given in parentheses. 2n=40; North America, Louisiana (8043).

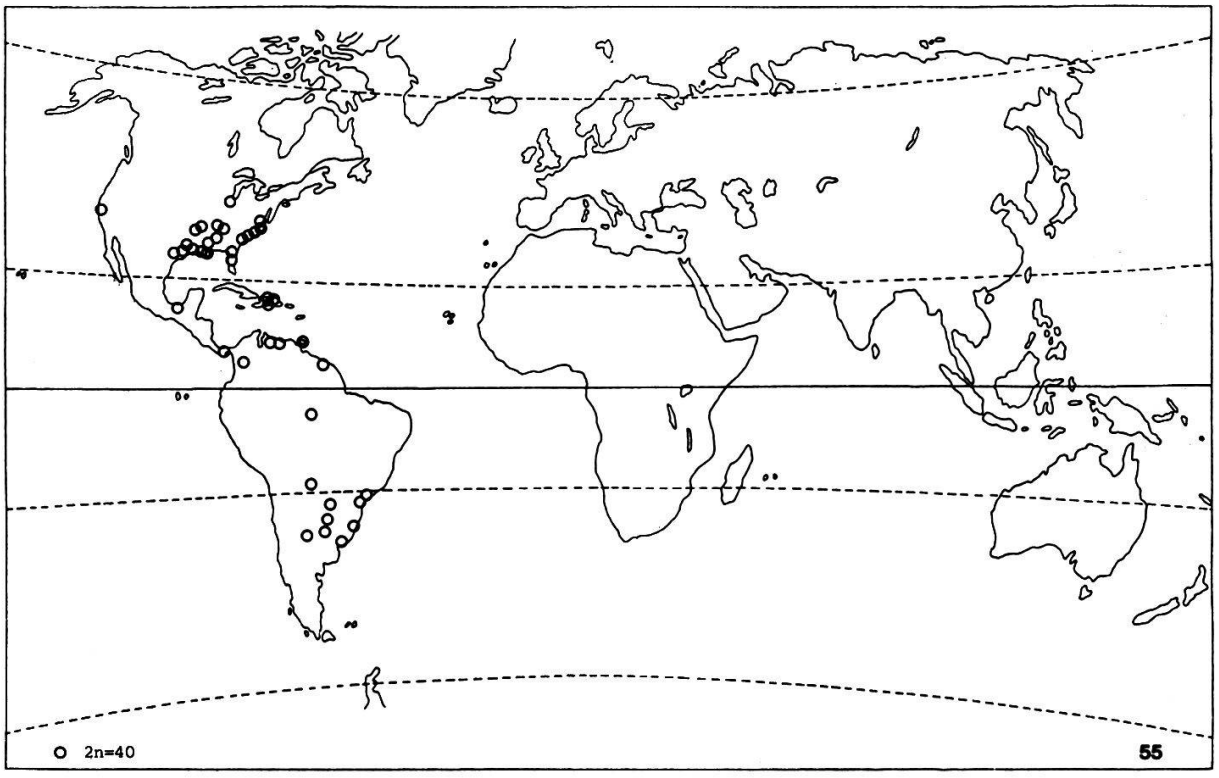


Fig. 55. *Lemna valdiviana*: geographical distribution of the studied material. Some stations in North America as well in South America are not included.

clone, intra-individual variation was observed; the cells carrying respectively 40 and about 55 chromosomes, the case corresponded both to mixoploidy as well as aneusomaty.

No cytological data on *L. valdiviana* were published hitherto bar the preliminary report by the author (URBANSKA-WORYTKIEWICZ 1975). At the present time, *L. valdiviana* has been separated from *L. minuscula* (LANDOLT 1980, see p. 19 of this volume); its only valid chromosome number known so far remains accordingly 2n=40.

3.3. *Wolffiella* Hegelm.

Out of nine taxa that form the genus *Wolffiella*, seven were studied. It should be noted, however, that only about one third of the material examinated from 67 localities consisted of population samples, representing respectively *W. lingulata* (4), *W. oblonga* (7) and *W. gladiata* (10); the remaining 46 samples represented clonal cultures. Chromosomes of *Wolffiella* were generally slightly larger than those occurring within the genus *Lemna*, their average length being 1.4 µ. Chromosome size variation was noted in all studied taxa, but no interspecific differences could have been established. The chromosomes of *Wolffiella* tended to be more uniformly and stronger stained than those of *Lemna* and it might be supposed that heterochromatic sectors were rather infrequent. Metaphase plates were often rather clustered so that

Table 7. Cytological variation within the genus *Wolffiella*

Taxon	Intra-individual variation		Variation within populations		Racial variation		N of the studied samples
	Aneu-somaty	Mixo-ploidy	Aneu-ploidy	Poly-ploidy	Aneu-ploidy	Poly-ploidy	
W. hyalina	-	-	-	-	-	-	5
W. neotropica	-	-	-	-	-	-	4
W. Welwitschii	-	-	-	-	-	-	3
W. lingulata	-	+	-	-	-	+	15
W. oblonga	-	+	-	-	-	+	20
W. gladiata	-	-	-	-	-	-	18
W. denticulata	-	-	-	-	-	+	2

accurate counts were difficult to obtain.

Cytological variation observed within the genus *Wolffiella* corresponded to the general pattern described in *Spirodela* and *Lemna*, but was rather limited (Tables 7, 8). On the whole, intra-individual variation was represented solely by four mixoploid strains, the case of *Wolffiella oblonga* being rather peculiar (see p. 71). Intra-populational variation was not observed. The studied material proved to be most frequently tetraploid, other levels of polyploidy being observed only exceptionally (Table 9). It should be remembered, however, that the informative value of the present results is particularly limited in the case of *Wolffiella*; it is not excluded that a more pronounced cytological variation could have been found within the genus, had a more ample material been investigated.

Table 8. Cytologically uniform and heterogenous samples found within the studied material of genus *Wolffiella*

Taxon	Uniform samples	Heterogenous samples			Total
		Aneusomaty	Mixoploidy	Mixed populations	
W. hyalina	5	-	-	-	5
W. neotropica	4	-	-	-	4
W. Welwitschii	3	-	-	-	3
W. lingulata	13	-	2	-	15
W. oblonga	18	-	2	-	20
W. gladiata	18	-	-	-	18
W. denticulata	2	-	-	-	2

Table 9. Chromosome numbers found in cytologically uniform samples of the genus *Wolffiella*

Taxon	Number of samples									To-
	2n=20	2n=30	2n=36	2n=40	2n=42	2n=50	2n=60	2n=70	2n=80	tal
W. hyalina	-	-	-	5	-	-	-	-	-	5
W. neotropica	-	-	-	4	-	-	-	-	-	4
W. Welwitschii	-	-	-	3	-	-	-	-	-	3
W. lingulata	2	-	-	9	-	2	-	-	-	13
W. oblonga	-	-	-	17	-	-	-	1	-	18
W. gladiata	-	-	-	18	-	-	-	-	-	18
W. denticulata	1	-	-	1	-	-	-	-	-	2

3.3.1. *Wolffiella hyalina* (Delile) Monod

2n=40 (Fig. 57)

Only five clonal samples of *Wolffiella hyalina* were examined; in the whole material, tetraploid chromosome number 2n=40 was invariably found. No intra-individual variation was observed.

W. hyalina was not cytologically studied hitherto.

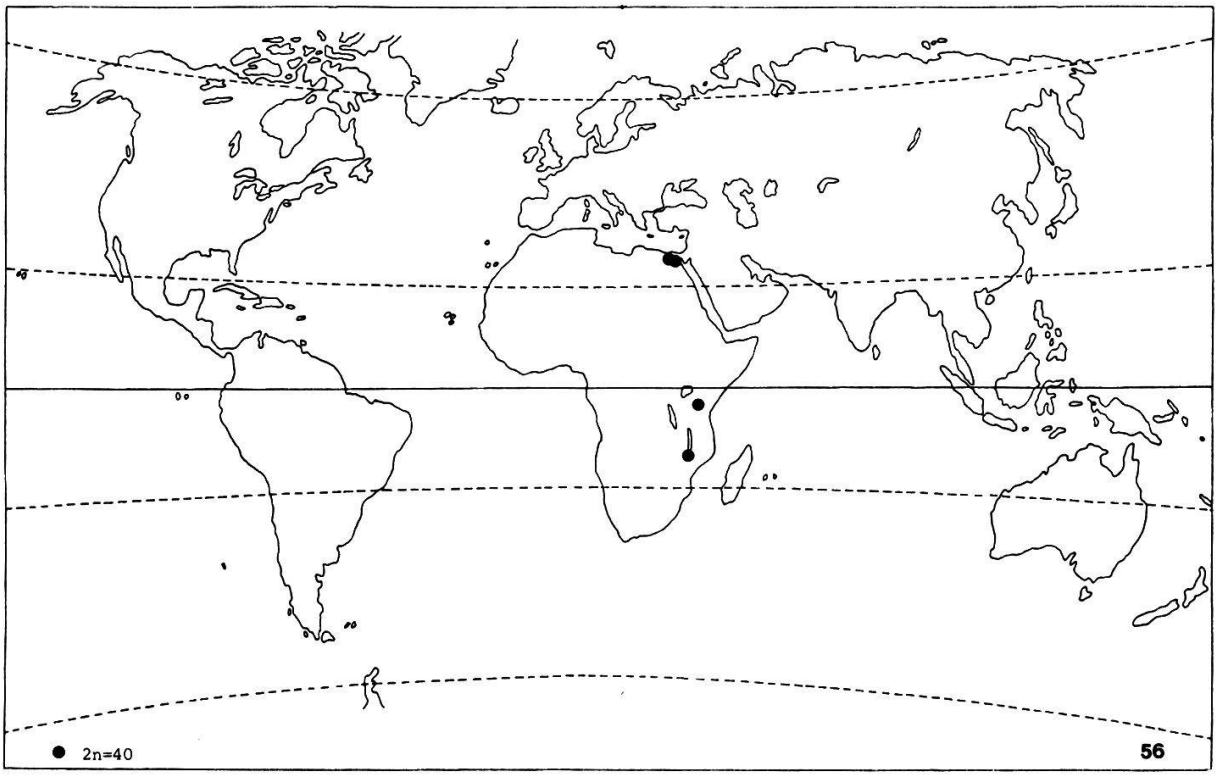


Fig. 56. *Wolffiella hyalina*: geographical distribution of the studied material. One station is not indicated.

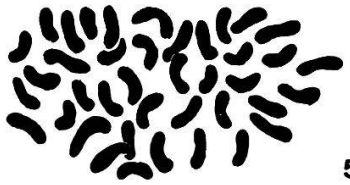


Fig. 57. *Wolffiella hyalina*: somatic metaphase. Collection number is given in parentheses. 2n=40; Africa, Malawi (7426).

3.2.2. *Wolffiella neotropica* Landolt

2n=40 (Fig. 58)

Four clonal samples of *W. neotropica* studied from the limited distribution area of this taxon were cytologically uniform, only tetraploid chromosome number being observed. *W. neotropica* was not studied so far.

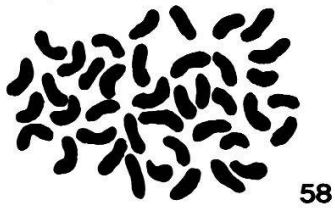


Fig. 58. *Wolffiella neotropica*: somatic metaphase. Collection number is given in parentheses. 2n=40; South America, Brazil (7290).

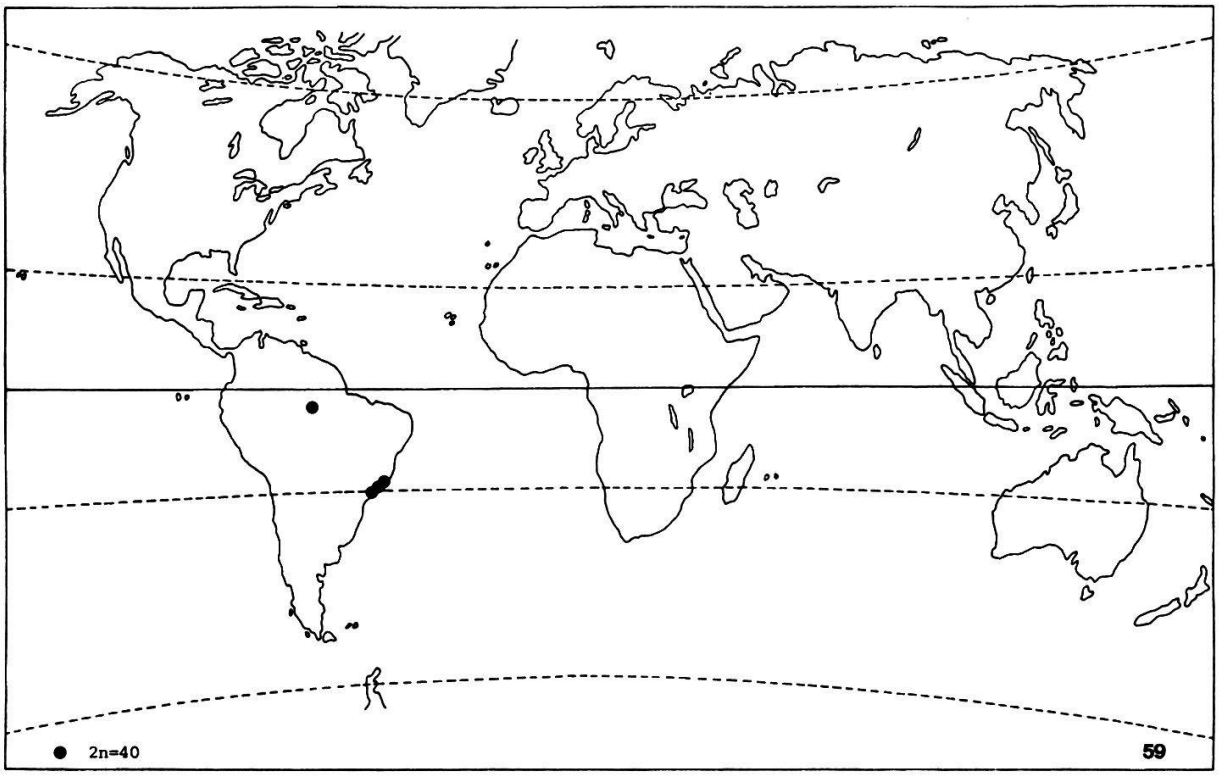


Fig. 59. *Wolffiella neotropica*: geographical distribution of the studied material.

3.3.3. *Wolffiella Welwitschii* (Hegelm.) Monod

2n=40 (Fig. 60)

Out of several strains of *W. Welwitschii* obtained on request from various parts of its geographical distribution area, only three clones could have been studied; the other perished before reaching a suitable developmental stage. Only the tetraploid chromosome number 2n=40 was found, no cytological variation being noted.

Wolffiella Welwitschii was not studied cytologically hitherto. DAUBS (1965) referred only to his morphological studies carried out in the herbarium specimens; chromosome number cited by FEDOROV (1969) is therefore apparently based on some misunderstanding.

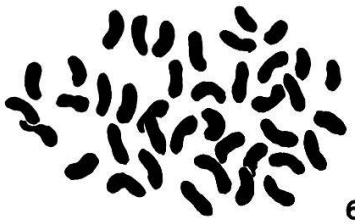


Fig. 60. *Wolffiella Welwitschii*: somatic metaphase. Collection number is given in parentheses. 2n=40; South Africa, Natal (8252).

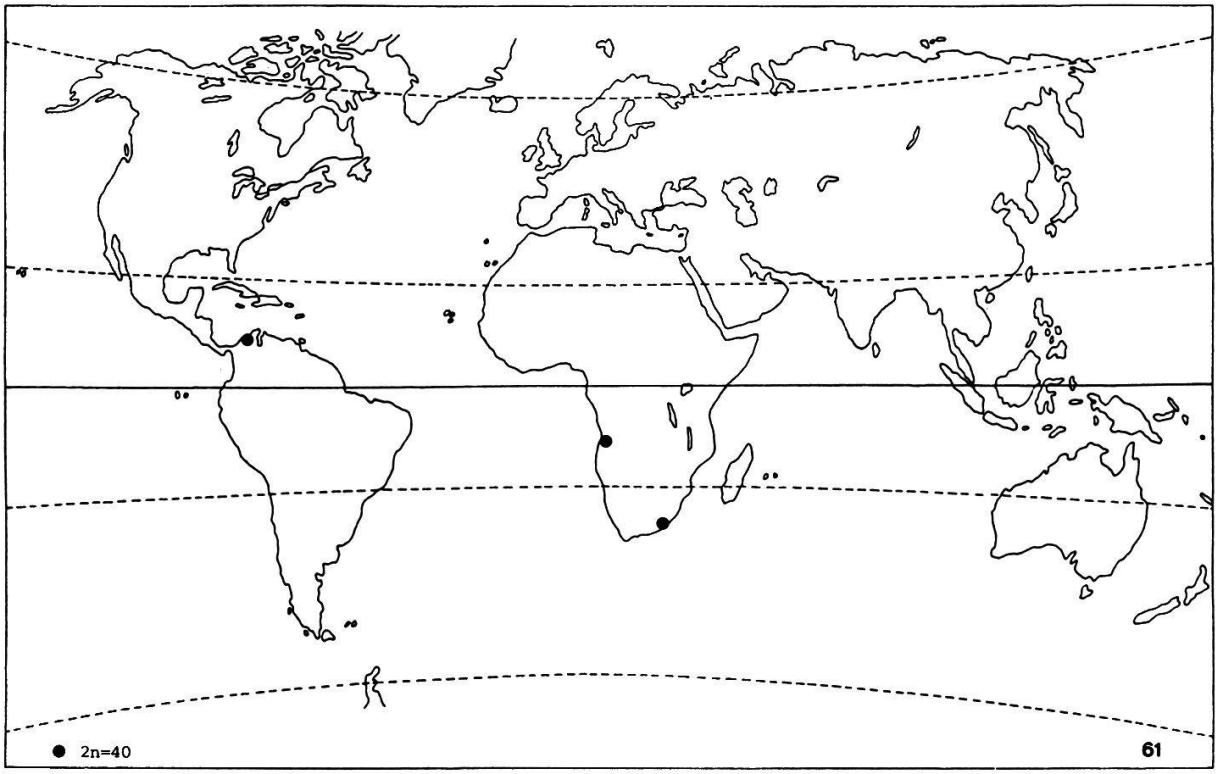


Fig. 61. *Wolffiella Welwitschii*: geographical distribution of the studied material.

3.3.4. *Wolffiella lingulata* (Hegelm.) Hegelm.

2n=20, 40, 50 (Figs 63-65)

W. lingulata was studied from 15 localities; only four population samples were examined. The material was for the most part cytologically uniform, mixoploid clones being observed only twice. It is interesting to note, however, that either case revealed a different pattern of mixoploidy, 2n=40, 20 and 2n=40, ~ 50 being respectively found. Polyploid differentiation occurring within *Wolffiella lingulata* comprised three levels i.e. diploid, tetraploid and pentaploid.

The only previous data on chromosome numbers of *Wolffiella lingulata* are

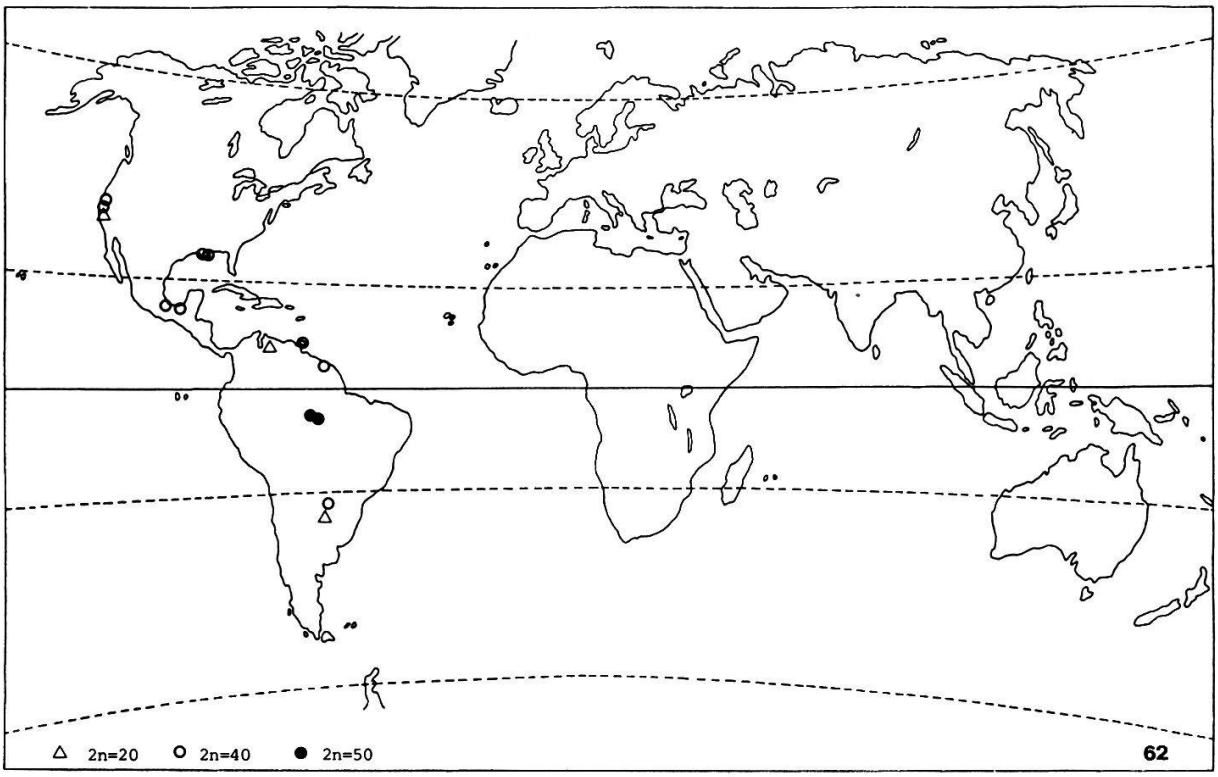
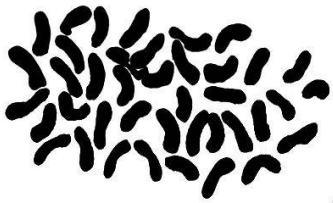


Fig. 62. *Wolffiella lingulata*: geographical distribution of the studied material. Two tetraploid stations are not indicated.

those of DAUBS (1965) who reported about 42 chromosomes in the material of an unspecified origin.

63



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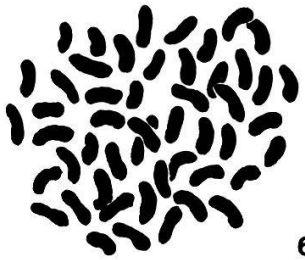


65

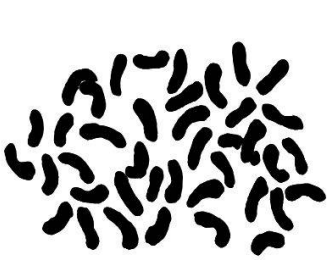
Figs 63-65. *Wolffiella lingulata*: somatic metaphases. Collection numbers are given in parentheses. 63. 2n=20; South America, Argentina (7725). 64. 2n=40; North America, California (8141). 65. 2n=50; South America, Brazil (7292).

3.3.5. *Wolffiella oblonga* (Phil.) Hegelm.

2n=40, 70 (Figs 66, 67)

On the whole, 20 samples of *Wolffiella oblonga* were studied from various parts of the distribution area of this American taxon. Out of this material, seven samples were taken in wild populations in North America, two comprised sterile cultures obtained in certain time intervals from two different laboratories each, and the remainder corresponded to the usual strains raised from single fronds.

Intra-individual variation observed in *Wolffiella oblonga* was rare, but either of the two mixoploid clones represented a different case. In one clone, the habitual for the duckweeds single-genome difference was observed (2n=40, ≈ 50). The other one, however, did not conform to this pattern; in the material received in 1968 from one source a septaploid chromosome number 2n=70 was found, whereas both cultures obtained respectively in 1971 and 1973 from another laboratory were invariably tetraploid (2n=40). It should be added that another clonal material (collection numbers 7169, 8393) obtained twice in 1968 and 1976 proved to be fairly stable cytologically, only 2n=40 being found.



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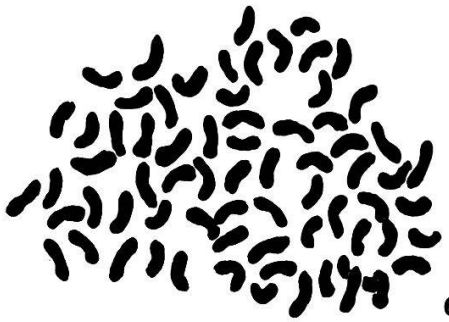


67

Figs 66-67. *Wolffiella oblonga*: somatic metaphases. Collection numbers are given in parentheses. 66. 2n=40; North America, Louisiana (8031). 67. 2n=70; South America, Brazil (7201a).

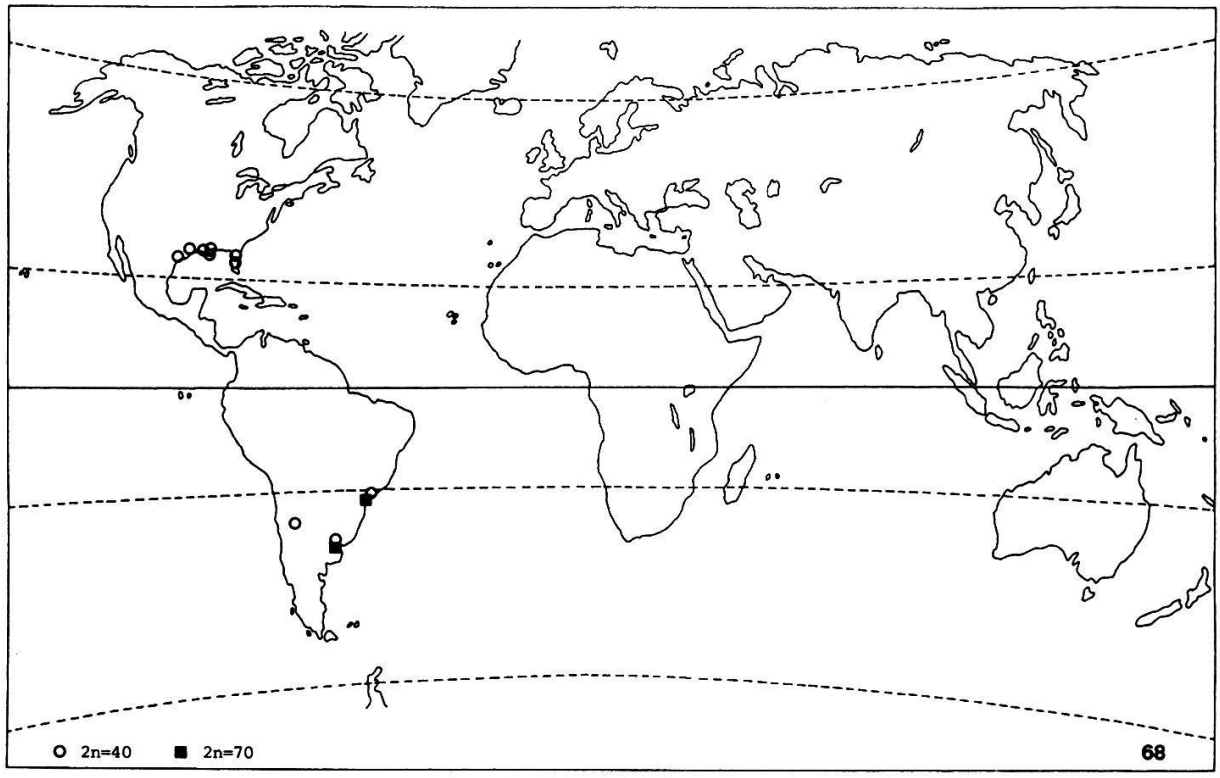


Fig. 68. *Wolffiella oblonga*: geographical distribution of the studied material. Some tetraploid stations are not indicated.

Most of the studied samples of *Wolffiella oblonga* were cytologically uniform; the only clone representing in this group a chromosome number different from 2n=40 was the septaploid material from Brazil (Fig. 67).
Wolffiella oblonga was previously studied only by DAUBS (1965) who reported an approximate chromosome number 42 but did not present any information on the origin of his material.

3.3.6. *Wolffiella gladiata* (Hegelm.) Hegelm.
2n=40 (Fig. 70)

Wolffiella gladiata was studied from 18 localities, ten population samples being included. Only tetraploid chromosome number 2n=40 was found.

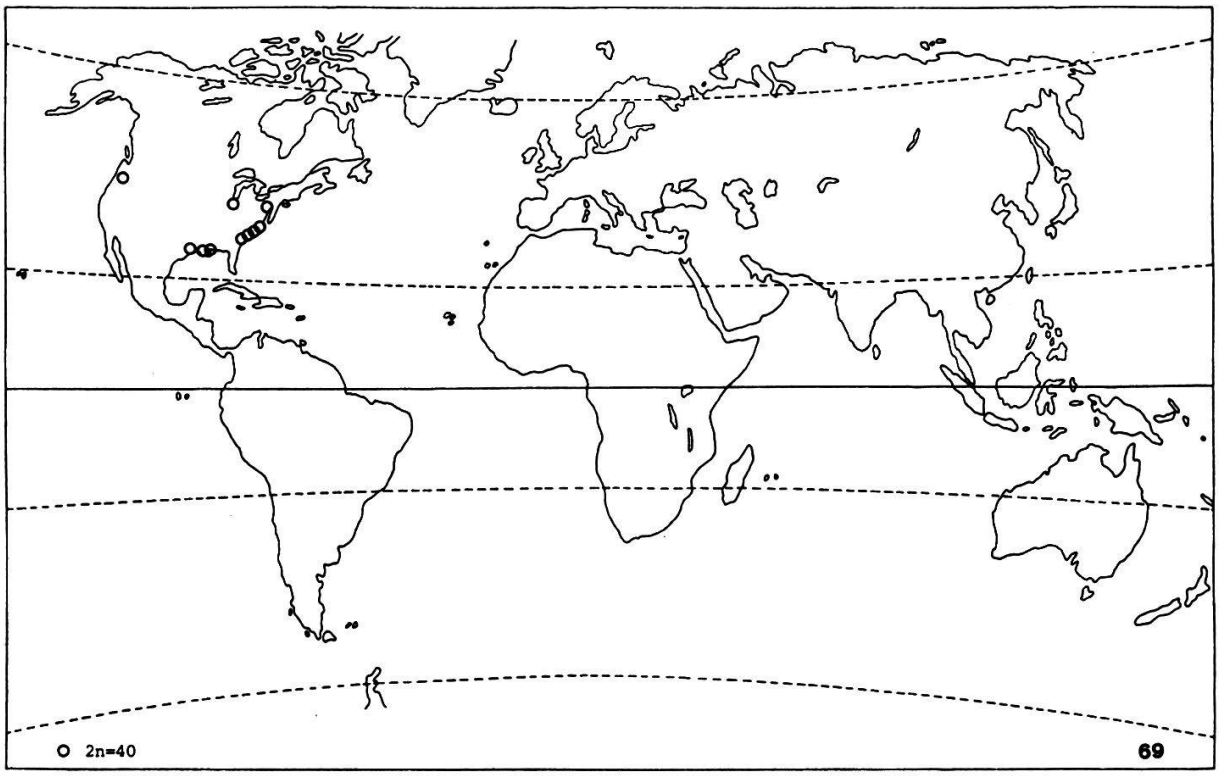


Fig. 69. *Wolffiella gladiata*: geographical distribution of the studied material. Some stations are not indicated.

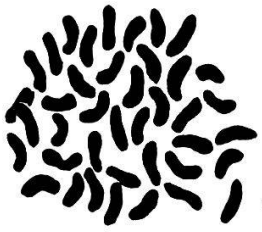
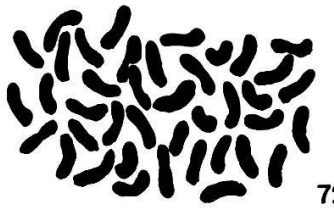


Fig. 70. *Wolffiella gladiata*: somatic metaphase. Collection number is given in parentheses. 2n=40; North America, Texas (8066).

Previously, DAUBS (1965) reported 2n=42 for *Wolffiella gladiata*; precise origin of this material, assigned by DAUBS to *W. floridana*, remains unknown.

3.3.7. *Wolffiella denticulata* (Hegelm.) Hegelm.
2n=20, 40 (Figs 71-72)

Only two clonal samples of this taxon, exceedingly rare and localized in South Africa, were studied. Each of them represented a different chromosome number viz. 2n=20 and 2n=40. No intra-individual variation was observed. Chromosome numbers of *Wolffiella denticulata* are given here for the first time. DAUBS (1965) studied only the herbarium specimens; the reference in FEDOROV's chromosome atlas of the Angiosperms (FEDOROV 1969) is therefore unvalid.



Figs 71-72. *Wolffiella denticulata*: somatic metaphases. Collection numbers are given in parentheses. 71. 2n=20; South Africa, Natal (7454). 72. 2n=40; South Africa, Natal (8221).

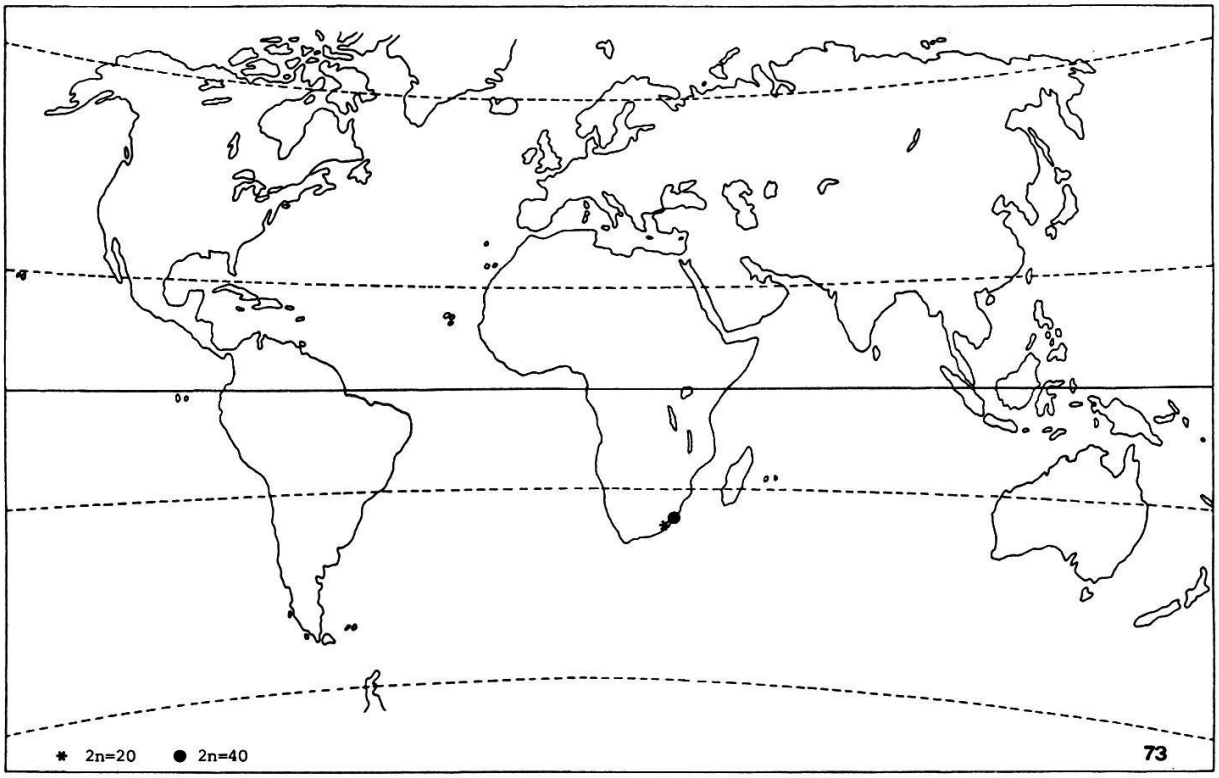


Fig. 73. *Wolffiella denticulata*: geographical distribution of the studied material.

3.4. *Wolffia* Horkel

The genus *Wolffia* was rather well represented in the studied material, all taxa but one viz. *W. elongata* Landolt being examined cytologically. On the whole, 252 samples were investigated; however, number of population samples taken in the wild was limited (36).

Although the smallest among the duckweeds, *Wolffia* had the largest chromosomes that most frequently stained well revealing no particularly diversified arm structure. However, localization of the centromere region was very often impossible; chromosomes of *Wolffia* tended as well to stick together in metaphase plates. Chromosome size differences occurring within taxa of *Wolffia* were most frequently not very pronounced, an average chromosome length being 1.7 μ.

Table 10. Cytological variation within the genus *Wolffia*

Taxon	Intra-individual variation		Variation within population		Racial variation		N of the studied samples
	Aneu-somaty	Mixo-ploidy	Aneu-ploidy	Poly-ploidy	Aneu-ploidy	Poly-ploidy	
W. microscopica	-	-	-	-	-	+	2
W. brasiliensis	+	-	-	-	-	+	63
W. borealis	+	-	-	-	-	+	18
W. australiana	-	-	-	+	-	+	13
W. angusta	-	-	-	-	-	-	3
W. arrhiza	-	+	-	-	-	+	32
W. columbiana	-	+	-	+	-	+	87
W. globosa	-	+	-	+	-	+	34

Table 11. Cytologically uniform and heterogenous samples found in the studied material of the genus *Wolffia*

Taxon	Uniform samples	Heterogenous samples			Total
		Aneusomaty	Mixoploidy	Mixed populations	
W. microscopica	2	-	-	-	2
W. brasiliensis	59	1	-	3	63
W. borealis	16	2	-	-	18
W. australiana	12	-	-	1	13
W. angusta	3	-	-	-	3
W. arrhiza	30	-	2	-	32
W. columbiana	80	-	6	1	87
W. globosa	31	-	2	1	34

Intra-individual cytological variation occurring within the genus *Wolffia* comprised mostly mixoploidy, aneusomaty being much less frequent (Tables 10,11). On the other hand, mixed population samples represented aneuploid and polyploid differentiation in an equal frequency; on the whole, however, intra-populational variation was rare.

Polyploid differentiation occurring within the genus *Wolffia* was very pronounced, a continuous range of euploid chromosome numbers from 2n=20 up to 2n=80 being found (Table 12). Except for *Wolffia angusta*, all the studied taxa revealed more than one chromosome number. The representative of the whole family single-genome-difference pattern was particularly distinct in

Table 12. Chromosome numbers found in cytologically uniform samples of the genus *Wolffia*

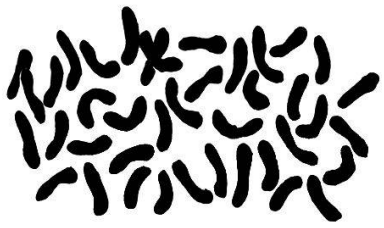
Taxon	Number of samples									To-
	2n=20	2n=30	2n=36	2n=40	2n=42	2n=50	2n=60	2n=70	2n=80	tal
W. microscopica	-	-	-	1	-	-	-	-	1	2
W. brasiliensis	1	-	-	46	-	10	1	-	1	59
W. borealis	1	6	-	9	-	-	-	-	-	16
W. australiana	2	-	-	10	-	-	-	-	-	12
W. angusta	-	-	-	3	-	-	-	-	-	3
W. arrhiza	-	1	-	19	-	3	5	1	1	30
W. columbiana	-	7	-	60	-	12	-	1	-	80
W. globosa	-	1	-	22	-	3	5	-	-	31

Wolffia arrhiza. It should be stressed, however, that the tetraploid chromosome number 2n=40 was clearly prevailing in the studied material (Table 12).

3.4.1. *Wolffia microscopica* (Griff.) Kurz

2n=40, 80 (Figs 74-75)

Only two clonal samples originating from the limited distribution area of *W. microscopica* were studied. Each of them represented a different level of polyploidy (2n=40, 2n=80). The previous results of ROY and DUTT (1967) suggest a rather complex cytological differentiation occurring within *W. micro-*



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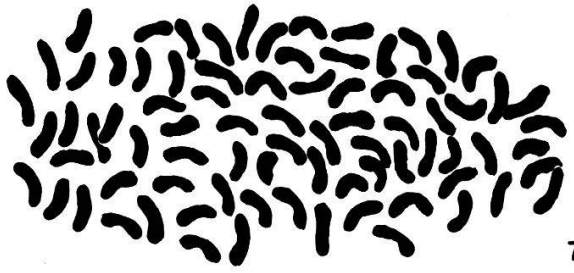


75

Figs 74-75. *Wolffia microscopica*: somatic metaphases. Collection numbers are given in parentheses. 74. 2n=40; Asia, India (7238). 75. 2n=80; Asia, India (8359).

scopica, for these authors observed the gametic chromosome number 2n=35 that should correspond to yet another polyploid cytotype i.e. 2n=70.

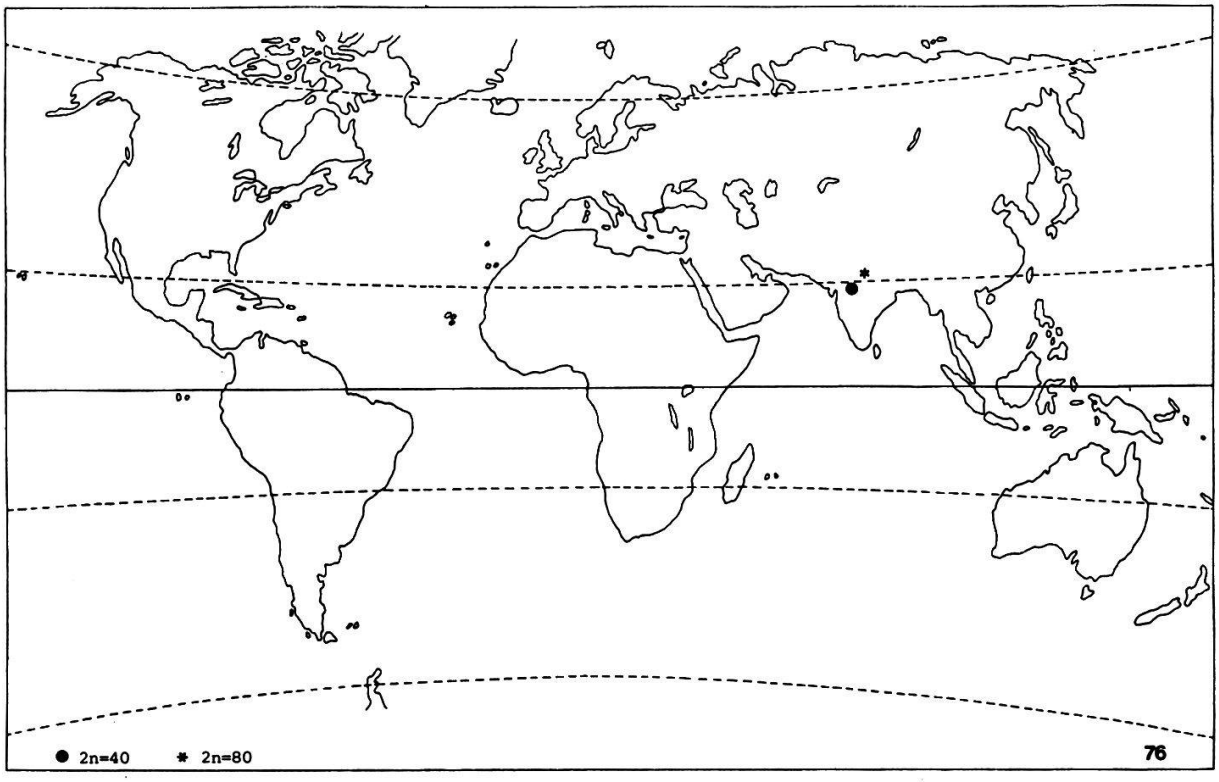


Fig. 76. *Wolffia microscopica*: geographical distribution of the studied material.

3.4.2. *Wolffia brasiliensis* Weddell

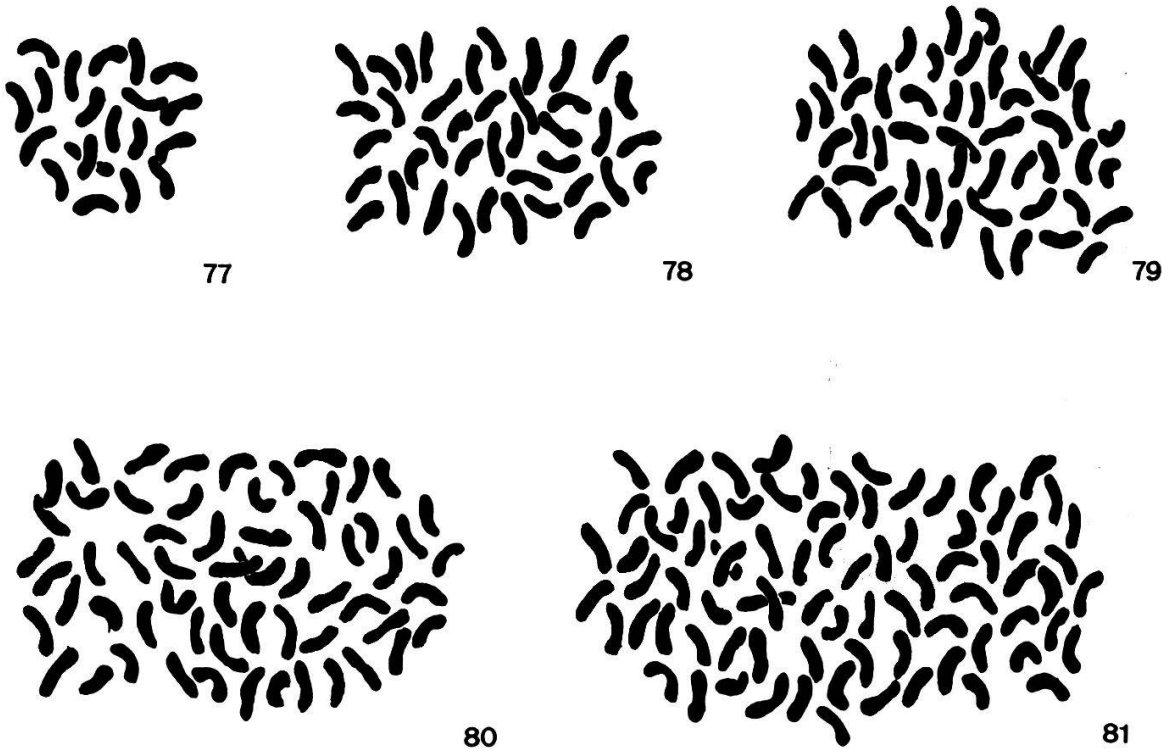
2n=20, 40, 50, 60, 80 (Figs 77-81)

W. brasiliensis was studied from 63 localities, population samples representing 36.5% of the examined material.

Intra-individual variation within *W. brasiliensis* was exceptionally rare, only a single case of aneusomaty (2n=40, 44) being observed. Mixed populations consisted of euploid and aneuploid units, but were equally infrequent. On the other hand, polyploid differentiation was distinct, numerous chromo-

some numbers being found in cytologically uniform samples (Figs 77-81). According to expectation, the tetraploid chromosome number occurred most frequently in the studied material. It is interesting to not that as much as ten pentaploid samples were found, five of them being taken in wild populations whereas the other five represented clonal cultures.

Wolffia brasiliensis was not cytologically investigated so far except for a brief study of KWANYUNEN (personal communication) who examined a culture issued from one of our pentaploid (2n=50) clones and counted only 2n=42.



Figs 77-81. *Wolffia brasiliensis*: somatic metaphases. Collection numbers are given in parentheses. 77. 2n=20; North America, Texas (7773). 78. 2n=40; North America, Mexico (7311). 79. 2n=50; North America, Texas (8088). 80. 2n=60; North America, Illinois (7104). 81. 2n=80; North America, Arkansas (8027).

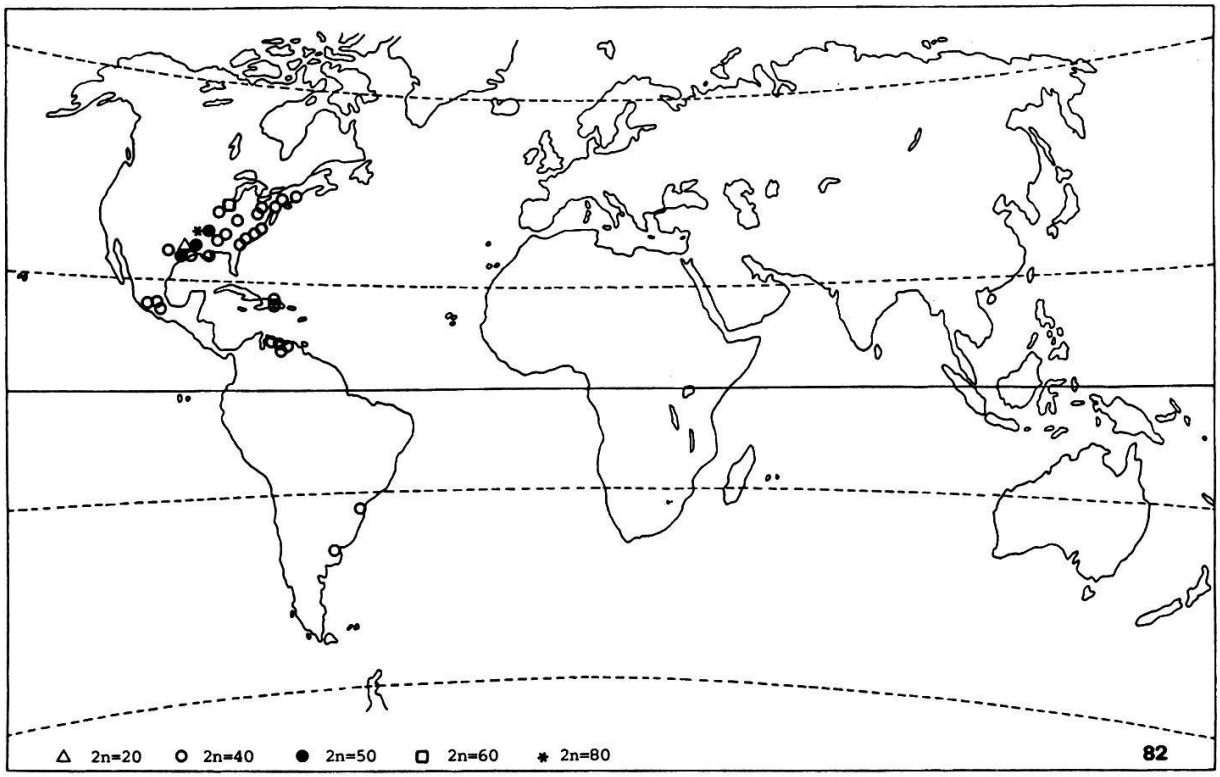


Fig. 82. *Wolffia brasiliensis*: geographical distribution of the studied material. Numerous tetraploid stations are not indicated.

3.4.3. *Wolffia borealis* (Engelm.) Landolt

2n=20, 30, 40 (Figs 84-86)

On the whole, 18 samples of *W. borealis*, mostly consisting of clonal cultures, were investigated. Intra-individual variation was observed only twice, aneusomatic fronds representing in either case different polyploidy levels (2n=20, 23; 2n=40, 38). Intra-populational variation was not found. On the

other hand, *W. borealis* revealed an interesting pattern of polyploid differentiation, diploid, triploid and tetraploid chromosome numbers being found; 2n=40 occurred most frequently.

The only record published hitherto on *Wolffia borealis* is that of MOORE (see DORE 1957) who studied this taxon under the name of *Wolffia punctata* and

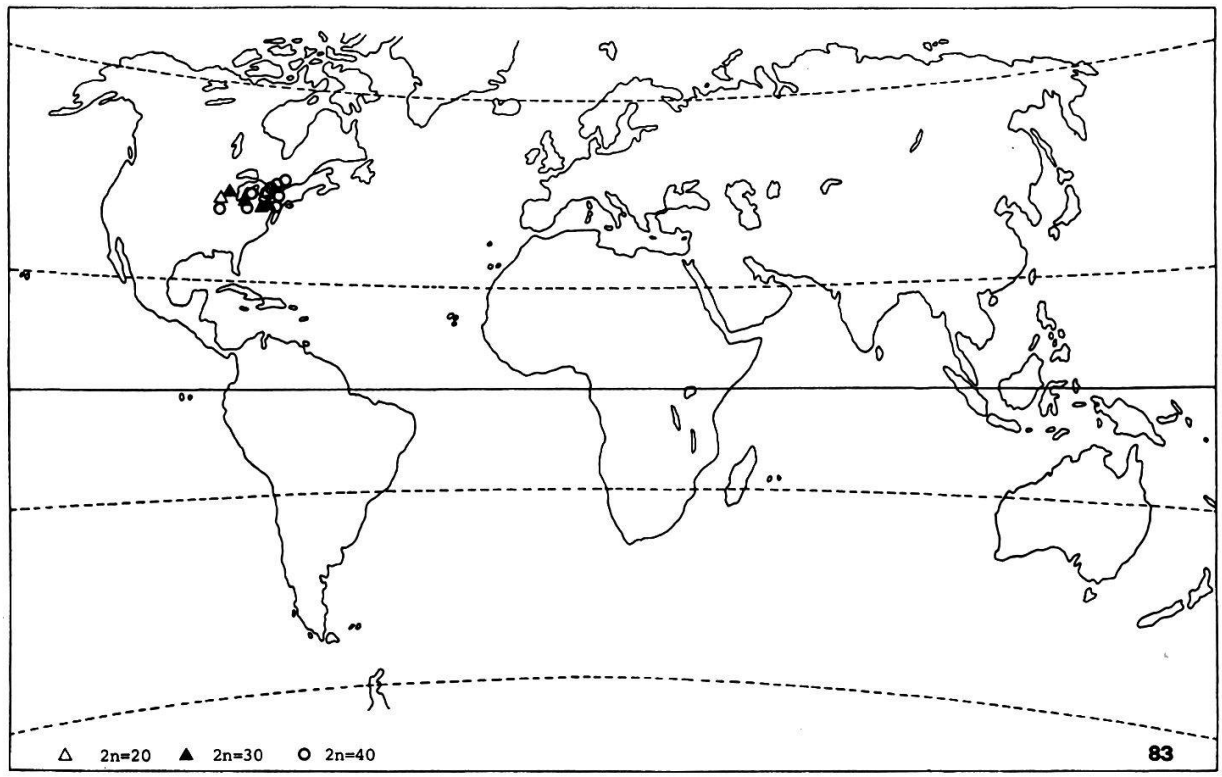
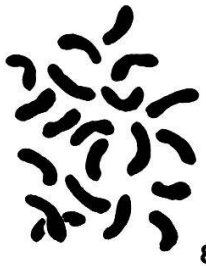


Fig. 83. *Wolffia borealis*: geographical distribution of the studied material. Some tetraploid stations are not indicated.

found about 40 chromosomes in a material from Canada. The present results are thus partly confirmed by the previous data.



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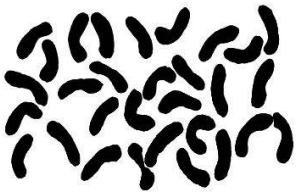

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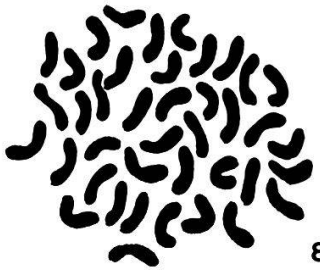


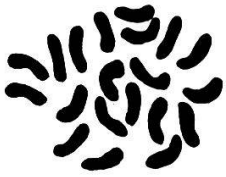
86

Figs 84-86. *Wolffia borealis*: somatic metaphases. Collection numbers are given in parentheses. 84. 2n=20; North America, Wisconsin (7690). 85. 2n=30; North America, Ohio (8587). 86. 2n=40; North America, Canada, Ontario (7577).

3.4.4. *Wolffia australiana* (Benth.) Hartog & Plas

2n=20, 40 (Figs 87, 88)

Wolffia australiana was studied from thirteen localities; only two population samples were taken in the wild, the remainder representing the clonal cultures. No intra-individual variation was observed.



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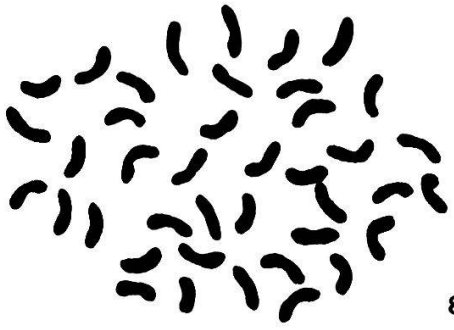


88

Figs 87-88. *Wolffia australiana*: somatic metaphases. Collection numbers are given in parentheses. 87. 2n=20; South Australia, Glencoe West (7819). 88. 2n=40; New Zealand, Nort Canterbury (7540, 8647).

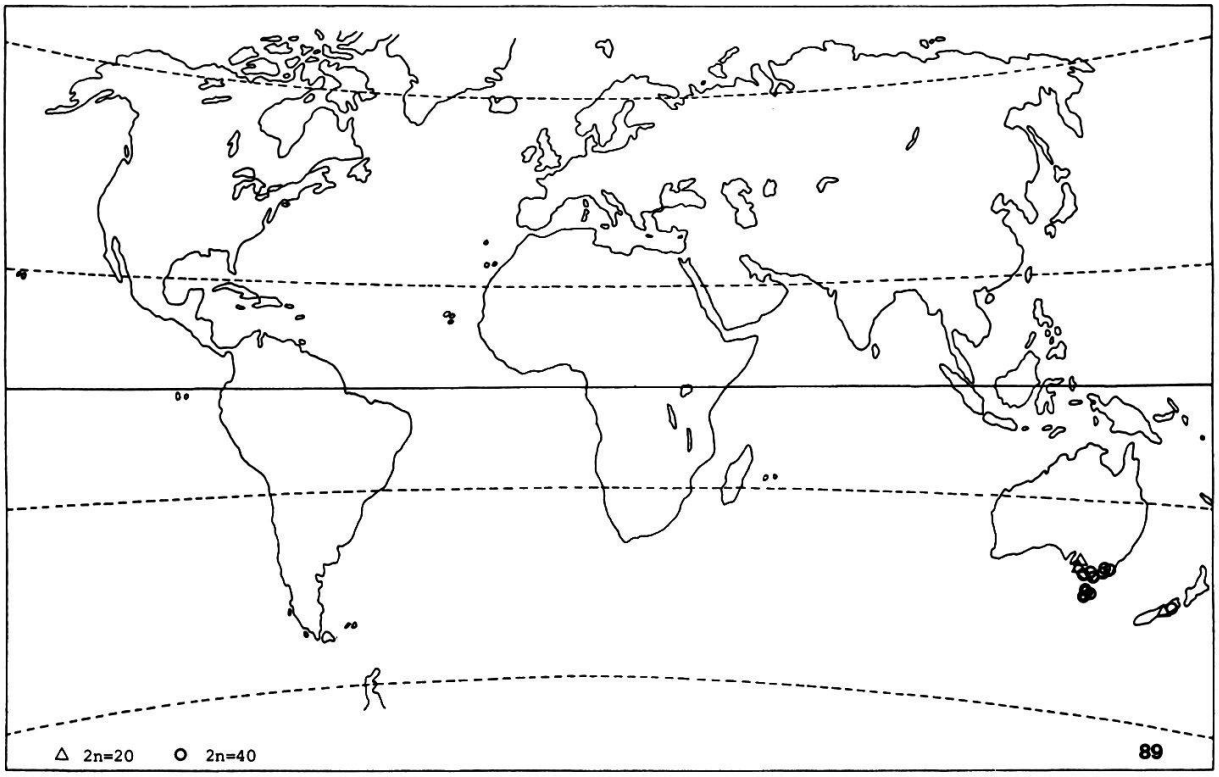


Fig. 89. *Wolffia australiana*: geographical distribution of the studied material. Some tetraploid stations in Tasmania and Australia are not included.

The limited informative value of cytological data obtained on clonal material of the duckweeds is well exemplified by the only mixed population sample originating from New Zealand. The clonal material obtained on request in 1971 was invariably diploid; however, the population sample taken by ourselves in 1979 in the wild comprised in fact both diploid and tetraploid units, the latter ones positively representing the majority (17 vs. 2).
Cytologically uniform material of *Wolffia australiana* was mostly tetraploid; in addition to ten 40chromosomic samples, two diploid ones originating from South Australia were found.
W. australiana was not cytologically studied hitherto.

3.4.5. *Wolffia angusta* Landolt

2n=40 (Fig. 91)

The Australian taxon *Wolffia angusta* was studied only from three localities. The clonal samples proved to be cytologically uniform, only tetraploid chromosome number being found.

Wolffia angusta was studied cytologically for the first time in the course of the present work.

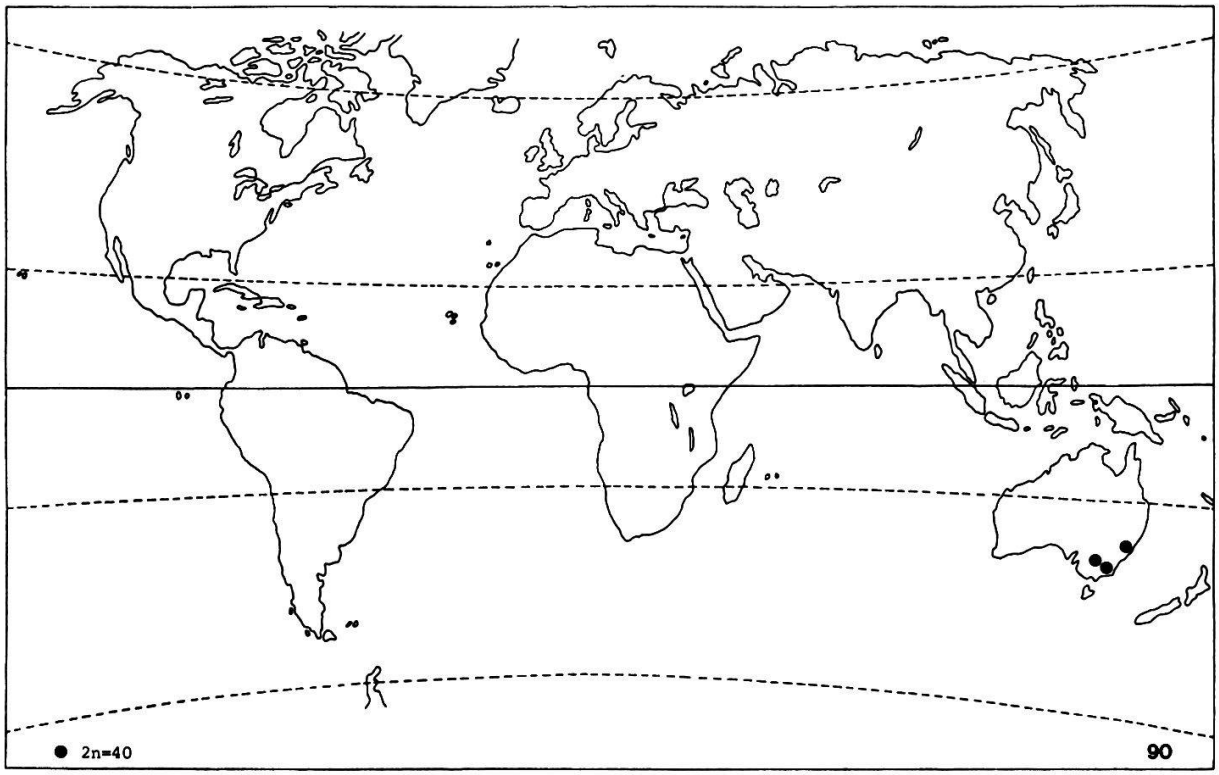


Fig. 90. *Wolffia angusta*: geographical distribution of the studied material.

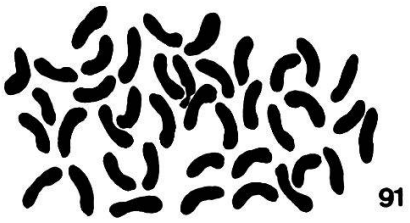


Fig. 91. *Wolffia angusta*: somatic metaphase. Collection number is given in parentheses. 2n=40; Australia, Victoria (7480).

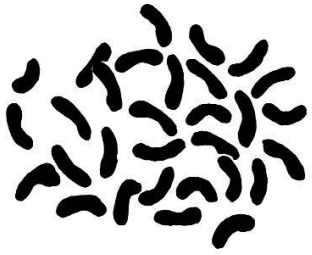
3.4.6. *Wolffia arrhiza* (L.) Horkel et Wimmer

2n=30, 40, 50, 60, 70, 80 (Figs 92-97)

Wolffia arrhiza was studied from 32 localities in Europe and Africa, all samples but one representing the clonal material.

Intra-individual variation within *W. arrhiza* was found only twice; the otherwise tetraploid clones revealed most frequently aneuploid chromosome numbers that corresponded, however, to higher levels of polyploidy (2n=40, 76; 2n=40, 50, 74). The latter clone, studied twice in 1966 and 1973 after having been obtained from two independent sources, revealed in the first series the cytological variation, whereas the second culture was uniformly tetraploid. KWANYUNEN (personal communication) found in turn an aneuploid chromosome number 2n=62 in a different culture of the same clone. It seems therefore that the intra-individual variation occasionally occurring in *Wolffia arrhiza* may sometimes be rather complex.

Cytologically uniform samples of *Wolffia arrhiza* represented five different cytotypes, the tetraploid one being the most frequent. The present results suggest thus a more pronounced cytological differentiation in *W. arrhiza* than indicated by the previous reports (2n=50, BLACKBURN 1933; 2n=44-46, LAWALREE 1943; 2n=50, WCISLO 1970).



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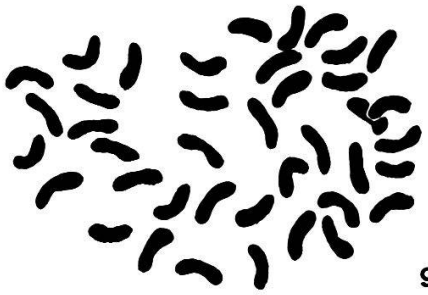

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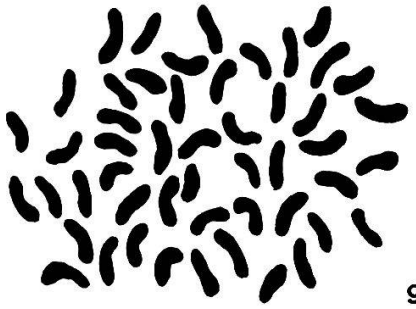

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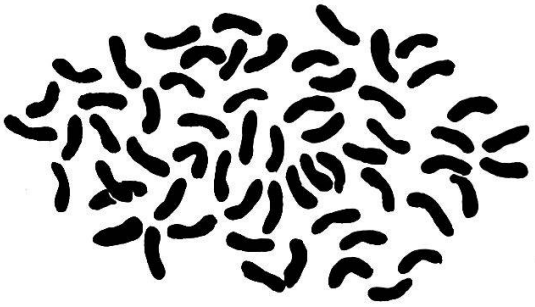

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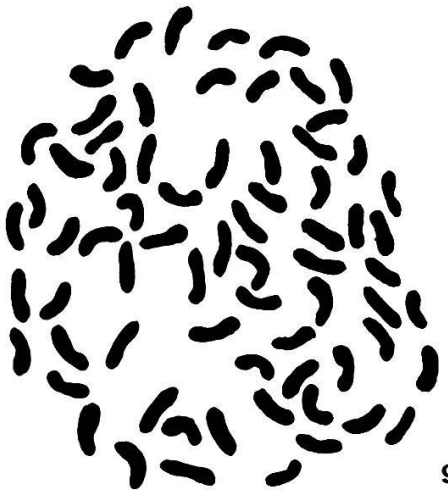

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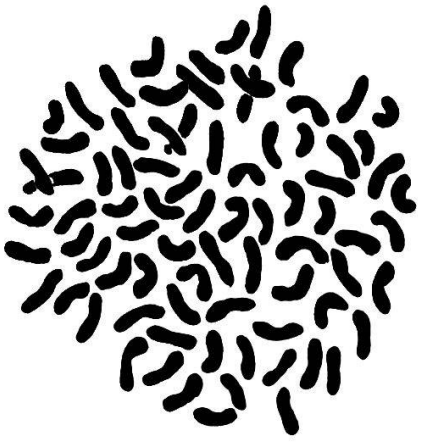


97

Figs 92-97. *Wolffia arrhiza*: somatic metaphases. Collection numbers are given in parentheses. 92. 2n=30; South Africa (7251). 93. 2n=40; Europe, Italy (8272). 94. 2n=50; Africa, Uganda (7193). 95. 2n=60; Europe, Yugoslavia (7699). 96. 2n=70; Europe, Netherlands (7158). 97. 2n=80; Europe, Portugal (7196).

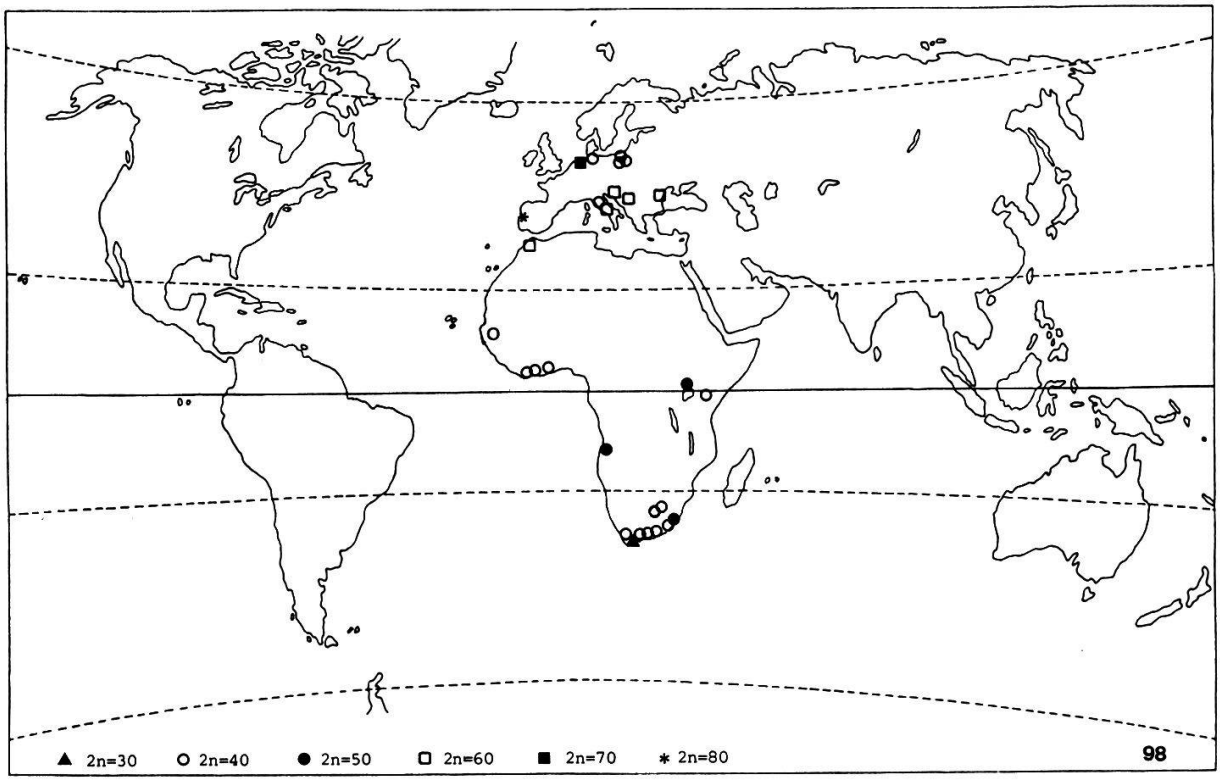


Fig. 98. *Wolffia arrhiza*: geographical distribution of the studied material. Some tetraploid stations are not indicated.

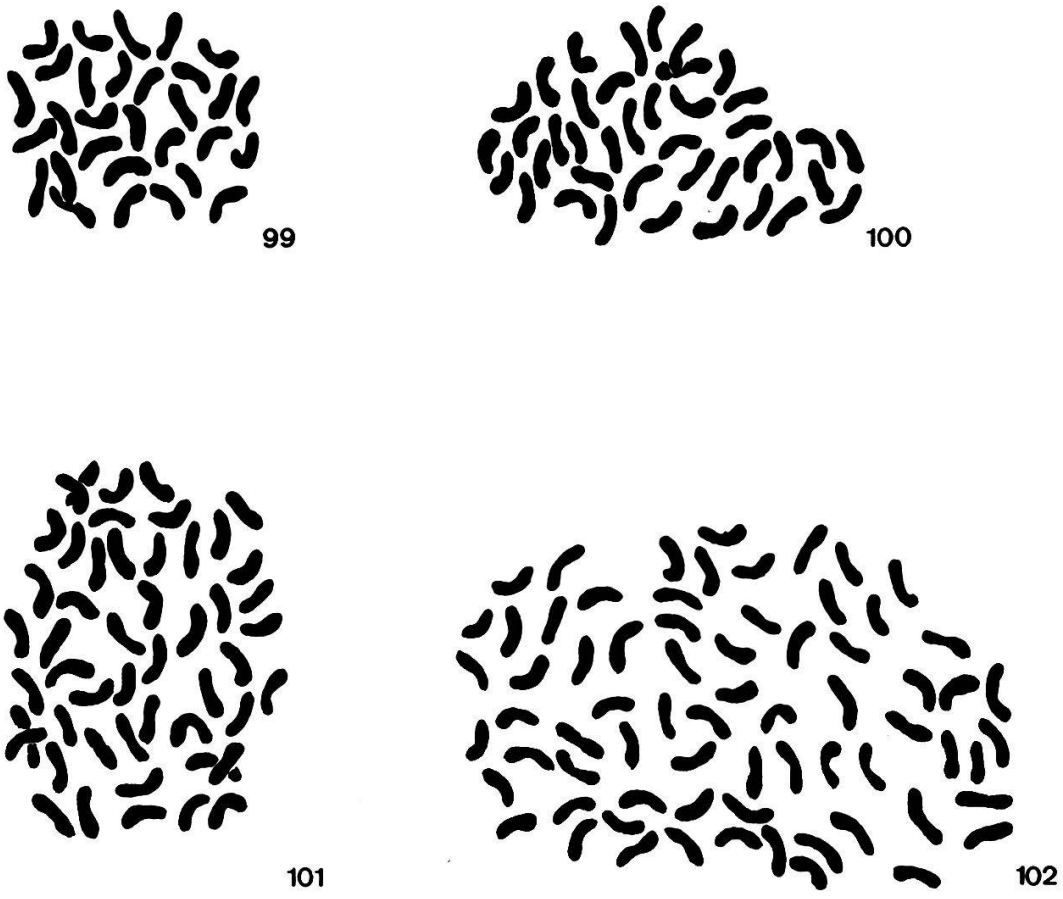
3.4.7. *Wolffia columbiana* Karsten

2n=30, 40, 50, 70 (Figs 99-102)

Wolffia columbiana was studied from 87 localities distributed in various parts of America. The examined material comprised 27 population samples taken in the wild, the remainder being represented by clonal cultures.
Intra-individual variation within *Wolffia columbiana* was rare. Only the mixoploidy was observed, all cases corresponding to the familiar for the duckweeds single-genome- or several-genome-difference pattern. A singular form of mixoploidy was found in a single clone, repeatedly obtained in 1968 and 1973 from two laboratories: in the first series, only 2n=50 was observed, whereas the second series was invariably tetraploid. It should be added that KWANYUNEN (personal communication) counted in still another part of this clone a hypertetraploid chromosome number 2n=42.

The only mixed population sample revealed tetra- and octoploid units, corresponding thus to a complete multiplication of the 40chromosomic complement.

Polyploid differentiation occurring within *Wolffia columbiana* was rather pronounced. Four different levels of polyploidy were found, the tetraploid chromosome number being, as usual, most frequently observed. Pentaploid samples were rather numerous in the studied material (Table 12).
The only report previously published on cytology of *Wolffia columbiana* is that of DAUBS (1965) who counted about 42 chromosomes in a material of unspecified origin.



Figs 99-102. *Wolffia columbiana*: somatic metaphases. Collection numbers are given in parentheses. 99. 2n=30; Canada, Ontario (7787). 100. 2n=40; North America, Texas (8077). 101. 2n=50; South America, Argentina (7231). 102. 2n=70; South America, Argentina (7716).

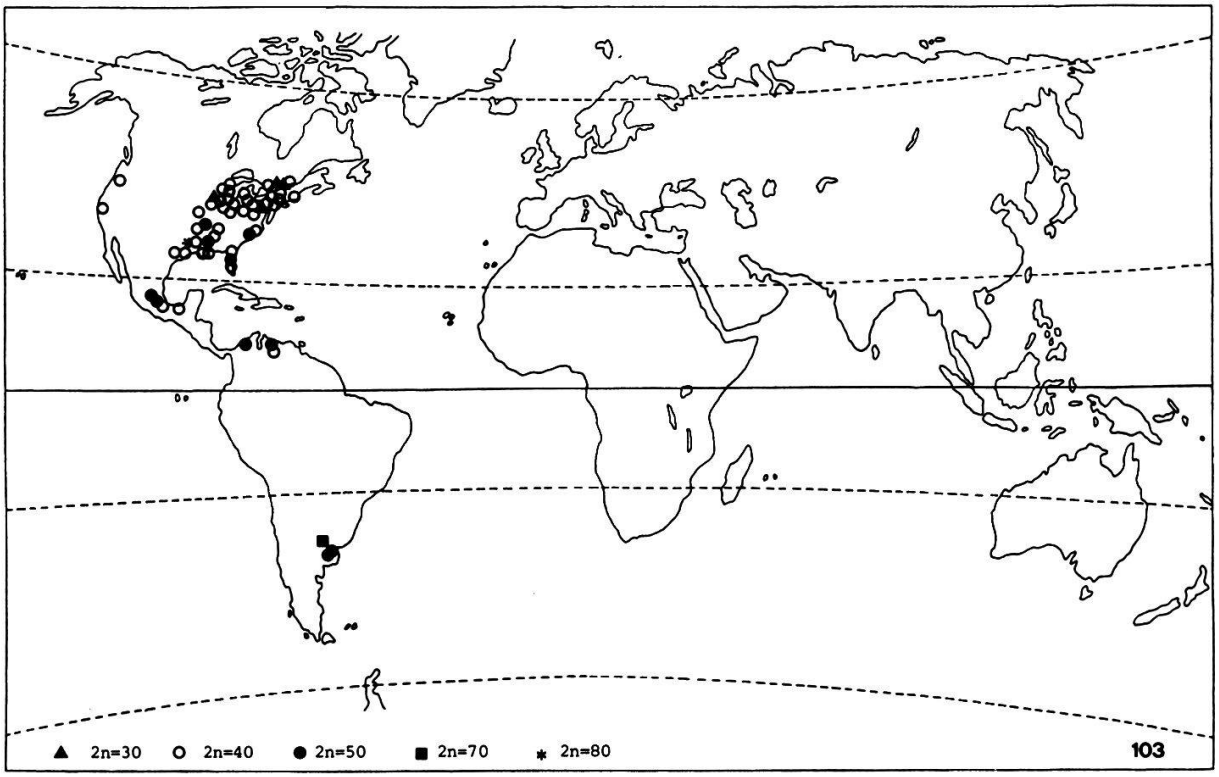


Fig. 103. *Wolffia columbiana*: geographical distribution of the studied material. Numerous tetraploid stations in North America are not indicated.

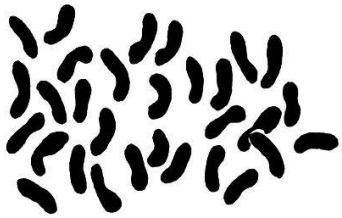
3.4.8. *Wolffia globosa* (Roxb.) Hartog & Plas

2n=30, 40, 50, 60 (Figs 104-107)

On the whole, 34 samples of *Wolffia globosa* were studied from various parts of its large distribution area; all but two represented clonal cultures. Intra-individual variation within *W. globosa* was observed only twice, the respective mixoploid clones having 2n=40, 70 and 2n=40, 80. Intra-populational variation was found in the sample consisting mostly of hexaploid units (2n=60), but comprising also a few triploid ones (2n=30).

Cytologically uniform samples of *W. globosa* represented four different levels of polyploidy (2n=30, 40, 50, 60); tetraploid chromosome number occurred in about two thirds of the studied material.

Wolffia globosa was not studied cytologically hitherto, bar the observations



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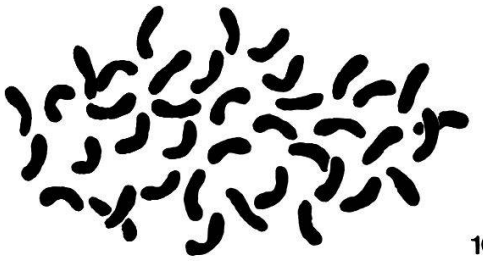

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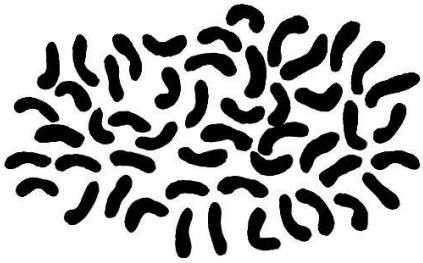

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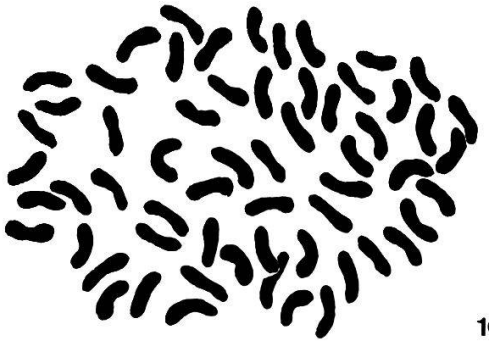

107

Figs 104-107. *Wolffia globosa*: somatic metaphases. Collection numbers are given in parentheses. 104. 2n=30; Africa, Zimbabwe (7524). 105. 2n=40; Africa, Tanzania (7340). 106. 2n=50; Asia, Indonesia (8356). 107. 2n=60; North America, California (8152).

of KWANYUNEN (personal communication) who found a hypertetraploid chromosome number 2n=46 in another part of the clone that was evaluated as tetraploid (2n=40) by the present author a few years before.

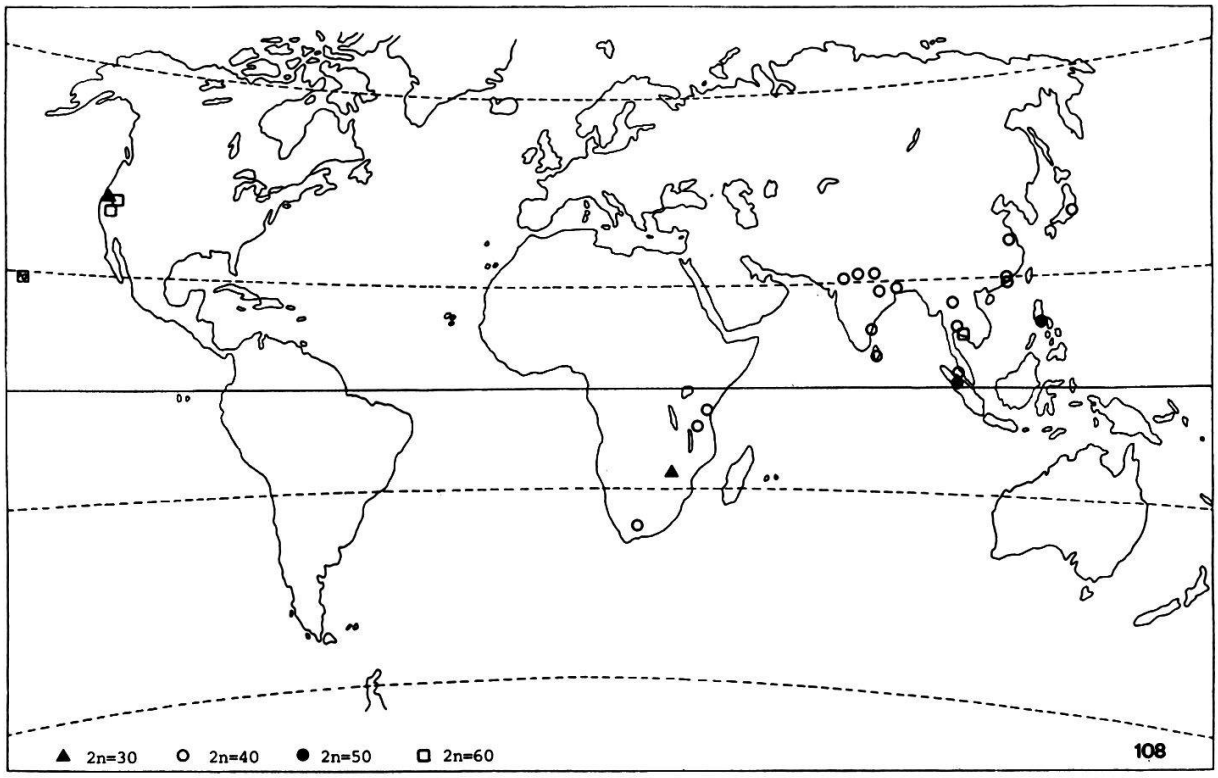

Fig. 108. *Wolffia globosa*: geographical distribution of the studied material. Numerous tetraploid stations are not indicated.

Discussion

Vegetative propagation in flowering plants represents a low-risk strategy of proliferating the genotype but avoiding all hazards involved in the sexual reproduction. The family of *Lemnaceae* offers an excellent example of such strategy, the predominant vegetative propagation accompanied by the spontaneous fragmentation of clones and reinforced by the production of turions in some taxa being a great advantage for survival and dispersion. However, a scientist studying variation within the duckweed family is faced with the dilemma of the sample choice. On the one hand, the genotype identification in wild populations of the *Lemnaceae* is practically impossible with current methods; for this reason, the useful suggestions recently made by HARPER and

WHITE (1974) and HARPER (1977) about distinguishing between genets and ramets do not seem applicable. On the other hand, a study carried out in a sterile clonal culture does give some information on an individual variation, but has an indicative rather than a definitive value, the laboratory conditions being obviously quite different from the natural environment of the duckweeds; furthermore, it cannot be decided whether the observed details are representative of a given population or represent fortuitous aberrations, only a single genotype being frequently investigated. In the present study we tried, in some cases, to compare both these aspects, but further investigations are indispensable to elucidate some of the results obtained on cytological variation within the *Lemnaceae*. The explanations offered here are thus admittedly speculative.

Clonal multiplication results in an increased longevity of given genotypes; it allows therefore for the maintenance of particular gene combinations, the genetic variation being accordingly rather limited in most cases (e.g. GRANT 1971, WILLIAMS 1975, ABRAHAMSON 1980). The duckweeds conform to this trend; as far as the cytological variation is concerned, intra-individual and intra-populational variation was only occasionally observed in the course of the present study, the respective frequencies being 3.3.% and 1.5%. The *Lemnaceae* correspond in this respect to the concept of WILLIAMS (1975) who distinguished mitotically standarized asexual offspring from meiotically diversified sexual progeny.

The stabilizing effect of vegetative propagation embraces as well its influence upon occasionally appearing mutations. Of a particular interest are in this respect mutations of the genome; as vegetative propagation permits to by-pass the detrimental effects of low fertility and/or vigour known in aneuploids and odd polyploids, the deviating chromosome numbers may be transferred to next generations. The recurrent pattern of cytological variation occurring within the whole family of *Lemnaceae* strongly suggests that the asexual reproduction plays an important rôle in differentiation mechanisms operating within this group. Intra-individual variation being apparently carried through numerous cell generations, the daughter fronds may receive various chromosome number. An aneusomatic frond could thus occasionally give rise to both eu- and aneuploid groups; mixoploid fronds could in turn contribute to the formation of groups representing different levels of polyploidy. It is also con-

ceivable that, depending on current environmental conditions, population can contract or expand; some clones might then become locally abundant and eventually colonize the whole areas, whereas the other ones disappear. The occurrence of cytologically uniform clones and colonies of the *Lemnaceae* that represent chromosome numbers deviating from the habitual for the duckweeds 2n=40 points out towards the importance of vegetative propagation to the development and maintenance of populations; in this respect, the present paper can be considered as yet another contribution to the ample documentation existing on the subject (e.g. COTTAM 1954, HARBERD 1961, ANDERSON and LOUCKS 1973, WIGHAM 1974, STEWARD and ORNES 1975, URBANSKA-WORYTKIEWICZ 1977, 1977a, 1979, 1980).

The cytological variation occurring within the family of *Lemnaceae* offers some interesting aspects. Aneusomaty was frequently considered as the result of some mitotic disturbances occurring with a particular frequency in taxa with a strong vegetative propagation (e.g. SNOAD 1955, SHARMA 1956, SINHA 1962, MEYER 1965, RYCHLEWSKI 1967). As far as the *Lemnaceae* are concerned, pronounced mitotic deviations were but exceptionally observed. It cannot be excluded that some minor deviations or/and elimination of a few chromosomes might sometimes have passed unnoticed; it seems, however, that mitotic aberrations are rather ancillary to some other factors influencing the aneusomaty in the duckweeds. Another explanation could be structural rearrangements of chromosomes, in particular fragmentations and/or translocations (BROOKS 1940, SHARMA and DAS 1954). Numerous taxa of the *Lemnaceae* manifest some differences in chromosome size within their sets; there are also indications that some chromosome sectors might be heterochromatic. It is therefore conceivable that some structural rearrangements might indeed occur; however, a positive evidence in this respect is still missing, chromosomes of the *Lemnaceae* being highly unsuitable for karyotype analysis that calls perhaps for more refined preparation techniques than those used in the present study.
Aneuploidy occurring within the family of *Lemnaceae* might as well result from a selective endoduplication, only a part of the nucleus being involved in the multiplication process. DUNCAN (1954) who studied aneusomaty in *Paphiopedilum wardii* found out that only three chromosome types were particularly liable to endoduplication, the remainder of the chromosome complement being much more

stable. Aneuploid plants occurring within diploid populations of *Cardamine pratensis* (URBANSKA-WORYTKIEWICZ and LANDOLT 1974) proved to be polysomic, the smallest pair of chromosomes being involved in this variation. GLAESS (1957) observed aneusomaty in the liver cells of rats and suggested that deviating chromosome numbers resulted from a selective endoduplication operating in chromosome groups that accounted for the viability of particular aneuploid nuclei. Results of BREMER (1949, 1959, 1961) concerning some *Saccharum*-hybrids point out that a preferential endoduplication may not only appear in vegetative tissues but also influence occasionally reproductive cells.

A preferential endoduplication as the mechanism accounting for the aneuploidy within the *Lemnaceae* remains, for the time being, an alternative open to verification. On the other hand, it seems to be a sole plausible explanation for the peculiar pattern of euploid differentiation occurring within the family.

Euploid chromosome numbers found within the *Lemnaceae* form on the whole a continuous range i.e. 2n=20, 30, 40, 50, 60, 70, 80; differences between particular levels of polyploidy correspond to a single genome, the number ten being regarded as basic for the family. As far as the intraspecific differentiation is concerned, 17 out of 21 taxa that possessed more than one euploid chromosome number corresponded, at least partly, to the single-genome-difference pattern. Mixoploid individuals carried chromosome numbers that most frequently differed from each other by a single genome; in addition, odd genome differences were sometimes observed (e.g. 2n=40, 60; 2n=40, 70; 2n=50, 80). Intra-individual polyploid differentiation is obviously well-known both in plants and animals; however, the type represented by the *Lemnaceae* seems to be rather infrequent. A comparable case represents *Zephyranthes mesochloa* propagating principally by bulbs; SHARMA and GOSH (1954) observed in somatic cells of this Amaryllid a wide range of euploid chromosome numbers (2n=42, 48, 60, 66, 72) and supposed that the multiplication of chromosomes possibly involved only members of a single genome (x=6). SHARMA and DE (1956) proposed the analogous explanation for the peculiar differentiation observed in somatic tissues of *Dioscorea alata* (2n=30, 40, 50, 70). It should be added that later on, MARTIN and ORTIZ (1963) found in *Dioscorea alata* a still wider range of euploid differentiation identical with that occurring within the family of *Lemnaceae*.

We are inclined to think that endoduplication might influence the polyploid differentiation occurring within the duckweeds. Patterns of variation observed in the mixoploid individuals suggest that a selective endoduplication might occur, sometimes repeatedly, in some cells of tetraploid plants. On the other hand, the octoploid chromosome number might result from a complete doubling of the 40chromosomic set. As mentioned before, nearly all mitoses were apparently normal and no pronounced deviations that might lead to a restitution were observed; they could not have remained undetected in our ample material originating from 1500 habitats and comprising very numerous fronds. It seems hardly acceptable anyway that either mitotic aberrations or structural rearrangements of chromosomes should regularly raise chromosome numbers just for a single genome. A detailed study on the *Lemnaceae* dealing with intervening phases of the nuclear cycle should be most desirable, as conclusive data are lacking.

Origin and significance of euploid chromosome numbers lower than 2n=40 remain ambiguous. It might be that 2n=20 and 2n=30 partly represent issues of some reversion process, reduction of chromosome numbers being sometimes observed in somatic tissues of plants (e.g. HUSKINS 1948, KITANI 1963, FELDMAN et al. 1966, BROWN and STACK 1968, STACK and BROWN 1969, SEGMEN 1971); however, no structures corresponding to a somatic reduction were found in the studied material of the duckweeds. Each of the clones with 2n=20 or 2n=30 that represented only 3.9% of the whole examined material originated from a different locality, so that the results offer no information as to the actual structure of the populations; it should be noted in this context that in two populations fixed in the wild that respectively comprised 2n=20, 40 and 2n=30, 60, fronds with the lower chromosome number represented the minority. On the other hand, 55.9% of all diploid and triploid clones were found within the genus *Spirodela*; it cannot therefore be excluded that, in some cases, chromosome numbers 2n=20 and 2n=30 might indicate some ancestor types. This suggestion, however, requires further verifications; studies on cytological variation within populations of *Spirodela* from South and Central America and especially those on *S. intermedia* should be particularly important in this respect.

Some aspects of cytological variation observed in the studied material suggest that the *Lemnaceae* may sometimes be cytologically instable. In our previous paper (URBANSKA-WORYTKIEWICZ 1975) we reported intriguing fluctuations in chromosome numbers observed in a clonal culture of *Lemna minor* over a few-year-period; comparable cases were occasionally found in the course of the present work. For instance clonal material of *Wolffia columbiana* sent us from two independent sources in 1968 and 1973 revealed a different chromosome number viz. 2n=50, 2n=40 in either series; the cultures of *Wolffiella oblonga* first received in 1968 from one source and then twice (1971, 1973) from another laboratory, had in the first series 2n=70, in both others 2n=40. Two strains of *Lemna aequinoctialis*, studied by the present author in 1970 and 1973, were invariably pentaploid (2n=50); this year, they were sent on request to Japan, where chromosome numbers representing a higher level of polyploidy i.e. 2n=78, 81 were found (TAKIMOTO, personal communication). Cytological instability in plants is little known, well-documented cases being very rare in the literature (e.g. BRITTON and HULL 1956, LEWIS 1962, 1970, 1970a, LEWIS et al. 1971, FAVARGER 1975, 1978); it should be noted that these reports deal mostly with more or less continuous variation, whereas in the *Lemnaceae* different polyploidy levels were usually revealed. No long-range study, except the outstanding contribution of LEWIS (1970) has included so far the effect of time upon chromosomal variability within a single wild population; investigations in clonal material of some *Lemnaceae* carried out over a longer time-span should be most interesting.

In conclusion, a comment upon a general philosophy of the chromosome counts in cytologically difficult groups should be offered. In his excellent review, FAVARGER (1978) pointed out towards two principal causes of discrepances appearing in the literature viz. 1) possible errors and 2) infraspecific differentiation comprising not only geographical but also less known intra-individual and intra-populational variation. Our results obtained on the *Lemnaceae* differ partly from other reports. We don't qualify those data as erroneous, preferring to consider them as indications of the complex cytological variation occurring within the family of *Lemnaceae*. The duckweeds are not only exceedingly difficult as far as a chromosome study is concerned, but also present great problems when their morphology is examined. According to LANDOLT

(1980, see p. 13 of the present volume) "... it is sometimes difficult to distinguish between particular species without having observed living plants at various developmental stages". This dynamic approach seems advisable in further studies on cytological variation in the *Lemnaceae*, for it gives more chance of coming to satisfactory conclusions when we ask how much of what we find is accident or design.

Summary

Cytological variation was studied in 30 taxa of the family of *Lemnaceae*, material from 1500 localities being examined.
The duckweed family offers an excellent example of a low-risk life strategy based upon a predominant or exclusive vegetative reproduction, its genetic variation being accordingly limited. The recurrent pattern of cytological variation observed within the *Lemnaceae* strongly suggests that the asexual reproduction plays an important and stabilizing rôle within this group.
Three levels of cytological variations were observed:
1) intra-individual variation occurring in form of aneusomaty and/or mixoploidy;
2) intra-populational variation (aneuploidy or polyploidy);
3) "racial" differentiation corresponding to clones and populations that were cytologically uniform yet represented various cytotypes.

Euploid chromosome numbers of the *Lemnaceae* formed a continuous range viz. 2n=20, 30, 40, 50, 60, 70, 80, the tetraploid number 2n=40 being positively the most frequent. Mixoploid individuals as well as populations and taxa possessing more than one euploid chromosome number conformed most frequently to a curious single-genome-difference pattern; it is supposed that a selective endoduplication might influence this variation.
Origin and significance of euploid chromosome numbers lower than 2n=40 remain ambiguous. 2n=20 and 2n=30 might partly result, on the one hand, from some reversion processes; on the other hand, particular frequency of these numbers observed within some taxa of the genus *Spirodela* might indicate some ancestor types. The problem remains open to further verifications.
Some aspects of cytological variation suggest that the duckweeds may sometimes be cytologically instable; long-range studies, comprising ageing clonal cultures, are advised.
In conclusion, a comment upon a general philosophy of the chromosome counts in cytologically difficult groups is offered.

Zusammenfassung

An 30 Arten der Familie der Lemnaceen wurde die zytologische Variation untersucht. Insgesamt fanden 1500 Proben verschiedener Herkünfte Berücksichtigung.

Die Familie der Lemnaceen liefert ein ausgezeichnetes Beispiel einer Lebensstrategie mit vorwiegend oder ausschliesslich vegetativer Vermehrung und entsprechend beschränkter genetischer Variabilität. Das innerhalb der Lemnaceen beobachtete Muster der zytologischen Variation deutet darauf hin, dass die asexuelle Fortpflanzung für diese Verwandtschaftsgruppe eine wichtige stabilisierende Rolle spielt. Es wurden drei Stufen zytologischer Variation beobachtet:

1. Intra-individuelle Variation in Form von Aneusomatie und/oder Mixoploidie;
2. Variation innerhalb der Populationen in Form von Aneuploidie oder Polyploidie;
3. "Rassen"-Bildung: zytologisch einheitliche Klone und Populationen bilden voneinander verschiedene Zytotypen.

Die euploiden Chromosomenzahlen der Lemnaceen entsprechen einer fortlaufenden Reihe von 2n=20, 30, 40, 50, 60, 70, 80. Die tetraploide Zahl 2n=40 war weitaus am häufigsten vorhanden. Mixoploide Individuen, wie auch Populationen und Arten die mehr als eine Chromosomenzahl aufwiesen, zeigten sehr oft ein eigenartiges Muster von Chromosomenzahl-Unterschieden in einem einzigen Genom. Es wird vermutet, dass eine selektive Endoduplikation an diesem Muster mitwirkt.

Die Entstehung und Bedeutung der euploiden Chromosomenzahlen unterhalb von 2n=40 sind unklar. Einerseits könnten die Zahlen 2n=20 und 2n=30 als Rückbildung verstanden werden; andererseits deutet die besondere Häufigkeit dieser Chromosomenzahlen bei der Gattung *Spirodela* auf ursprüngliche Verhältnisse hin. Das Problem muss noch weiter abgeklärt werden.
Einige Aspekte der zytologischen Variation lassen vermuten, dass die Lemnaceen gelegentlich zytologisch instabil sein können. Langfristige Untersuchungen an alternden Klonen sind wünschenswert.
Zum Schluss werden einige Betrachtungen über Chromosomenzählungen bei zytologisch schwierigen Verwandtschaftsgruppen angestellt.

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