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Contribution to the Cytotaxonomy and Cytogeography of the Flora of the Western Himalayas (with an attempt to compare it with the Flora of the Alps). Part III.

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In the last part of this series the cytological studies on several families of the Sympetalae are concluded. [1])

Gesneriaceae

The family *Gesneriaceae* comprises 85 genera and 1100 species (Willis, 1966), and is distributed in tropical and subtropical regions of both the hemispheres.

Fourteen genera, some of which are monotypic, are restricted to China. Few species of the genus *Streptocarpus* have their habitat in South Africa and Madagascar. The monotypic genus *Rhabdothamnus* is endemic to New Zealand. Some genera are found growing in the New World also. Three species of the genus *Klugia* grow in Southern India and one species in Mexico.

The family is represented in India (after Hooker, op. cit.) by 129 species, some of which grow at low and medium altitudes in Himalayas (subtropical and temperate Himalayas). The number of species of *Gesneriaceae* is smaller in Western Himalayas than in Eastern Himalayas. Six species belonging to three different genera are endemic to some mountains of Europe (Balkan Peninsula, and Pyrénées).

Clarke (in Hooker, 1885) classified the family, on the basis of capsule characters, into five tribes: *Trichosporeae, Didymocarpeae, Leptoboeae, Epithemeae* and *Eucyrtandreae.* Later Fritsch (1895) made a revision of the classification with some alterations. He divided the family into two subfamilies, *Cyrtandroideae* and *Gesnerioideae* on the basis of flower

[1]) The publication of this series was made possible by a generous contribution of the State of Neuchâtel (Switzerland).

Table 7: *OROBANCHACEAE*

Taxa	Source and altitude	Collection number	Chromosome number n	2n	Level of ploidy	Previous report
	Species from the Western Himalayas studied by the author (A)					
Subfamily Orobanchaceae bicarpellatae Genus Orobanche (Tournef) G. Beck Section Osproleon Wallroth						
Orobanche epithymum D.C.*	Basudhara, 3800 m Kumaon	2012	19	–	4x	
O. kashmirica Clarke*	Balthal, 2900 m Kashmir	4279	19	–	4x	
	Species from Europe studied by the author (B)					
O. alba Stephan. (= *O. epithymum* D.C.)	Jura Hills, Neuchâtel Switzerland	–	19	–	4x	
Section Trionychon Wallroth *O. purpurea* Jacq.	Plateau de Ceillac, 1600 m, French Alps (Prof. C. Favarger)	–	12	24	2x	

* Chromosome number of the species reported for the first time

characters: the flower is hypogynous in the first subfamily, whereas it is more or less epigynous in the second. These two taxa represent two lines of parallel evolution from nearly actinomorphic flowers to zygomorphic flowers. Each subfamily is again divided into several tribes. The subfamily *Cyrtandroideae* is predominantly distributed in the Indomalayan region.

Cytological investigations undertaken up to now were mostly confined to chromosome counts. Main contributors are Sugiura (1939), Thathachar (1942), Rogers (1954), Eberle (1956), Fussell (1958), Ratter (1963), Ratter and Prentice (1964), Lee (1962a, 1966a, b) and Contandriopoulos (1966). Most of the earlier chromosome studies have been on material from different botanical gardens.

Our cytological investigations are reported on Table 8.

Discussion

Didymocarpus Wall. (syn. *Roettlera* Vahl.) of the subfamily *Cyrtandroideae*, tribe *Didymocarpiae*, is a genus consisting of 120 species (Willis, 1966), distributed in India, Malaya, South China and Madagascar, Australia and tropical Africa. Hooker (1885) has described 40 species from India.

D. pedicellata Br. occurs in subtropical W. Himalayas between an altitude of 800 to 1400 m in damp places. Distribution is confined to Kumaon only. Chromosome number at MI is counted as 18 bivalents (Fig. 143).

Didissandra Clarke. comprises some 33 species, 30 of which are distributed in India and China, while 3 species are reported from India alone.

D. lanuginosa Clarke. is met in temperate Himalayas at an altitude of 1200 m in damp places. No species is met in Kashmir. Fig. 144 shows 10 bivalents at MI of meiosis.

Chirita Hamm. is a large genus of *Gesneraceae* comprising 80 species distributed in Indomalayan regions (Willis, op. cit.). Three species are described from India by Hooker (op. cit.).

C. bifolia Don. Prodr. is collected from Bowali (1600 m). It is common at this altitude in Kumaon. Chromosome counts clearly show 12 bivalents and 4 univalents at diakinesis of meiosis (Fig. 145).

C. pumila Don. Prodr. occurs in subropical Himalayas at an altitudinal range of 500–1800 m in rare localities, as small groups. Four bivalents were counted at MI of meiosis (Fig. 146).

Platystemma Wall. of the tribe *Championieae* is a monotypic genus represented only in the Himalayas. It is a small herb with violet flowers.

P. violoides Wall. is found in Mussoorie and Nainital regions of Kumaon in abundance on the walls along roadsides. Counting of chromosomes reveals 20 bivalents at MI of meiosis. Secondary association of bivalents seems to be a feature at this stage (Fig. 147). Later course of meiosis is normal.

Six species of *Rhynchoglossum* Blume. of the tribe *Klugieae*, are reported from Indomalaya and Formosa (Willis, 1966).

R. obliquum Blume. is common up to 1500 m in the W. Himalayas. Chromosome number is 18 bivalents at MI (Fig. 148).

Table 8: *GESNERIACEAE*

Taxa	Source and altitude	Collection number	Chromosome number n	2n	Level of ploidy	Previous report
Subfamily Cyrtandroideae						
Tribe Didymocarpeae						
Didymocarpus pedicellata Br.*	Ranibag, 1400 m Nainital	2575	18	–	4x	
Didissandra lanuginosa Clarke*	Ranikhet, 1900 m	2557	10	–	2x	
Chirita bifolia D. Don*	Bowali, 1850 m	2582	14	–	4x	
C. pumila D. Don	Nainital, 1900 m	2581	4	–	2x	n = 4, Ratter 1963
Tribe Championieae						
Platystemma violoides Wall.*	Nainital, 1900 m	2559	20	–	4x	
Tribe Klugieae						
Rhynchoglossum obliquum Blume*	Garampani, 1400 m	2030	18	–	4x	

* Chromosome number of the species reported for the first time

Six species belonging to five genera of *Gesneriaceae* have been studied in the present work. The chromosome numbers of five of them were reported for the first time.

The cytological data of Sugiura (1940) and Thathachar (1942) enabled them tho assess x = 9 as the basic number of the genus *Didymocarpus.* On this basis, *D. pedicellata* (n = 18) is on a tetraploid level. The basic number of the genus *Didissandra* seems to be x = 10 *(D. lanuginosa).*

Chirita pumila, with n = 4, provided the lowest base number of the genus (cf. Ratter, 1963). *C. bifolia* (n = 14) might have arisen from x = 4, or from another base number probably x = 7 which is one of the basic numbers suggested for the family by Sugiura (1940). In the light of the present work, a review of the chromosome counts in the genus *Chirita* clearly indicates that the genus possesses several basic numbers (x = 4, (7), 9) probably starting from the lowest number x = 4. The gametic number 14 does not necessarily come from x = 7, but perhaps through amphidiploidy between 4 and 10.

The high chromosome number n = 20 of *Platystemma violoides* showed a polyploid origin. The secondary pairing of bivalents at MI in this species may provide another support to this conclusion.

Rhynchoglossum obliquum with n = 18 also seems to be polyploid on a basic number 9.

From the literature and from the current data, it may be concluded that polyploidy played an important role in chromosomal evolution of the 5 genera of *Gesneriaceae* currently studied.

The inclusion of the genera *Chirita* and *Didymocarpus* as sections of a large genus, *Roettlera, in Fritsch's* classification seems to be well supported by the similarity of their basic chromosome numbers (x = 4 and x = 9). Besides, in *Chirita,* we have species with n = 14 and n = 17. The few representatives of the family in Europe are comparatively high polyploids, and *Ramonda serbien* (Contandriopoulos, op. cit.) has the highest somatic number (2n = 96) counted hitherto in *Gesneriaceae,* after *Aeschynanthus ellipticus* (Ratter and Prentice, 1969).

Ramonda, Haberlea and *Jankaea* are paleopolyploid genera. A migration from Himalayas or China is not likely for the European *Gesneriaceae.* It seems more probable that they would derive from a stock of *Gesneriaceae* already present in South Europe at the middle Tertiary.

Acanthaceae

The family *Acanthaceae* including 250 genera and 2500 species (Willis, 1966) is the ninth largest family of dicotyledonous plants. According to fossil records of *Strobilanthes* obtained by Velenovsky and Viniklar (1931), it is believed that the *Acanthaceae* date back to the Cretaceous period. This pantropical family has four centers of distribution: Indomalaya *(Strobilanthes* and *Andrographideae),* Brazil *(Ruellia),* Central America *(Aphelandreae* and *Odontonema)* and Africa *(Barleria).* In Europe, it is represented by only a few species of the genus *Acanthus,* which grow in the Mediterranean region. No species of this family has reached

Central Europe. About twelve genera are found throughout the Tropics. These include the two largest genera of the family: *Justicia* and *Ruellia* with 325 and 225 species, respectively (Grant, 1955). Subtropical species are found in Australia, South Africa, China, Japan and the United States. Nineteen genera have species both in Africa and Asia (Willis, 1949). Nearly 120 genera are monotypic and restricted in range.

Acanthaceae are considered by many botanists to have been derived from the *Scrophulariaceae* or stocks ancestral to them. Bessey (1915) placed the family in the *Scrophulariales;* Wettstein (1924), Engler and Diels (1936) and Emberger (1960) placed it in the order *Tubiflorae* and Bentham and Hooker (1876) and Hutchinson (1948) in the order *Personales.*

Hooker (1885) reported 49 genera and 250 species under *Acanthaceae* from British India. They grow at altitudes which range from plain level to about 2100 m. The members are predominantly represented at lower altitudes between plain level and 1800 m beyond which only a few species ascend.

Clarke (in Hooker op. cit.) has divided the family into 5 tribes: *Thunbergieae, Nelsonieae, Ruellieae, Acantheae* and *Justicieae.* Lindau (1895) also using pollen characters in his classification, distinguished four subfamilies: *Nelsonioideae, Mendoncioideae, Thunbergioideae* and *Acanthoideae,* the last one comprising numerous tribes. Van Tieghem (1908) proposed to group the first three taxa of Lindau in a separate familiy: *Thunbergiaceae,* whereas the last one constitutes the *Acanthaceae, sensu stricto.* Bremekamp (1938, 1948, 1953) using chiefly characters of the sporoderm has proposed many changes in the internal taxonomy of the family but he was not followed by Melchior (1964). An interesting discussion upon these taxonomical problems was made by Long (1970).

Important contributions with respect to the cytology of this family have been made by Sugiura (1936a, b, 1939, 1940), Bowden (1940), Narayanan (1951a-d), Rangaswamy (1941), Mukherjee (1952), Grant (1955), Joseph (1961), Ellis (1962), Miège (1962), Mangenot and Mangenot (1962), Kaur (1965, 1966), De (1963, 1966), Bhat and Tandon (1967), Verma and Dhillon (1967), Mehra and Gill (1968), Kaur and Nizam (1970).

Our cytological results are reported on Table 9.

Discussion

Chromosome numbers of 12 species are new reports out of the 31 species of *Acanthaceae* belonging to 15 genera presently studied. The lowest chromosome number observed is n = 9 in *Strobilanthes dalhousianus* and *Justicia quinque-angularis* while the highest number is n = 42 in *Lepidagathis purpuricaulis.* Most of the species investigated so far have rather high chromosome numbers which makes the assessment of polyploidy difficult. In general, the chromosome size is small, except in the species of *Barleria.*

Thunbergia shows 3 basic numbers, x = 7, 8 and 9 (Darlington & Wylie, op. cit.). The present finding of n = 14 for *T. erecta* (a perennial species cultivated in Northern India) places the taxon from Haldwani at a tetraploid level on x = 7. This report differs from the previous counts of 2n = 52 (Narayanan, 1951), 2n = 56 (Grant, 1955) and 2n = 64 (Mangenot and Mangenot, 1962), thereby indicating intraspecific polyploid and perhaps aneuploid races in the species. The chromosome numbers of *Thunbergia* known so far (Bolkhovskikh, op. cit.) suggest that variation in chromosome number has been important in speciation in this genus.

Hygrophila spinosa and *H. polysperma* with n = 16 agree with the results of earlier authors (Table 9A) except for Sugiura's report (1940) of 2n = 24 for the former species. Darlington & Wylie (l.c.) suggested x = 12, 16 as base numbers

for *Hygrophila* while Grant (1955) considered 8 as the probable basic number of the genus. Grant (1955) states that „*Hygrophila* appears to be a natural group since these chromosome number determinations were representative of both the Old and New World species". The subsequent observations of De (1966) and of Miège (1962) have confirmed the somatic number 2n = 32. Therefore, it seems that this genus is a paleopolyploid one with basic number x = 8.

Ruellia tuberosa shows intraspecific aneuploidy with 2n = 32 (Sugiura, 1936b; Narayanan, 1951a) and 2n = 34 or n = 17 (Narayanan, 1951a; Grant, 1955; Ellis, 1962; De, 1963; and author). Darlington & Wylie (l.c.) suggested x = 16, 17, 18 as base numbers for *Ruellia*. De (1966) regarded 16 as the basic number of the genus and suggested that numbers 2n = 34 and 36 could have arisen through aneuploid addition of one or two chromosomes, respectively. As all of the 25 species of *Ruellia* studied by Grant (1955) have 2n = 34, we are inclined to think that 17 is the basic (secondary) number of this genus and that 2n = 32 or 36 represents exceptional cases of aneuploidy. *Ruellia* also would be a paleopolyploid genus.

Aechmanthera tomentosa with n = 15 confirms the previous finding of Verma & Dhillon (1967). Since *Aechmanthera* is a small genus of three species, x = 15 may be the basic chromosome number. This genus is again a paleopolyploid one.

Hemigraphis latebrosa with n = 14 is cytologically studied for the first time. Grant (l.c.) recorded n = 14 and 2n = 28 for *H. drymophila* and considered 7 as the probable basic number of the genus. However, Kaur (1965) has counted 2n = 26 in *Hemigraphis rupestris*. (See Fig. 149 for the present count).

Strobilanthes is a large genus with 250 species (Willis, op. cit.) growing in tropical Asia and Madagascar. Hooker described about 150 species from India. Most of the species are shrubs or subshrubs with perennial habit. Many occur gregariously, forming almost the sole undergrowth in forests. This is one of the rare genera of *Acanthaceae* growing up to the alpine regions. For example, *S. wallichii* Nees grows up to 3200 m. *S. atropurpureus* Nees is confined to the Western Himalayas from Kashmir to Nepal between 1800 and 2300 m.

S. dalhousianus Clarke is a suberect shrub, restricted to the Western Himalayas, frequent between 1800–2400 m. This species exhibits morphological variation. (1) The comparison between the normal type and a variant is made in Table 9B. Both the type and his variant have the same gametic number n = 9. This genus is interesting from a cytomorphological angle. Seven, presently studied species show gametic chromosome numbers 9, 11, 13, 14, 16 and 20, respectively, indicating the probable role of dysploidy in the evolution of species. Four species (*S. atropurpureus* n = 16, *S. glutinosus* n = 14, (Figs. 150–153), *S. quadrangularis* n = 11 and *S. wallichii* n = 20) are chromosomally known for the first time. *S. alatus* with n = 16 agrees with Mehra and Gill's report (1968); *S. dalhousianus* and *S. anisophyllus* showing gametic chromosome numbers 9 and 13, respectively, agree with the counts of Verma and Dhillon (1967). According to Grant (l.c.) 7 and 10 (5) are probably the basic numbers from which the polyploid series arose. In the light of the present results, it seems likely to ascertain the following basic numbers for this genus: x = 6, 7, 8, 9, 10, 11.

(1) **Picture 6 shows the morphotypes of *Strobilanthes dalhousianus*.**

Blepharis boerhaaviaefolia with n = 14 differs from the chromosome count of n = 13 by Kaur (1966). The genus seems to be polybasic with x = 6, 7, 8, 9 (cf. Miège, 1962). (See Fig. 155).

Barleria gibsoni (n = 20) is chromosomally studied for (Fig. 154) the first time. *B. prionitis* with n = 20 supports the chromosome count of this species by De (1966) but disagrees with the carlier finding of 2n = 30 by Narayanan (1951a). Narayanan (1951a) reported 2n = 34, 36, 38 and 40, for varieties of *Barleria cristata* with withe, pink, striped and blue flowers, respectively. Reports by other workers on the same species are n = 20 or 2n = 40 (Ellis, 1962; De, 1963; Verma & Dhillon, 1967; the present study) and 2n = 38 (Grant, l.c.). The chromosome numbers known in the genus are 2n = 30, 34, 36, 38, 40, 42 (cf. De, 1966). This evidently points out the significant role of aneuploidy in evolution at intra- and interspecific level within the genus. According to De (1966), 15 could be taken as the basic number of the genus since 30 is the lowest zygotic number in *Barleria.* In the present state of knowledge, it is very difficult to know if the genus *Barleria* is polybasic (x = 7, 8, 9, 10) or if the numbers differing from 2n = 40 are brought about by fragmentations and fusions.

Three cytotypes are known in *Crossandra undulaefolia* Salish. (= *infundibuliformis* Nees.) with n = 19 or 2n = 38 (Grant. 1955; Ellis, 1962; Verma & Dhillon, 1967; and present study), 2n = 20 (Narayanan, 1951a), and 2n = 60 (De, 1966). De (l.c.) took x = 10 as the basic number for the genus and thought that the origin of the 2n = 38 complement came through the loss of one chromosome from the gametic set at tetraploid level. As Mangenot and Mangenot (1962) have found 2n = 42 in *Crossandra flava,* the same alternative as in the genus *Barleria* (x = 7, 9, 10 or an aneuploidy from 2n = 40) seems to be applicable to *Crossandra.*

Lepidagathis purpuricaulis showing n = 42 is reported (Fig. 156) for the first time. *L. cuspidata* with n = 11 agrees with the report of Verma & Dhillon (1967). Miège (1962) attributed the basic number x = 10 to this genus, because *L. anobrya* from Africa possesses 2n = 20. Therefore, it seems likely that *Lepidagathis* would be polybasic with x = (7), 10 and 11, but the somatic number 42 (see Bolkhovskikh *et al.*) may also proceed from 2n = 40 through aneuploidy.

Out of the five species of the genus *Justicia,* studied (Figs. 159, 157) cytologically, the chromosome number of *J. diffusa* (n = 9) and (Fig. 158). *J. pubigera* (n = 14) are recorded for the first time. For their chromosome numbers, the species *J. simplex* (n = 18) (*), *J. quinqueangularis* (n = 9) are in line with earlier authors (See Table 9A). The chromosome number of *J. gendarussa* differs from that found by other authors (2n = 32, Narayanan, 1951a; 2n = 30, Joseph, 1961) but agrees with the count of Basak (1959). Darlington & Wylie (l.c.) have suggested x = 14 as the basic chromosome number of the genus *Justicia,* and De (op. cit.) x = 12. Grant (1955) and Long (1970) believed 7, 8, 6 or 9 to be probable basic numbers for this genus.

The discovery of species with 2n = 18 allows us to conclude that 9 is one of the basic numbers of the genus *Justicia,* the other ones being 6, 7, 8. With regards to the gametic numbers 13 and 15, they probably originated through amphidiploidy (6 + 7 and 6 + 9) and this fact stresses the role of polyploidy in the evolution of this genus.

(*) *J. simplex* has also a diploid race with n = 9 (Pal, 1964 in Bolkhovskikh *et al.*).

The chromosome number of *Adhatoda vasica* was found to be n = 17 by many workers (see Table 9A) including the author, but intraspecific polyploidy in this species was established by Grant (l.c.) who reported 2n = 56. According to Grant (l.c.) x = 7 is the basic number of the genus, and *A. vasica* would be a „tetraploid in comparison to *Justicias* with 28 chromosomes". In the view of the author, x = 17 is also a basic number for the genus but a secondary one which perhaps came from 9 + 8 through amphidiploidy. This opinion would imply that in a single species, *Adhatoda vasica,* the three basic numbers 7, 8 and 9 existing in *Justicia* are represented.

Haploid chromosome number 26 for *Rungia parviflora* is (Fig. 160) reported for the first time. The two species cytologically studied earlier show a great difference in their diploid chromosome numbers: *R. repens* with 2n = 20 (Narayanan, 1951a; Ellis, 1962) and *R. pectinata* with 2n = 50 (De, 1966). De (1966) has suggested x = 10 as the basic number of the genus. In the light of the results on *Dicliptera (videte infra),* a genus from the same tribe, it appears that one basic number of *Rungia* is x = 13, besides x = 10. As regards the somatic number 2n = 50 considered by De as pentaploid, it could also proceed from 2n = 26 through aneuploidy.

Two species of *Dicliptera* were currently investigated. *D. bupleuroides* (n = 13) and *D. roxburghiana* (n = 13) show the lowest chromosome number in the genus so far recorded. In contrast, *D. assurgens* and *D. brachiata* having somatic number 2n = ca. 80 (Grant, 1955) are representatives of higher polyploids of the genus. These two species are perhaps hexaploids with 2n = 78 (= 6 x 13). Besides x = 13, this genus seems to possess x = 10 and x = 12 (Bolkhovskikh *et al.,* op. cit.).

Chromosome number of *Peristrophe speciosa* (n = 15) is the first chromosome report for the species. The gametic chromosome number 15 observed for *P. bicalyculata* agrees with Ahuja (1955) and Verma & Dhillon (1967) but differs from 2n = 20 reported by Narayanan (1951a). It is suggested that x = 15 may be considered as one of the basic numbers of the genus *Peristrophe,* the other ones being x = 10 and perhaps x = 7.

Three facts are striking in the karyology of the *Acanthaceae* studied here.

1. Out of fifteen genera, twelve are polybasic; besides, the two genera in which the basic number is x = 15 or x = 17, are probably polybasic too, because these numbers could have arisen secondarily from x = 7, 8 and 9 through amphidiploidy. Grant (1955) has determined the following basic numbers (5), 6, 7, 8, 9, 10 and 11 in the same family. The present observations are entirely in agreement with Grant's assertion and no gametic chromosome number was discovered which could not be explaned with such a basis. Most of the genera are built upon 7, 8 and 9 which are considered by Grant as predominant. Such a situation makes the use of chromosome numbers in the taxonomy and phylogeny of the *Acanthaceae* somewhat problematical. Grant thinks that „the frequency of basic chromosome numbers of 7, 8 and 9, and the extensive range of chromosome morphology suggest the reticulate nature of the genera and species". It may also be explained as a case of parallel evolution of the caryotype (Favarger, 1962).

2. The gametic numbers of most of the species hitherto studied in the *Acanthaceae are relatively high.* No gametic number lower than x = 9 was reported, and many

Table 9: *ACANTHACEAE (A)*

Taxa	Source and altitude	Collection number	Chromosome number n	2n	Level of ploidy	Previous report
Subfamily Thunbergioideae						
Thunbergia erecta T. Anders.+	Haldwani, 400 m	2028	14	–	4x	2n = 52, Narayanan 1951 2n = ca. 56, Grant 1955 2n = 60, Mangenot & Mangenot 1957 2n = 64, Mangenot & Mangenot 1962
Subfamily Acanthoideae						
A. Contortae						
Tribe Hygrophileae						
Hygrophila polysperma T. Anders.	Haridwar, 300 m	2097	16	–	4x	2n = 32, Grant 1955
H. spinosa T. Anders.	Pinjore, 400 m	2070	16	–	4x	2n = 32, Rangaswamy 1941 Miège 1962 Grant 1955 2n = 24, Sugiura 1937, 1940 n = 16, Verma & Dhillon 1967 Mehra & Gill 1968
Tribe Strobilantheae						
Hemigraphis latebrosa Nees*	Kasauli Road, 800 m Kalka	2058	14	–	4x	
Aechmanthera tomentosa Nees	Thogave, 1000 m Kumaon	2048	15	–	?	n = 15, Verma & Dhillon 1967
Strobilanthes glutinosus Nees *	Bowali, 1850 m	2051	14	–	4x	
S. quandrangularis Clarke *	Didihut, 1500 m Kumaon	2044	11	–	2x	
S. dalhousianus Clarke	Nainital, 1900 m	2580	9	–	2x	n = 9, Verma & Dhillon 1967
S. anisophyllus T. Anders.	Chandigarh, 300 m	2065	13	–	nx	n = 13, Verma & Dhillon 1967
S. alatus Nees	Nainital, 1900 m	2573	16	–	4x	n = 16, Mehra & Gill 1968
S. wallichii Nees *	Nainital, 1900 m	2022	20	–	4x	
S. atropurpureus Nees *	Tangmarg, 2100 m Kashmir	4320	16	–	4x	
Tribe Ruellieae						
Ruellia tuberosa L.	Dehra Dun, 450 m	2605	17	–	?	2n = 32, Sugiura 1936 2n = 34, Bowden 1940, 1945 2n = 32, 34, Narayanan 1951 Grant 1955 Ellis 1962 De 1963
Tribe Barlerieae						
Barleria prionitis L.	Pinjore, 400 m	2098	20	–	4x	2n = 30, Narayanan 1951 2n = 40, Raman & Kesavan 1964, 1965 n = 20, De 1963
Barleria cristata L.	Chamoli, 700 m Kumaon	2027	20	–	4x	2n = 34, 36, 38, 40, Narayanan 1951 2n = 38, Grant 1955 2n = 40, De 1963 n = 20, Ellis 1962 Verma & Dhillon 1967
B. gibsoni Dalz.*	Chandigarh, 300 m	2064	20	–	4x	
B. Imbricateae						
Tribe Acantheae						
Blepharis boerhaaviaefolia Pers.+	Pinjore, 400 m	2073	14	–	4x	n = 13, Kaur 1966
Crossandra infundibuliformis Nees	Chandigarh, 300 m	2054	19	–	4x	2n = 20, Narayanan 1951 2n = 38, Grant 1955 2n = 60, De 1963 n = 30, De 1963 n = 19, Ellis 1962 Verma & Dhillon 1967
Lepidagathis cuspidata Nees	Nainital, 1900 m	2515	11	–	2x	n = 11, Verma & Dhillon 1967
L. purpuricaulis Nees*	Jeolikot, 1400 m Nainital	2517	42	–	12x	
Tribe Justicieae						
Justicia gendarussa L.	Dehra Dun, 450 m	2078	14	–	4x	2n = 28, Basak 1959 2n = 30, Joseph 1964 2n = 32, Narayanan 1951a
Justicia pubigera Wall.*	Chamoli, 700 m Kumaon	2018	14	–	4x	
J. quinqueangularis Koen.	Surajpur, 350 m	2069	9	–	2x	2n = 18, Ahuja & Natarajan 1957 n = 9, Verma & Dhillon 1967
J. diffusa Willd.*	Garampani, 1000 m	2563	9	–	2x	
J. simplex D. Don	Garampani, 1000 m	2565	18	–	4x	2n = 36, Grant 1955 Ellis 1962 n = 9, Pal 1964 n = 18, Verma & Dhillon 1967 n = 14, Mehra & Gill 1968
Adhatoda vasica Nees	Kathgodam, 500 m	2529	17	–	nx	2n = 34, Hardas & Joshi 1954 Mukherjee 1952 2n = 56, Grant 1955 n = 17, Verma & Dhillon 1967 Mehra & Gill 1968
Tribe Odontonemeae						
Subtribe Diclipterinae						
Peristrophe bicalyculata (Vahl) Nees	Bageswar, 1400 m	2043	15	–	?	2n = 20, Narayanan 1951 2n = 30, Verma & Dhillon 1967 n = 15, Ahuja 1955
P. speciosa Nees*	Kalka, 600 m	2056	15	–	?	
Rungia parviflora Nees *	Hanumanmandir, 1600 m	2025	26	–	?	
Dicliptera roxburghiana Nees	Nainital 1900 m	2511	13	–	2x	n = 13, Verma & Dhillon 1967
D. bupleuroides Nees	Govindghat, 2100 m Nainital	2539	13	–	2x	n = 13, Verma & Dhillon 1967

* Chromosome number of the species reported for the first time
\+ A new chromosome report for the species

Table 9B: Salient morphological features of the morphotypes of *Strobilanthes dalhousianus*

Characters	Normal	Variant
Locality and altitude	Nainital, 1900 m	Nandaprayag, 1400 m
Habitat	Shady places	Open dry places
Habit	Erect, branched	Semi-erect, profusely branched
Stem	Four-angled, thick, hairy	Cylindrical, thin, non-hairy
Leaves	Opposite, arrangement with one large and small leaf on either side	Opposite, arrangement with one large and small leaf on either side
Length of lamina	18–25 cm	6–10 cm
Breadth of lamina	4–6 cm	1.5–2.0 cm
Inflorescence axis	Short	Long

Table 9C: *Hypothetical basic numbers of different genera of acanthaceae (in brackets)*

	Probable basic numbers x =	Gametic numbers observed (the lowest is underlined)
Thunbergia	7, 8, 9	*9*, 14, 16, 24, 28, 32
Hygrophila	8	*16* (Sugiura: 12)
Ruellia	17 (= 8 + 9)	*17* (16?, 18?)
Aechmanthera	15 (= 7 + 8)	*15*
Hemigraphis	(6?), 7, 13 (= 6 + 7)	*13*, 14
Strobilanthes	6, 7, 8, 9, 10, 11	*9*, 10, 11, 15, 16, 20
Blepharis	6, 7, 8, 9	*12*, 13, 15, 17
Barleria	(7), (8), 9, 10 (15 = 7 + 8)	*15*, 19, 20
Crossandra	7, 9, 10	*10*, 19, 21, 30
Lepidagathis	6, 7, 10, 11	*10*, 11, 12, 21, 42
Rungia	(6?), (7?), 10, 13 (= 6 + 7)	*10*, 26
Dicliptera	6, 7, 10, 13 (= 6 + 7)	*13*, 20, 24
Peristrophe	7, (8), 10, 15 (= 7 + 8)	*10*, 15, 21
Justicia	6, 7, 8, 9	*9*, 12, 13, 14, 15, 16, 17, 18
Adhatoda	7, (8), (9), 17 (= 8 + 9)	*17*, 28

Table 10: *PLANTAGINACEAE*

Taxa	Source and altitude	Collection number	Chromosome number n	2n	Level of ploidy	Previous report
	Species from the Western Himalayas studied by the author (A)					
Plantago major L.	Ranikhet, 1900 m	2596	18	–	6x	2n = 12, Löve & Löve 1965a, etc. (cf. Bolkhovskikh *et al.* 1969)
	Pahalgam, 2100 m Kashmir	4221	6	–	2x	
P. lanceolata L.	Tangmarg, 2100 m Kashmir	4220	6	–	2x	2n = 12, 24, 96, McCullagh 1934 2n = 12, Mulligan 1961b (for others, cf. Bolkhovskikh *et al.* 1969)
	Species from Europe and Asia studied by the author (B)					
P. major L.	Neuchâtel, Switzerland	–	–	12	2x	
P. lanceolata L.	Neuchâtel, Switzerland	–	–	12	2x	
P. asiatica L.	East Siberia (Moscow) U.S.S.R.	–	–	36	6x	2n = 12, McCullagh 1934 2n = 24, Fujiwara 1956a Subramanyan & Kamble 1966 2n = 36, Rahn 1966
P. intermedia Gilib.*	S. de Peney, Chanée, N. Grand Bois, Switzerland	–	–	12	2x	
P. media L.	Jura Mountains, Neuchâtel Switzerland	–	12	–	4x	2n = 12, 24, Raba 1954, 1957, 1966 2n = 24, McCullagh 1934 etc. (cf. Bolkhovskikh *et al.* 1969)

* Chromosome number of the species reported for the first time

Table 10C: Analysis of cytomorphological characters of *P. major* L. from W. Himalayas and Europe

Characters	Nainital 1900 m	Lahorkhet 2100 m	Dehra Dun 450 m	Kedarnath 3600 m	Srinagar 1650 m	Gulmarg 2700 m	Khilanmarg 3000 m	Neuchâtel Switzerland	Simplon/Valais Switzerland
Habitat	Marshy clay soil in shady places	Wet sandy soil, exposed place	Wet sandy soil	Open, grassy ground	Wet clay soil, near roads	Open grassy ground with large population	On grassy meadows, widespread population	Open ground with clay and sandy soil	Roadsid open places
Growth habit	Semi-erect	Erect	Erect	Upper leaves erect with prostrate lower leaves	Ascendent	Prostrate	Prostrate	Semi-erect	Semi-erect
Plant height cm	60	50	60	6	40	6	3.5	45	35
Aver. no. of leaves	18	14	16	9	8	10	5	12	15
Length of petiole cm	30–35	16–20	15–25	2–3	4–7	4–5	0.7–2.0	10–13	9–14
Shape of leaves	Radial,	Radial,	Light	Light	Bright	Creen, Green,		Light	
Shape of leaves	Radial, lanceolate, dark green	Radial, green, lanceolate	Light green, lanceolate	Light green, non-hairy leaf surface	Bright green, oval shape with wavy margin	Green, ovate, hairy surface	Green, ovate, with wavy margin	Light green, ovate, undulate margin	Light green, ovate, undulate margin
Length of leaves cm	10–15	11–14.5	20–25	3–4.5	10–12	3–5	1.3–3	12–14	8–11
Breadth of leaves cm	2.5–3.5	2.2–4.8	3–7	2–2.8	4–6	2.3–2.5	0.7–2	8–10	7–8
Length of the scape cm	7–8	3–4.5	10–14	2–4	15–30	3–4.5	1–4.8	20–22	14–16
Nature of the spike	Laxed	Laxed	Laxed	Cylindrical	Cylindrical	Cylindrical, compact	Short compact with laxed flowers	Semi-compact	Compact
Length of spike cm	8–10	3–4.6	13–18	1.6–3	14–40	1.6–3.5	0.7–2	12–15	9–11
No. of seeds per capsule	7–10	5–10	8–10	7–8	5–7	8–10	7–9	7–9	8–9
Stomatal size μ	34 μ x 24 μ	32 μ x 22 μ	32 μ x 22 μ	29 μ x 18 μ	28 μ x 18 μ	31 μ x 20 μ	30 μ x 20 μ		
Chromosome (n)	18	18	6	6	6	6	6	6	6

species possess such gametic numbers as 13, 14, 15, 16, 17 suggesting an old phenomenon of polyploidization. Therefore, some genera, as *Ruellia* and *Aechmanthera,* were regarded by the author as paleopolyploids (Favarger 1961). This fact is in line with the finding of a high percentage of polyploidy in the tropical African flora by Mangenot & Mangenot (1962). Moreover, from these high (secondary) basic numbers, more recent polyploids have arisen which would be classified by Favarger (op. cit.) as meso- and neo-polyploids. The family *Acanthaceae* seems to have already undergone a very long evolution during which *ancestral species with low basic chromosome numbers* have disappeared. However, this evolution is not completed and has been pursued by recent phenomena of polyploidization (see under 3.).

3. As a survey of the literature points out, intraspecific polyploidy and aneuploidy are very frequent in the family *Acanthaceae.* The multiplicity of chromosome numbers can be partly explained by a misidentification of the species or by wrong counts, but an important part of this variation is certainly not an artificial one. Unfortunately, nothing is known about geographical distribution or ecology of these „chromosome races". It would be very important in the future to give more attention to these aspects. The presence of such neopolyploids in a tropical flora is somewhat astonishing. Perhaps it was favoured by the herbaceous habit of numerous *Acanthaceae,* by recent or subrecent events such as changes of climate and migrations, or also by the influence of man.

Plantaginaceae

This small family of *Bicarpellatae* consists of 3 genera with 270 species (Willis, 1966). Hooker has described 10 species from India. Hegi (1914) recorded 15 species of *Plantaginaceae* from Central Europe. The members are annual or perennial herbs. Many of them have a vast distribution.

Systematic treatment of the family was first made by Barnéoud (1845). Decaisne (1852) split the genus *Plantago* into 17 sections. Harms and Reiche (1895) classified the family into 3 genera: *Litorella, Plantago* and *Bougueria.* The genus *Plantago* was split again into 2 subgenera: *Euplantago* and *Psyllium.* The subgenus *Euplantago* was divided into 11 sections. Pilger (1937) made a detailed systematic study of the family on the basis of the system adopted by Harms and Reiche.

Even though cytological investigations have been made by many authors (McCullagh, 1934; Böcher, 1943; Böcher *et al.,* 1953, 1955; Rahn, 1957; Ono, 1954 and Cartier, 1970), the great phenotypic variability, a characteristic feature of the members of the family, especially of the genus *Plantago,* still remains as an interesting aspect to study. Hence, a detailed cytomorphological study was undertaken now on two species: *Plantago major* and *P. lanceolata* (1), both growing in abundance in Himalayas and in Europe.

The cytological results of the present investigations are recorded on Table 10.

(1) Böcher (1943) has accurately studied the variation and biology of *P. lanceolata* from Europe. Hence, detailed study of this species from Europe is not attempted here.

Plantago major is a highly polymorphous species distributed from circumpolar arctic regions to Alaska, U.S.A., Europe, Africa, Asia minor, Central Asia, Himalayas, Siberia, Tibet, Mongolia, China, Manchuria, Korea, Saghal, Kuril, Formosa and Malaysia.

Cytological investigations were made on young roots of *P. major,* from seeds collected in W. Himalayas, at various altitudes and latitudes. Meiosis was studied from the flower buds fixed at Neuchâtel and at the Simplon in Switzerland. Chromosome counts were made too on the seed samples received from 50 different places in Europe. It could be observed that in the whole of Europe (see Table 10C), *P. major* grows as diploid (2n = 12). In Himalayas, the populations studied are diploid in Kashmir and in Mussoorie regions (Fig. 161), but those from Kumaon region uniformily revealed a hexaploid chromosome number (Fig. 162). Since, both the chromosomal types possess morphological variation, a comparison was made for different characters between the two cytotypes collected from different places (Table 10C). In a previous paper (Favarger et Vasudevan, 1972), it was supposed that the hexaploid plants from Kumaon belong to *P. asiatica.*

A karyotypical study of the somatic complement of a (Fig. 166) hexaploid *P. asiatica* obtained from the Botanical Garden of Moscow and collected in East Asia revealed 11 chromosome pairs with median centromere, 6 chromosome pairs with submedian centromere and the remaining 1 pair with subterminal centromere. One pair of the chromosomes with subterminal centromere also possessed a pair of satellites, and one pair of median chromosomes possessed a secondary constriction. The chromosome size in general resembled the size of chromosomes in diploid (2n = 12) *P. major* (Favarger and Vasudevan, 1972). As to the morphology of this Asiatic plant, it was similar to that of the plant collected in Kumaon (see under).

A clear example of cytomixis was observed in an individual (n = 6) from Mussoorie. At MI of the meiosis, cytoplasmic connections with chromatin contents were observed between the PMC's (Fig. 163). Some PMC's showed as many as 8 bivalents instead of the normal number of six, while few others showed one, two or five bivalents in a cell (Fig. 163). At AII, lagging chromosomes were not uncommon. About 15% pollen sterility was observed after staining the pollen with acetocarmine. The plant with cytomixis also showed a partial failure in seed setting.

P. lanceolata Linn. is a perennial species which occurs in the W. Himalayas from Kashmir to Kumaon at an altitude between 1500–3400 m. It normally grows on open grassy ground. It is very common in Europe.

Chromosome number of plants both from Europe and the Himalayas, as determined from meiosis, is n = 6 at MI. Morphological variation is found to be prevalent in this species as in *P. major.* A Table (10C) summarizing the variability of morphological types observed in different parts including different altitudes in W. Himalayas, is given.

P. intermedia Gilib. collected in Switzerland revealed (Fig. 164) a somatic number of 2n = 12. Somatic complement consists of 5 pairs of chromosomes with median centromere, and one pair with submedian centromere. Two pairs of the chromosome set possess satellites. The chromosome count of this species is made for the first time. (Fig. 165).

Discussion

It is interesting to note that in *Plantago major sens. lat.,* all the populations from Europe, so far examined, are diploids; the nearest allied species, *P. intermedia* Gilib. (one population studied) is diploid too. In so far as it may be possible to adopt a definite position in a very confused situation, the Asiatic polyploids belong to the following taxa:

P. major var. *asiatica* Decne. = *P. asiatica* L.

Tetraploids and hexaploids in Japan
(besides diploids after McCullagh, 1934)

Hexaploids from East Siberia
(the present author)

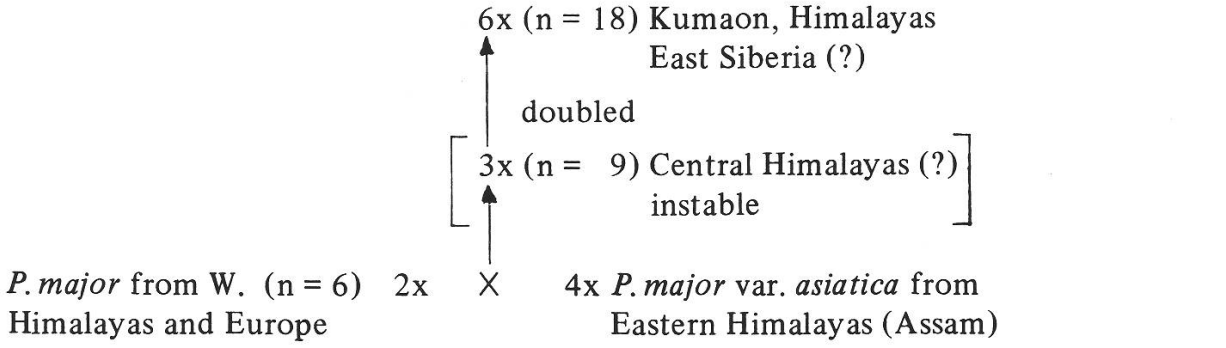
Tetraploids from Assam (Eastern Himalayas)
(Subramanyam and Kamble, 1966)

Hexaploids from Kumaon (Western Himalayas)
(the present author)

P. major var. *japonica* (Fr. et Sav.) O. Ktze = *P. japonica* Franch. et Savat.

Hexaploids in Japan (McCullagh, 1934,
besides diploids, Sinotô, 1925 etc.)

All these polyploids are localized on the borders of the area of *P. major sens. lat.* In the present state of knowledge, it is difficult to know if the Western Himalayan area of the hexaploids is, or is not, connected with that of the East Siberian one, through Tibet and Mongolia. In a previous paper (Favarger and Vasudevan, 1972), it was supposed that the hexaploids from Kumaon originated through amphidiploidy between the diploid *P. major* from Kashmir and the tetraploid plants from Assam. This suggestion may be depicted as follows:



One does not know up to what point the East Siberian populations depend on the Himalayan hexaploids. In Japan, where diploids are found besides tetraploids and hexaploids, a similar evolution of the whole complex could have taken place, perhaps at an earlier time, since the taxa *P. japonica* and *P. asiatica* seem to be more differentiated in this country.

Regular bivalent formation with normal meiosis and 100% pollen fertility noticed in the hexaploid *P. major* from Kumaon gives enough evidence to believe that the „race" is an allohexaploid. Occurrrence of both intraspecific and interspecific polyploidy in many species of *Plantago* has already been noticed by many authors (McCullagh, 1934; Böcher *et al.*, 1953, 1955; Ono, 1953;

Gorenflet, 1960 and Cartier, 1970). Extensive geographical distribution covering a vast area with various ecological nitches may be one of the causes of the successful establishment of polyploids in the genus. The evolutionary significance of the cytomixis found in an individual from Mussoorie (Himalayas) is worth considering here. Viable pollen grains developed from the aberrant FMC of the plant showing cytomixis, may probably lead to the polyploid or aneuploid race of the species. This assumption is further supported by the presence of partial seed setting in the taxon with cytomixis. This individual may be perhaps a hybrid between a diploid *P. major* and a diploid *P. asiatica* (?) which would be existing in Central Himalayas but has not been reported yet.

In the collective species *P. coronopus* L., Gorenflot (1960) believed that the tetraploid populations, in which meiosis is regular without multivalents, arose from the doubling of the chromosome sets of hybrids between different microspecies from the complex. In her excellent paper on the biosystematics of some *Plantago* species, Cartier (1970) showed that all the tetraploid populations of *P. alpina* and *P. serpentina* are allopolyploids, some coming from interspecific hybrids, the others from intraspecific hybrids. In the *Oreades* section too, the polyploids observed in West Asia are supposed to have arisen through hybridization between several diploid *subspecies* differing in karyotype, followed by doubling of the chromosome sets. For example, the ssp. *saxatilis* possesses a satellitiferous chromosome from ssp. *atrata,* and another one from the ssp. *spadicea.*

In *Plantago major sens. lat.,* the karyotype of the ssp. *intermedia* so far observed, is not exactly the same as that of *P. major* ssp. *major,* and some differences were observed too in hexaploid *P. asiatica* from the Far East. Therefore, it is likely that the polyploids from Japan, East Siberia and the Kumaon Himalayas are segmental allopolyploids (Stebbins, 1947) although no multivalents were noticed, or genomic allopolyploids though the apparent differenciation of the two chromosome sets from the parents is very slight.

A last problem is the taxonomy. The morphological differences on which Pilger (op. cit.) based his specific separation of *P. asiatica* from *P. major,* seem to be rather unimportant. Neither in the hexaploids from Kumaon, nor in the plant from Russian Far East, the bract was really separated from the calix and the latter stalked. As to the number of seeds per fruit, it varies largely in both diploids and hexaploids from W. Himalayas; moreover, the average value is a little higher in the hexaploids (see Table 10C). On the contrary, the East Siberian plants have 4–5 seeds per fruit, as indicated by Hara (1956) and by Ohwi (1965) for *Plantago asiatica* from Japan. Therefore, it seems more likely that the hexaploids from the Russian Far East are linked with the Japanese plants.

In the present author's opinion, it would be more convenient to treat *P. asiatica* as a *subspecies* from *P. major* instead of treating it as an independent species.

The extensive morphological variability present in both diploid as well as hexaploid *P. major* (1) from W. Himalayas and their subsequent overlapping make it difficult to distinguish whether the variation is a genetically controlled or environmentally adapted phenomenon. This aspect requires an experimental study of large populations under the same environment.

(1) Pictures 7 and 8 show morphological variants in the diploid and hexaploid races of *P. major.*

Intraspecific morphological variability is a common phenomenon among the members of the genus *Plantago* (*P. coronopus,* Böcher *et al.,* 1953, 1955, Gorenflot, 1959; *P. maritima,* Gregor, 1938; *P. media,* Rahn, 1957). In the present investigation, the extent of morphological variation appeared clearly when individuals of *P. major* with 3.5 cm and 90 cm height are recorded with a lot of intermediates in between (see Table 10C). In *P. lanceolata,* the variation in plant height is noticed from 11 cm to 50 cm. The other characters mentioned in the Table (10C) show the range of variation to which each trait is subjected.

The worldwide distribution of some species of *Plantago* is one of the reasons for such a great amount of morphological specialization of the genus in the process of their adaptation to the various climatical, ecological and edaphic conditions. Table 10C points out that the morphological variation in both *P. major* and *P. lanceolata* takes place even under the same ecological or geographical conditions. Reduced size of the species at higher altitudes is apparently due to low temperature, a greater amount of light and probably the constant subjugation to wind at higher elevation. Though the variation is influenced by environment to a certain extent, the occurrence of more than one morphotype under similar ecogeographical conditions evidently suggests a genetical basis for this phenomenon.

The report of an aneuploid race with 2n = 13 in *P. coronopus* by Böcher *et al.* (1953) adds sufficient proof to establish that cytological evolution in *Plantaginaceae* has arisen through interspecific and intraspecific euploidy coupled with aneuploidy.

III. General Discussion

The present cytological investigation concerns 197 plant species from the Western Himalayas and 52 species from Europe, especially from the Alps, belonging to ten families of the *Sympetalae (Tubiflorae + Gentianaceae).* The chromosome number of 69 Himalayan species are new reports while 16 numbers differ from those of the literature. Out of the alpic plants, 5 species were cytologically investigated for the first time while in *Scrophularia canina,* a new chromosome number was discovered (n = 12).

The main results were already discussed under each family. The author will summarize here some data of general interest in two fields i.e., that of cytotaxonomy and that of cytogeography and history of the flora.

Part 1. Cytotaxonimical aspects

a) Cytotypes and their taxonomic status

Ever since an intensive cytological examination of Linnean species has been undertaken, cytologists have detected many species with more than one chromosome number. This phenomenon is more frequent in the so-called „collective species", having a wide geographical distribution and morphological variability. About 7% of the flora of Central Europe consists of such intraspecific „chromosome races" (cf. Tischler, 1950); in the last twenty years, this number has greatly increased. Until now, chromosome counts of Western Himalayan plant species show about 4.6% of „polyplotypes" out of the total number of 570 species for which the chromosome number is known.

In the present investigation, the author could notice cytotypes in *Gentiana carinata* Griseb (n = 10, 20), *Solanum nigrum* L. (n = 12, 24, 36), *Scrophularia himalensis* Royle (n = 12, 24), *Veronica anagallis* L. (n = 18, 27) and *Plantago major* L. (n = 6, 18) growing in W. Himalayas. A comparative account of the morphological features of these chromosome races was given in various Tables in the text.

Other species in which several chromosome races were observed by various authors in Himalayas or in India as a whole, are for example, *Centaurium pulchellum* (Sw.) Druce (n = 18, 27, 36), *Trichodesma indicum* (L.) RBr (n = 11, 22 in India), *Convolvulus pluricaulis* Choisy (n = 18, 2n = 36, n = 10), *Cuscuta reflexa* Roxb. (n = 14, 15, 16, 21), *Scrophularia variegata* Bieb. (n = 12, 24), *Veronica beccabunga* L. (n = 9, 2n = 36), *Veronica hederifolia* L. (n = 9, 18 and 2n = 54), *Thunbergia erecta* T. Anders. (n = 14, 2n = 56), *Crossandra infundibuliformis* Nees. (n = 19, 2n = 20, 60), *Justicia simplex* D. Don (n = 9, 18) and *Adhatoda vasica* Nees. (n = 17, 2n = 56) ([1]).

Interesting enough is the fact that in many species growing in Western Himalayas and having a large geographical distribution (Europe, Central Asia, and/or America), the chromosome number found in the Himalayas is not the same as that found by the present author or other workers in other parts of their area. It is the case for exemple in: *Centaurium pulchellum, Asperugo procumbens, Lycopsis arvensis, Lithospermum arvense, Scrophularia scopolii, Pedicularis oederi, Phryma leptostachya.*

The taxonomic position of intraspecific chromosome races is a much disputed actual problem. We look into this situation through a simple definition of species brought forth by Mayr (1940) who considers species as „groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups". The Swedish taxonomist Nannfeldt (1938) was the pioneer taxonomist to advocate for specific rank of the chromosome races; he says: „As soon as chromosome races (polyplotypes) are morphologically distinct and thus, recognizable to the taxonomist, they had better to be recognized as species, even if the morphological characters are small". Later on, following Nannfeldt, Löve (1951, 1954), Löve and Raymond (1957), Valentine and Löve (1958) advocated a specific rank for all the taxa differing in chromosome number. Löve (1952) believes that morphologically indistinguishable polyploids are not in existence either in North Europe or in other areas as well (cf. Valentine, 1950), a point on which many disagreed. However, Smith (1933), Smithwhite (1954),

([1]) **But there is a possibility that the polyploid plant studied by Grant comes from Malaysia.**

Böcher (1961), De Litardière (1939) and Guinochet (1942–1943) are among those who stand against the absolute reliance on the chromosome numbers for taxonomic divisions. Favarger (1956) expressed the opinion that taxonomic treatment of chromosome races should not be governed by the single criterion of chromosome number, but by other morphological characters too. According to him, races differing in chromosome number may be elevated to the rank of subspecies or varieties depending on the cases. Davis and Heywood (1963) have also disapproved the idea of ranking diploids and polyploids belonging to a single collective species, as distinct species, no matter what the degree of morphological differenciation is.

The intraspecific chromosome races recorded in *Gentiana carinata* Griseb., though revealing morphological differences (see Table 10) are not significant as both races are found in Kashmir Himalayas. Only after studying the type material and after comparing it with the morphology of the races, may any speculation on the taxonomic status of these races be possible. Also, it would be prudent to assess the reproductive isolation the races possess.

The polyploid complex of *Solanum nigrum* L. demonstrates definite morphological characteristics (differences in growth habit, size of the plant, fruit colour, number of seeds per fruit, pollen size, stomatal size) which can be used for assessing the taxonomic status of different cytotypes. The correlation of morphological characteristics with chromosome number of different races observed in the present investigation seems to be a sufficient reason to give specific rank to each cytotype. The hybridization studies between different races by Tandon and Rau (1966) provided additional evidences for the reproductive isolation existing among the races.

The diploid taxon of *Scrophularia himalensis* found only in the Kashmir region of W. Himalayas is geographically isolated from the tetraploid race growing in the Kumaon Himalayas. The morphological features noticed in the diploid taxon, especially the non-branching, tall habit of growth, differ considerably from those of the tetraploid one with branching nature. A critical comparison of the type specimen with races studied here, may tell us whether the latter may or may not be placed in a different taxonomic unit.

The tetraploid *Veronica anagallis* L. is found only in Kashmir while the hexaploid race is found in Punjab and Kumaon. The tetraploid is characterized by more or less ovate leaves, while the hexaploid possesses ovate-lanceolate leaves.

In addition to this, many other characters of taxonomic value (see Table 6C) show distinct differences between the races. On the basis of these differences, Khoshoo and Khushu (1966) proposed a subspecific rank for the races. But a hybridization study between the races and a thorough comparison with the type material of the species *V. anagallis* L. and various closely resembling varieties of the same, may indicate the exact taxonomic status to be given; it seems to the present author that a specific rank for the races should be given here as in the various chromosome races of *V. hederifolia* by Fischer (1967).

The diploid race of *Plantago major* has a wide Eurasiatic distribution, but the hexaploid race is restricted to Central Himalayas and Eastern Asia. The variability of morphological characters noticed in the diploid taxon is more or less shared by the hexaploid also. Hence, a sharp distinction on mophological grounds is difficult to make between diploid and hexaploid chromosome races of *P. major.*

The hexaploid *P. asiatica* L. resembles the diploid *P. major* in all morphological features. The present author failed to observe a morphological distinction between *P. major* and the material of *P. asiatica* growing in extreme Siberia. Hence, the hexaploid taxon may be placed at the subspecific level.

A number of other species listed above, showing two or more chromosome numbers require a thorough morphological study with the aid of the type specimen before drawing any conclusion about their taxonomic status.

b) Aneuploidy

Aneuploid chromosome number variation is one of the cytological mechanisms for the origin of new species, and probably also of many genera. The most extensive aneuploid series in the plant kingdom is to be found in the genus *Carex* in which haploid numbers ranging from n = 6 to n = 56 have been reported and in which every number from 12 to 43 is represented by one or more species (Stebbins, 1950). Aneuploid chromosome number variation was observed in a large number of the genera studied currently. Intraspecific aneuploid races were noticed in *Cuscuta reflexa* (n = 14, 15, 16). In the light of the present work, previous records indicate the presence of aneuploid race in *Ipomaea coccinea* (2n = 28, 30), *Convovulus arvensis* (2n = 48, 50), *Barleria cristata* (2n = 34, 36, 38, 40), *Blepharis boerhaaviaefolia* (2n = 26, 28) and *Justicia gendarusa* (2n = 28, 30, 32). If different aneuploid numbers were noticed by different authors, it is not unlikely to suppose that in some cases, the discrepancy lies in wrong counts or in mistakes in identification of the material. However, in a number of well studied species of the European flora, an aneuploid process of intraspecific differentiation was observed without any doubt for example in *Cardamine pratensis* (Lövquist, 1956, Landolt and Urbanska, 1971), *Erysimum grex. grandiflorum* (Favarger, 1964, 1972) and *Carduus defloratus* (Favarger and Küpfer, 1970).

Intrageneric aneuploidy is found to be very prevalent in many genera of the *Scrophulariaceae, Acanthaceae* and *Verbenaceae,* whereas their role is confined to few genera only in *Gentianaceae, Boraginaceae* and *Solanaceae.* In the *Scrophulariaceae,* the genus *Veronica* possesses an extensive aneuploid series (n = 7, 8, 9, 14, 18, 20, 21, 23, 26, 27); *Scrophularia* has n = 8, 9, 10, 11, 12, 13, 15, 17, 24, 25; *Pedicularis* has n = 6, 7, 8; and *Verbascum* has n = 15, 16 and 18. In the *Acanthaceae,* an aneuploid series prevails in the genera *Ruellia* and *Barleria;* the evolution of the species is attributed to this phenomenon (De, 1966). The present work, revealing a series of haploid numbers in *Strobilanthes* (n = 9, 11, 13, 14, 16, 20) is again a clear indication of intrageneric aneuploidy operating as a mechanism in the speciation. In the *Verbenaceae,* the species evolution in the genus *Callicarpa* is attributed to aneuploidy by Sharma and Chatterjee (1963). In the genus *Myosotis,* gametic numbers vary from n = 12, 18, 24, 25, 26, 27, whereas in *Heliotropium,* the series shows n = 11, 12, 32. In the *Gentianaceae,* the genera *Gentiana* and *Swertia* make use of aneuploidy for the evolution of new species, since the Himalayan species studied here and belonging to the former genus has shown gametic number n = 9, 10, 13, whereas the latter demonstrates n = 8, 9, 10 and 13. Intrageneric aneuploidy is responsible for species origin in *Plantago* also, where the gametic number varies from n = 4–6.

The missing numbers in the aneuploid series might have been non-investigated ones. The variable nature of genera in their response to aneuploidy may be attributed to genetic factors, but this variability indicates the active stage of evolution to which these genera are comparatively subjected.

The current investigations have brought about new proofs to the fact that many genera are polybasic. To what extent is it possible to affirm that one of these basic numbers is more primitive than the others remains a question. It is likely too that at the birth of one genus, there is a time of variability for the chromosome number and that after it, the more favourable and stable chromosome number, and often several of them are fixed. In neighbouring genera, it seems that a parallel evolution of the karyotype has taken place (Favarger, 1962).

Various causes have been put forth by many workers for the incidence of aneuploidy. Weijer (1952) expressed that aneuploidy results from partial return to the basic number by the progeny of a triploid, whereas Tuschnjakova (1929) attributed the phenomenon to non-disjunction. MacMahon (1936) and Richardson (1933) suggested aneuploidy to be due to fragmentation while Duncan (1945) stood against this view, suggesting „B" chromosome as the cause of aneuploidy.

c) Meiotic abnormalities

The majority of the taxa currently investigatet show normal pairing of chromosomes at diakinesis. They undergo regular meiotic segregation and normal pollen grain formation. The disturbed meiotic instances are treated below:

1. Desynapsis:

Several types of deviations from regular pairing of chromosomes have been reported in the literature and one of the most interesting is desynapsis. The term desynapsis has often been used when chromosomes pair normally at pachytene but begin to fall apart at diplotene and commonly remain unpaired at diakinesis and metaphase I.

Depending on the degree of failure in pairing, Prakken (op. cit.) classified desynapsis into three groups: weak, medium strong and complete, on the basis of percentage of chromosome pairing. Although there are several cases of desynapsis reported in various plants and animal species, only a few of them are known to be completely desynaptic (*Datura,* Bergner *et al.*, 1934; *Hevea,* Ramaer, 1935; *Allium,* Levan, 1940; *Alopecurus,* Johnson, 1944). Desynapsis noticed in *Solanum nigrum* (n = 24) in the current work, falls in Prakken's medium strong category. But desynapsis noticed in *Withania somnifera* (n = 24) is weak.

As stated above, the frequency of bivalent formation was very low at both diakinesis and MI. Lack of chromosome homology cannot be used to explain the failure of chromosome pairing since the normal plant showed regular pairing of chromosomes. Differences in environmental conditions cannot be responsible for the deviation from the normal pairing since both types of plants were grown under similar conditions. It is possible that desynapsis has a genetic basis; the fact that one desynaptic plant occurred leads one to suspect the possibility of spontaneous gene mutation.

2. Secondary association:

The phenomenon of secondary association was first observed by Kuwada (1910) in *Oryza sativa.* It is believed that the post-synaptic association results from residual affinity between different chromosomes. The real significance as an expression of ancestral homology of associated bivalents was first realized by Lawrence (1931). Secondary pairing of bivalents is generally noticed from late diakinesis to MII. According to Lawrence (op. cit.), it indicates allopolyploidy, and he considers that the degree of such an association is a measure of the phylogenetic age of the form concerned.

Secondary pairing of chromosomes was reported in many plants: *Calceolaria clibrani* (Srinath, 1940), *Digitalis purpurea* (Buxton and Newton, 1928), *Verbascum phoeniceum* (Lawrence, 1931), *Angelonia grandiflora* (Rghavan and Srinivasan, 1940), *Striga* (Kumar and Abraham, 1941) and *Russelia* (Pal, 1961), a *Scrophulariaceae* in which chromosome size is comparatively small which is, according to Srinath (1940), one of the attributes of a secondary association. In all these cases, secondary pairing has been taken as a criterion of homology of associated bivalents and has been used to determine the basic chromosome number of the species studied. The pioneer work in this line was that of Nandi (1936) in rice, in which the basic number is ascertained as 5 on the basis of secondary pairing though the haploid number is 12.

In the present work, secondary association of bivalents was noticed in *Russelia sarmentosa* and in *R. juncea* (1) in the *Scrophulariaceae* and in *Platystema violoides* in the *Gesneraceae.* The number of chromosomes and the extent of their associations, however, have been found to vary from cell to cell in the same anther. These associations do not cause any irregularities in the subsequent stages of meiosis.

The concept of secondary association and the interpretations based on it have been frequently criticized. Sax (1931, 1932) could not recognize the secondary association described by Darlington *et al.* (1930) in *Pyrus,* since it was not realized in other genera. Clausen (1931b) expressed the need for caution in interpreting the origin of basic chromosome numbers from the secondary association. On the contrary, Catcheside (1937) concluded that it is a real phenomenon and suggested that *Brassica oleracea* n = 9 is a hyperploid derived from an ancestor with the haploid number x = 6.

Various causes have been ascribed for secondary association. Unfavourable temperature and habitats are reported to be two of the causes (cf. Kobayashi, 1952). Thomas and Revell (1946) have demonstrated that heterochromatic regions have a tendency to associate at meiosis in *Cicer arietinum* and that this phenomenon is related to the activity of ribonucleic acid.

According to Stebbins (1950, p. 362), „secondary association can be considered as an actual phenomenon which, in many instances, suggests the polyploid nature of a species or a genus but which may be considerably modified by segmental interchange, duplication of chromosome segments and other phenomena not at

(1) **The present author has studied these species cytologically but has not included them in the Table.**

all related to polyploidy. It is, therefore, not a reliable index of the exact basic haploid number possessed by the original ancestors of a group". Since the cytological findings of a large number of species of *Scrophulariaceae* were not in line with the basic number x = 5 suggested by Raghavan and Srinivasan (l.c.) the writer is of the opinion that secondary association should not be relied upon for the assessment of basic number in the absence of evidences from other sources.

3. Cytomixis:

In the course of the present investigation, cytomixis was noticed in *Pedicularis megalantha* (n = 8) and *Limnophila roxburghii* (n = 18) in the *Scrophulariaceae* and in *Plantago major* (n = 6) in the *Plantaginaceae.*

Gates (1911), working with *Oenothera gigas,* named the phenomenon of extrasion or passage of chromatin material from the nucleus of one pollen mother cell into the cytoplasm of adjoining pollen mother cells as „cytomixis". This process was described as early as 1901, in the pollen mother cells of *Crocus vernus* (Kornicke), and the epidermal layers of several other monocotyledons plants (Miche, 1901).

The extrusion of chromatin material may affect a series of cells. Gates (1911) reported that cytomixis takes place at the same time in all the pollen mother cells of a given anther in *Oenothera gigas* and always in the same direction. However, Kattermann (1933) found that movement was not uniform in direction and the contents of one cell could often be seen in two or three neighbouring cells. The phenomenon in *Pedicularis megalantha* and *Plantago major* was found to take place between two neighbouring cells with the transfer of a varying amount of chromatin material. It was noted that the nucleus of the cell undergoing cytomixis may often remain behind (Gates, 1911) or pass *piecemeal* into the cytoplasm of the neighbouring cell (Youngman, 1931). Though commonly cytomixis was found to occur from leptotene to metaphase-I (Kihara and Lilienfeld, 1934), cases are also known where cytomixis occurred at a stage as late as second telophase (Stebbins, 1932). But the phenomenon observed in the present material is almost restricted at MI.

In many cases, the diminution of chromosome number has been attributed to cytomixis. Yamashita (1937) considered nuclear migration to be the cause of a group of cells with reduced chromosome numbers in *Triticum.* Kihara and Lilienfeld (1934) believed that pollen mother cellls with reduced chromosome number might have arisen as a result of cytomixis. They also suggested the probable role of cytomixis in polyploidy. The observation of few PMC's with less chromosome number or little chromatin material in the present material, especially in *Plantago major,* agrees with the previous observations.

In *Pedicularis megalantha* and *Plantago major,* the cell wall may be defective and may possess narrow connections through which chromosome material passes.

Since cytomixis can bring about variation in chromosome numbers in the gametes, the possibility that cytomixis might have played a role in the production of aneuploid plants cannot be ruled out. The intraspecific polyploidy (n = 18) noticed in *Plantago major* has probably evolved through the help of cytomixis in the remote past.

Part 2. Cytogeographical aspects

An attempt to compare the alpine flora of the Western Himalayas with the orophilous flora of the Alps.

Since the works of Hagerup (1931) and Tischler (1935), statistics of polyploids have been carried out on the flora of rather numerous parts of the world, especially in Europe and North America (Löve, 1949; Reese, 1958) and in tropical Africa (Mangenot and Mangenot, 1962). It seemed interesting to us to establish the percentage of polyploid taxa in the samples of the flora of the Western Himalayas that we have been studying (Table 11). The percentage of polyploids obtained is low (37.1%). However, this result is unreliable for the following reasons: first of all, the statistics concern only the ten families of gamopetalous. Sokolovskaya and Strelkova (1938) have insisted on the necessity of working especially on the *Graminaceae* because of the importance of their sociological characteristics. On the other hand, and though we have mainly prospected the upper levels of vegetation, our collections have also included plants of the tropical, subtropical and montane (or mediterranean) levels. That is the reason why we have presented another set of statistics which seems to us more representative, that is, based on the whole lot of species with ecological optimum above 3300 m of altitude (alpine and subalpine levels including the level of the high mountains forests) which are the genuine orophilous plants after Favarger (1972). We have listed all

Table 11

	W. Himalayas			
	No. of species cytologically studied	Diploids	Polyploids	% of polyploidy
Gentianaceae	22	18	4	18.2
Convolvulaceae	15	11	4	26.7
Boraginaceae	26	21	5	19.2
Verbenaceae	7	4	3	42.9
Solanaceae	27	19	8	29.6
Scrophulariaceae	59	37	22	37.3
Orobanchaceae	2	–	2	100.0
Gesneriaceae	6	2	4	66.7
Acanthaceae	31	11	20	64.5
Plantaginaceae	2	1	1	50.0
Total	197	124	73	37.1

the orophilous species growing in the Western Himalayas whose chromosome numbers have been determined, most often by Mehra and his students and by other Indian workers (including our own results). This represents an amount of 191 taxa distributed in 31 families.

Among the orophilous plants of the Western Himalayas, there are 44% of polyploids and 56% of diploids.

Other statistics dealing with the 570 species of the flora of the W. Himalayas (known chromosome number), growing above 1800 m, that is, in what is called the temperate and alpine Himalayas (Hooker, op. cit.), have given us the same relative proportions of diploids and polyploids.

The difference between the first statistics and the following ones seems to show that in the ten gamopetalous families studied by the author, the percentage of polyploids is lower than in the whole flora. However, in the two families of *Acanthaceae* and *Gesneriaceae,* the percentage of polyploidy is relatively high (see p. 187).

So the orophilous flora of the Western Himalayas and probably all the extropical flora of this chain is characterized by a percentage of polyploids rather low, of about 44%.

However, it must be added that only about 1/3 of these floras was hitherto cytologically studied.

The orophilous flora from several other mountainous ranges in Asia was investigated by Sokolovskaya and Strelkova (1938) with the following results:

	Pamir	Altaï	Caucasus
Number of species studied	150	200	164
% of polyploids	85%	65%	50.5%

Our own results on the W. Himalayan flora mostly differ from those obtained from the Pamir range which lies not very far north, and also from those of the Altaï mountains; however, they come near the results from the Caucasus range, though they are still lower than the latter.

To explain the relatively low percentage of polyploids in the Western Himalayas, some authors will perhaps put forward the rather low latitude of this chain ($30^0 - 35^0$ N.). As a matter of fact, Sokolovskaya ([1]) has shown in East Asia a south-north gradient of increasing polyploidy rather similar to that observed in Europe by Tischler, Löve and Reese (op. cit.).

	Primorye Territory	Sakhaline	Kamchatka	Koriakian Land
Number of species studied	218	156	160	119
% of polyploidy	44.1%	51.5%	58.7%	58.3%

([1]) 1960, 1963, 1966.

However, as far as mountainous ranges are concerned, the influence of the latitude will be corrected by altitude and many other factors, so that the relation of polyploidy with latitude will be defeated.

The „climatic" explanation will be partly correct because the ecological conditions to which the orophilous plants are submitted in Pamir are very severe, much more than in the Western Himalayas.

As early as 1954, Miège, discussing the distribution of the polyploid species from the genus *Dioscorea* in tropical Africa and in south Europe, and Favarger (1954) about the nival flora of the Alps, have pointed out that the Hagerup-Tischler's explanation did not apply either to the tropical regions or to the high mountains floras.

In this connection, an important proof has been given by Mangenot and Mangenot (1962) who showed that the flora of the high forests of Western Africa numbered 85–90% of polyploids.

To explain the low percentage of polyploids in the orophilous flora of Caucasus, Sokolovskaya and Strelkova (1940) have put forward a historical geobotanical explanation. Thus, when the question of polyploidy deals with historical geobotany, it is necessary to change the method of percentage of polyploids, for, as Favarger showed it (1961), polyploids considered with a historical outlook do not all have the same value. Therefore, the above author has proposed the method which he has called: „spectrum of relative oldness of a flora" in which he perceives old elements: palcopolyploids + diploids; elements of a middle age: mesopolyploids, and young elements: neopolyploids + taxa having differentiated „chromosome races" on the same territory.

Thanks to this method, Favarger has compared the nival flora of the Alps to that of S.W. Groënland. Johnson and Packer (1967) used it to analyze the flora of a particular region of Alaska.

The next table allows us to compare the spectrum of relative oldness of the orophilous flora between the W. Himalayas and the Swiss Alps (Table 12). Though, the proportion of species cytologically studied is still low in the Himalayas (27% to 29%), we think that we are able to conclude from the comparison that *the orophilous flora of W. Himalayas is richer in old elements than the flora of the Alps, and is at the same time poorer in elements (M) of a middle age and in recent elements (N + R).*

After its present composition, the orophilous flora of the W. Himalays does not show any genetical affinities with the tropical or subtropical flora of the lower levels.

After the geologists, at the time of the upheavel of the Himalayas, the Indian peninsula has separated from the chains in process of upheavel by the whole extent of the Téthys. The contact between the peninsular tropical flora and the true Himalayan flora took place only at the Pliocene, even at the Pleistocene (Legris, p. 420) and, at that time, the orophilous plants had already differentiated. However, it is most probable that at the time of the orogenic movements, the flora of low Himalayan countries, in the North as well as on the beaches of the Téthys, was a subtropical flora. Still, at the Pleistocene, the flora of the Valley of Kashmir studied by Puri (op. cit.) was partly composed of tropical genera. As Scharfetter (1929) has shown, some genera of this arcto-tertiary flora have been able to adapt

Table 12

	Orophilous flora of the Western Himalayas (above 3300 m)	Flora of the nival level of the east part of the Swiss Alps (after Favarger 1961)
Number of species (after Hooker's flora for the Himalayas)	651	220
Number of species cytologically known	184 (1)	204
Paleopolyploids (P)	12%	3.9%
Diploids (D)	54.3%	53.0%
	66.3%	56.9%
Mesopolyploids (M)	24.4%	30.9%
Neopolyploids (N)	4.4%	6.8%
„Chromosome races" (R)	4.9%	5.4%
	9.3%	12.2%

(1) The difference between this number and the number 191 reported (p. 000) and included in the statistics of the rough percentage of polyploids is due to the fact that in the last calculation, we have added to the diploid species, the diploid races of the species presenting such a differentiation

N.B. The results obtained on all the species (570) growing above 1800 m (temperate and alpine Himalayas) are very similar:

P + D = 68.9%
M = 22.5%
N + R = 8.6%

to the conditions of high mountains, for ex.: *Wulfenia amherstiana* (Himalayas) and *W. carinthiaca* (Alps) and the Rhododendrons. Others have gone through more important genetical modifications and have produced the numerous species of *Primula, Saxifraga, Androsace, Gentiana* which are found in the Alps as well as in the Himalayas. The southern branch of the arctotertiary flora related to the Mediterranean flora and even to the African flora which produced numerous orophytes in the Alps does not seem to have produced many Himalayan orophytes. The only ones which might be quoted are: *Rubia tibetica, Jurinea spec., Nepeta spec.* It is possible that the establishment of the Mediterranean group in the Kashmir valley is not very ancient. Puri (op.cit.) thinks that in the valley of Kashmir, climatic changes happened, in the direction of more xeric conditions, as the beginning of the Pleistocene which involved the destruction of the tropical flora of Liddarmarg.

In conclusion, the author believes that the orophilous flora of the Western Himalayas was differentiated at the Tertiary, from elements of the arcto-tertiary flora (mainly from the boreal and asiatic branch) which produced psychrophilous species, and that this phenomenon took place through gradual speciation (without polyploidization). The same has happened in the Alps too, but from

other stocks and in a different manner, so that there are nowadays, few similarities between the orophilous floras of the Alps and of the Western Himalayas, *at the specific level.*

After a first provisional estimation, the orophilous flora of the W. Himalayas includes about 650 species. It is likely that about 200 species were described since the publication of Hooker's flora, which gives a total of ca. 850 species, a number which can be compared with that published by Favarger (1972) for the Alps, i.e. 1049 species, though it is smaller. From these 650 species, only 88 (i.e., 13.5%) are also growing in the Alps. As Engler (1879) has already noted, all the orophilous species common to the Alps and to the Himalayas, are met in Siberia too, or in the Arctic region.

The family *Gentianaceae* gives a good example of the independent differentiation of orophytes in the Alps and in the W. Himalayas (Table 13).

It can be seen that in the W. Himalayas, there are many species of *Swertia* (a single species in the Alps). No representative of the genera *Jaeschkea* nor *Halenia* is known in Europe. The distribution of the *Gentiana spec.* into the different tribes is very different too in the Alps and in our country. A single species, *Pleurogyne carinthiaca* is common to both chains ([1]).

In the genus *Pedicularis,* the sections *Siphonanthae* and *Ortorrynchae* including about 15 species in the W. Himalayas are not represented in the Alps where ten species of *Rhyncholophae* are growing, whereas only two are met in the W. Himalayas.

From the previous considerations, it would be likely to conclude that the orophilous flora of the W. Himalayas is of the same date as the flora of the Alps. Now, how can this greater richness in old forms be explained?

Two main reasons can be put forward:

1. The Himalayan flora was certainly much less disturbed by the Quaternary glaciations than the flora of the Alps.

2. Besides the orophytes, differentiated on the spot from arctotertiary ancestors, the Western Himalayas received several orophytes from the neighbouring ranges of mountains, i.e. those of Central Asia and chiefly from the Western Chinese mountains (through the Eastern Himalayas). The importance of this chain as link will never be too estimated. It is well known that in the Chinese and Japanese regions, the arcto-tertiary flora was much better preserved. These exchanges took place without long migrations, because the W. Himalayas were not far from the centers of origin of these taxa.

On the contrary, it seems likely that some genera of the alpic flora such as *Primula* section *Auricula, Androsace* section *Aretia,* many species of *Gentiana* have originated in Central Asia and have undergone, at the end of the Tertiary, very long migrations from their centers to Europe during which they became polyploids (Kress, 1963).

This explanation agrees entirely with that proposed by Sokolovskaya and Strelkova for the Caucasian orophilous flora. Interesting enough, the present work

([1]) *Gentiana tenella* of the Alps seems to be replaced in the W. Himalayas by *G. duthiei.*

Table 13

	Number of species in each genus	
	W. Himalayas	Alps
Genus *Gentiana* (incl. *Gentianella*)	36	38
Swertia	15	1
Pleurogyne	4	1
Halenia	1	–
Jaeschkea	2	–

	Number of species of each section of the genus *Gentiana*	
	W. Himalayas	Alps
Subgenus *Gentiana*		
Section *Coelanthe*	–	5
Pneumonanthe	–	2
Frigida	5	2
Aptera	3	1
Isomeria	2	0
Chondrophylla	17	1
Thylacites	–	4
Cyclostigma	–	9
Subgenus *Gentianella*		
Section *Crossopetalum*	2	1
Amarella	5	11
Arctophila	1	–
Comastoma	1	2

gives some examples suggesting a rather recent migration of taxa from Central Asia to Europe: *Lycopsis arvensis, Asperugo procumbens, Solanum nigrum, Veronica grex hederifolia,* in which the Himalayan taxa are diploids, whereas the corresponding taxa from Central Europe (including alpic region) are higher polyploids. However, we must say that in three other cases: *Plantago asiatica-major, Pedicularis oederi, Scrophularia scopolii* ([1]), the Himalayan populations, or parts

([1]) The case of *Scrophularia scopolii* must be verified.

of them, are polyploid, but it does not imply that these plants were coming from Europe (for the case of *Plantago,* see Favarger and Vasudevan, 1972).

To conclude, the author cannot agree with Legris' assertion (op. cit., p. 444), when he says about the orophilous flora from W. Himalayas: „le froid et l'intensité des radiations ultraviolettes sont les causes de nombreuses mutations et d'un pourcentage élevé de polyploïdes et d'hybrides. Ces caractéristiques d'une flore jeune expliquent que l'Himalaya ait pu jouer le rôle d'un centre de dispersion vers les régions tempérées". The flora of the W. Himalayas is poorer in polyploids than the Alps and it has preserved a greater number of ancient taxa.

Summary

In the present paper, a series of cytological studies on numerous species from Western Himalayas and Europe belonging to several families of *Sympetalae* is concluded. Some chromosome numbers were determined for the first time; others differed from earlier determinations. Intraspecific polyploidy was observed in *Plantago major* (n = 6, 18) in populations from W. Himalayas. The intrageneric cytological evolution of all genera studied was tentatively explained and new basic numbers (x) have been suggested for many genera (see discussion of the families).

A special note is made on the role played by aneuploidy in evolution. Various meiotic abnormalities like desynapsis, secondary association and cytomixis are discussed.

An analysis of the extent of polyploidy in the ten families of the current investigation showed 37% polyploidy in Western Himalayas. It is significant to note that the tropical families *Gesneriaceae* and *Acanthaceae* possessed a higher percentage of polyploidy. Separate statistics of orophilous plants of Western Himalayas showed 44% polyploids and 56% diploids. A comparison of polyploidy in the flora of the alpine level of the eastern part of the Swiss Alps and in the orophilous flora of the Western Himalayas, on the basis of „polyploid spectrum" of Favarger, proved that the orophilous flora of Western Himalayas is richer in old elements and poorer in elements of middle age (M) and in recent elements (N+R). This difference is attributed by the author to the weaker influence of quarternary glaciations in the Himalayas and to exchanges, without long migrations, with the flora of Western Chinese mountains through the Eastern Himalayas.

Zusammenfassung

Cytotaxonomische und cytogeographische Untersuchungen an Pflanzen aus dem Himalaya im Vergleich zu verwandten Pflanzen aus den Alpen. Teil III.

Diese Arbeit bildet den Schluss einer Serie cytologischer Untersuchungen an zahlreichen Arten sympetaler Familien aus dem westlichen Himalaya und aus den Alpen. Manche Chromosomenzahlen wurden erstmals bestimmt; andere waren von früheren Bestimmungen verschieden. Intraspezifische Polyploidie wurde bei Plantago major (n = 6, 18) aus dem westlichen Himalaya beobachtet.
Die intragenerische cytologische Entwicklung der untersuchten Gattungen wird diskutiert und für mehrere Gattungen werden neue Grundzahlen (x) vorgeschlagen (siehe Diskussion der Familien). Die Bedeutung der Aneuploidie für die Entwicklung wird untersucht; verschiedene Abnormitäten der Meiose (Desynapsis, sekundäre Assoziation, Cytomixis) werden diskutiert.

Die untersuchten Arten aus zehn Familien ergaben einen Polyploidiegrad von 37% für den westlichen Himalaya. In den tropischen Familien der *Gesneriaceae* und *Acanthaceae* war der Polyploidiegrad besonders hoch. Unter den orophilen Arten des westlichen Himalayas fanden sich 44% polyploide und 56% diploide. Ein Vergleich der Polyploidie in der Flora der alpinen Stufe der östlichen Schweizer Alpen und in der orophilen Flora des westlichen Himalayas auf der Grundlage des „polyploiden Spektrums" von Favarger zeigt, dass der westliche Himalaya reicher an alten Florenelementen und ärmer an jüngeren Florenelementen ist. Dieser Unterschied zu den Verhältnissen in den Alpen wird dem geringeren Einfluss der quarternären Vergletscherungen im Himalaya und den Beziehungen zu den Bergen Westchinas zugeschrieben.

Fig. 140: Orobanche epithymum D.C. n = 19 MI.
Fig. 141: Orobanche alba stephan n = 19 MI.
Fig. 142: Orobanche kashmirica Clarke n = 19 MI.
Fig. 143: Didymocarpus pedicellata Br. n = 18 MI (1600 x).
Fig. 144: Didissandra lanuginosa Clarke n = 10 MI.
Fig. 145: Chirita bifolia D. Don n = 14 Diakinesis.
Fig. 146: Chirita pumila D. Don n = 4 Late Diakinesis.
Fig. 147: Platystemma violoides Wall. n = 20 MI, secondary association of bivalents are noticed.
Fig. 148: Rhynchoglossum obliquum Blume n = 18 MI.
Fig. 149: Hemigraphis latebrosa Nees n = 14 (1600 x).

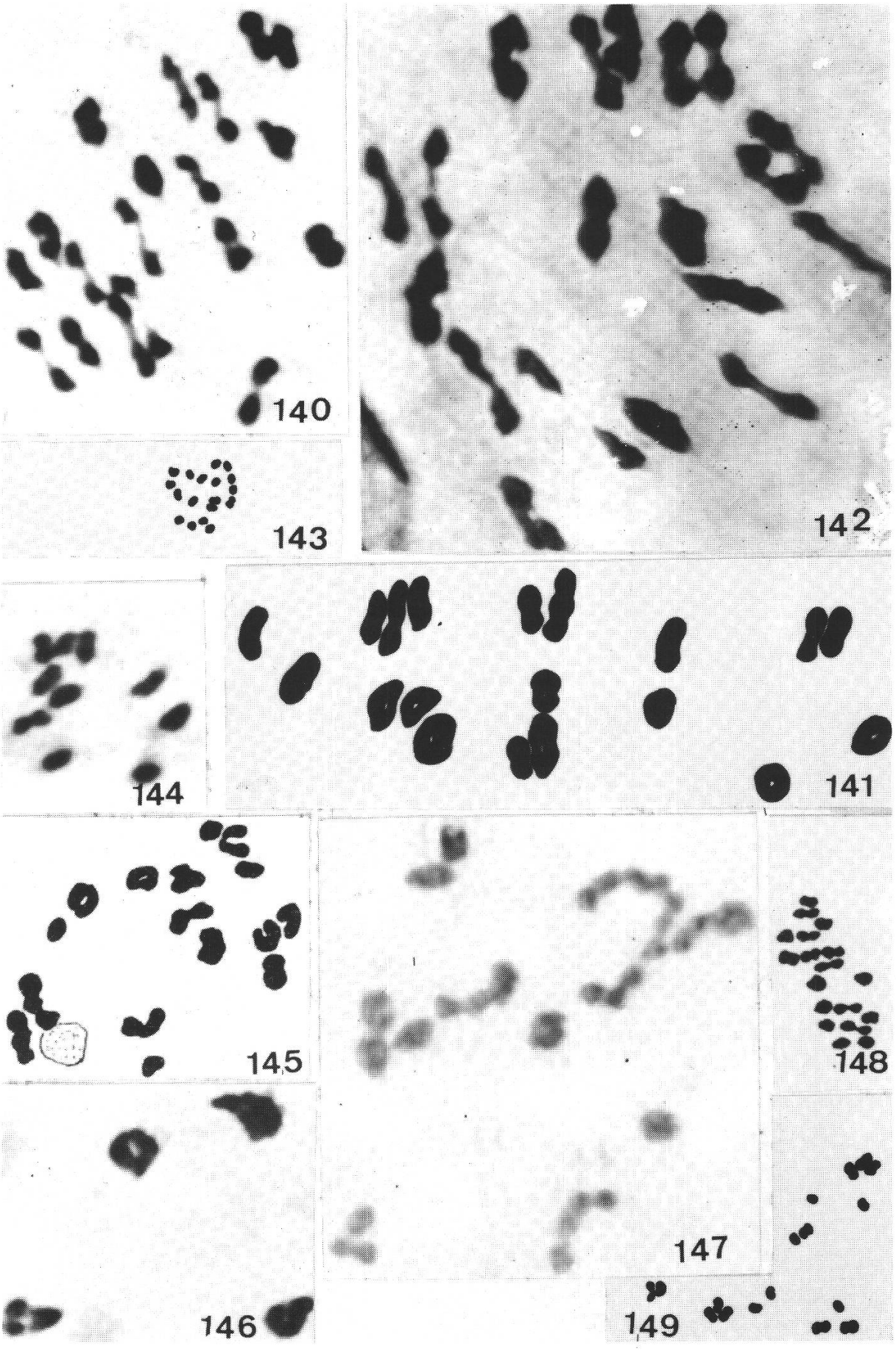
Fig. 150: Strobilanthes glutinosus Nees n = 14 MI.
Fig. 151: Strobilanthes quandrangularis Clarke n = II AI.
Fig. 152: Strobilanthes wallichi Nees n = 20 MI.
Fig. 153: Strobilanthes atropurpureus Nees n = 16 MI.
Fig. 154: Barleria gibsoni Dalz. n = 20 AI.
Fig. 155: Blepharis boerhaaviaefolia Pers n = 14 AII (1600 x).

Fig. 156: Lepidagathis purpuricaulis Nees n = 42 MI.
Fig. 157: Justicia gendarussa L. n = 14 AI.
Fig. 158: Justicia pubigera Wall. n = 14 MI.
Fig. 159: Justicia diffusa Willd. n = 9 Late Diakinesis.
Fig. 160: Rungia parviflora Nees n = 26 AI.
Fig. 161: Plantago major L. n = 6 MI.
Fig. 162: Plantago major L. n = 18 MI.
Fig. 163: Plantago major L. n = 6, showing cytomixis. Note a PMC with one bivalent.
Fig. 164: Plantago intermedia Gilib. 2n = 12 showing two pairs of satellites.
Fig. 165: Plantago intermedia Gilib. 2n = 12 idiogram.
Fig. 166: Plantago asiatica L. 2n = 36 idiogram.

Fig. 167: Cytological races of *Gentiana carinata* Griseb. (n = 10, 20).
Fig. 168: Cytological races of *Solanum nigrum* L. (n = 12, 24, 36).
Fig. 169: Cytological races of *Scrophularia himalensis* Royle (n = 12, 24).
Fig. 170: Cytological races of *Veronica anagallis* L. (n = 18, 27).
Fig. 171: Varieties among the tetraploid race of *Veronica anagallis* L.
Fig. 172: Morphotypes of *Strobilanthes dalhousianus* Clarke.
Fig. 173: Morphological races among the diploid race of *Plantago major* L. (n = 6).
Fig. 174: Morphological races among the hexaploid race of *Plantago major* L. (n = 18).

Fig. 175: *Cactus* vegetation in subtropical Western Himalayas (Rampur in Siwalik) 1000 m.
Fig. 176: *Quercus incana* forest in Mussoorie Hills (1900 m).
Fig. 177: *Betula utilis* and *Abies spectabilis* growing in the subalpine zone of W. Himalayas. (In Garhwal 2700–3000 m).
Fig. 178: *Pinus gerardiana* growing in the inner dry zone of W. Himalayas at 2000 m (Sutlej valley behind Simla).
Fig. 179: *Picea exelsa* in Kashmir (3000 m).
Fig. 180: *Cedrus deodara* in Kumaon region of W. Himalayas.

Fig. 181: *Abies spectabilis* and *Acer* species in Kashmir.
Fig. 182: *Abies pindrow* forest in Gulmarg (2700–3000 m) in Kashmir.
Fig. 183: Timberline in Kumaon (3600 m).
Fig. 184: Alpine Juniperous meadows in Kashmir (3500 m).
Fig. 185: Avvalley in Ladakh, the dry cold desert of W. Himalayas. Upperslopes of mountains are nearly barren and herbaceous vegetation is found along the river banks.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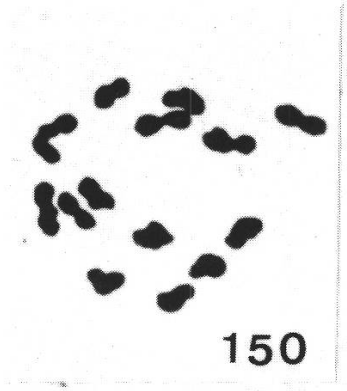
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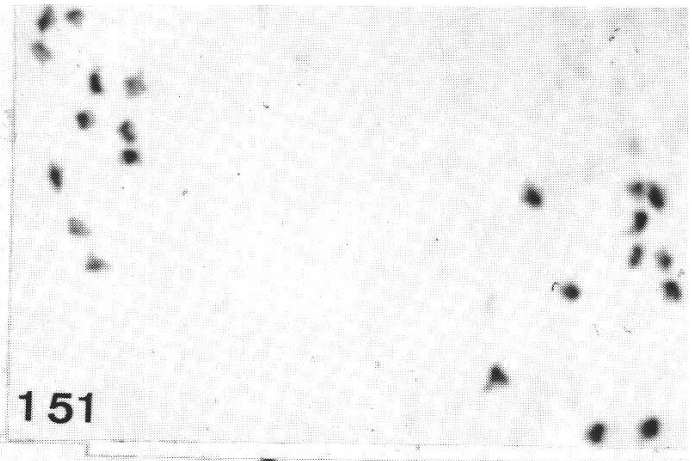
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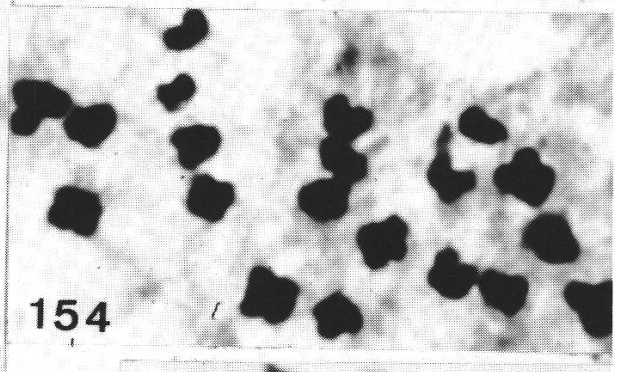
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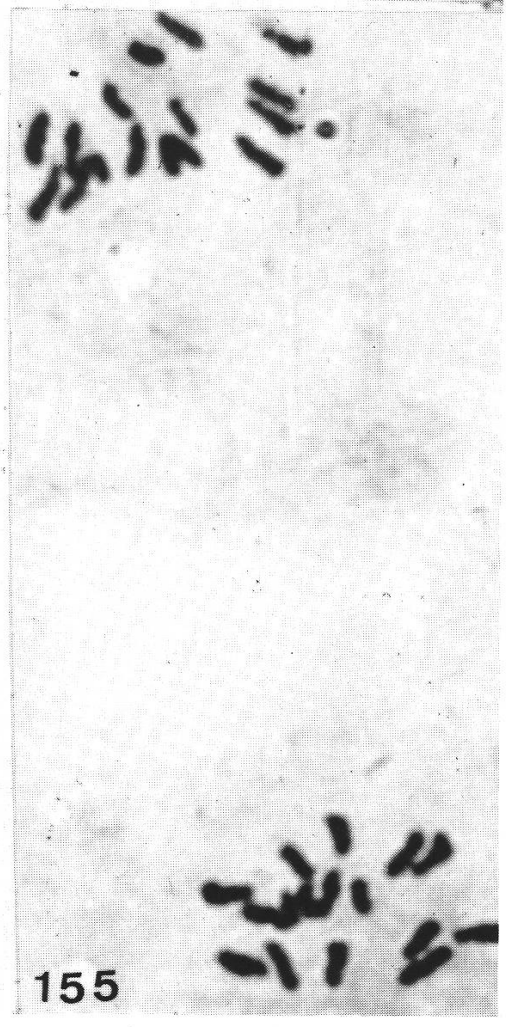
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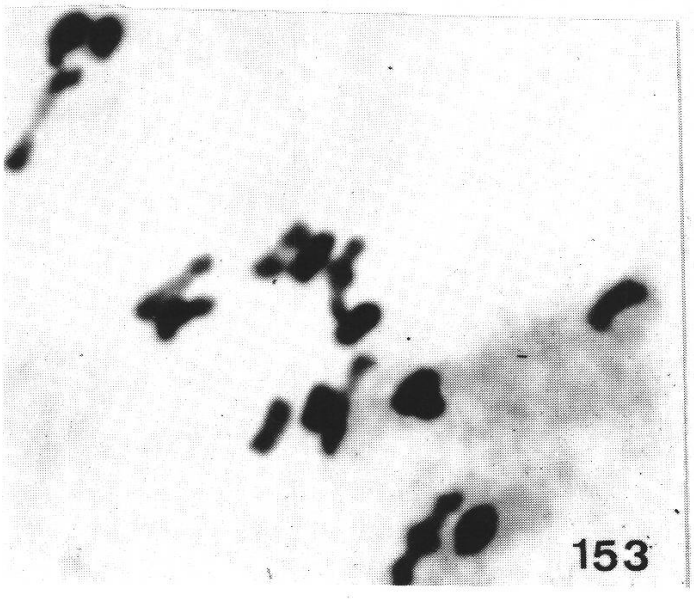
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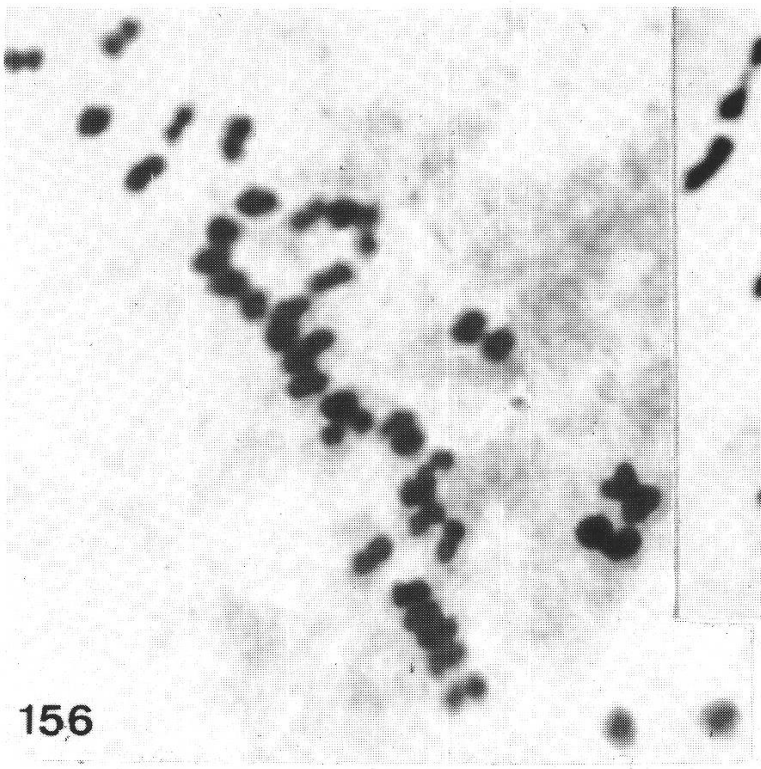
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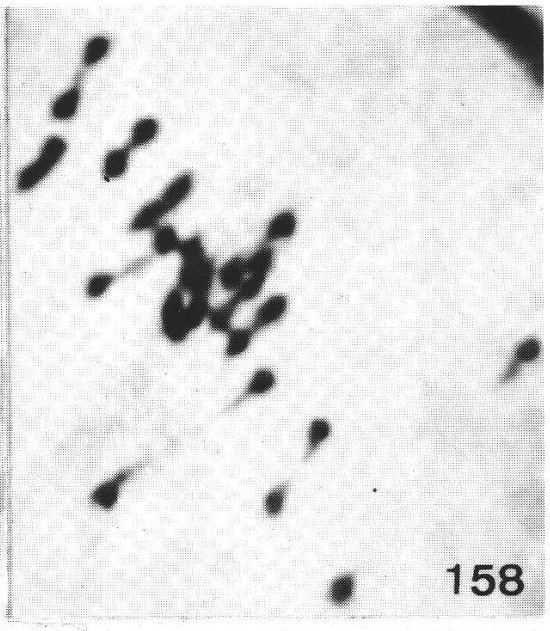
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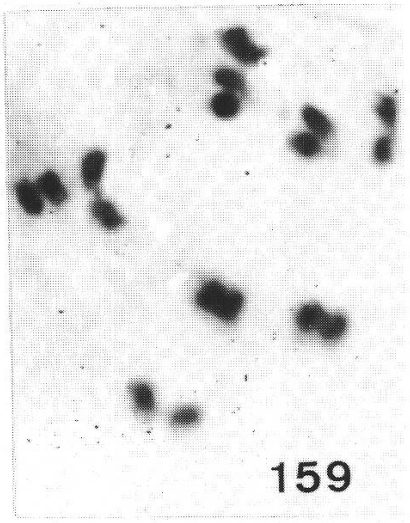
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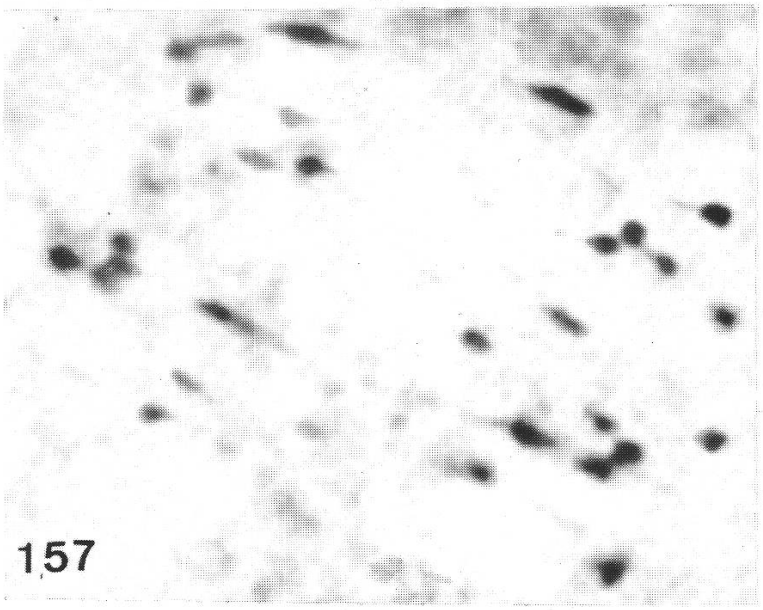
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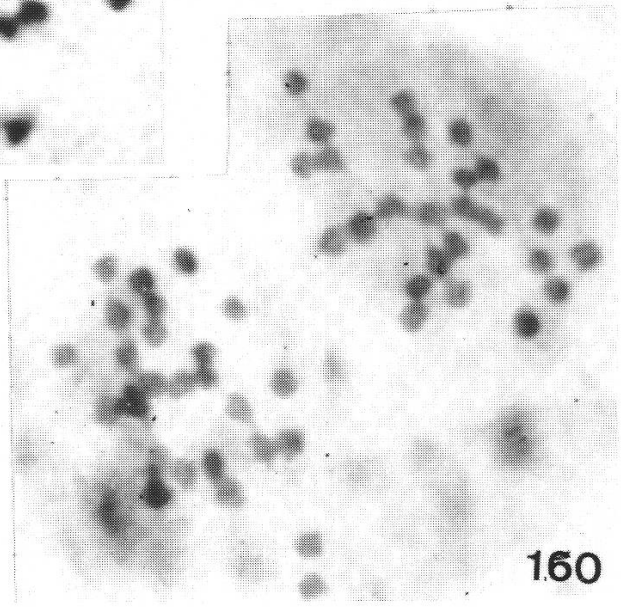
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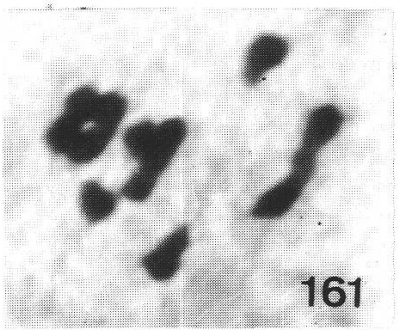
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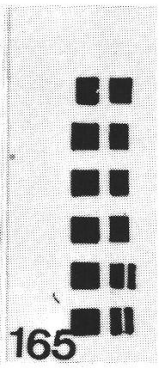
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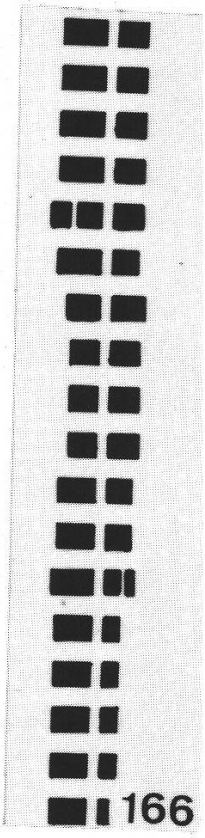
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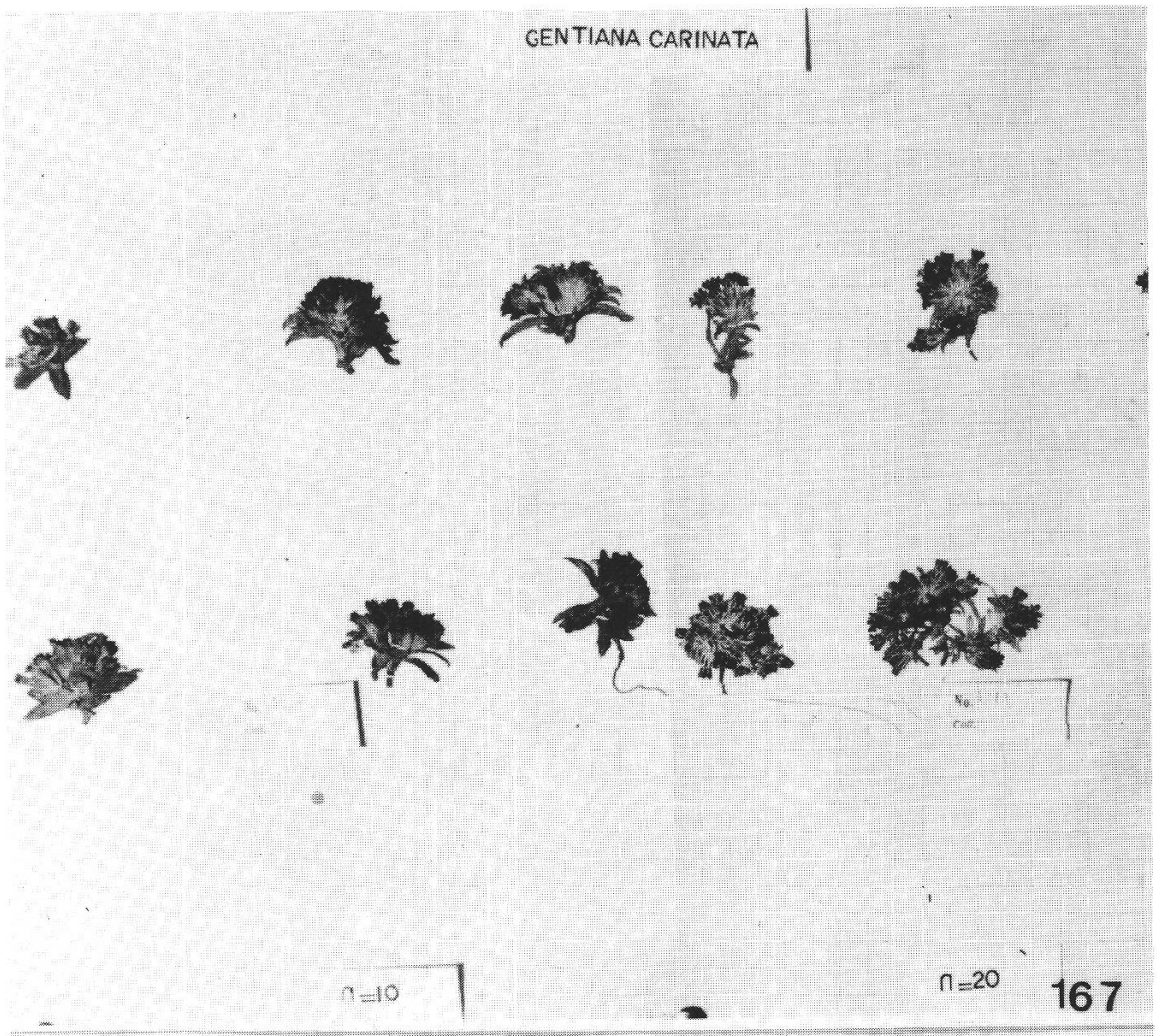
GENTIANA CARINATA
n=10
n=20
167

SOLANAM NIGRUM
n=24
n=36
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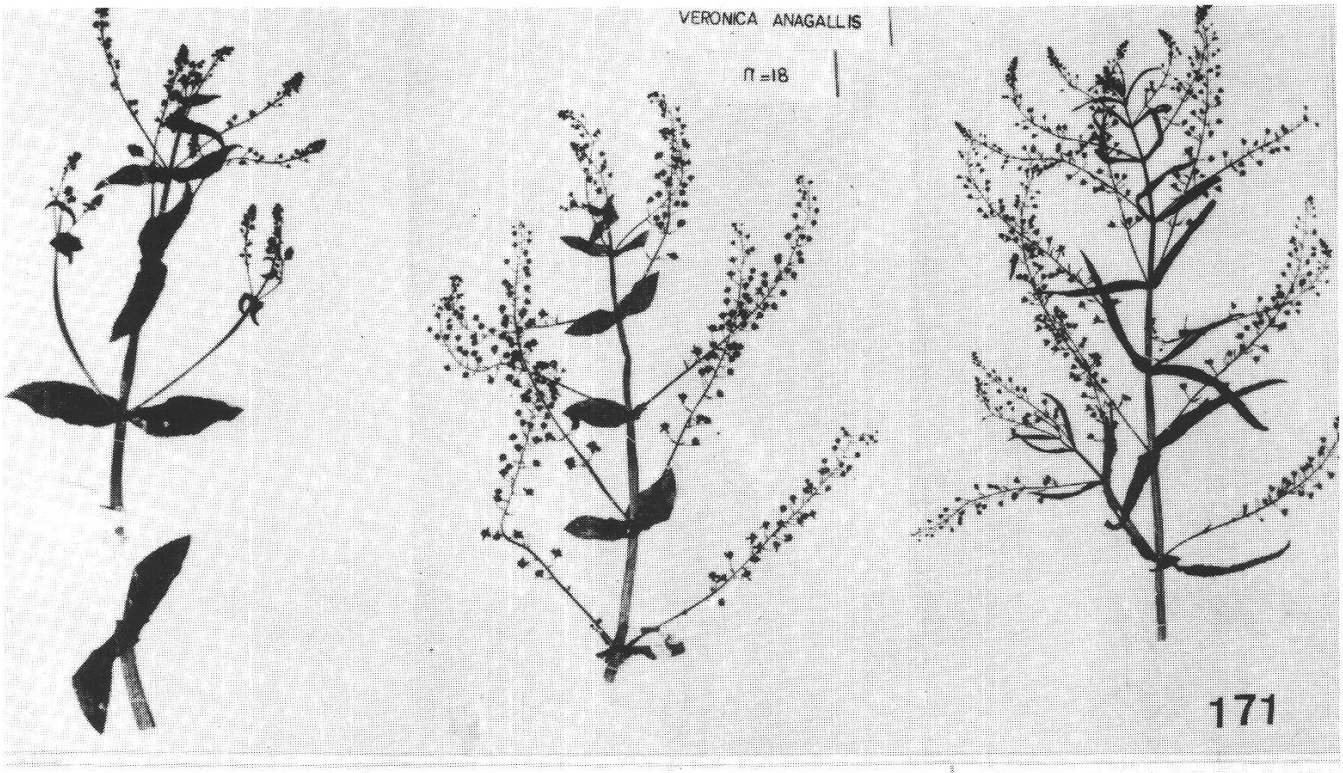
SCROPHULARIA HIMALENSIS
n=12
n=24
169

VERONICA ANAGALLIS
n=27
170


VERONICA ANAGALLIS
n =18
171

STROBILANTHES DALHOUSIANUS
172

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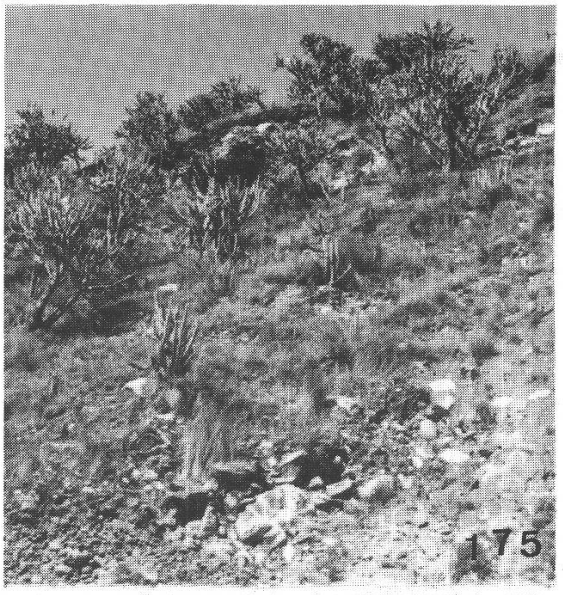
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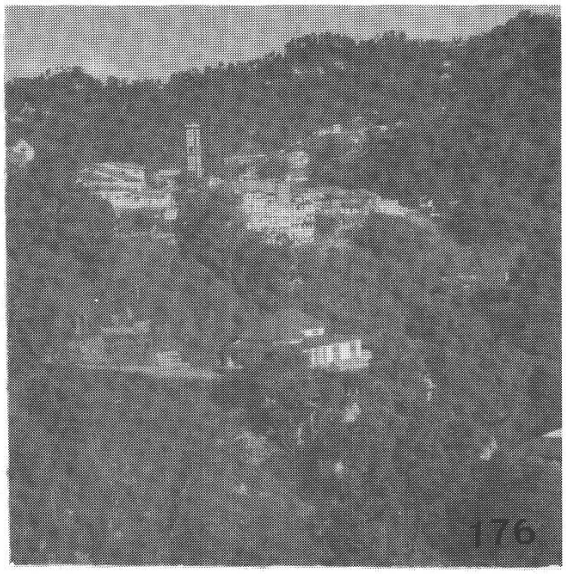
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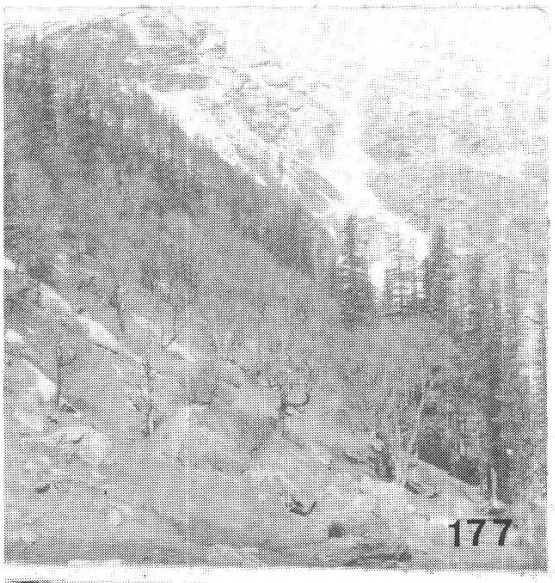
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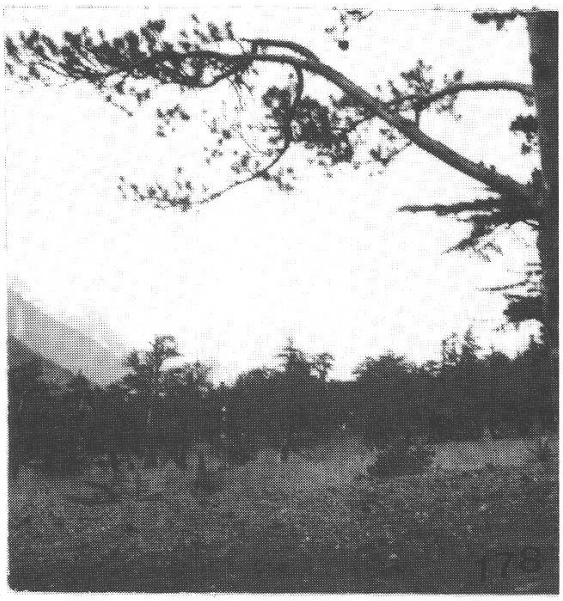
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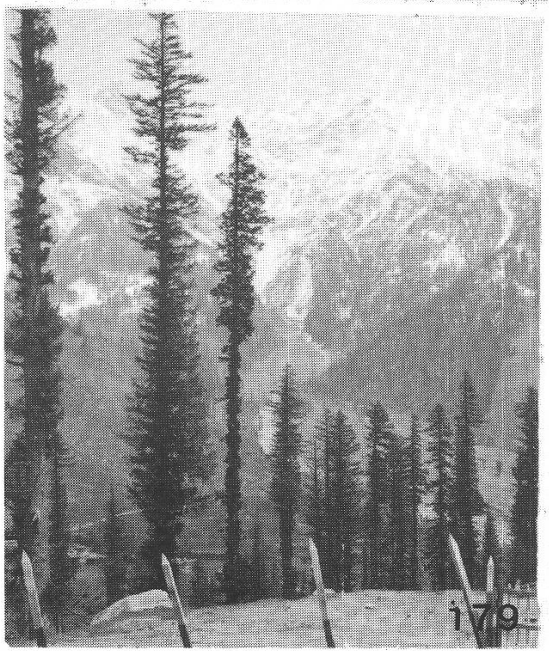
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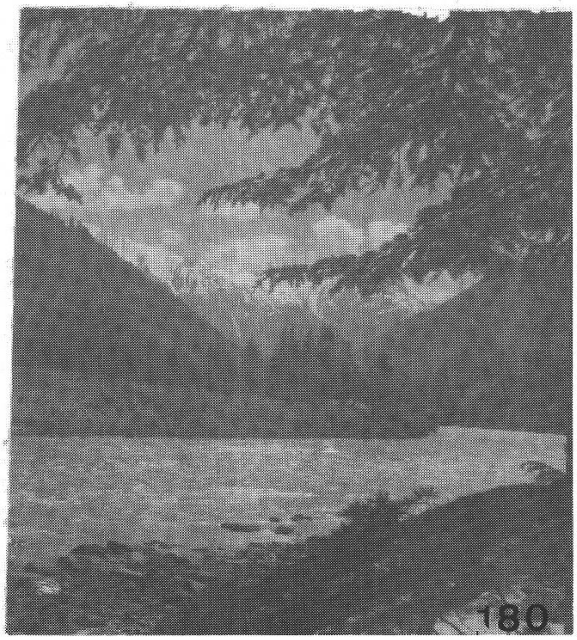
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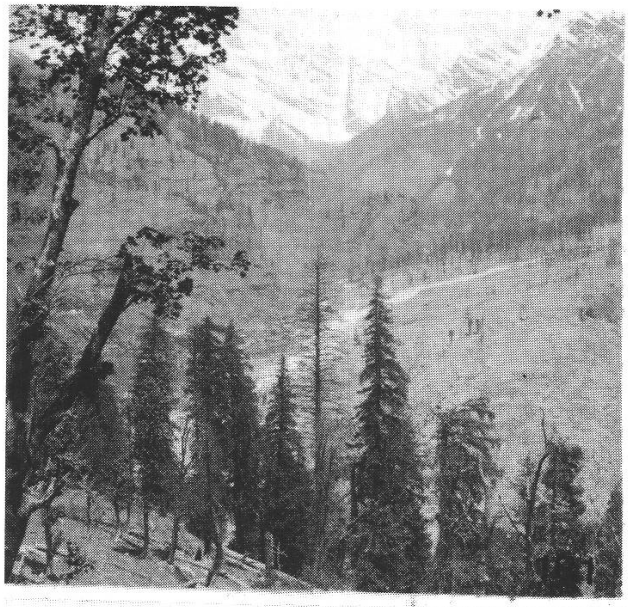

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