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SYSTEMATIC STUDIES IN THE BALSAMINACEAE

by

© Alina E. Zinov'eva-Stahevitch

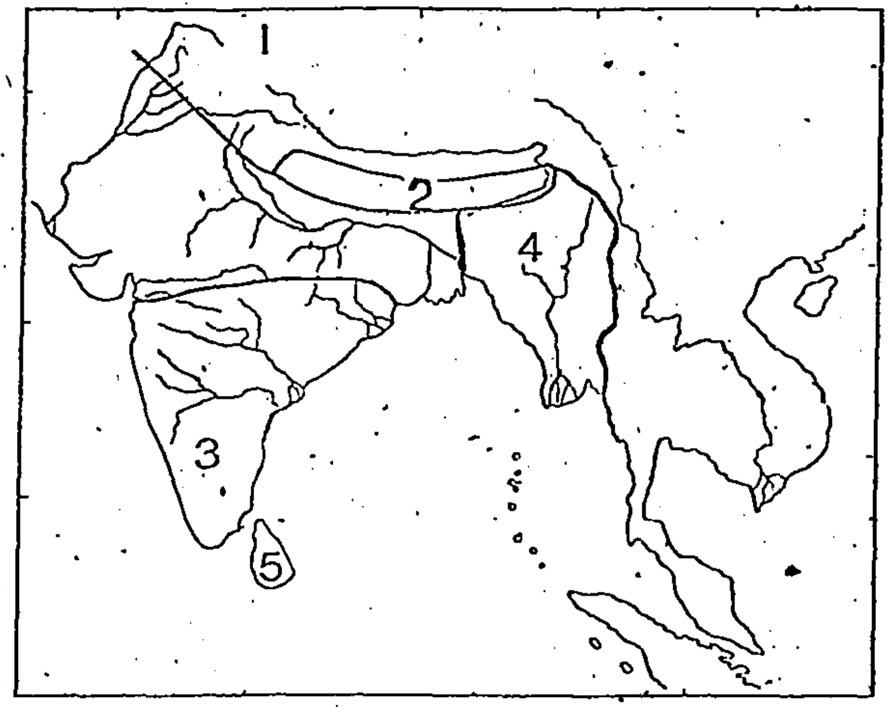
A thesis submitted to the Faculty of Graduate
Studies and Research in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

Department of Plant Science
Macdonald Campus
McGill University
Montreal

August, 1981

Phytogeographic Provinces of British India according to the scheme used by Sir Joseph Hooker in his monographs of Impatiens L.

1. Western Himalayan Region
2. Eastern Himalayan Region
3. Deccan Region
4. Burmese Region
5. Ceylonese Region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DEDICATION

This thesis is dedicated to Sri Mohamed Ismail of the Government Botanic Garden at Ootacamund and to his son Siraj for the enormous effort they made in helping me carry out my field studies in India. Without their knowledge and support this thesis would not exist.

CLAIM TO ORIGINAL RESEARCH

The study reported in this thesis constitutes the original research of the author, and the following are the most important contributions to the knowledge of the taxonomy of the Balsaminaceae:

1. The manner in which the fruit capsules dehisce is described accurately for the first time. The results indicate that Series A and Series B are more distinct than previously thought, but the genus _Hydrocera_ Blume now appears less distinctive than has been proposed.

2. Chromosome number determinations are reported for the first time for seven species: _I. cinnabarina_ Grey-Wilson ($n = 8$, $2n = 16$), _I. coelotropis_ Fisch. ($2n = 34$), _I. dalzellii_ Hk.f. ($2n = 16$), _I. flanaganae_ Hemsl. ($2n = 16$), _I. gordoni_ Horne ($n = 8$, $2n = 16$), _I. pulcherrima_ Dalz. ($n = 6$, $2n = 12$), and _I. usambarensis_ Grey-Wilson ($2n = 16$).

3. New chromosome numbers were found in _I. goughii_ Wt. ($2n = 40$), _I. parasitica_ Bedd. ($n = 7$) and _I. viscosa_ ($2n = 32$).

4. Idiograms are given for ten species for the first time.

5. The presence of satellite chromosomes are reported in seven new species.

6. This is the first study of meiotic irregularities in non-cultivated _Impatiens_ species which included lagging

chromosomes, bridges, secondary associations, micronuclei, abnormal quartets, and pollen grains of varying size.

7. This is the first comprehensive review of the genera of the Balsaminaceae. Little evidence was found to support their retention.

ACKNOWLEDGEMENTS

I would like to express my appreciation to:

Dr. William F. Grant, my thesis director, for his support and encouragement throughout my years of graduate study;

The staff of the Maharashtra Association for the Cultivation of Science for allowing me to use the facilities of their institution. The staff of the Botanical Survey of India (Southern Circle);

Dr. B.A. Razi for organizing and guiding my first major collecting trip in India;

Dr. B. Stone of the University of Malaysia for organizing my collecting trip in Malaysia;

Dr. Roland Loiselle, Chairman of the National Committee on the Plant Gene Resources of Canada and Dr. Tibor Rajhathy, Director of the Ottawa Research Station; for their assistance in advice and help in the importation of the living plant material used in these studies;

Dr. John Simmonds and his staff (Ottawa Research Station, Ornamentals Section) for propagating the collections following importation;

Dr. Constance Nozollillo of the University of Ottawa for cutting of <u>Impatiens</u>;

The staff of the Royal Botanic Gardens, Kew, for <u>Impatiens</u> cuttings;

The Curators and staff of the herbaria whose specimens were used in this study;

Dr. Luc Brouillet, Curator of the McGill University Herbarium, for our numerous discussions;

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My daughter, Lara Beate, for her patience and good humor through what for her must have been trying years.

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ABSTRACT

Ph.D. Alina E. Zinov'eva-Stahevitch Plant Science

SYSTEMATIC STUDIES IN THE BALSAMINACEAE

Plant collections, field and herbarium studies were used to evaluate classifications of Impatiens. Accepted interpretations of the perianth are questioned, and a program of developmental studies on several categories of inflorescences proposed. The fruit has been incorrectly described. It is of two types, differing in manner of dehiscence. Chromosome numbers are an inadequate taxonomic character because of parallel cytoevolution. Karyotypes were prepared, but it was found that homologues were not distinguishable. A technique for Hy-banding was developed, and homeologues in plants of I. leschenaultii Wall. identified. It is proposed that Hy-banding can identify marker chromosomes which will be a more efficient character than complete karyotypes. The classifications of Impatiens are discussed, and it is concluded that one founded on flower-pollinator relationships is the best, although convergence is a problem. The genera of the Balsaminaceae are reviewed. It is concluded that these show only slight deviations from Impatiens, and are rejected.

RESUME

Ph.D. Alina E. Zinov'eva-Stahevitch Plant Science

SYSTEMATIC STUDIES IN THE BALSAMINACEAE

On a utilisé des collections de plantes, et des études sur le terrain et en herbier, pour évaluer les classifications du genre Impatiens. L'interprétation classique du périanthe est mise en doute, et un programme d'étude du développement des inflorescences est proposé. Le fruit avait été incorrectement décrit; on en retrouve deux types, qui diffèrent par leur mode de déhiscence. Les nombres chromosomiques constituent un caractère taxonomique inadéquat, à cause du parallélisme présent au cours de l'évolution cytologique. Des caryotypes ont été préparés, mais on n'y pouvait distinguer les homéologues. On a donc développé une technique pour teindre les bandes Hy, et on a identifié les homéologues chez des plants d'I. leschenaultii Wall. On suggère que les bandes Hy peuvent servir à déterminer des chromosomes marqueurs, qui représenteraient des caractères plus sûrs que le caryotype complet. On discute des classifications antérieures d'Impatiens, et on conclut qu'un système fondé sur les relations fleur-pollinisateur serait le meilleur, bien que la convergence présente un problème. Les genres de Balsaminaceae sont révisés. La conclusion qui ressort de cette étude est qu'ils ne représentent que des déviations mineures d'Impatiens. Ils sont donc rejetés.

TABLE OF CONTENTS

INTRODUCTION

Impatiens L. is a large subcosmopolitan genus with its main centers of diversity in the Old World tropics and subtropics. Beginning with Hooker (1868), numerous authors have failed to arrive at a satisfactory classification of *Impatiens*. A review of the literature, together with field and herbarium studies, soon indicated the major problems. Since the middle of the last century all treatments [except the superficial, if occasionally valuable, one by Warburg and Reiche (1895) in Prantl and Engler's *Natürliche Pflanzenfamilien*] have been regional in nature, and therefore inadequate for recognizing major phylogenetic trends. Furthermore, the complex and fragile flower (which is a major evolutionary unit in *Impatiens*) does not lend itself well to preservation in herbarium specimens. Fresh material is not easily procured. Only about 30 species have ever been maintained in botanical collections, and many of the tropical and subtropical species are endemic to small, geographically and politically inaccessible regions. As a result of these problems, *Impatiens* has acquired the not altogether warranted reputation of being the most difficult of all Angiosperm genera (Hooker, 1868; 1909b). Consequently, in this century few botanists (with the notable exception of Schulze, Huynh, Clevenger, Bhaskar, and Grey-Wilson) have undertaken studies in *Impatiens*. This is unfortunate, for the genus offers a broad range of excellent topics for systematic studies.

The original goal of my research was the cytotaxonomy of

Impatiens, undoubtedly an overly ambitious project, which was inspired by the paper by Jones and Smith (1966) on the cytogeography of the genus. Initally, I planned to concentrate on the species of peninsular India because I knew that they had recently been revised. I had enormous faith that the taxonomy of the genus was on a relatively firm basis, for it had been the last major undertaking by a very eminent botanist of the last century. The more I looked at herbarium specimens and, even more importantly, at populations in the field, the less I could see the merit of existing classifications. It finally became evident that no significant progress in the cytotaxonomy of Impatiens could be made as long as the only available frame of reference was an artificial, and often bizarre, classification. At this point, the decision was made to develop into a well-rounded taxonomist capable of making one's own judgements rather than a narrow specialist forever dependent on the decisions of others. The thesis which follows is a first attempt to initiate this development.

CHAPTER I

ECONOMIC IMPORTANCE

ECONOMIC IMPORTANCE

Impatiens is the only genus in the Balsaminaceae which is of economic importance. Several species have long been valued in floriculture for their highly decorative flowers, long blooming season, and tolerance to deep shade (Howitt, 1968). Approximately 30 "species" (Table 1) have been cultivated, but only a few of these have spread beyond local or conservatory culture. The first of these (Fig. 1), the garden balsam (I. balsamina L.), is a native of southern Asia, and probably was introduced into Europe from Goa by the Portuguese sometime in the 16th century (Bailey, 1900). This species is said to have reached England by the end of the 16th century, having been described in Gerard's Herball published in 1597. The second common cultivar (Fig. 2) is I. walleriana Hk.f. (I. sultani Hk.f. and I. holstii Engl. et Warb.) commonly known as 'Patience Plant', 'Patient Lucy' or 'Busy Lizzy'. A native of Tropical East Africa, I. walleriana was introduced into cultivation by the Royal Botanic Gardens, Kew, at the end of the 19th century, and soon became a staple window box and bedding ornamental (Murphy, 1978).

In the early 1970's, Impatiens ornamentals underwent a spectacular rise in sales primarily as a result of their high resistance to air pollution (Adedipe and Barrett, 1972) and the introduction of new, compact "elfin" varieties of I. walleriana (Winters, 1973). By 1977, Impatiens ranked third in retail sales as a bedding ornamental in North America (Voight, 1978; Chong, 1979).

The cultivation of Impatiens is not restricted to civilized peoples. The aborigines of Papuasia grow Impatiens in gardens and along village tracks (Winters, 1973). It has been suggested that "New Guinea Impatiens"

Table 1

Species of *Impatiens* which have been brought into cultivation as ornamentals.

Species	Source area
A. Garden Ornamentals	
1. *I. amphorata* Edgw.	W. Himalayas
2. *I. balsamina* L.	India
3. *I. hawkeri* Bull	Papuasia
4. *I. herzogii*[1]	Papuasia
5. *I. holstii* Engl. & Warb.[2]	Tropical East Africa
6. *I. linearifolia* Warb.[1]	Papuasia
7. *I. mooreana* Schlecter[1]	Papuasia
8. *I. petersiana* Rehd.[3]	--
9. *I. schlecteri* Warb.[1]	Papuasia
10. *I. sultani* Hk.f.[2]	Tropical East Africa
11. *I. walleriana* Hk.f.	Tropical East Africa
B. Conservatory Ornamentals	
1. *I. auricoma* Baill.	Comoro Island
2. *I. balfourii* Hk.f.	Himalayas
3. *I. chrysantha* Hk.f.	Himalayas
4. *I. comorensis* Baker	Comoro Island
5. *I. cuspidata* W. & A.	India
6. *I. falcifer* Hk.f.	Himalayas
7. *I. flaccida* Arn.	S. India, Sri Lanka
8. *I. glandulifera* Royle	Himalayas

Table cont'd.

Table 1 (cont'd)

Species	Source area
9. I. grandiflora Hemsl.	Madagascar
10. I. hookeriana Arn.	S. India, Sri Lanka
11. I. jerdoniae Wt.	S. India
12. I. niamniamensis Gilg	Tropical Africa
13. I. oliveri Wt.	Tropical East Africa
14. I. oppositifolia L.	S. India, Himalayas
15. I. marianae Reichb.	India
16. I. platypetala Lindl.	Java, Celebes
17. I. psittacina Hk.f.	Thailand
18. I. repens Moon.	Sri Lanka

[1] Synonymous with I. hawkeri Bull sensu lato (Grey-Wilson, 1980a).

[2] Synonymous with I. walleriana Hk.f. sensu lato (Grey-Wilson, 1978; 1980g).

[3] Referrable to either I. hawkeri Bull Group 9 or I. walleriana (Grey-Wilson, 1980a).

[4] Catagory B includes the species in A.

Fig. 1. *I. balsamina* L.

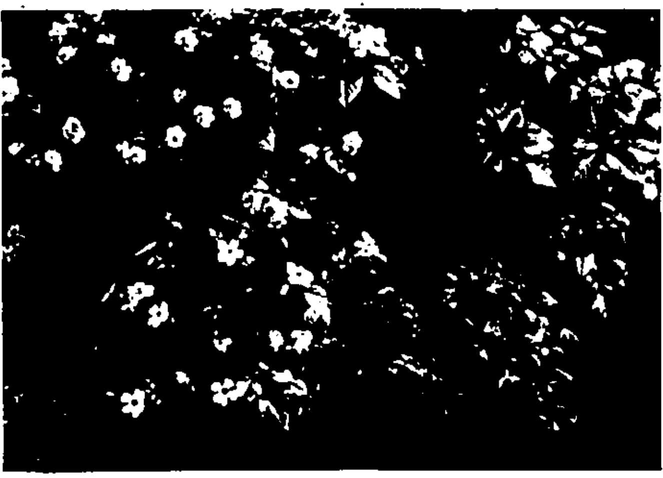


Fig. 2. *I. walleriana* Hk.f.

are all derived from I. hawkeri Bull, and that the many different lines with their huge flowers and brightly variegated foliage, are the result of centuries of breeding and selection by the indigenous population (H.B.S. Womersley, personal communication; Grey-Wilson, 1980a). A collection of New Guinea Impatiens (Fig. 3) was introduced into North America by the United States Department of Agriculture and the Longwood Foundation (Winters, 1973) and has since then revolutionized the Impatiens market.

The potential of Impatiens as ornamentals has by no means been exhausted. As the eminent American Horticulturist L.H. Bailey observed in 1900:

> "The genus Impatiens abounds in species that will probably have horticultural value, although relatively few are now in cultivation outside botanical collections... This beautiful genus has not been much developed horticulturally. Great numbers of species, hybrids, and interesting forms may be expected to appear in cultivation in the future. The genus has immense possibilities for productive horticultural work."

The potential of Impatiens for the development of new ornamentals has been recently discussed by two taxonomists. Bhaskar (1975), in his study of South Indian Impatiens, proposed 12 species for cultivation, namely, I. chinensis L., I. cuspidata W. and A., I. flaccida Arn., I. fruticosa D.C., I. gardneriana Wt., I. grandis Heyne, I. hookeriana Arn., I. maculata Wt., I. parasitica Bedd., I. phoenicea Bedd., I. pulcherrima

Figure 3

New Guinea _Impatiens_

Dalz., and I. talbotii Hk.f. His list was limited to species that could be grown at Mysore in the Indian lowlands. A much greater number of attractive species can be grown in the temperate zone where the climate more closely approaches that of the South Indian hills (Russell, 1980). Grey-Wilson (1980g) suggested that numerous African Impatiens are suitable for cultivation including: I. rosulata Grey-Wilson, I. rubromaculata Warb., I. lukwangulensis Grey-Wilson, I. eryaleia Launert, and I. flammea Gilg. Since most Impatiens perform well at low temperatures, and so require relatively moderate outlays of energy, the commercial demand for them is likely to increase in the future.

Although the main economic impact of Impatiens is as ornamentals, several species have been used as medicinals, prophylactics, dyes and oils (Table 2). Perhaps the most widespread medicinal application is as a topical salve against a variety of irritant syndromes (Table 2A), including stinging nettle (Thomson and Sifton, 1922), burns in India (Rao, 1914) and Papuasia (Winters, 1973), and eczema among the Zulus (Riley, 1963), Indians (Rao, 1914) and Amerindians (Schaffer et al., 1951-52). As a curative for poison ivy, the sap of I. capensis and I. pallida is still a popular folk remedy in rural New England (Gibbons, 1966). Josselyn (1672) reports that macerated leaves and stems of I. capensis mixed with hog grease were the favored Amerindian ointment for bruises. Rao (1914) noted that I. balsamina was used in India as a treatment for ulcers. Little is known of the pharmaceutical properties of Impatiens species, but our native I. capensis and I. pallida contain

Table 2

Uses of *Impatiens* other than as ornamentals

A: Medicinals, prophylactics

Species	Treatment	Where used	Reference
I. balsamina L.	eye disease	S. India	Rao, 1914
	ulcers	S. India	Rao, 1914
	eczema	S. India	Rao, 1914
I. capensis Meerb.[1]	bruises	N. America	Josselyn, 1672
	eczema	N. America	Schaffer *et al.*, 1951-52
	poison ivy	N. America	Gibbons, 1966
	emetic	N. America	Pammel, 1911
	diuretic	N. America	Pammel, 1911
I. chinensis L.	gonorrhea	S. India	Rao, 1914
	burns	S. India	Rao, 1914
I. glandulifera Royle[2]	diuretic	Europe	Pammel, 1911
I. hawkeri Bull[3]	burns	New Guinea	Winters, 1973
I. hochstetteri Warb.[4]	eczema	S. Africa	Riley, 1963

Table cont'd.

Table 2 cont'd.

Species	Treatment	Where used	Reference
I. noli-tangere L.	diuretic	Europe	Warburg and Reiche, 1895; Pammel, 1911
	emetic	Europe	Warburg and Reiche, 1895; Pammel, 1911 Schauenberg and Paris, 1977
	antihemorrhoidal	Europe	Warburg and Reiche, 1895
	cathartic	Europe	Warburg and Reiche, 1895; Schauenberg and Paris, 1977
	nettles	Europe	Thomson and Sifton, 1922
I. pallida Nutt.	eczema	N. America	Schaffer *et al.*, 1922
	poison ivy	N. America	Gibbons, 1966

B. *Dyes*

Species	Pigment	Use	Where used	Reference
I. balsamina L.	red	cosmetic	India, China, Japan	Warburg and Reiche, 1895
I. capensis Meerb.[5]	orange	coloring dried salmon	N. America	Nuttall, 1818
	orange or yellow	coloring cloth	N. America	Nuttall, 1818
I. tinctoria A. Rich	black	cosmetic	Ethiopia	Warburg and Reiche, 1895

Table cont'd.

Table 2 cont'd.

C. Food

Species	Use	Source	Where used	Reference
I. balsamina L.	oil (culinary and fuel)	seed	India	Warburg and Reiche, 1895; Rao, 1914
I. capensis Meerb.	vegetable	stems, leaves, young plants	N. America	Gibbons, 1966
I. glandulifera Royle[2]	oil (culinary and fuel)	seed	W. Himalayas	Warburg and Reiche, 1895
I. racemosa DC.	oil (culinary and fuel)	seed	E. Himalayas	Warburg and Reiche, 1895

---

[1] Either as I. biflora Walt. or I. fulva Nutt.

[2] As I. roylei Walp.

[3] As I. mooreana Schlecter

[4] As I. marlothiana G.M. Schulze

[5] As I. fulva Nutt.

the powerful anti-fungal agent 2-methoxy-1,4 napthoquinone (Schaffer et al., 1951-52). A second major medicinal role of Impatiens has been as purgatives (Table 2A). The Eurasian-American vicariads I. noli-tangere and I. capensis as well as the Himalayan I. glandulifera are strong emetics, diuretics, and laxatives, and were widely used as such in Europe (where the 1st species is naturalized) until the middle of the 19th century when they fell into disfavor due to the violence of the reaction they produced (Warburg and Reiche, 1895; Pammel, 1911). It should be noted, however, that one recent work on herbal medicines (Schauenberg and Paris, 1978) does recommend I. noli-tangere as an effective diuretic and emetic. It may be these expurgatory properties which have caused all three species to be implicated in livestock poisoning (Long, 1917; Pammel, 1911). However, the evidence is entirely circumstantial, and as Steyermark (1963) points out, I. capensis is frequently grazed by white-tailed deer without any adverse effects.

Several species of Impatiens have been employed as dyes (Table 2B). In India, China, and Japan, a red pigment extracted from the bruised petals of I. balsamina has been used as a cosmetic for the coloring of hands, nails and feet (Warburg and Reiche, 1895). Amerindians anticipated the modern food processing industry in the use of extracts of I. capensis to color dried salmon. Amerindians and later European colonists used the floral pigments of this species as a dye for cloth. The African species, I. tinctoria A. Rich. derives its specific epithet from the fact that the tuber yields a black pigment which was used in Ethiopia for the ritual dying of hands and feet (Hooker, 1868; Warburg and Reiche, 1895).

Finally, it should be noted that <u>Impatiens</u> species have occasionally been used as food sources (Table 2C).

CHAPTER II

A DICTIONARY OF VERNACULAR NAMES FOR *IMPATIENS*

5

A DICTIONARY OF VERNACULAR NAMES FOR IMPATIENS

One problem which I have encountered over and over again while doing field work is not knowing the word for Impatiens in the local dialect. I have yet to encounter rural populations in which the individuals cannot immediately direct you to good collecting localities if only one knows the vernacular name. Exploding the capsules of Impatiens appears to be a popular pastime (albeit mainly of childhood) the world over. On the other hand, given the sketchy knowledge of English found in most of rural Asia, it is often impossible to explain what one is looking for by describing the plant. I remember one particulary frustrating morning lost while a most accommodating, but hopelessly puzzled village headman dragged me all over the Pykarra Downs in an attempt to discover exactly what wretched plant the "crazy memsahib from Kan-a'-da" was collecting. (To this day I cannot decide whether his generous allotment of his time was the result of his enthusiasm for the local flood-control project funded by Canadian money, or, what is more likely, the result of the innate Indian kindness to the mentally ill.) Upon my return to Ootacamund, I asked Mohamed Ismail for the Tamil word for Impatiens which he wrote out phonetically. Then he gave me the Maylayama name, explaining that the villagers at Pykarra were immigrants from Kerala who still spoke their mother tongue rather than Tamil. Later I was able to verify the names in Rao (1914). So that was how this little dictionary began, and it has proven quite useful in the field. I have given no authorities for the

English names because these I have picked up while collecting in Eastern North American, mainly in New England.

Some common names for *Impatiens*

Language	Common Name	Reference
Arabic	Bahâ	Bedevian, 1936
Chinese	Fêng Hsien Hua	Steward, 1958
English	Jewelweed	--
	Lady's earrings	
	Snapweed	
	Touch-me-not	
French	Balsamine	Bedevian, 1936
	Impatiente	Provancher, 1862
	N'y touchez pas	
German	Ruhr-mich-nicht-an	Kosch, 1965
	Springkraut	
Hindi	Gul-mehndi	Rama Rao, 1914
Italian	Balsamina	Bedevian, 1936
	Belluomo	
	Gelosia	
Japanese	Tsuri-Fune-Sō Zuku	Ohwi, 1965
Malay	Inai	Ridley, 1922
Maylayama (S. India)	Mecchingom Pily	Rama Rao, 1914
Marattra (Cent. India)	Tereda	Cooke, 1901

Cont'd...

Language	Common Name	Reference
Papuasian	Kontip	Winters, 1973
Sinhalese	Kudalu-mal	Fernando, 1954
(Sri Lanka)	Gal-demata	
Samoan	Patiale	Christophersen, 1935
Tamil	Pylee	Rama Rao, 1914
	Vastla	
Turkish	Kina çiç	Bedevian, 1936

CHAPTER III

MATERIALS AND METHODS

MATERIAL AND METHODS

The research reported here was primarily based on four types of evidence:

I. Herbarium Specimens

Morphology, flowering, and fruiting periods, and general distribution patterns were studied using the Balsaminaceae collections at the following institutions: BKF, BK, BLATT, BO, BSI, CAN, DAO, K, KLU, MH, MT, MTMG, NY, and PDA. In addition, studies were carried out using the collections of three herbaria which are not registered with the International Bureau for Plant Taxonomy and Nomenclature (Lanjouw and Stafleu, 1964): Maharashtra Association for the Cultivation of Science, M.A.C.S. (Pune, Maharashtra); University of Mysore, Manasagangotri (Mysore, Karnataka); and the United Planters Association of South India (Munnar, Kerala). A representative sample of photographs made by the staff of the M.A.C.S. for my permanent records is given in Appendix I of this section. All data were entered on permanent cards, and in some cases, drawings made.

II. Field Work

Observations of Impatiens species in their natural environment, and collections of seeds and tubers for future studies were carried out in South India during 1976-77, and in Sri Lanka, Malaysia and Indonesia from July-September, 1977. Tubers of the Scapigerous species did not survive shipment to North America. Furthermore, percent seed germination was initially very low, a problem encountered by other workers as well (Clevenger, 1971; Bhaskar, 1975; Grey-Wilson, 1980b).

Only a few common species were obtained through seed banks. As a result, research requiring living material (cytological studies, for example) could not progress. Therefore, it was necessary to undertake a second collecting trip to South India (October-November, 1979) to obtain fresh material for study. A supplementary collection of living plants had been deposited at the Government Botanic Garden, Ootacamund (Tamil Nadu) in 1977 in case seed germination caused problems. Unfortunately, during a change in administration, this collection was inadvertently destroyed, necessitating the duplication of the material collected during 1976-77. During the 1979 trip, seed collections were supplemented by living material which was brought back to Canada by permission of the Quarantine Division of Agriculture Canada. The material was prepared for shipment to North America by the following procedure:

1. The Government Botanic Garden at Ootacamund was used as a base. It was chosen for the following reasons:
    a. The presence of greenhouse facilities and of staff, trained in the propagation and maintanence of plants, who were willing to care for material while the author was in the field.
    b. A suitable climate. In the Old World Tropics, <u>Impatiens</u> is almost exclusively an orophytic genus. In my experience, few species occur at elevations below 1000 meters and it is not uncommon to find them at the highest elevations (which in South India is about 3000 meters). The plants which I had tried to raise in Pune (elevation 1000 meters) during 1976-77 did very poorly.

Bhaskar (1975) encountered similar problems at Mysore (elevation about 500 meters). Since it was critical that the plants be healthy if they were to survive transport to North America (the problems encountered in shipping _Impatiens_ have been discussed by Winters, 1973), it was essential to maintain them in a sufficiently cool environment between the time of collection and the time of transport. Ootacamund at an elevation of 2,300 meters provides an ideal climate for tropical _Impatiens_, and the surrounding region is in fact a major center of diversity for the genus in the Indian subcontinent.

2. Whole plants were collected in various hill stations, rich in _Impatiens_ species (localities are given in Table 1), immediately wrapped in wet newspapers (plants packed in plastic bags begin to rot within a few hours), and a numbered tag was included in each packet. Field data were entered on the corresponding sheet in a specially prepared notebook (Fig. 1) supplied by Dr. V. Vartak of the Maharashtra Association for the Cultivation of Science. In the case of the Scapigerae, as much soil as possible was washed from the tubers. Some representative species are shown in Appendix 2 of this section.
3. At the end of each day, plants were unwrapped and cuttings made or in the case of the Scapigerae, infloresences and damaged leaves removed. On subsequent days, cuttings and tubers were checked for freshness, and unhealthy material

Table 1

Field collections of *Impatiens*

Species	Locality
I. acaulis Arn.	
(= *I. gracilis* Bedd.)	Materan, Maharashtra[1]
(= *I. gracilis* Bedd.)	Fritzgerald Ghat, Mahableshwar, Maharashtra
(= *I. acaulis* arn.)	Adam's Peak, Sri Lanka
I. appendiculata Arn.	Pussellawa, Sri Lanka
I. balfourii Hk.f.	Botanic Garden, Besançon, France (Himalayas)[2]
I. balsamina L.	
var. *arcuta* Hk.f.	Kollur Ghat, Karnataka Madhuairibetta, Karnataka Poonachi, Anamalais Hills, Tamil Nadu
I. balsamina L.	
var. *balsamina*	Parvati Hill, Pune, Maharashtra Mahableshwar, Maharashtra Khandala Maharashtra Karla Caves, Maharashtra
I. balsamina L.	
var. *coccinea* Hk.f.	Ootacamund, Niligri Hills, Tamil Nadu
I. balsamina	Baja Caves, Maharashtra
var. *rosea*	Khandala, Maharashtra Londvala, Maharashtra Karla Caves, Maharashtra

Table 1 continued

Species	Locality
I. balsamina L. var. azaleiflora	Cultivar, Pocha's Seed Farm, Pune, Maharashtra
I. balsamina L. var. camelliflora	Cultivar, Pocha's Seed Farm
I. campanulata Wt.	Sim's Park, Coonoor, Tamil Nadu Tiger Shola, Pulney Hills, Tamil Nadu Pambar Shola, Pulney Hills, Tamil Nadu Bombay Shola, Pulney Hills, Tamil Nadu Attakatti, Anamalai Hills, Tamil Nadu Waynaad Estate, Devicolam, Kerala Lockert Gap, Kerala Rajmalai, Anamudi Peak, Kerala Royal Botanic Gardens, Kew (India)
I. cinnabarina Grey-Wilson	Royal Botanic Gardens, Kew (Africa)
I. chinensis L. var. chinensis	Mercara Downs, Karnataka Government Botanic Garden, Ootacamund, Niligri Hills, Tamil Nadu
I. chinensis L. var. rupicola (Hk.f.) Bhask.	Shimoga, Karnataka
I. chonoceras Hassk.	Bogor-Tjiboidas Highway, Java
I. clavicornu Turz.	Pykarra Downs, Niligri Hills, Tamil Nadu Valley View, Niligri Hills, Tamil Nadu
I. coelotropis Fisch.	Rajmalai, Kerala

Table 1 continued

Species	Locality
I. cordata Wt.	Devicolam, Kerala Rajmalai, Anamudi Peak, Kerala Munnar, Kerala
I. curtisii Hk.f.	Maxwell's Hill, Malaysia
I. cuspidata W. & A.	Frog Hill, Niligri Hills, Tamil Nadu Lamb's Rock, Coonoor, Tamil Nadu Kundahs, Niligri Hills, Tamil Nadu Sim's Park, Coonoor, Tamil Nadu Munnar, Kerala Upper Vagavurai, Kerala
I. dalzellii Hk.f. & T.	Mahableshwar, Maharashtra
I. diversifolia Wall.	Pykara Downs, Niligri Hills, Tamil Nadu
I. elegans Bedd.	Poonachi, Anamalais Hills, Tamil Nadu Soliyar Submergible Area, Anamalai Hills, Tamil Nadu Valparai, Anamalais Hills, Tamil Nadu
I. flaccida Arn. var. flaccida	Valparai, Anamalais Hills, Tamil Nadu Wynaad Estate, Devicolam, Kerala Kandy, Sri Lanka
cv. 'alba'	University of Ottawa (Sri Lanka)
I. flanaganae Hemsl.	Royal Botanic Gardens, Kew (Africa)

Table 1 continued

Species	Locality
I. fruticosa DC.	Lamb's Rock, Coonoor, Niligri Hills, Tamil Nadu
	Naduvattum, Niligri Hills
	Gudalur, Niligri Hills, Tamil Nadu
I. gardneriana Wt.	Dhoni Hills, Kerala
	Thakarpaddy Bridge, Calicut, Kerala
	Chundala, Kerala
I. glandulifera Royle	Essen, Germany (introduced)
I. gordoni Horne	Royal Botanic Gardens, Kew (Seychelles)
I. goughii Wt.	Kodaikanal, Pulney Hills, Tamil Nadu
	Naduvattum, Niligris Hills, Tamil Nadu
	Waverly Estate, Anamalais Hills, Tamil Nadu
	Munnar to Upper Vaguvarai, Kerala
	Wynaad Estate, Devicolam, Tamil Nadu
I. griffithii Hk.f.	Kedah Peak, Malaysia
I. hawkeri Bull	Royal Botanic Gardens, Kew (New Guinea)
	Ottawa Research Station
I. henslowiana Arn.	Tiger Shola, Pulney Hills, Tamil Nadu
	Lockert Estate, Devicolam, Kerala
	Lockert Gap, Kerala, Tamil Nadu
	Upper Vaguvarai to Munnar, Kerala
	Nur Eliya, Sri Lanka
	Royal Botanic Gardens, Kew (unknown)

Table 1 continued

Species	Locality
I. hookeriana Arn.	Sim's Park, Coonoor, Niligri Hills, Tamil Nadu Coonoor-Coimbatore Highway, Niligri Hills, Tamil Nadu Royal Botanic Gardens, Kew (unknown)
I. javensis (Bl.) Steud.	Mt. Gedé, Java
I. kleinii W. & A.	Khandala, Maharashtra Calicut, Kerala Lockert Gap, Kerala Dohni Hills, Kerala Mercara Downs, Karnataka
I. latifolia L.	Naduvattum, Niligri Hills, Tamil Nadu Lamb's Rock, Coonoor, Niligri Hills, Tamil Nadu
I. lawii Hk.f. & T.	University of Mysore, Manasagangotri (India)
I. lenta Hk.f.	Nalliambudi, Palghat, Kerala
I. leptopoda Arn.	Royal Botanic Gardens, Kew (Sri Lanka) Horton Plains, Sri Lanka
I. leschenaultii Wall.	Woodhouse, Niligri Hills, Tamil Nadu Dodabetta Peak, Niligri Hills Beirim Shola, Pulney Hills, Tamil Nadu Upper Vaguvarai, Kerala
I. levingei Hk.f.	Lamb's Rock, Coonoor, Tamil Nadu
I. linearifolia Warb.	Ottawa Research Station (New Guinea)

Table 1 continued

Species	Locality
I. macrophylla Gardn.	Nur Eliya, Sri Lanka
I. maculata Wt.	Attakatti to Valparai, Anamalai Hills, Tamil Nadu Naterikal, Tamil Nadu Andaparai Shola, Anamalai Hills, Tamil Nadu Devicolam, Kerala Upper Vaguvarai, Kerala
cv. 'Miss Swiss'	Ottawa Research Station
I. modesta W. & A.	Naduvattum, Niligri Hills, Tamil Nadu Anamudi Peak, Kerala
I. niamniamensis Gilg	Royal Botanic Gardens, Kew (Africa)
I. niligrica Fisch.	Pykarra Falls, Niligri Hills, Tamil Nadu
I. onchidioides	Fraser's Hill, Malaysia Mt. Gedē, Indonesia
I. oppositifolia L.	Mahableswar, Maharashtra
I. pandata Barnes	Anamudi Peak, Kerala Hatchery, Rajmalai, Kerala
I. parasitica Bedd.	Lockert Estate, Devicolam, Kerala Hatchery, Rajmalai, Kerala Anamudi Peak, Kerala
I. parviflora DC.	Staynor Park, Montreal (introduction)

Table 1 continued

Species	Locality
I. phoenicea Bedd.	Bombay Shola, Pulney Hills, Tamil Nadu Pambar Shola, Pulney Hills, Tamil Nadu Rajmalai, Kerala
I. platypetala Lindl. var. *platypetala*	Mt. Gedē, Java Royal Botanic Gardens, Kew (Indonesia)
var. *nematoceras* (Miq.) Steen.	University of Ottawa (Indonesia)
var. *nivea* Bakh. *ex* Steen.	Tjiboidas, Java
var. *aurantiaca* (Teysm. *ex* Kds.) Steen.	Royal Botanic Gardens, Kew (Celebes)
I. *pseudoviola* Gilg	Royal Botanic Gardens, Kew (Africa)
I. pulcherrima Dalz.	Fritzgerald Ghat, Maharashtra
I. pusilla Heyne	Naduvattum, Niligri Hills, Tamil Nadu
I. radicans Z. & M.	Mt. Gedē, Java
I. repens Moon	Ottawa Research Station (Sri Lanka) Royal Botanical Gardens, Kew
I. ridleyi Hk.f.	Batu Caves, Selangor, Malaysia
I. scabrida DC.	Botanic Garden, Besançon, France (Himalayas)

Table 1 continued

Species	Locality
I. scabriuscula Heyne	Doddabetta Peak, Niligri Hills, Tamil Nadu
I. scapiflora Heyne	Jog Falls, Shimoga, Karnataka
var. *scapiflora*	Abbe Falls, Mercara, Karnataka
	Dhoni Forest, Kerala
	Lockert Gap, Kerala
	Tambracheri Ghat, S. Wynaad, Kerala
var. *pseudo-acaulis* Bhask.	Frog Hill, Niligri Hills, Tamil Nadu
(= *I. rivalis* Wt.)	
I. schlecteri Warb.	University of Ottawa (New Guinea)
I. sodeni Engl. & Warb. *ex* Engl.	Royal Botanic Gardens, Kew (Africa)
	Royal Botanic Gardens, Kew (Africa)
I. tangachee Bedd.	Munnar, Kerala
	Umaiya Malai, Kerala
I. taprobanica Hiern.	Ramboda, Sri Lanka
I. tenella Heyne	Gudalar, Niligri Hills, Tamil Nadu
	Naduvattum, Niligri Hills, Tamil Nadu
I. tomentosa Heyne	Glen Morgan Estate, Niligri Hills, Tamil Nadu
	Base Station, Pulney Hills, Tamil Nadu
I. truncata Thw.	Elk Plains, Sri Lanka
I. umbellata Heyne	Rajmala, Kerala
I. usambarensis Grey-Wilson	Royal Botanic Gardens, Kew (Africa)

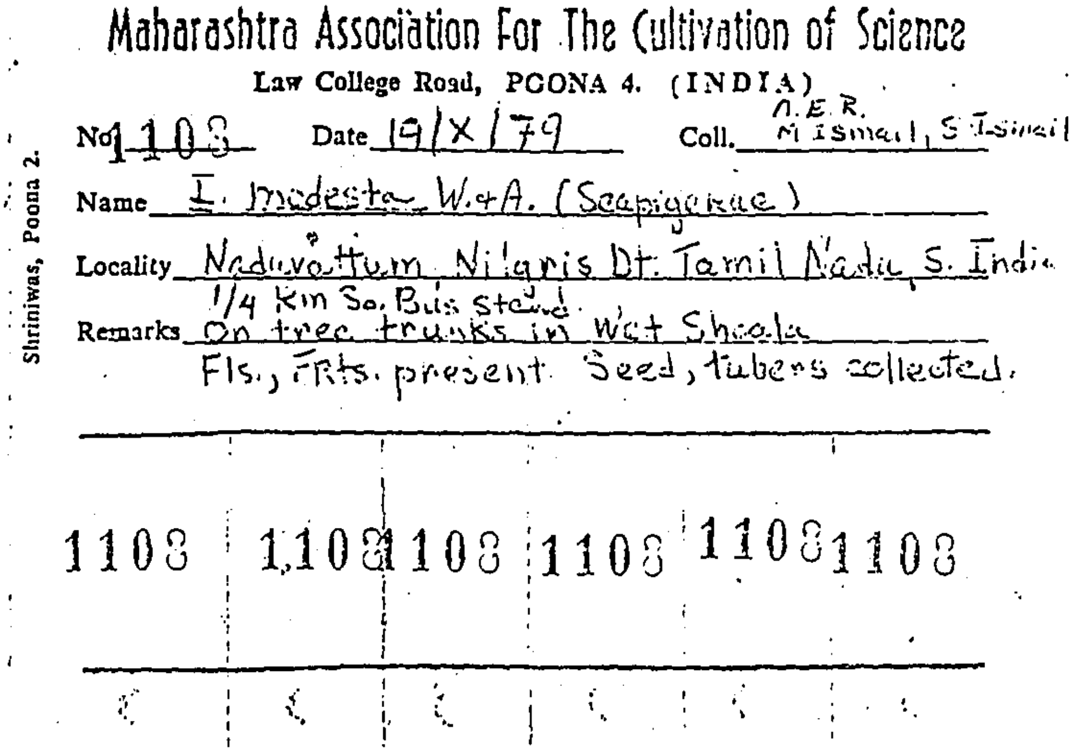
Table 1 continued

Species	Location
I. viscida Wt.	Pambar Shola, Pulney Hills, Tamil Nadu Silver Cascade, Pulney Hills, Tamil Nadu Tiger Shola, Pulney Hills, Tamil Nadu
I. viscosa Bedd.	Tambracheri Ghat, Calicut Dt., Kerala
I. walleriana Hk.f.	
(single-flowered)	Cultivar, Atwater Market, Montreal
(double-flowered)	Cultivar, Sheridan's Nursery, Montreal
I. wrayii Hk.f.	Perak, Malaysia

[1] If country not indicated = India.

[2] Region where taxon is native.

Figure 1



Maharashtra Association For The Cultivation of Science

Law College Road, POONA 4. (INDIA)

No 1108 Date 19/X/79 Coll. A.E.R. M. Ismail, S. Ismail

Name I. modesta W.&A. (Scapigerae)

Locality Naduvattum Nilgiris Dt. Tamil Nadu, S. India 1/4 Km So. Bus stand.

Remarks On tree trunks in Wet Shola

Fls., Frts. present. Seed, tubers collected.

1108 1108 1108 1108 1108 1108

Shriniwas, Poona 2.

Sample of page from notebook supplied by Dr. V. Vartak for field collecting data.

discarded, then rewrapped in wet newspapers which were not allowed to dry out at any time. An individual collecting trip never lasted more than five days to insure that the material would arrive at Ootacamund in good condition.

4. Once back at the Botanic Garden, fresh cuttings were prepared to insure that tissues were in prime condition. The scapigerous species were scrubbed with a fine-grade child's toothbrush to loosen all roots and soil particles, and rinsed. The Epiphyticae were propagated from stem cuttings. Tags labelled with the collection number were fastened to the stem of each cutting or, in the case of the scapigerous species to a petiole. The material was dipped in the fungicide "Benlate" (1.0 g/l) and then into rooting hormone ("Seradix 1").

5. Agriculture Canada had agreed to permit the introduction of the live material as rooted cuttings or tubers on the condition that the original roots were removed and that the plants be re-rooted in a sterile medium other than sterilized sphagnum moss. Two methods were used:

    a. Plastic basins were purchased in the local market, and these were half-filled with half-strength Hoagland's (Hoagland and Arnon, 1938) culture solution in which one-quarter tablet of a commercial algacide (active ingredients: monuron and simazine), sold for aquaria use, was added. Cuttings were inserted into "Rootrainers" purchased from Spencer-Lemaire Industries Ltd. of Edmonton, Alberta (Book style "Fives" with a volume of 7 cm^3 and a nominal size of 2.5 cm X 2.5 cm X 10 cm), which were then inserted into the basin (Fig. 2). The solution was changed every three days.

b. The Scapigerae were rooted by an alternative technique.

Plastic sheeting was used to line the tray portion of the "Rootrainers" and these were filled with vermiculite brought from North America, since artificial rooting media are not available in India. The tubers were inserted, and the vermiculite was kept moist with half-strength Hoagland's solution. Initially there was a problem with algae, but the algacide was found to be an effective deterrent to their growth. The cuttings of some species (e.g. I. henslowiana Arn., I. phoenicea Bedd.) rotted easily and could not be rooted by the technique described in (a), and so were rooted by the second method. Since midday temperatures were relatively high in the greenhouse, the plastic basins were kept covered with wet newspapers during the hottest periods of the day. Material collected early in the trip rooted well (the perennials generally having less of a mortality rate than the annuals as is to be expected). Material collected in the last two weeks did not have sufficient time to develop roots.

7. Since certain regions of India, including the Nilgri Hills in which Ootacamund is situated are infested with Golden Nematode (Heterodera rostochiensis Wr. 1923), a phytosanitary inspection was carried out by the plant pathologist at the

Figure 2

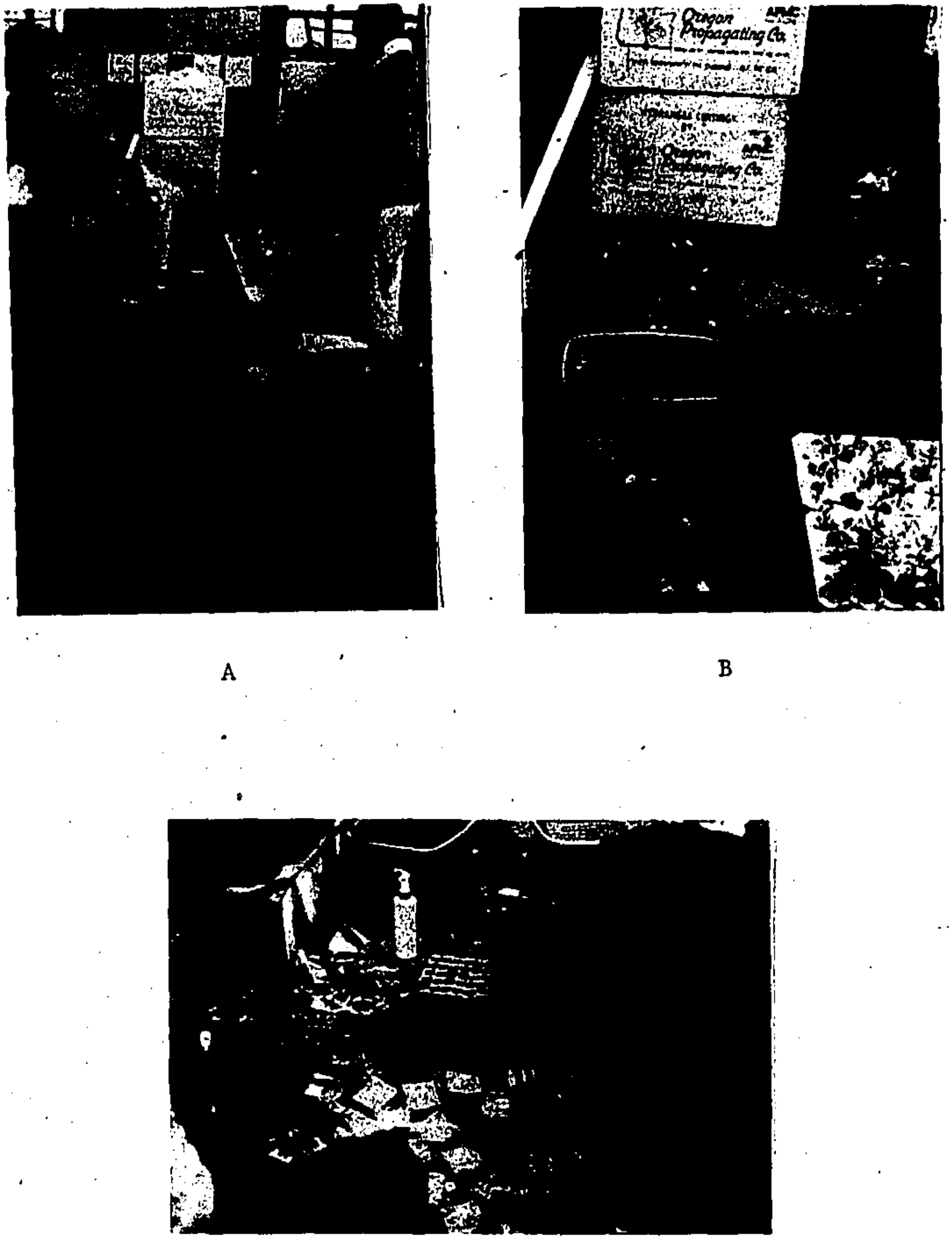
Preparation of Plant Material
For Shipment to North America

A. Staff of Government Botanic Garden, Ootacamund, maintained plants for author.

B. Plants in rootrainers in plastic containers of Hoagland's nutrient solution, or, in case of species which are difficult to root, in vermiculite. Boxes in background were used for shipment to North America.

C. Mohamed Ismail (right) and Siraj wrap rooted cuttings prior to shipment.

Figure 2



A

B

C

State Potato Research Station (Ootacamund), and when all the material was found to be free of infestation a certificate was issued.

8. Material was prepared for transport as follows:

   a. Plants were removed from the sterile medium, dipped in "Benlate", and inserted in a small mound of vermiculite which had been heaped on a square of cotton gauze several layers thick (these were all handcut and folded from rolls of surgical gauze since individual squares were not available). The edges of the gauze were gathered and fastened with string tied around the base of the plant. The vermiculite ball was then dipped in "Benlate", and laid on newspapers to drain. (Fig. 2).

9. The plants were packed in the "rootrainers" and the "rootrainers" were stacked in heavy waxed cartons (60 cm X 45 cm X 41 cm) of commercial nursery stock which were provided by J.D. Carrière Greenhouses, Baie d'Urfé, Québec. The cartons had been lined with 0.6 cm styrofoam sheets to minimize temperature fluctuations during transport. Since the nearest airport to Ootacamund is at Bangalore, an eight hour trip by local bus was necessitated. (There is an air terminal at Coimbatore which is three hours by bus from Ootacamund but it is only serviced by the Indian Airlines Aerobus whose luggage compartment doors are too narrow for containers the size of the cartons.). It was feared that the luggage rack of the bus might prove too hot for the plants

so ice was procured, wrapped in plastic garbage bags and added to the space between the stacked trays and the carton flaps. This proved an unwise decision because enroute the ice melted and drenched the plants, hastening rot. The trays had to be removed on arrival and the plants left to air dry overnight.

10. A general phytosanitary inspection was carried out at Pune by the staff of the Maharashtra Plant Quarantine Office and a certificate issued.
11. The material was then brought to Montreal and immediately taken to the Ottawa Research Station of the Central Experimental Farm where it was unpacked and placed in propagating benches. It was then maintained by Dr. J. Simmond and his staff in the Ornamentals Section until it was sufficiently established to be brought to Macdonald College. The Scapigerae were maintained in Petri dishes filled with moist perlite which provided a more mechanically stable substrate than vermiculite. The tubers were checked daily and rotten ones (less than 10%) were discarded. When good root and shoot development was observed, the plants were transferred to a peat-loam-sand (3:2:1) mixture which was thought to approximate their natural substrate. No exact figures were kept as to how many plants survived transport and were successfully propagaged, but we have estimated that the figure was about 75% (by comparison, the U.S.D.A. - Longwood Foundation Expedition to Papuasia had a survival rate of less than 50%; Winters, 1973). Since in

most instances a number of plants from several populations of the same species were collected, in most cases this did not represent significant losses, except for two species, I. phoenicea Bedd. and I. umbellata Heyne, where there were no survivors. Another species, I. maculata Wt. has not bloomed so far.

The following modification of procedures would undoubtedly yield an even higher survival rate:

1. The use of "plant-a-plug" containers produced by Plant-a-Plug Systems (Crossett, Arkansas) for storing and transporting plants while doing field work. A certain number of plants rotted even when wrapped in wet newspapers. Others were injured in the period between collection in the field and storage in wooden crates (for subsequent transport to Ootacamund). Local buses which are usually the only mechanized means of transportation in rural India are unbelievably crowded. The pack would protect the plants from jostling by passengers.
2. The application of "Benlate" on the evening following collection despite the inconvenience of carrying a container for the solution. Even more important is the use of an antibiotic in addition to a fungicide. The major damage to plants was apparently due to bacteria. The plant pathologists at the M.A.C.S. suggested that the suppression of fungi was a stimulus to increased bacterial activity. At their suggestion, the plants were dipped in a solution containing tetracyline (10 mg/l).

3. The addition of insolation batting between the carton sides and the inner styrofoam sheets in the containers used for air transport. The numerous assurances by the staff of British Overseas Airways that temperatures in the hold do not fall below freezing were belied by the unhealthy vivid green color and icy feel of the plants when they were opened for quarantine inspection in Montreal. Some of the perennial South Indian <u>Impatiens</u> species endure a brief period of freezing temperatures (in mid-December), but others are restricted to localities or times of the year in which temperatures are much higher (i.e. about 15°C).
4. Packing tubers and cuttings individually. To conserve space, several tubers or cuttings were wrapped together. If one began to rot, it was necessary to unwrap the packet, discard the rotten specimen, and clean the others to which in some cases microorganisms had already spread.

III. <u>Greenhouse Material</u>

The plants collected in India together with some species which were germinated from seed have been retained for observation and study. The following maintenance program is carried out:

1. All plants are repotted twice annually in a mixture of equal parts peat-loam-sand in which they do better than in one which approximates their natural substrates high in organic matter.
2. Fertilization is carried out every two weeks, using 20-20-20 (a soluble fertilizer containing N,P,K, chelated trace elements and sequestered nutrients) or "Liquid Seaweed" (a non-toxic

organic fertilizer).

3. Pruning is done every three months.
4. During the summer, the plants are shaded with temporary screens.

Despite the effort in maintaining this collection, it has proved invaluable in providing numerous insights into the fruit, flower, and vegetative characters as well as ecological, phenological, and reproductive phenomena which one can never observe in herbarium specimens.

IV. Taxonomic Literature

It was realized that a major problem with all studies on the Balsaminaceae has been their limited scope as compared to the full range of variation found in the family. This has often led to erroneous conclusions in the light of later research. For this reason an effort was made to obtain and study as many taxonomic works dealing with Balsaminaceae as possible. The most valuable of these were Agnew (1974), Backer and van den Brink (1963), Baker (1877), Barnes (1938, 1939, 1944), Beddome (1859, 1874), Bhaskar, (1975), Blatter (1933), Comber (1934), Cooke (1901), De Candolle (1824), Don (1831), Fernando (1954), Fischer (1930), Fyson (1915, 1932), Gamble (1915), Gilg (1909), Grey-Wilson (1980g), Handel-Mazzetti (1933), Hooker (1868; 1874-75; 1904-06; 1908b; 1909a,b,c; 1910a,b; 1911a,b,c), Hooker and Thomson (1859), Hutchinson and Dalziel (1927), Huynh (1968a,b), Mathew (1962), Moore (1972), Nairne (1894), Ohwi (1965), Perrier (1933), Ridley (1922), Riley (1963), Rydberg (1910), Santapau (1961, 1967), Schulze (1944), Sebastine (1960), Sebastine and

Vivekanathan (1967), Shetty and Vivekanathan (1971), Shimizu (1970), Trimen and Hooker (1893), Warburg (1897), Warburg and Reiche (1895), and Wight and Arnott (1834). Others are cited in references to specific points in later sections. Of at least equal importance, were illustrations of specific species which were obtained and studied; the richest sources are Hooker (1907, 1908a, 1910c) and Grey-Wilson (1980g). The complete list of illustrations is too extensive to list but is given in Index Londinensis (Stapf, 1929) and Worsdell (1941).

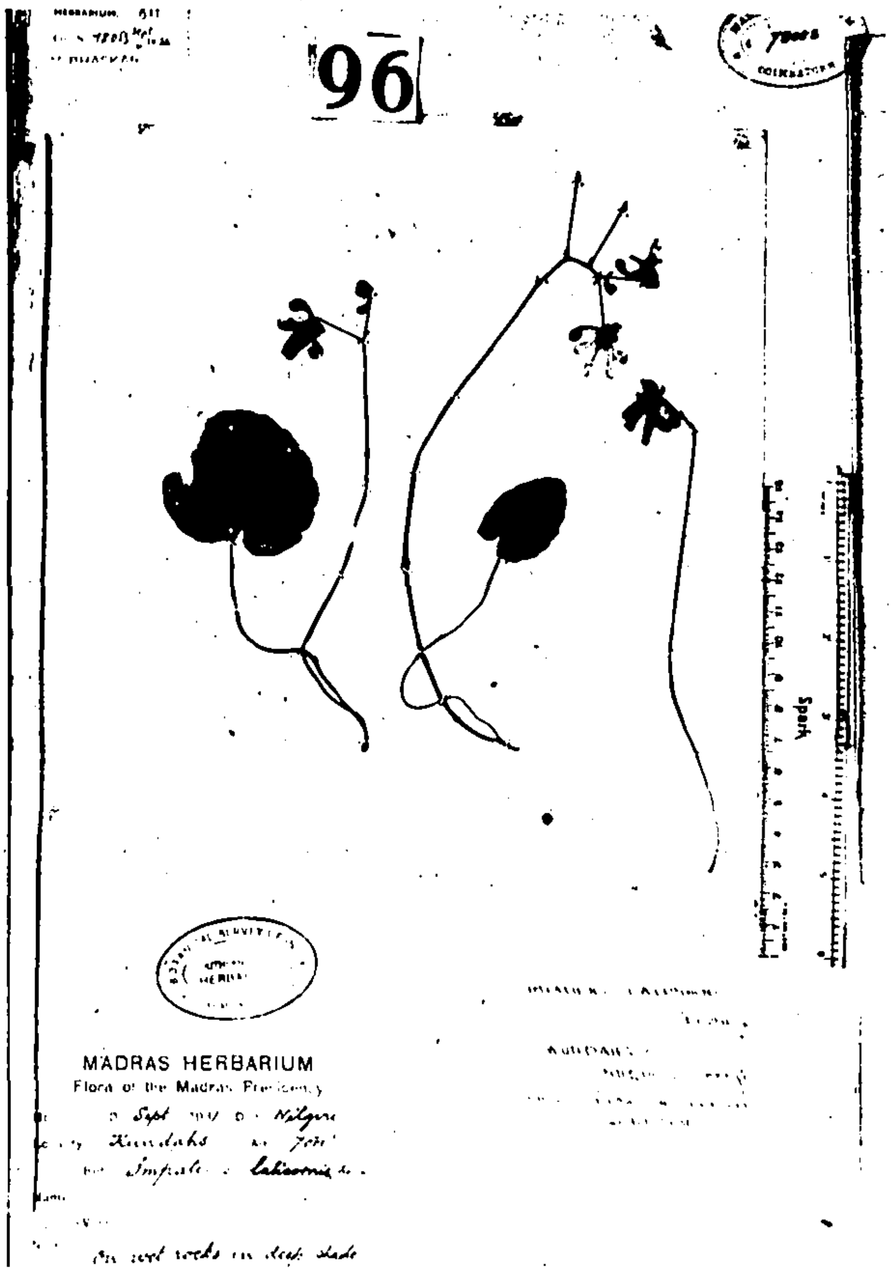
Other techniques used in the study of specific problems are detailed in the appropriate sections.

APPENDIX 1

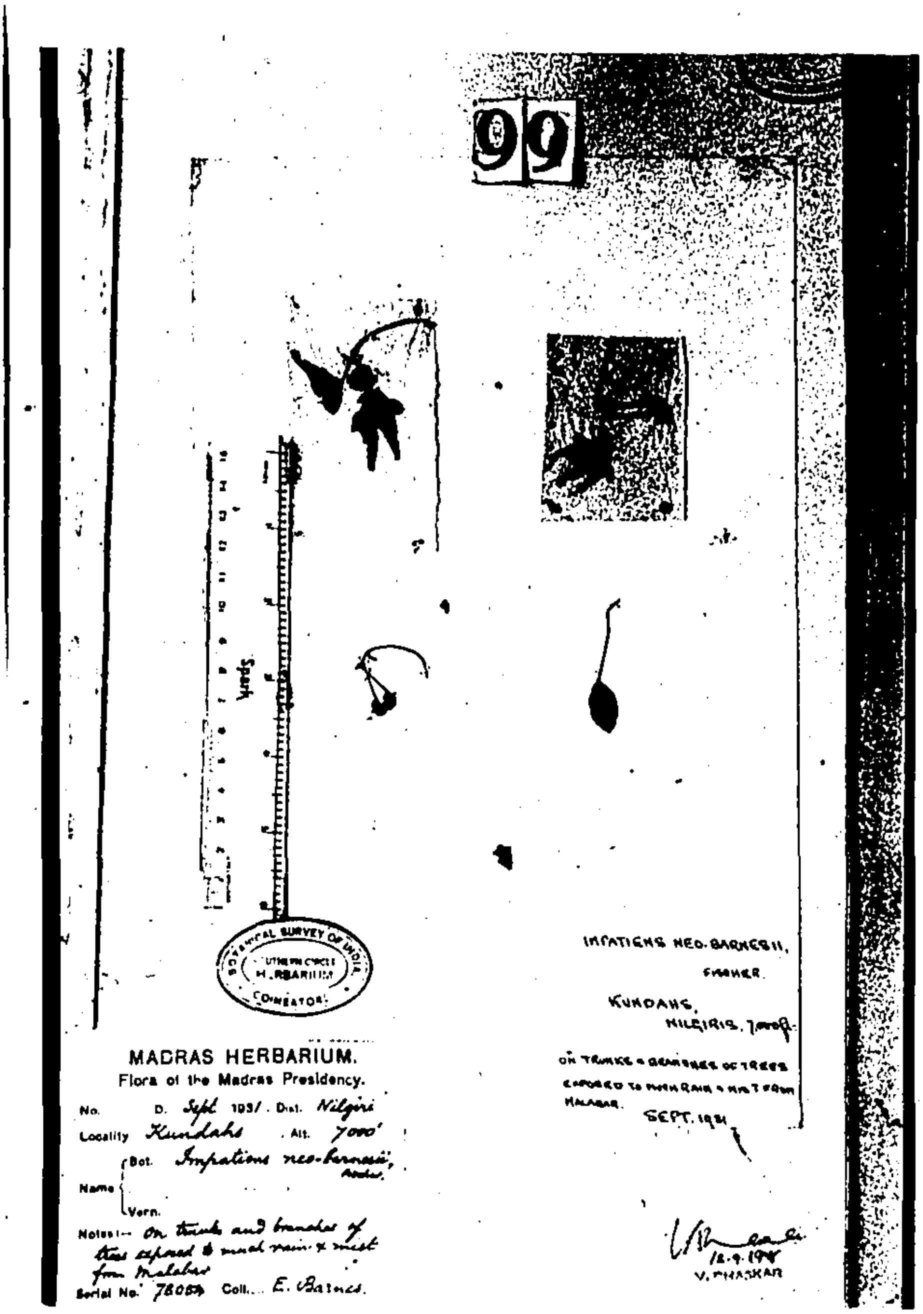
Photographs of some herbarium specimens examined at MH. Species are grouped according to classification of Hooker (1874-75; 1904-06).

SECTION SCAPIGERAE

(Species described after the publication of the Epitome)



Impatiens laticornis Fischer



MADRAS HERBARIUM.

Flora of the Madras Presidency.

No. D. Sept 1931. Dist. Nilgiri

Locality Kundahs . Alt. 7000'

Name Bot. Impatiens neo-barnesii, Fischer

Vern.

Notes:— On trunks and branches of trees exposed to much rain & mist from Malabar

Serial No. 78064 Coll... E. Barnes.

IMPATIENS NEO-BARNESII,

FISCHER.

KUNDAHS,

NILGIRIS, 7000ft.

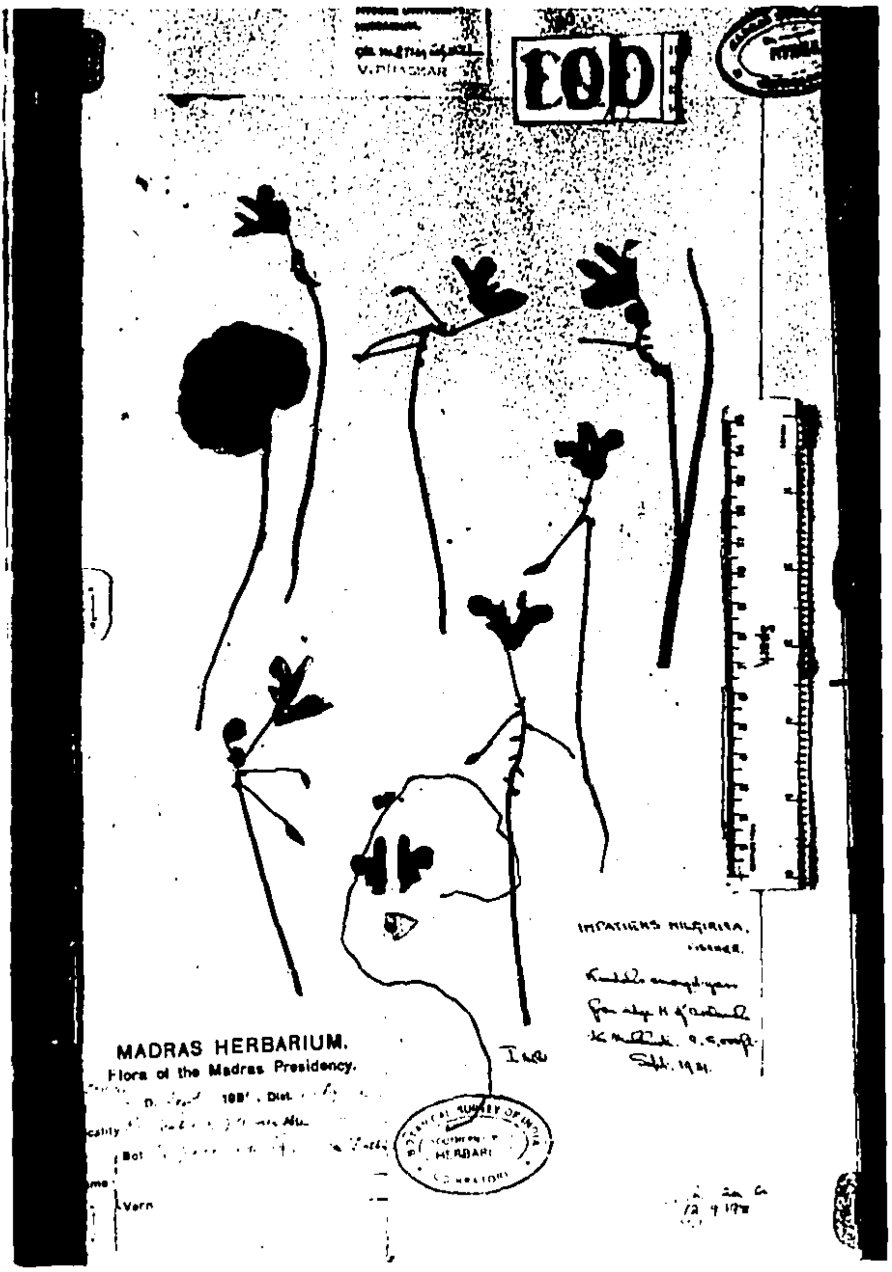
ON TRUNKS & BRANCHES OF TREES EXPOSED TO MUCH RAIN & MIST FROM MALABAR.

SEPT. 1931

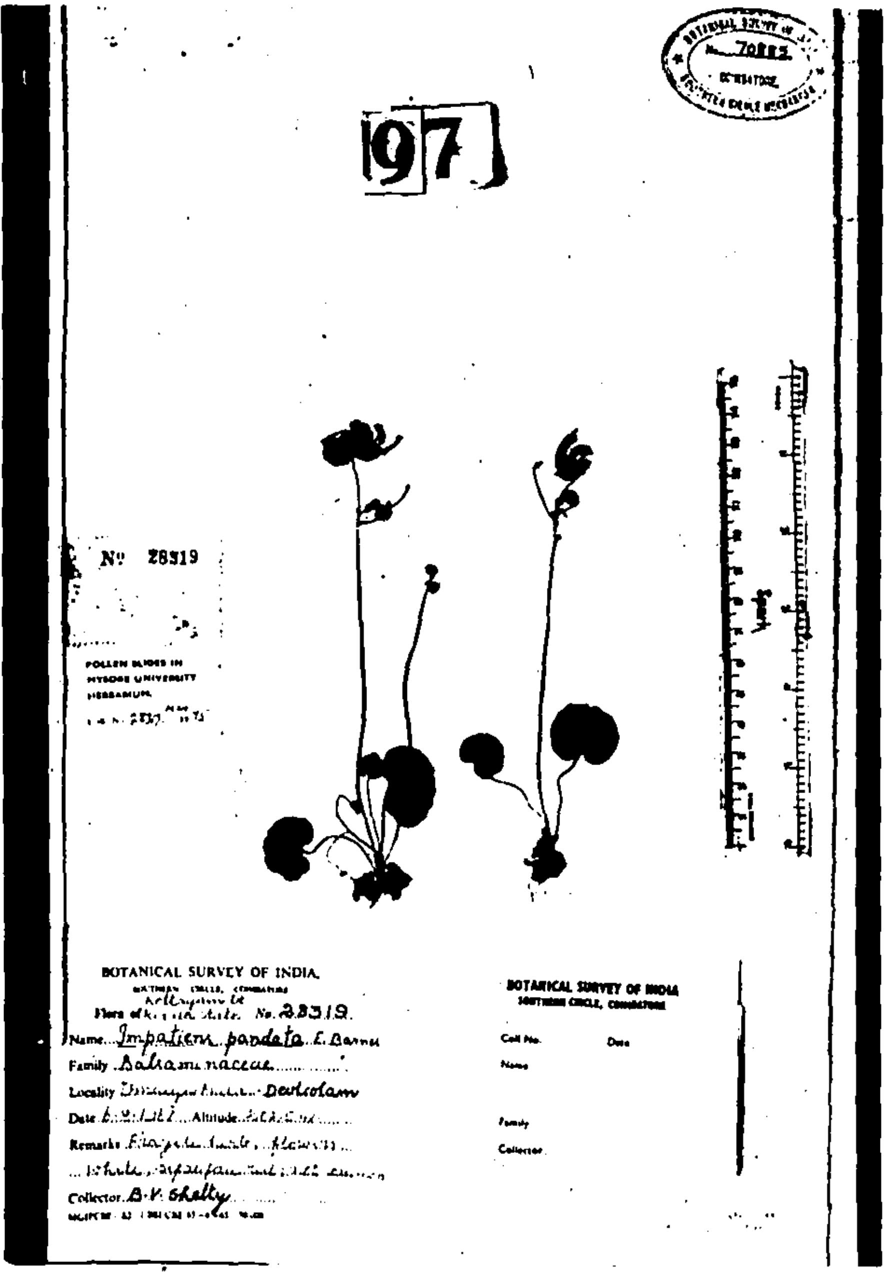
12.9.1958

V. BHASKAR

Impatiens *neo-barnesii* Fischer



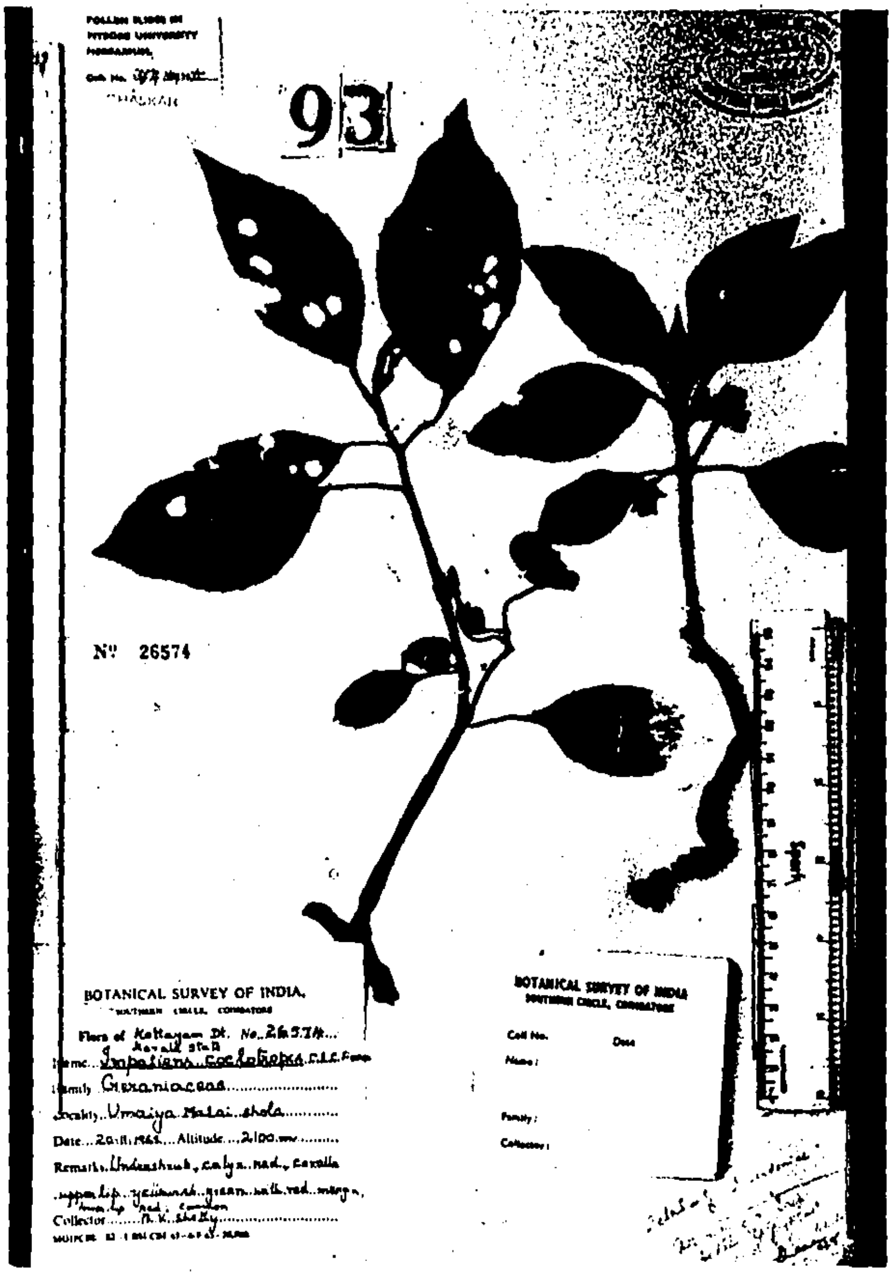
Impatiens nilgirica Fischer



Impatiens pandata Barnes

SECTION EPIPHYTICAE

Impatiens auriculata Wt.



BOTANICAL SURVEY OF INDIA.

Flora of Kottayam Dt. Kerala state No. 26574...

Name...Impatiens coelotropsis C.E.C. Fisch.

Family Geraniaceae.........

Locality..Umaiya Malai shola.........

Date...20.11.1965...Altitude...2100 m.........

Remarks. Undershrub, calyx red, corolla upper lip yellowish green with red margin, lower lip red, common

Collector.......B.K. Shetty.........

BOTANICAL SURVEY OF INDIA
SOUTHERN CIRCLE, COIMBATORE

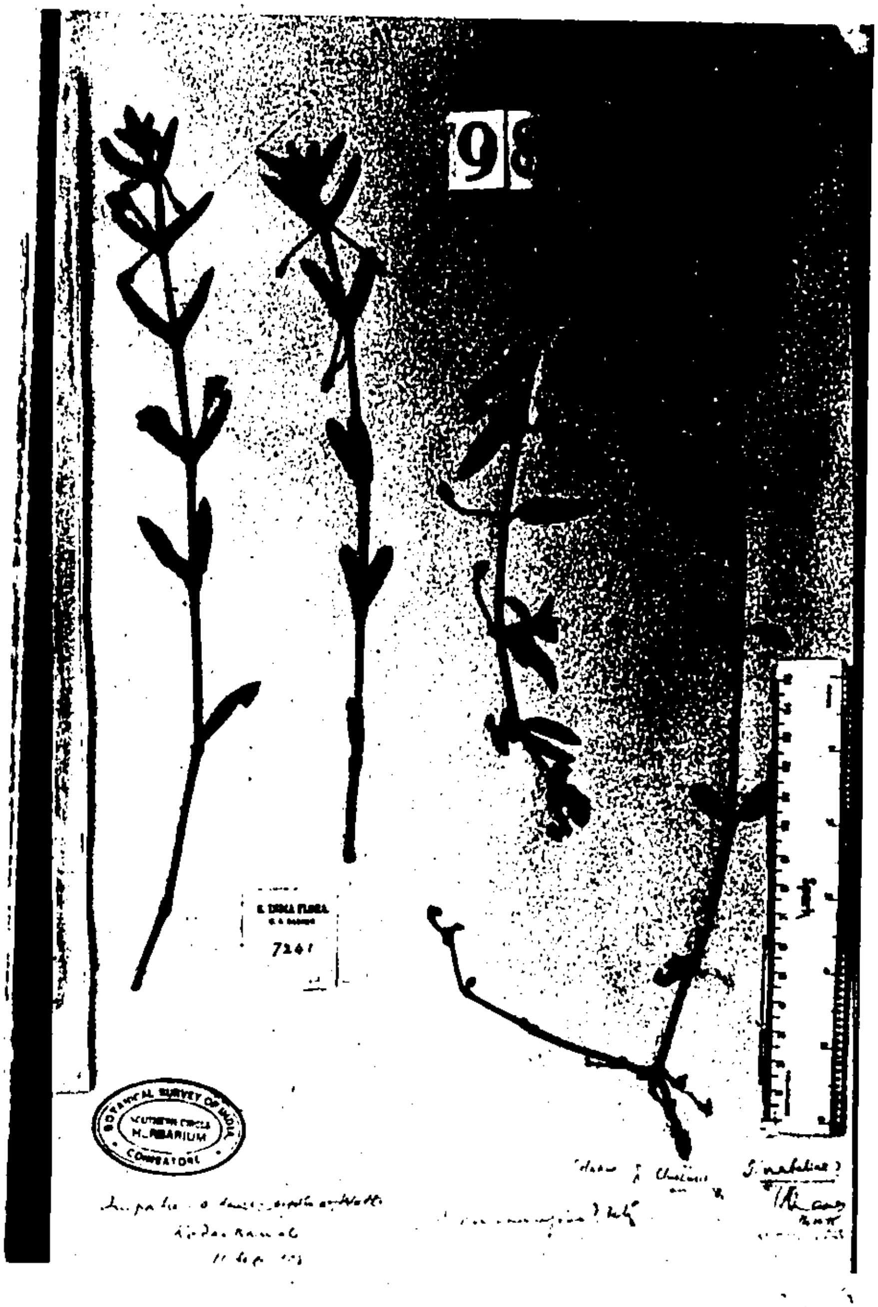
Coll No. Date
Name:
Family:
Collector:

Impatiens coelotropis Fischer

Impatiens jerdoniae Wt.

Impatiens parasitica Bedd.

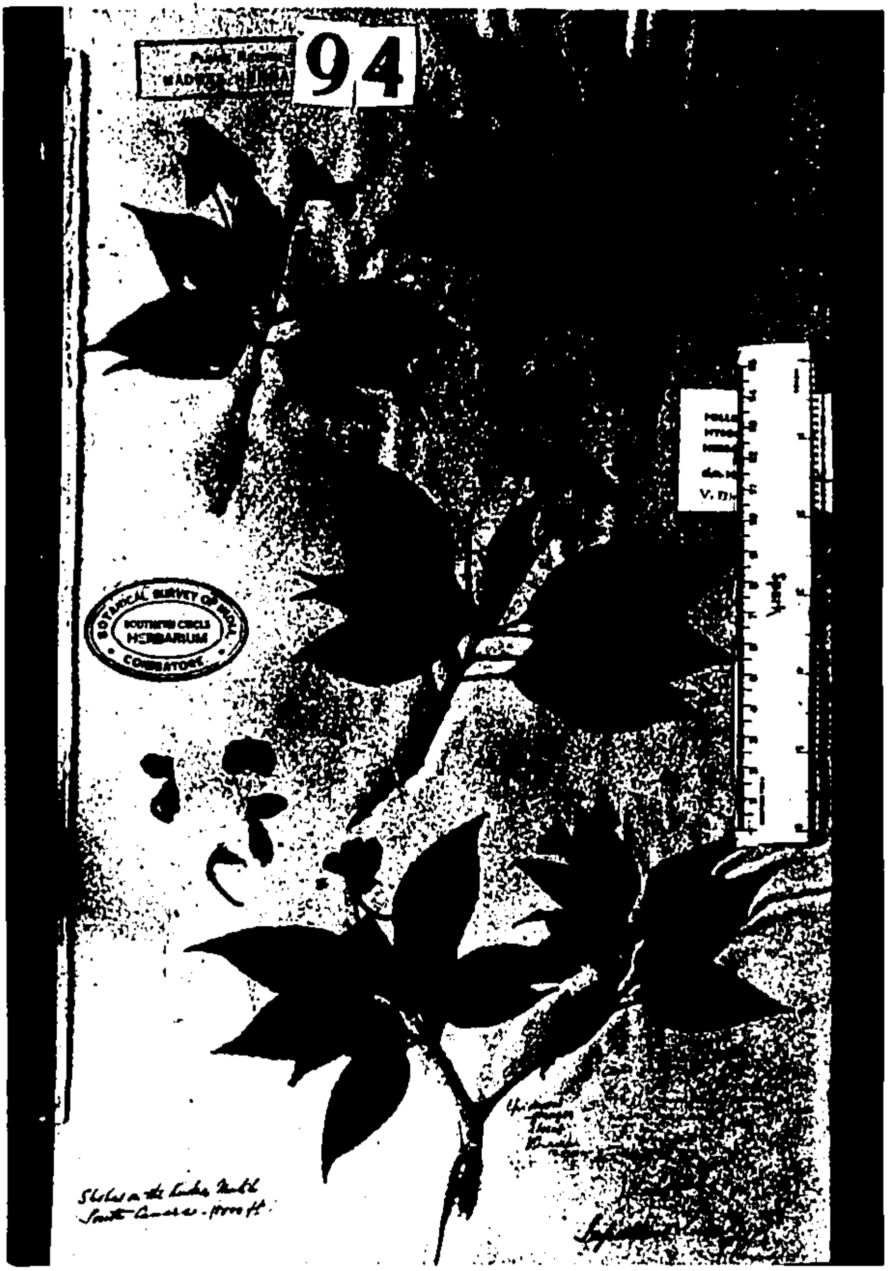
SECTION ANNUAE



Impatiens oppositifolia L. var. nataliae Bhask.

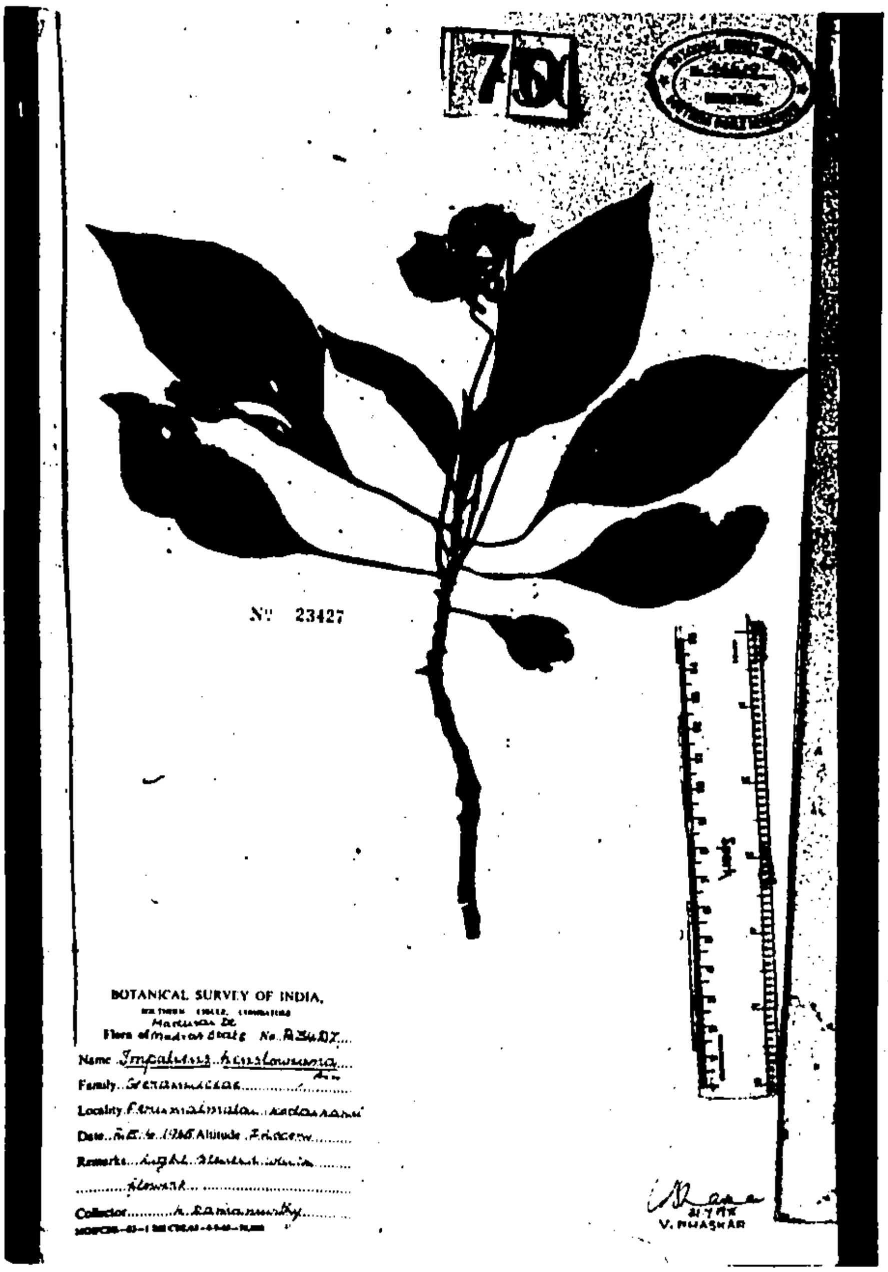
SECTION MICROSEPALAE

<u>Impatiens</u> <u>dasysperma</u> Wt.

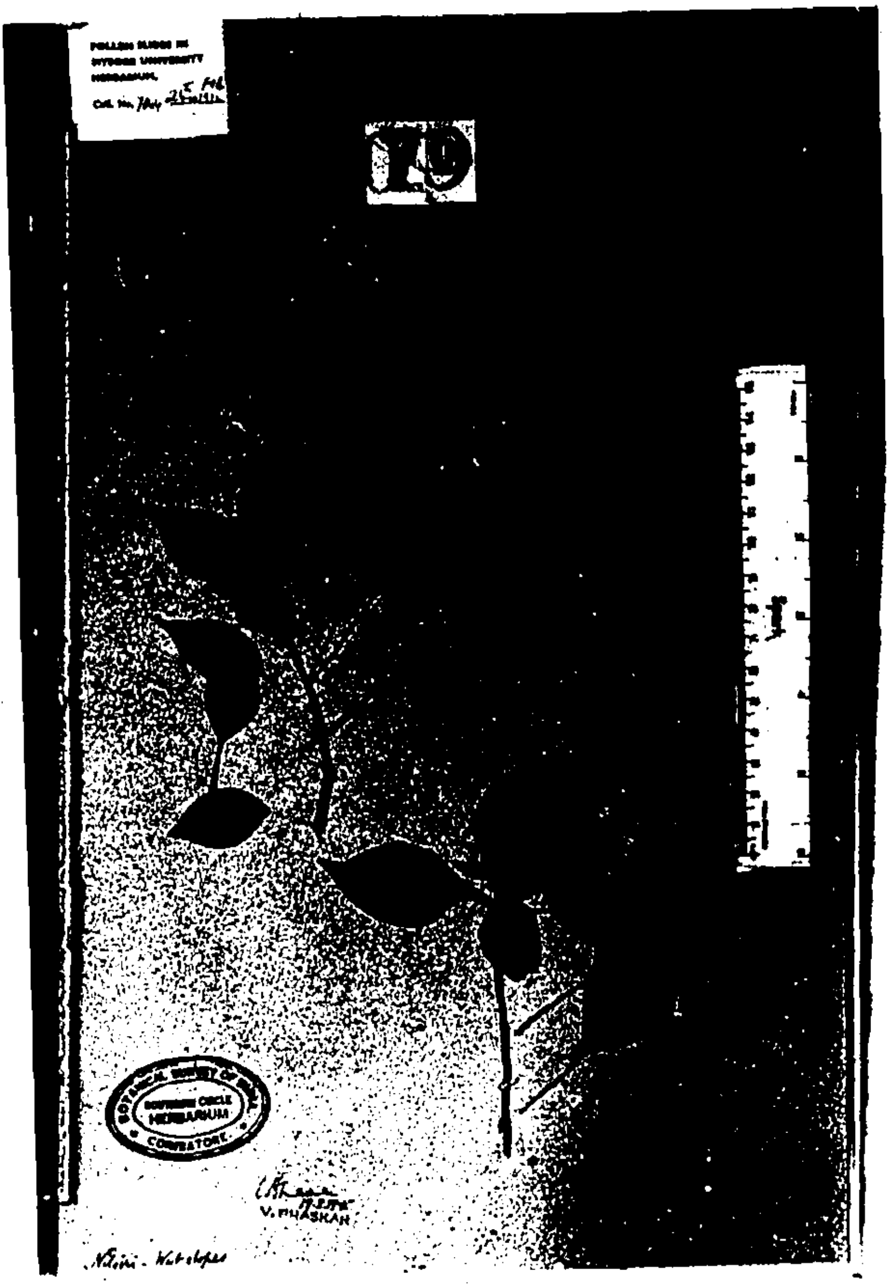


Impatiens latifolia L.

SECTION TOMENTOSAE



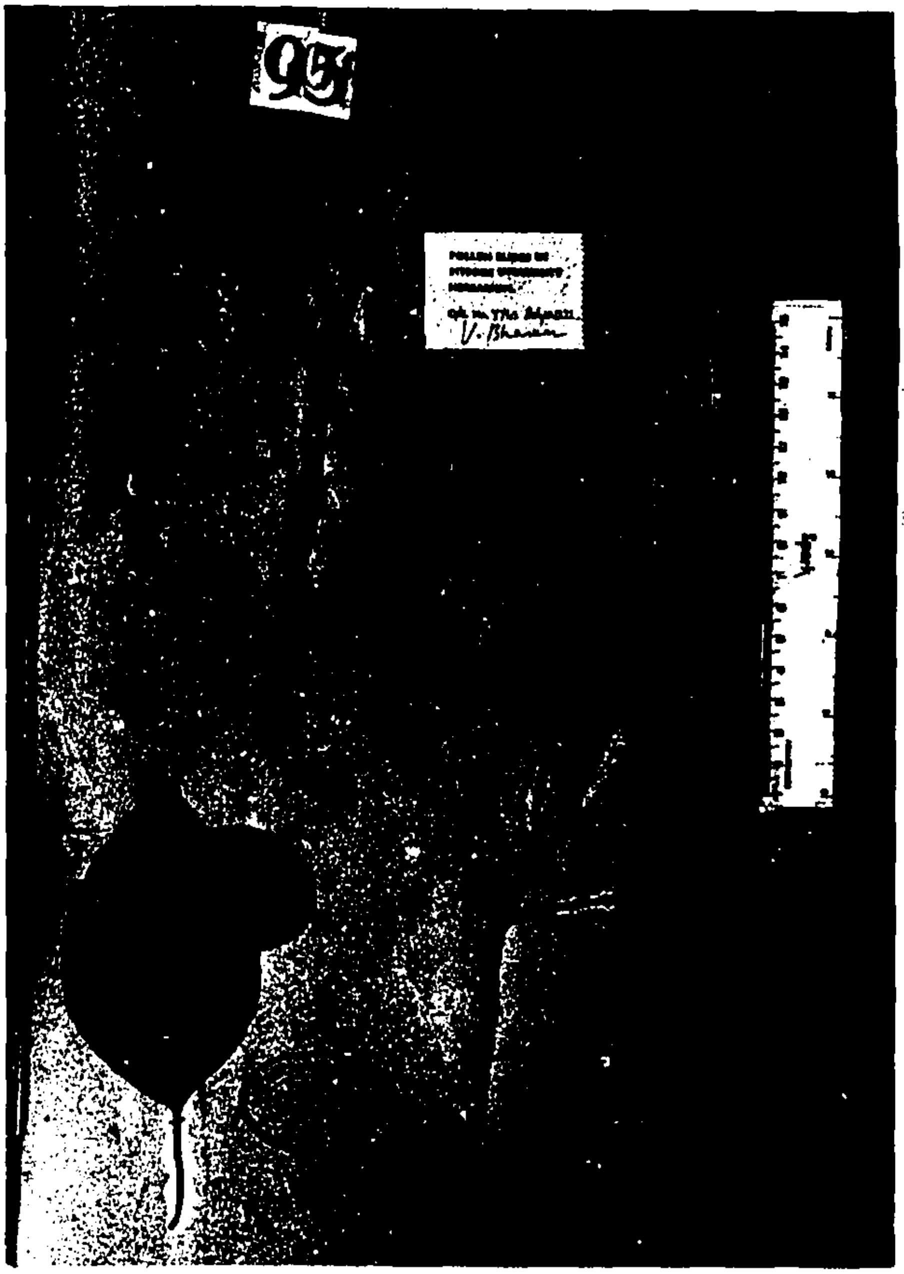
Impatiens henslowiana Arn.



Impatiens munronii Wt.

SECTION SUBUMBELLATAE

Impatiens cordata Wt.

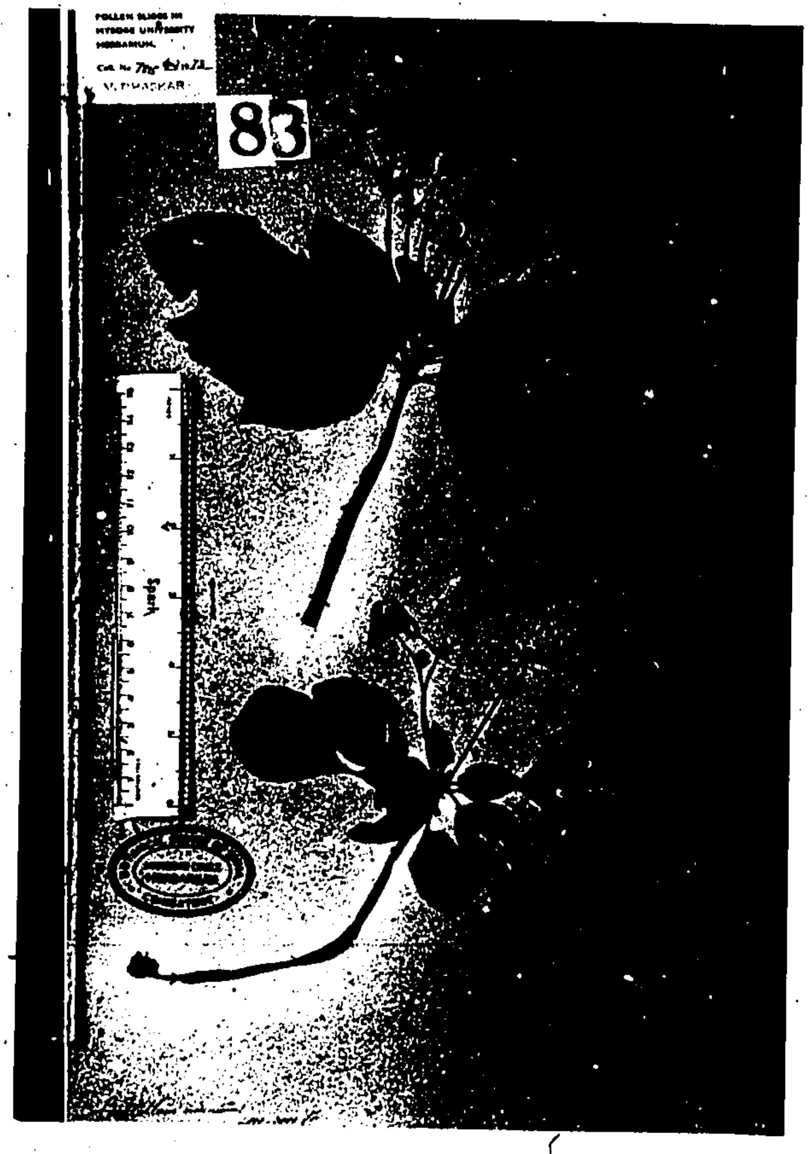


Impatiens disotis Hk.f.

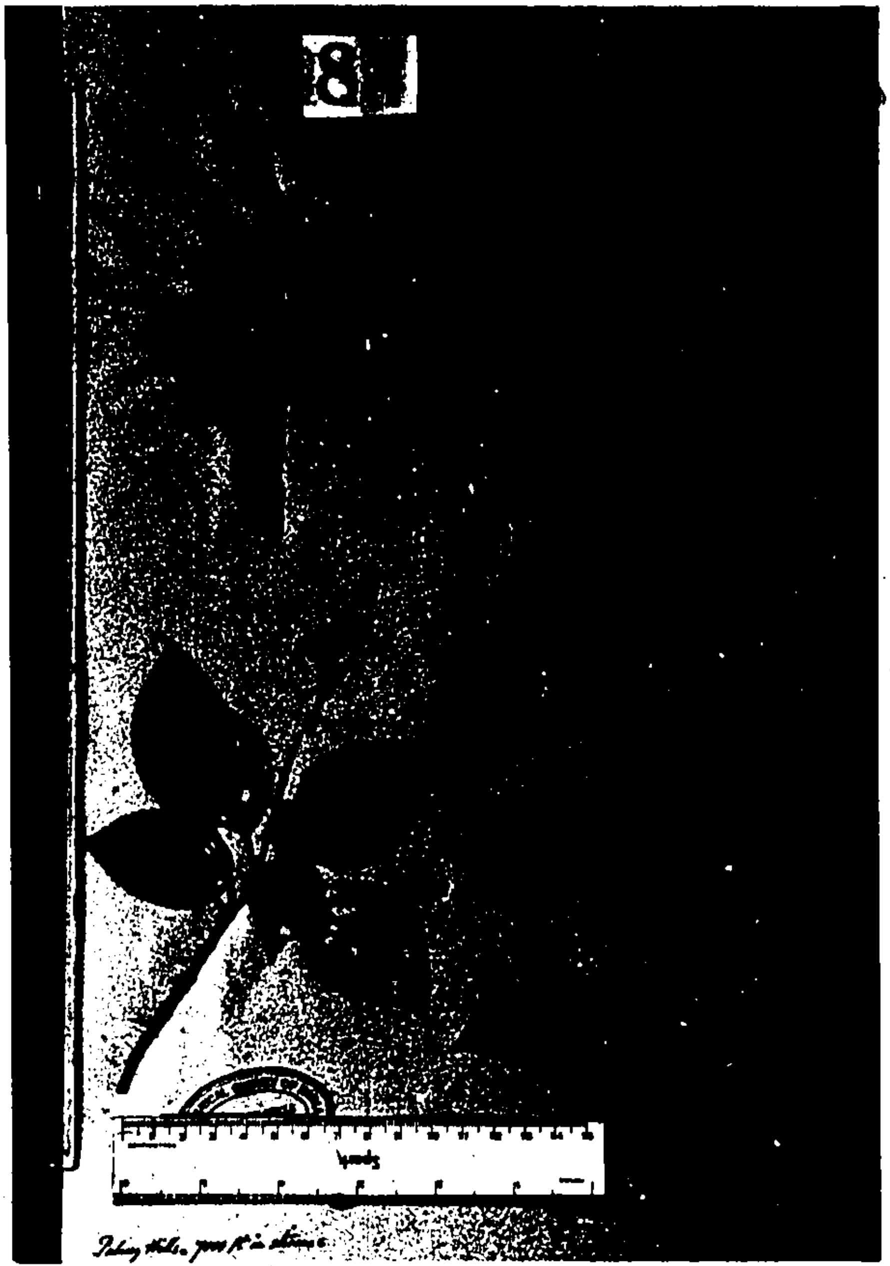
Impatiens fruticosa DC.

Impatiens grandis Heyne

Impatiens leptura Hk.f.



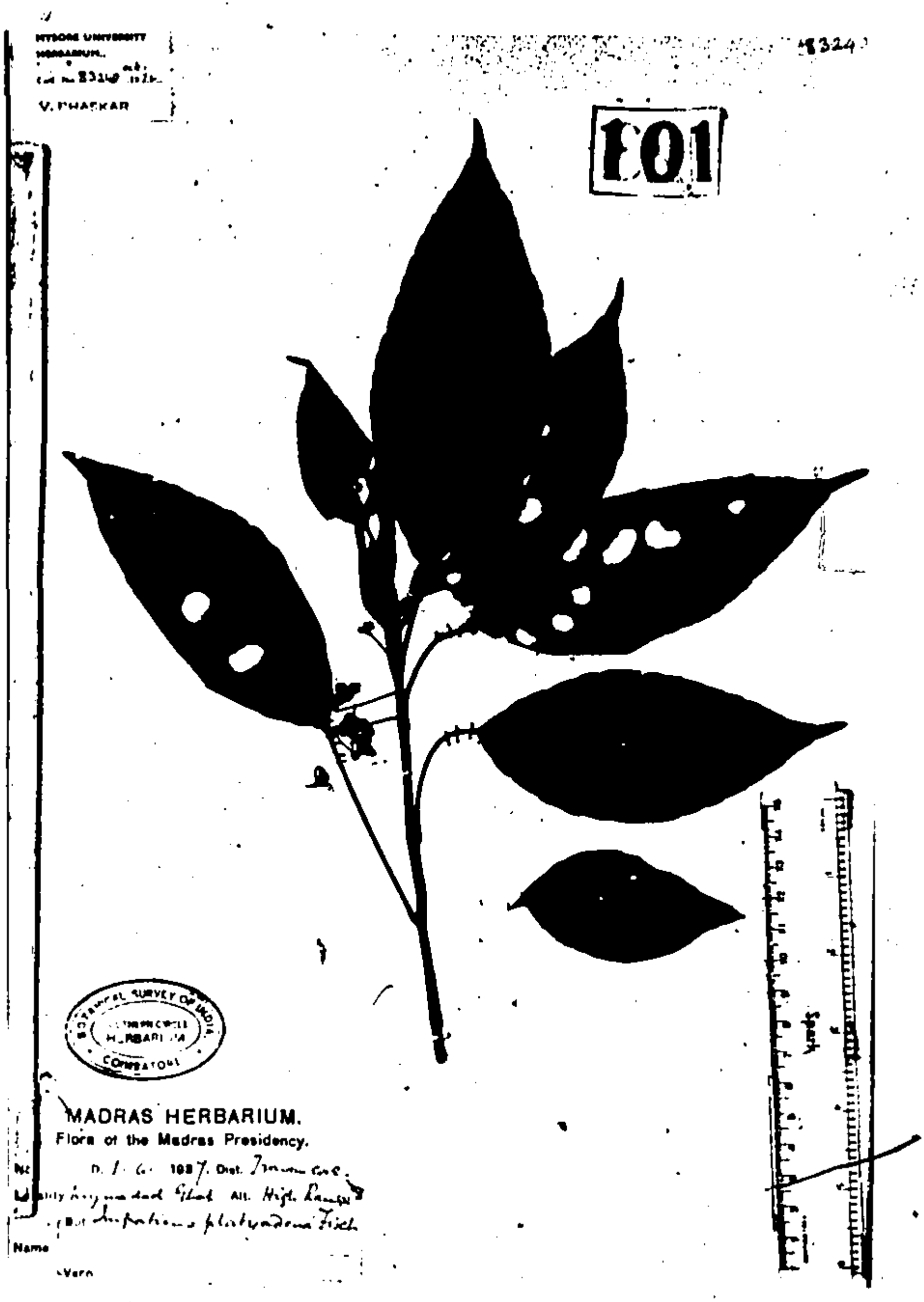
Impatiens umbellata Heyne



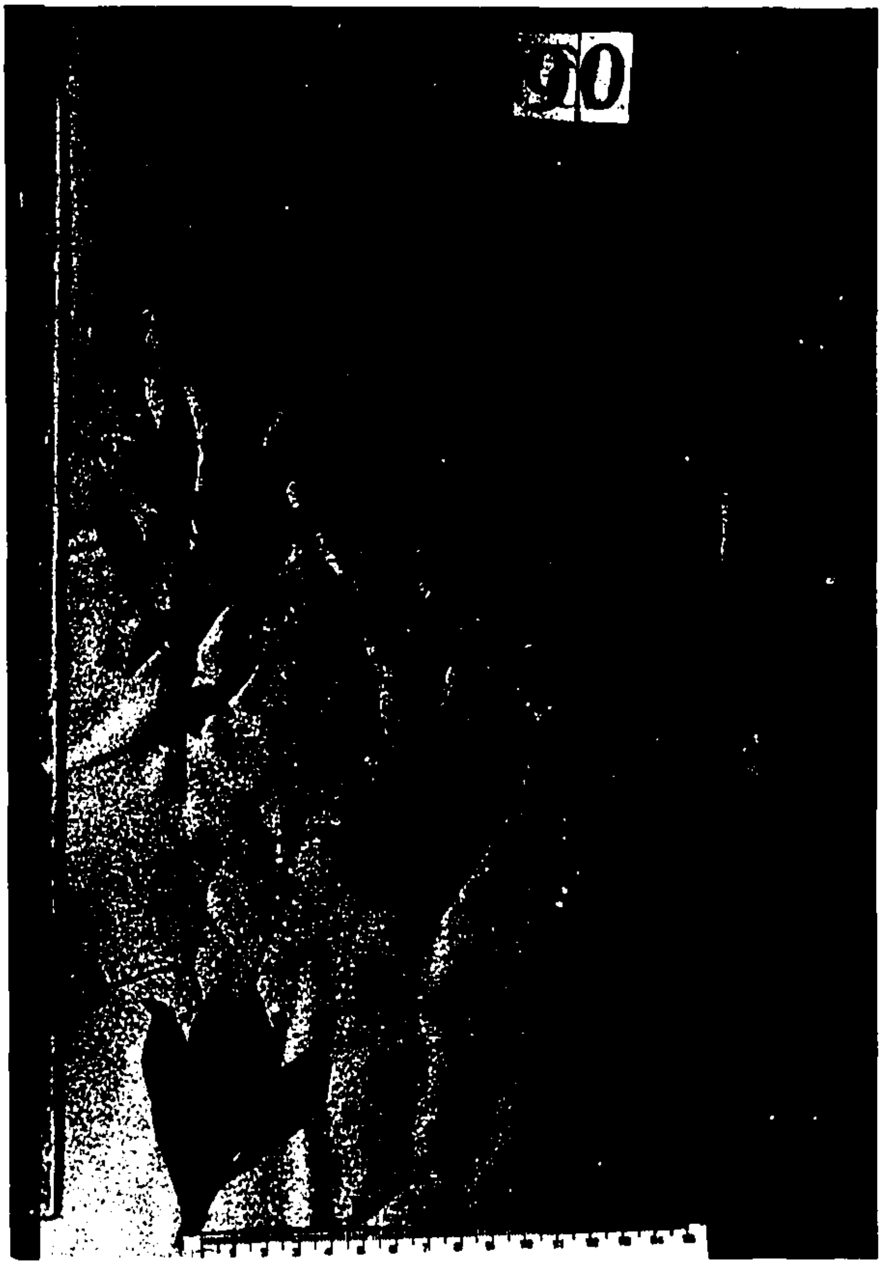
Impatiens viscida Wt.

SECTION RACEMOSAE

Impatiens phoenicea Bedd.



Impatiens platyadena Fischer



<u>Impatiens</u> <u>tangachee</u> Bedd.

<u>Impatiens</u> <u>wightiana</u> Bedd.

APPENDIX 2

Photographs of living plants collected in South India. Species arranged in Sections following classification of Hooker (1874-75; 1904-06).

Voucher specimens for the plants used in these studies will be deposited at MTMG with duplicates at MT and MH.

SECTION SCAPIGERAE

1. *I. acaulis* Arn. at Materan, a hill station in Maharshtra. This species grows on rocks in seasonal waterfalls.

2. *I. levingei* Hk.f. and *I. clavicornu* Turcz. in the greenhouse at Macdonald College. *I. levingei* is known from only one locality in the Niligri Hills.

3. *I. modesta* Wt. at Naduvattum in the Niligri Hills.

4. *I. niligirica* Fisch. at Pykarra, a new locality for this species.

SCAPIGERAE

Fig. 1. I. acaulis Arn.

Fig. 2. I. levengei Hk.f. and I. clavicrnu Turcz.

SCAPIGERAE Cont'd.

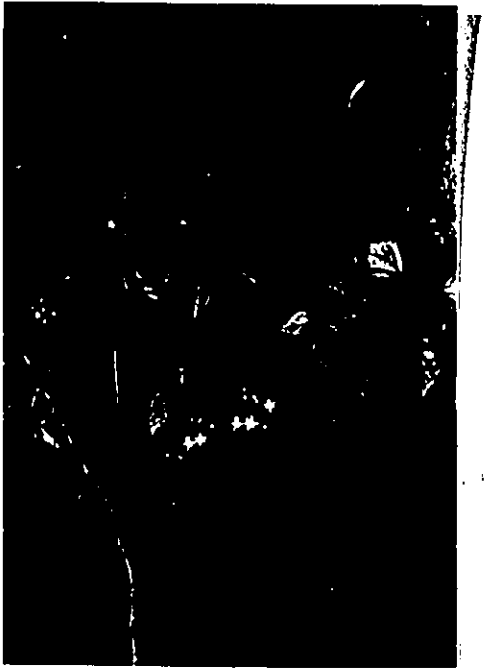


Fig. 3. I. modesta Wt.

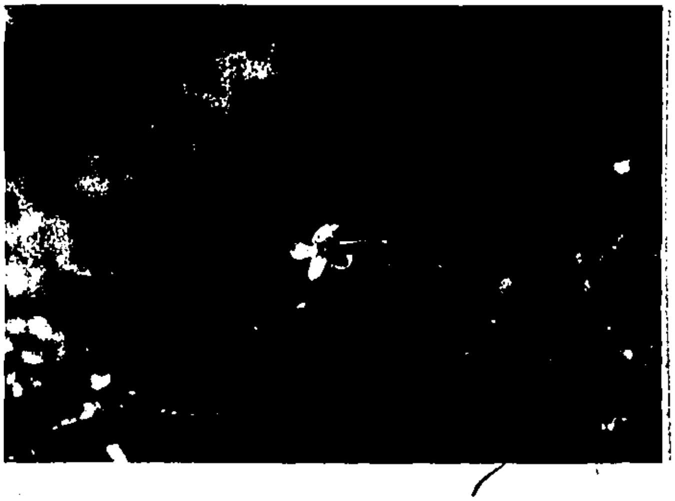


Fig. 4. I. niligrica Fisch.

SECTION EPIPHYTICAE

Fig. 1. *Impatiens parasitica* Bedd.

Grown from cuttings of plants collected at Lockert Gap, Devicolam, Travancore, High Range, Kerala.

Figure 1

Impatiens parasitica Bedd.

SECTION ANNUAE

1. I. dalzellii Hk.f. & T. grown from seed collected at Mahableshwar, a hill station in Maharashtra.

2. I. gardneriana Wt. grown from seed collected in Calicut Dt., Kerala.

3. I. pusilla Heyne growing at Pykarra in the Nilgri Hills of Tamil Nadu.

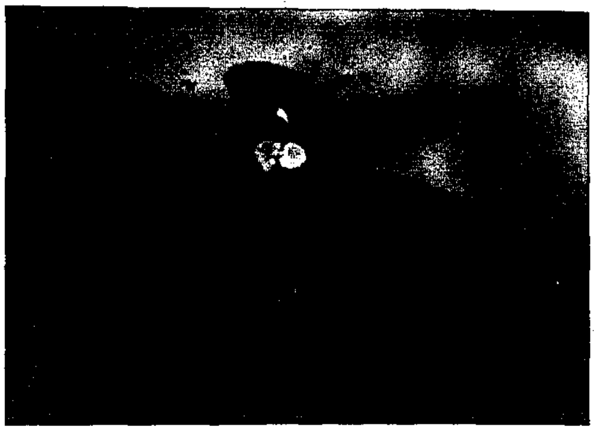


Fig. 1. I. dalzellii Hk.f. & T.

Fig. 2. I. gardneriana Wt.

Fig. 3. I. pusilla Heyne

SECTION ANNUAE Cont'd.

4. I. tenella Heyne at Frog Hill in the Nilgris.

5. I. tomentosa Heyne growing at the Glen Morgan Tea Estate (Nilgri Hills).

Fig. 4. I. tenella Heyne

Fig. 5. I. tomentosa Heyne

SECTION MICROSEPALAE

1. *I. balsamina* L. (wild type) grown from seed collected at Khandala, a hill station in Maharashtra.

2. *I. cuspidata* W.&A. at Lamb's Rock, Coonoor (the Nilgris, Tamil Nadu).

3. *I. flaccida* Arn., a Ceylonese species, is frequently cultivated in southern Asia.

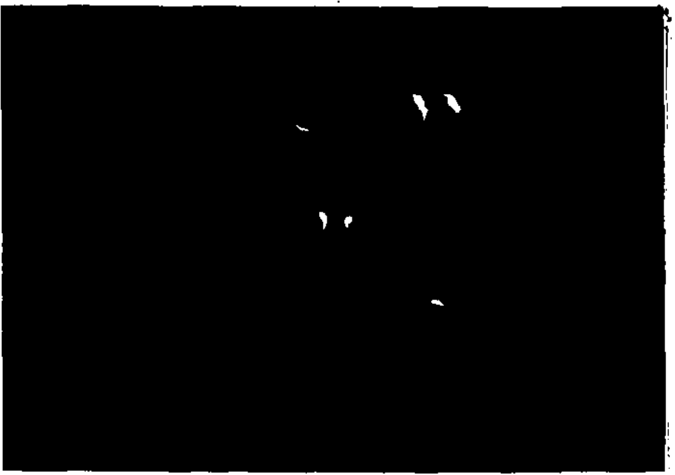


Fig. 1. I. balsamina L.

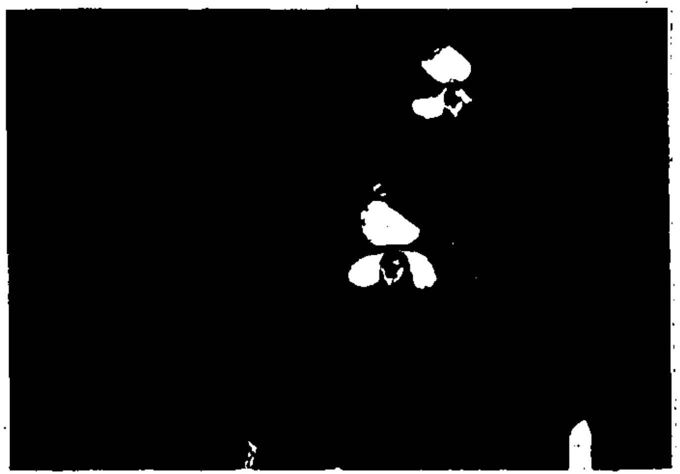


Fig. 2. I. cuspidata W.&A.

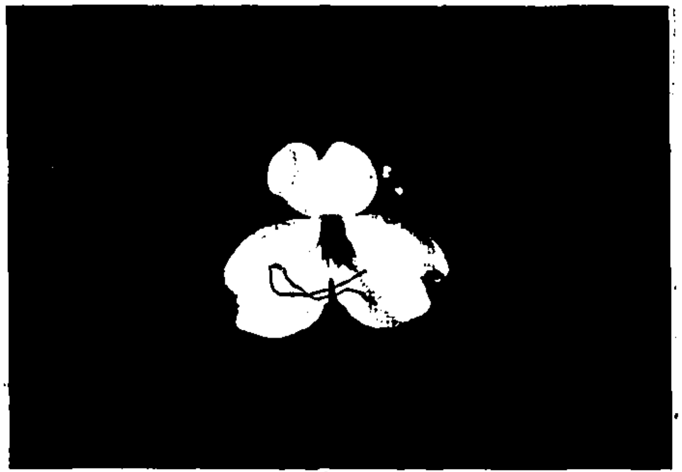


Fig. 3. I. flaccida Arn.

SECTION MICROSEPALAE CONT'D.

4. - 5. <u>I</u>. <u>leschenaultii</u> Wall., grown from seed collected between Pykarra and Naduvattum (the Nilgris, Tamil Nadu).
Fig. 4 Front view. Fig. 5 Side view.

MICROSEPALAE Cont'd.

Fig. 4. I. leschenaultii Wall.

Fig. 5. I. leschenaultii Wall.

SECTION MICROSEPALAE Cont'd.

6. *I. pulcherrima* Dalz. grown from seed collected at Mahalbleshwar, Maharashtra.

7. *I. repens* Moon is a native of Sri Lanka.

MICROSEPALAE Cont'd.

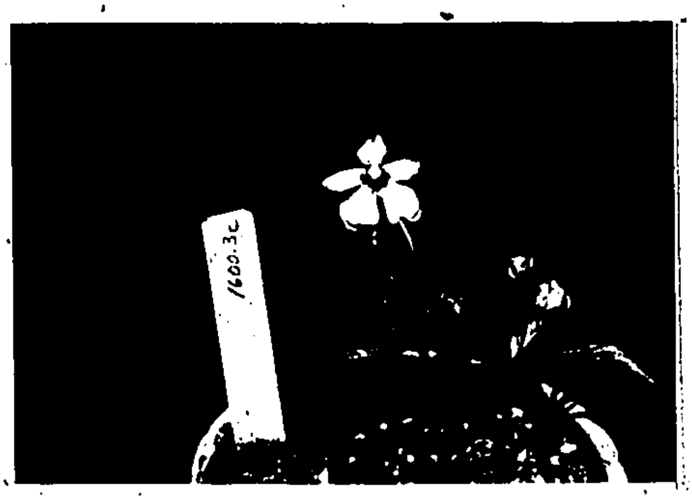


Fig. 6. *I. pulcherrima* Dalz.

Fig. 7. *I. repens* Moon

SECTION SUBUMBELLATAE

1. I. campanulata Wt. grown from cuttings collected at Tiger Shola (Pulney Hills, Tamil Nadu).

2. I. cordata Wt. growing in a roadside ditch at Rajmalai in the Travancore High Range.

3. I. elegans Bedd. from Sholiyar Dam in the Anamalai Hills of Tamil Nadu.

Fig. 1. I. campanulata Wt.

Fig. 2. I. cordata Wt.

Fig. 3. I. elegans Bedd.

SECTION SUBUMBELLATAE CONT'D

4. I. fruticosa DC. from Lamb's Rock, Coonoor.

5. I. goughii Wt. grown from seed collected in the Pulney Hills of Tamil Nadu. The plant is a tetraploid ($2n = 40$), the first such report for this species.

SUBUMBELLATAE Cont'd.

Fig. 4. I. fruticosa DC.

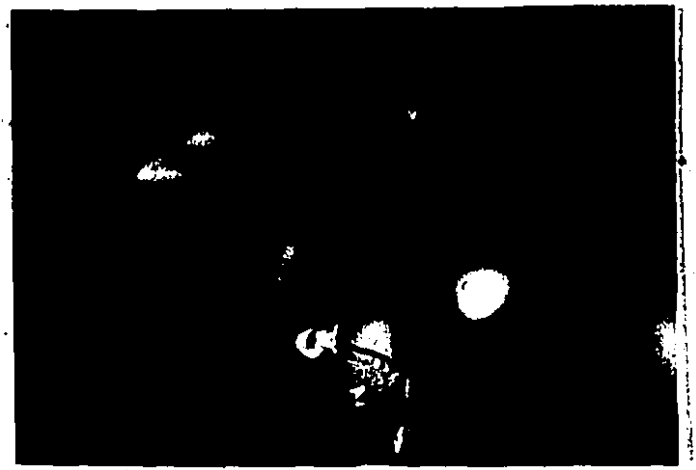


Fig. 5. I. goughii Wt.

SECTION SUBUMBELLATAE Cont'd.

6. I. hookeriana Arn. grown from cuttings collected at Sim's Park, Coonoor (the Nilgri Hills, Tamil Nadu).

7. I. viscida Wt. growing on wet rocks in the Pambar River in the Pulney Hills (Tamil Nadu).

SUBUMBELLATAE Cont'd.

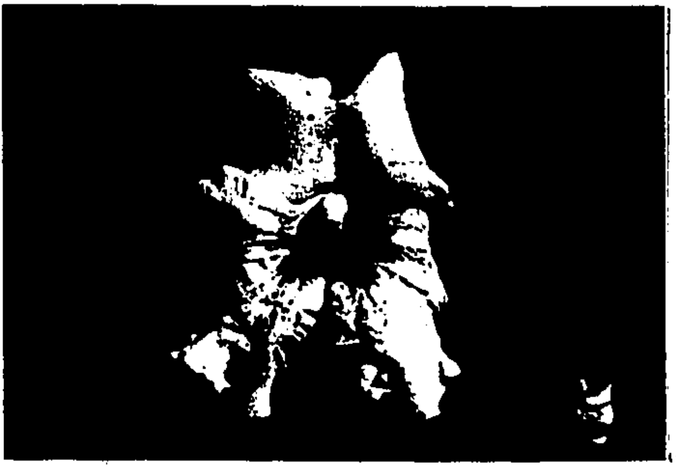


Fig. 6. I. hookeriana Arn.

Fig. 7. I. viscida Wt.

SECTION RACEMOSAE

1. I. maculata Wt. collected in the Anmalais ("Elephant Hills") of Tamil Nadu at an elevation of about 1,200 m.

2. I. phoenicea Bedd. growing in a shola along the Pambar River (Pulney Hills, Tamil Nadu) at approximately 2,500 m.

3. I. tangachee Bedd. (the specific epithet means "sister" in Tamil) grown from cuttings collected in the Travancore High Range. This species is semi-aquatic in its natural habitat.

RACEMOSAE

Fig. 1. I. maculata Wt.

Fig. 2. I. phoénica Bedd.

Fig. 3. I. tangachee Bedd.

CHAPTER IV

SELECTED FLORAL CHARACTERS

SELECTED FLORAL CHARACTERS

INTRODUCTION

The flower in Impatiens presents a series of complex problems in terms of its structure. The flower is highly zygomorphic which has made interpretation of its homologies difficult. Hooker (Huxley, 1918) despaired at arriving at a functional interpretation of the structural variations which he observed. Recently, the application of the principles of pollination biology to the taxonomy of the genus (Grey-Wilson, 1980g) indicates that a more workable taxonomy, based on evolutionary lines, can be developed.

TERMS USED IN DESCRIBING THE PERIANTH OF IMPATIENS

In the mature chasmogamous flower of most Impatiens species four types of perianth segments are evident. As one moves up the floral axis, one observes:

1. Sepals: There are usually two, but occasionally four; these are imbricate, foliaceous, and usually small. If four are present, the outer ones are generally larger than the inner ones (Fig. 1).

2. Pouch: This is interpreted as a sepal which has become elaborated into a gibbose structure, which is usually petaloid and terminates in a spur containing nectariferous tissue.

3. Odd petal: This petal is not fused to the other petals and lies below them on the floral axis; there is a marked abaxial ridge which is frequently chlorophyllous.

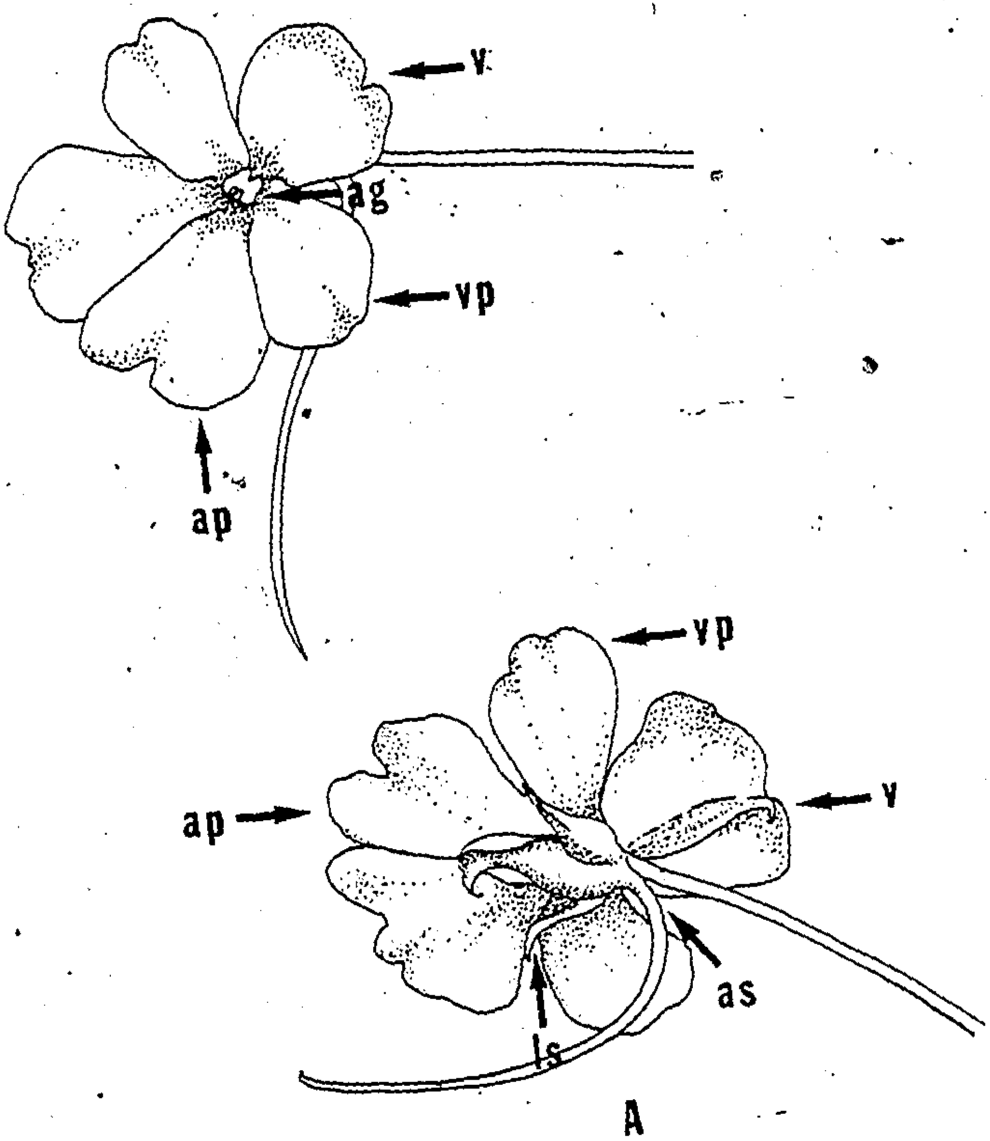
Figure 1

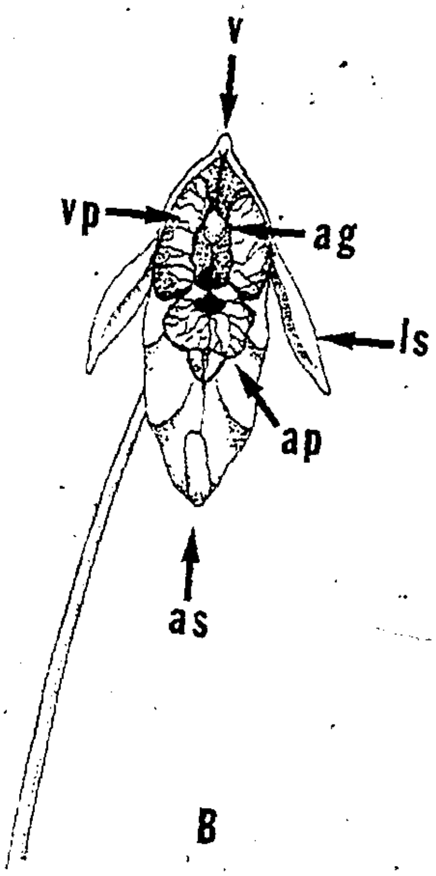
FLOWER PARTS IN IMPATIENS

A. I. hawkeri Bull, front and back view (Note costa).

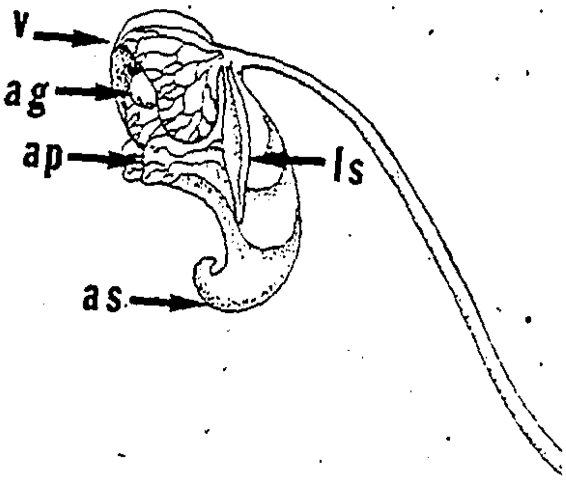
B. I. parasitica Bedd., front and side view

v = odd petal = vexillum
vp = vexillar petal
ap = antivexillar petal
ls = lateral sepals
as = pouch = antivexillar sepal
ag = cap of fused stamens over gynoecium


v
ag
vp
ap
vp
ap
v
as
ls
A



B



4. Fused petals: If one examines the venation, it is quite clear that there are four remaining petals, but as far as is known these are always at least pairwise connate, forming two wings. Each petal within a wing may be further elaborated into lobes.

Despite the apparently straightforward scheme presented here, the taxonomic literature is replete with confusion and inaccuracy with respect to the floral morphology of Impatiens. In the first place, in all species, the pedicel twists through 180° causing the flower to resupinate during ontogeny. Some authors have described the flower before and others after resupination. For ample demonstration of this point compare Henfrey(1860), Beddome (1874), Warburg and Reiche (1895), Gamble (1915) and Barnes (1939). Hooker and Thomson (1859) even reversed themselves in mid-treatment.

In the second place, because the perianth in many Impatiens is highly zygomorphic, the terms "sepal" and "petal" are insufficient to adequately describe the flower. A variety of terms have been used by different authors (Table 1), but none have gained universal acceptance. Ignoring Warburg and Reiche's system which is extremely awkward, there are two general philosophies as to terminology. One is to use orientational terms such as "lateral", "dorsal" and "posterior". The other is to use functional terminology such as is found in Hooker's scheme. Recently, it has been argued (Bhaskar, 1975; Grey-Wilson, 1980g) that orientational terms present no problem if one always uses them with respect to the mature, resupinated flower. In the first place, this is not borne out by the facts: even in the publications on Impatiens by these two authors, orientational terms have been reversed. Secondly, there is the tendency when using orientational terms to parenthetically

Table 1

Terminology for perianth segments in *Impatiens*

Unit	Author				
	Hk. f.[1] (1874-75) (1904-06)	Warburg and Reiche (1895)	Rydberg[2] (1910)		Grey-Wilson (1980g)
	sepals	sepals	lateral sepals		lateral sepals
	lip	lip	posterior/ saccate sepal		lower sepal
	vexillum (standard)	p2	dorsal petal		dorsal petal
 alae (wings)	lateral lobe	p4,p5	lateral petal	lateral united petals	upper petal
	terminal lobe	p1,p3	posterior petal		lower petal

---

[1] Followed by Bhaskar (1975).

[2] Followed by North American taxonomists.

add "by resupination" (Bhaskar, 1975; Grey-Wilson, 1977, 1980g), which suggests a certain lack of clarity in such a system. Finally, there is one issue which no author seems to have considered. Is it not somewhat short-sighted to propose terminology which is only to be used in the later stages of floral ontogenesis? This may be a perfectly adequate solution for the herbarium taxonomists, but undoubtedly a frustrating one for the morphologist or anatomist. Obviously, orientational terms are not suited to developmental studies of Impatiens, and would lead to utter confusion as the flower rotates, and what was dorsal becomes ventral.

It would appear then that a system based on functional terms would be more satisfactory in designating the perianth segments in Impatiens. We have the basis for such a scheme in Hooker's terminology in which he employed terms already in use for the Leguminosae and Orchidaceae (Hooker and Thomson, 1859). This system was followed by Bhaskar (1975) in his taxonomic revision of the South Indian Impatiens, but rejected by Grey-Wilson (1977, 1980g) because of his very understandable objection to Hooker's use of the terms "lip" and "lobe". The odd or saccate sepal of Impatiens is never a "lip" or "labellum", that is a landing platform. This role is carried out by the alae, and Grey-Wilson (1980g) has stressed the importance of the lower petals of the wings as a labellum. It is undoubtedly true that in the melittophilous and in some highly zygomorphic psychophilous and phalaenophilous Impatiens species only the lower petals are involved in this function. On the other hand, it is extremely difficult to believe that in those lepidoptera-pollinated species with fairly regular corollas (e.g. the I. walleriana aggregate, I. henslowiana Arn., and I. hawkeri sensu lato), it is not the alae taken as a whole which serve as a labellum. Thus it appears injudicious to use the term "lip" or its variants with respect to any corollar segment of Impatiens except in the context of an individual species. Furthermore, to refer to each petal of a wing as a "lobe" (as was done by Hooker) can only lead to further confusion since each petal may be subdivided into lobes (Fig. 1). On the other hand, Hooker's "vexillum" or "standard" seems preferable to Grey-Wilson's "dorsal petal (by resupination)". The following terminology is therefore proposed, and will be used throughout the remainder of this work:

1. Lateral sepals: for the one or two pairs of imbricate sepals.

2. Antivexillar sepal: for the odd sepal which is usually gibbous and often terminates in a spur. It will be further described by the adjectives "navicular", "saccate" or "bucciniform" (Grey-Wilson, 1980g).

3. Vexillum: for the odd petal with a narrow crest (which will be termed the costa) on one surface; the vexillum may be flattish or cucullate.

4. Alae (singular Ala): for the united petals or wings. These are divided into two parts: a vexillar petal which lies nearer to the vexillum and an antivexillar petal which lies further from the vexillum. "Lobes" refers to an elaboration within a petal. It should be noted that the "alae" in Impatiens are not strictly homologous to those found in the Leguminosae because in the latter each wing consists of one, not two, petals.

INTERPRETATIONS OF THE FLORAL PARTS IN IMPATIENS

Literature

It is generally believed that the flower of Impatiens is basically pentamerous. As a result of fusion, resupination and diversification, the flower now has become zygomorphic, and as a consequence, there have been several interpretations of the perianth segments:

1. All authors have interpreted the gibbose structure opposite the vexillum (which I term the antivexillar sepal) as a modified sepal. Bhaskar (1975) has argued that the occasional presence of 3-spurred teratoid flowers in *I. balsamina* L., in which all the sepals are apparently gibbose and spurred, is incontroversial proof of the validity of this hypothesis.
2. Knuth (cited in Henfrey,1860) is said to have proposed that the vexillum arose through the fusion of two lateral sepals which would explain the presence of only two of these in the modern Impatiens flower.
3. Hooker and Thomson (1859) pointed out that there are in fact some Impatiens species which have four lateral sepals. They credited Edgeworth with first having observed this feature in the Himalayan species, *I. amplexicaulis* Edgew. Hooker and Thomson reported also finding four lateral sepals in *I. longipes* Hk.f.& T., *I. urticifolia* Wall., and *I. arguta* Hk.f.& T. Consequently, they argued, the vexillum is merely a modified petal, and that the two missing sepals are simply suppressed in most Impatiens species.
4. This latter hypothesis gained support from a study of floral

development in I. glandulifera Royle by Payer (1857), who reported observing the rudiments of the two missing petals.

5. Grey-Wilson (1980f) argued that it is the anticous (that is vexillar) pair that has been lost in the course of evolution after he examined the vascularization in I. glandulifera Royle.

OBSERVATIONS

Five-sepaled Species

After reviewing a large body of literature on Impatiens, I have come to the conclusion that the nature of the floral organs is very imperfectly understood. With respect to so-called sepals three character states occur in the genus:

1. Five sepals always present (four lateral and one antivexillar).
2. Three sepals always present (two lateral and one antivexillar).
3. Sometimes three sepals (two lateral and one antivexillar), other times five (four lateral and one antivexillar).

Species which have been reported as having four lateral sepals are enumerated in Table 2; note that in some of these, which have been indicated by an asterisk, one pair of sepals may be either present or absent even on different flowers of the same plant (e.g. the Chinese species I. lasiophyton Hk.f.).

Contrary to previous authors (Bhaskar, 1975; Grey-Wilson, 1980g) the five-sepaled condition is by no means rare since it is reported to occur in at least 102 species of Impatiens although these form a small percentage of the balsam flora in all regions except China. Five-sepaled species have not been reported in any Malagasy, Ceylonese,

Table 2

Impatiens species having five sepals

Region	Species
African	1. I. fischeri[1]
	2. I. flanaganae[2]
	3. I. pohilii[3]
	4. I. rothii[4]
	5. I. tinctoria[5]
	6. I. quadrisepala[6]
	7. I. teitaenus[3]
W. Himalayan	1. I. amplexicaulis[7,a]
	*2. I. glandulifera[8,a]
	*3. I. scabrida[9]
E. Himalayan	1. I. arguta[10]
	2. I. drepanophylla[4]
	3. I. laevigata[11]
	4. I. leptoceras[9,a]
	*5. I. longipes[10]
	6. I. mishmiensis[4]
	7. I. nummularifolia[4]
	8. I. scitula[4]
	9. I. sulcata[11]

Table cont'd.

Table 2 Cont'd.

Region	Species
E. Himalayan (cont'd.)	10. *I. trichocladon*[4]
	11. *I. urticifolia*[11,a]
Burmese[c]	1. *I. arguta*[10]
	2. *I. chimiliensis*[12]
	3. *I. drepanophylla*[4]
	4. *I. gibbisepala*[4]
	5. *I. laevigata*[11]
	6. *I. manipurensis*[4]
	7. *I. micromeris*[4]
	8. *I. odontosepala*[4]
	9. *I. rubrolineata*[4]
	10. *I. wattii*[4]
Thai-Malaysian	1. *I. calcicola*[13]
	2. *I. claviger*[4]
	3. *I. cryptoneura*[4]
	4. *I. damrongii*[14]
	5. *I. harmandii*[4]
	6. *I. jurpiodes*[14]
	7. *I. juripa*[15,d]
	8. *I. longiloba*[13]
	9. *I. macrosepala*[4]
	10. *I. mirabilis*[4]

Table cont'd.

Table 2 Cont'd.

Region	Species
Thai-Malaysian (cont'd.)	11. I. opinata[13]
	12. I. parishii[4]
	13. I. ridleyi[4]
	14. I. scortechinii[4]
	15. I. tipusensis[16]
Indochinese	1. I. balsanae[4]
	2. I. claviger[4]
	3. I. harmandii[4]
	4. I. musyana[4]
	5. I. pygmaea[4]
Philippine	*1. I. burkei[4]
Chinese	1. I. abbatis[4]
	2. I. barbata[12]
	3. I. gasterocheila[4]
	4. I. holocentra[17]
	5. I. hongkongensis[3]
	*6. I. lasiophyton[4]
	7. I. leveillei[4]
	8. I. taronensis[17,e]

*Number of lateral sepals variable (2/4).

Table cont'd.

Table 2 Cont'd.

[1] authority = Warb.

[2] Bolus

[3] Grey-Wilson

[4] Hk.f.

[5] A. Rich

[6] R. Wilczek & G.M. Schulze

[7] Edgew.

[8] Royle

[9] DC.

[10] Hk.f. & T.

[11] Wall.

[12] Comber

[13] Craib

[14] Shimizu

[15] Hamil *ex* Hk.f.

[16] Henders.

[17] Hand.-Mzt.

[a] Hooker (1874-75; 1904-06) does not give the number of sepals; Warburg and Reiche (1895) state there are four sepals.

[b] This species occurs in both eastern and western Himalays, but 4-sepaled plants only in Sikkim (Hooker, 1974-75).

[c] Hooker (1904-06) lists five 4-sepaled species occuring in the Burmese region. Hooker (1909a) tabulates seven 4-sepaled Burmese species. I suspect that the discrepency is due to an omission in the Epitome (although the pagination is consecutive). This suggests that there is a missing page which includes descriptions of two new species with four sepals which were included in the later tabulation (Hooker, 1909a), but were not described elsewhere (having checked *Index Kewensis* supplements). Perhaps the missing species can be identified by examining Hooker's notes. Of the remaining five species, four are first described in Hooker (1910a) and one in Comber (1934).

[d] Hooker (1904-06) gives the number of sepals in *I. juripa* as two, Shimizu (1970) as four. It remains to be ascertained whether plants of *I. juripa* indeed have four sepals or whether they vary between two and four.

[e] The total number of 4-sepaled species in China is about 50 (Hooker, 1910b), but the present author does not have a complete description for all the Chinese *Impatiens*.

or Deccan taxa. No evidence was found that any of these species are particularly primitive. Two are tetraploids, I. mirabilis Hk.f. and I. ridleyi Hk.f., both of which are reported to have n = 17. I believe that I. mirabilis is related to the Deccan species in the section Epiphyticae, none of which have the five-sepaled condition.

As far as I have been able to ascertain the five-sepaled state tends to occur in clusters of closely related taxa, but these clusters are taxonomically and geographically isolated from each other which suggests that the five-sepaled condition has arisen repeatedly in unrelated groups of Impatiens. The allies of this group (the African I. stuhlmanni aggregate and the Malagasy I. longipedunculata aggregate) include only three-sepaled species. Another group of five-sepaled species is the Southeast Asian complex, including I. harmandii Hk.f., I. balansae Hk.f., I. musyana Hk.f. and I. pygmaea Hk.f., which is not related to I. tinctoria and its allies. A few species such as I. quadrisepala R. Wilczek & G.M. Schulze, I. teitaenus Grey-Wilson, I. mirabilis Hk.f. and I. burkei Hk.f. do not have any close relatives with five sepals.

Observations on bud development in species maintained in the greenhouse suggested an alternative interpretation of the five-sepaled condition in Impatiens. It was noted that in all species with only one pair of lateral sepals, the sepals open early in development long before the spur is fully developed. In contrast, in I. flanaganae Hemsl., the only five-sepaled species in which I have had the opportunity to follow bud ontonogenesis, the outer pair (the drawing in Grey-Wilson, 1980g shows the two pairs as lying side by side, but this was not the case in the material obtained from Kew) opens as described above, but the inner pair remains appressed to the bud almost until the time when the bud opens. Moreover, this inner pair is, as in almost all five-sepaled *Impatiens* species, much smaller and more membranous than the outer pair (Fig. 2). In fact, it was observed that the outer pair is very similar in size, appearance and texture to the subtending bract. A comparison of bracts and sepals in a number of species, revealed a great similarity between these two organs, and showed that in many cases they undergo parallel variation. To give just one example, in the Section Epiphyticae, *I. parasitica* Bedd. has minute linear bracts, while those of *I. coelotropis* Fisch. are large and ovate. Furthermore, it was found that in teratoid flowers of *I. balsamina* L., a gibbose and spurred structure occasionally replaces the normally minute subtending bract, a phenomenon previously reported by Simon (1975). It may be that the so-called outer sepals are in fact bracts, and that in most common types of *Impatiens* flower, there are no lateral sepals at all. Obviously, this problem only can be resolved following a thorough study of a number of species, but the presence of bracts apparently at the midpoint rather than the base of the pedicel in *I. cristata* Wall., *I. scabrida* DC., *I. glauca* Hk.f., *I. serrata* Benth., *I. serrulata* Hk.f. and their Eastern Himalayan and Burmese allies, as well as the apparently congested inflorescences of the African *I. stuhlmanni* aggregate, all indicate that inflorescence structure in *Impatiens* is in need of serious reevaluation, especially since none of the five-sepaled species are associated with solitary inflorescences.

Figure 2

Some variations in sepals found in *Impatiens*

A. *I. verrucifer* Hk.f. Sepals large, ovate and apiculate.

B. *I. attopeuensis* Hk.f. Sepals large, ovate and crassulate.

C. *I. ukagurensis* Grey-Wilson. Sepals minute and pubescent.

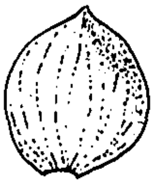
D. *I. indo-chinensis* Hk.f. Sepals minute and cuspidate.

E. *I. grandisepala* Grey-Wilson. Sepals very large and membranous.

F. *I. claviger* Hk.f. 1. Outer pair. 2. Inner pair.

G. *I. balansae* Hk.f. 1. Outer pair. 2. Inner pair.

C and E from Grey-Wilson (1980g); Others from Hooker (1908).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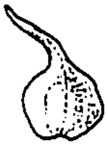
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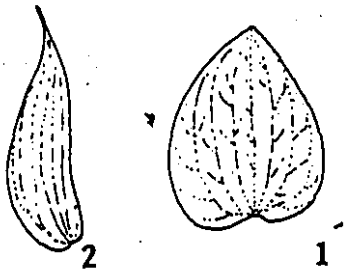

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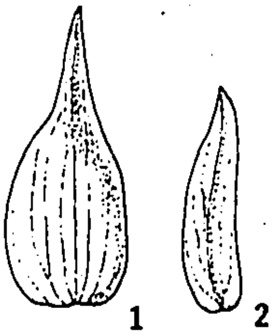

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Three-spurred flowers: Seeds of I. balsamina L. var. azaleiflora obtained from Pocha's Seed Farm (Pune, Maharashtra) showed a strong tendency to produce flowers with multiple spurs. These were examined and it was found that, at least in this particular line, the additional spurred sepals are not the result of a simple transformation of lateral sepals into gibbose and spurred ones. In the normal condition, there are three solitary flowers produced in each leaf axil, and the pedicel of each is subtended by a minute bract. Generally, when multi-spurred flowers are produced, there is a reduction in the number of flowers produced in that axil equal to the number of supernumerary spurs. That is, an axil in which there is a three-spurred flower has only one flower; while an axil with a two-spurred flower has in addition one single-spurred flower. If one examines these multi-spurred flowers carefully, one then discovers that the perianth parts have also doubled or trebled. Although only one androecium and gynoecium develop normally, there are small petaloid structures which undoubtedly represent the supernumerary reproductive organs since vestigal anther sacs can be observed. Although the small lateral sepals are usually absent in these teratoid flowers, they are occasionally present which suggests that they really fail to develop because of the extreme crowding of segments along the floral axis. The multi-spurred flowers, at least in this species, are the result of fusion during ontogenesis and do not constitute evidence that the spurred, gibbose structure in Impatiens evolved from a sepal.

Vestigal lateral sepals: From Table 2 it is evident that I. glandulifera Royle cannot be used as the sole basis for interpreting the calyx in Impatiens because it has at times two sepals, at other times, four. Consequently, it is not clear that the rudimentary protuberances and vascular traces reported by Payer (1857) and Grey-Wilson (1980f) respectively, are truly indicative of the primitive condition. This is particularly true since the second author earlier (1977) reported finding no evidence of vascular traces in I. walleriana Hk.f., a species which always has two sepals and, moreover, a much more primitive flower than does I. glandulifera. Obviously, the sepals must be reexamined systematically using species in each of the three categories which I have distinguished earlier.

An alternative hypothesis for origin of the vexillum: Although Knuth's interpretation of the vexillum as the product of two sepals was rejected by all later authors, there is no convincing proof to substantiate the alternative suggestion. Consequently, the problem should not be considered resolved. In examining numerous fresh flowers, I made the following observations:

1. The vexillum lies midway between the alae and the lateral sepals.
2. In all species, there is a costa at the midline on the abaxial surface of the vexillum, which is usually chlorophyllous, and the greenish color extends outward from the costa to form an ovoid region (Fig. 1). This feature is not readily seen in herbarium specimens, and is obscure in fresh material of some highly zygomorphic groups (including I. glandulifera Royle), but it is very prominent in many tropical taxa, especially those with relatively

actinomorphic flowers.

3. In many species, including I. repens Moon and I. platypetala Lindl., the apices of the lateral sepals are distinctly pigmented, presumably due to a concentration of anthocyanins. In these species, there is an identical pigment spot on the carina of the antivexillar sepal (which undoubtedly is homologous to the apex of a sepal), and again at the apex of the vexillar costa. This suggests that the vexillum may be a compound structure resulting from the fusion of the two missing lateral sepals with each other along their inner margins and which then fused with one of the petals. As will be seen in the final chapter, fusion of lateral sepals (in this case the antivexillar pair) has occured in at least one group of Impatiens. Hopefully, studies on early floral development will reveal the true nature of the vexillum.

FLOWER-POLLINATOR RELATIONSHIPS

Introduction

Pollination biology plays an important role in systematic botany for two reasons. In the first place, differences in pollinators may serve as an isolating mechanism between closely related taxa. Secondly, as Radford et al. (1974) have pointed out, different types of pollination mechanisms tend to select for different groups of taxonomic characters. Consequently, in anemophilous (wind pollinated) groups such as Quercus the species are distinguished on the basis of fruit, leaf and bark characters. On the other hand, in entomophilous (insect pollinated) groups, of which the Orchidaceae is a classical example, there has been enormous diversification and elaboration in floral structure, and it is the flowers rather than the vegetative organs which provide the taxonomist with a wealth of characters for distinguishing and classifying taxa.

Many _Impatiens_ species produce two types of flowers, a showy chasmogam and an inconspicuous cleistogam. The great elaboration of floral organs, including nectaries, the diversity of flower colors and pigments (Bohm and Towers, 1962; Clevenger, 1971) together with the highly sculptured pollen (Huynh, 1968a,b), all point to _Impatiens_ as an entomophilous group in which pollination biology has played a major evolutionary role.

Pollinators

Pollinators of _Impatiens_ have not been extensively studied, but it is reported (Table 3) that pollination by butterflies (psychophily), moths (phalaenophily), bees (mellitophily), and birds occurs in the genus. Given this diverse assemblage of pollinating agents, one would expect to find a concomitant diversity in flower types, for as Pijl and Dodson (1966) have pointed out, each of these pollinators is associated with a different type of flower. One would then expect an understanding of pollination biology in _Impatiens_ to provide taxonomic characters which would facilitate classification. Unfortunately, Hooker [whose difficulties with the flower of _Impatiens_ are extensively documented in his correspondence, edited by Huxley (1918)] was unable to unravel the functional significance of the different types of flowers found in _Impatiens_, and so turned primarily to the inflorescence characters as a basis for his classification.

Table 3

Reported pollinator-flower relationships in *Impatiens*

Pollinator		Species	Flower type	Color	Reference
Lepidoptera	1.	*I. flaccida* Arn. var. *flaccida*	A	P	Clevenger, 1971
	2.	*I. flaccida* Arn. var. *alba*	A	W	Clevenger, 1971
	3.	*I. garderneriana* Wt.	A	M	*Bhaskar, 1975
	4.	*I. grandis* Heyne	A	W	Clevenger, 1971
	5.	*I. irvingii* Hk.f.	A	P	Clevenger, 1971
	6.	*I. kamerunensis* Warb.	A	L	Clevenger, 1971
	7.	*I. pallide-rosea* Gilg	A	Pk	*Grey-Wilson, 1980g
	8.	*I. platypetala* Lindl. var. *platypetala*	A	P	Clevenger, 1971
	9.	*I. platypetala* Lindl. var. *aurantiaca* Teysm. *ex* Kds.	A	O	Clevenger, 1971[1]
	10.	*I. pseudoviola* Gilg	A	P	*Grey-Wilson, 1980g
	11.	*I. rubromaculata* Warb.	A	L	*Grey-Wilson, 1980g
	12.	*I. schlecteri* Warb.	A	R	Clevenger, 1971
	13.	*I. sodeni* Engl. & Warb. *ex* Warb.	A	Pk,W	Clevenger, 1971
	14.	*I. usambarensis* Grey-Wilson	A	O	*Grey-Wilson, 1980g
	15.	*I. walleriana* Hk.f.	A	V	Clevenger, 1971 *Grey-Wilson, 1980g

Table cont'd.

Table 3 cont'd.

Pollinator	Species	Flower type	Color	Reference
Aves	1. *I. capensis* Meerb.	B	W,Y,O	*Josselyn, 1672 *Wilson, 1821 *Pickens, 1944 *Russell, 1976
	2. *I. niamniamensis* Gilg	B	R	Meeuse, 1961
	3. *I. walleriana* Hk.f.	A	R	Grey-Wilson, 1980g
Hymenoptera	1. *I. amphorata* Edgew.	B	P	*Khoshoo, 1955
	2. *I. austrotanzanica* Grey-W.	B	R	*Grey-Wilson, 1980g
	3. *I. capensis* Meerb.	B	W,Y,O	Trelease, 1880[2] *Weatherby, 1917, 1919[2] *Carroll, 1919[2] Clevenger, 1971[3] *Russell, 1976
	4. *I. glandulifera* Royle	B	W,M,P	Clevenger, 1971 Valentine, 1971, 1978
	5. *I. noli-tangere* L.	B	Y,W	*Darwin (in Bennett, 1873) Valentine, 1978
	6. *I. pallida* Nutt.	B	Y	Clevenger, 1971 *Russell, 1976

Table cont'd.

Table 3 cont'd.

Pollinator	Species	Flower type	Color	Reference
Hymenoptera cont'd.	7. I. polyantha Gilg	B	W,Pk	*Grey-Wilson, 1980g
	8. I. repens Moon	B	Y	Clevenger, 1971
	9. I. scabrida DC.	B	Y	*Khoshoo, 1955 Clevenger, 1971
Diptera	1. I. capensis Meerb.	B	W,Y,O	*Carroll, 1919[2] *Russell, 1976 *Valentine, 1978
	2. I. glandulifera Royle	B	W,M,P	*Valentine, 1978
	3. I. parviflora DC.	B	Y	Coombe, 1956
Coleoptera	1. I. parviflora DC.	B	Y	Coombe, 1956

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*Based on field observations; A = flower relatively actinomorphic with shallow antivexillar sepal, filiform spur; B = flower highly zygomorphic, funnel-shaped; L = lavender; M = mauve; O = orange; P = purple; Pk = pink; R = red; W = white; Y = yellow.

[1] Given as I. aurantiaca Teysm.; [2] Given as I. biflora Walt.; [3] Given as I. capensis Thunb., which is a synonym for I. hochstetteri Warb.

Warburg and Reiche (1895) in Engler and Prantl's Natürliche Pflanzenfamilien made no significant alterations in this classification which first had been proposed by Hooker in the Flora of British India (1874-75), and one or the other of these two rather similar treatments has been followed by most subsequent taxonomists.

An entirely different approach was proposed by Perrier (1933) in his monograph on the *Impatiens* of Madagascar. It is in some ways a tragedy that the work of this brilliant French botanist has been overlooked by those working on the Balsaminaceae, perhaps because the apparently regional nature of his study suggests that it is not worth making the effort to overcome the language barrier which his monograph poses to many taxonomists. On the contrary, Perrier had a much better understanding of *Impatiens* than any of his better-known predecessors and his discussion is thoroughly modern in its grasp of dispersal, diversification, ecology, and parallel evolution. Perrier recognized that there are two major phylogenetic lines in *Impatiens* which differ in their floral morphology:

1. Species with a relatively flat corolla, large alae, a shallow antivexillar sepal, and diversely shaped, but often filliform, spurs. The flowers are pink, mauve, violet, purplish, or white (Vulgares group).
2. Species with a small vexillum, alae which are very reduced, and an antivexillar sepal which is shaped like a cornucopia. The flowers are red or purple (Humblotianae group).

These two types are illustrated in Fig. 1. In retrospect, it seems remarkable that Perrier was the first to observe this difference because the two common ornamental species exemplify this dichotomy;

I. walleriana Hk.f. has a vulgares-type flower and I. balsamina L., a humblotianae-type. The effectiveness of this scheme was amply demonstrated in Grey-Wilson's (1980g) revision of the African Impatiens which was based on the recognition of these two evolutionary lines (which he termed Type A and Type B flowers).

As Pijl and Dodson (1966) have pointed out, different groups of pollinators are associated with morphologically very dissimilar flower types; specifically:

1. Butterfly-pollinated flowers are usually delicate, white, pink, or mauve in color, with corollas which are relatively flat and open. The nectar source is deeply hidden (for example, at the tip of a long spur).
2. In contrast, the bee-pollinated flowers are mechanically strong, blue or yellow in color, with corollas which are zygomorphic, semi-closed and produce a great stereoscopic effect. The nectar source is not very deeply hidden (for example, in a short spur).

A comparison of the vulgares- and humblotianae-type flowers (Fig. 1) reveals that they are classic cases of butterfly- and bee-flowers. Furthermore, it is apparent that the species in Table 3 show a similar dichotomy.

If one considers the genus as a whole, it is obvious that the situation is much more complicated than this straightforward scheme would suggest. As the illustrations in Appendix 2 of Chapter III indicate, there are many species of Impatiens which are not readily accommodated in these two categories of butterfly- and bee-pollinated flowers. For example, there are white- pink- or purple-flowered species in which the vexillar petal is much reduced (I. cordata Wt., I. viscida Wt.). Grey-Wilson (1980g) has proposed that species with this type of flower are pollinated by solitary bees. The species in the section Scapigerae may involve two different groups of pollinators. The species with long-spurs (I. acaulis Arn., I. scapiflora Heyne) appear phalenophilous while the remaining species may be psychophilous (Fig. 3). It is partially for this reason that I have not followed the treatment of Bhaskar in uniting I. clavicornu Turz. and I. levingei (Appendix 2 of Chapter III). The former is a short-spurred, white-flowered species, while the latter is a long-spurred, purple-flowered species (they are also found in very different habitats). Perhaps the most notable deviations from the humblotianae-type flower, are the ornithophilous species such as I. niamniamensis Gilg (Fig. 3), I. volkensii Warb., and I. ulugurensis Warb. In these, the alae are fused along the inner margins of the antivexillar petals to form a single structure. It has been suggested that this provides a larger opening for birds than is provided by the primitive Type B flower. Plants of I. niamniamensis grown in the greenhouse displayed cauliflory, which according to Pijl and Dodson (1966) is a common feature of ornithophilous species.

The contrast between the two basic flower types together with the phenomenon of resupination led Grey-Wilson (1980g) to speculate on the evolution of the flower in Impatiens. His arguments can be summarized as follows:

1. The ancestor had a pentamerous flower with free and equal perianth segments. Since the flower was wholly actinomorphic,

Figure 3

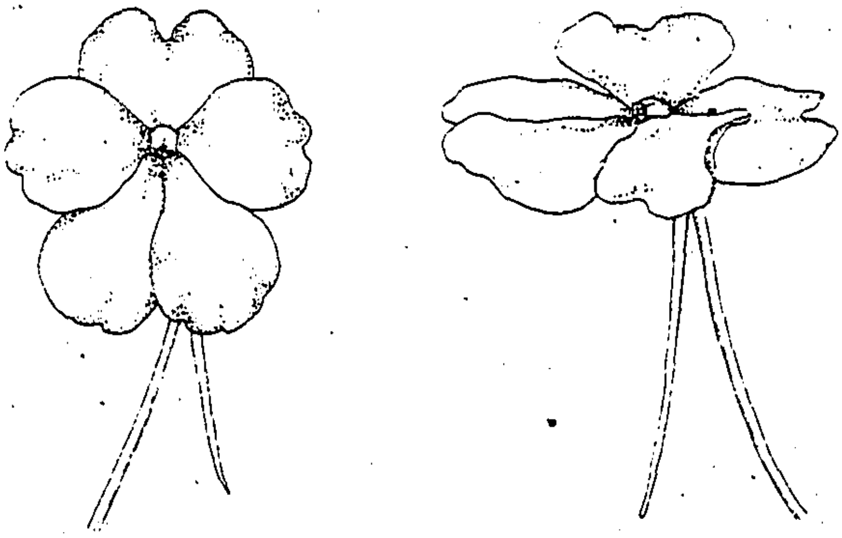
DIFFERENT FLOWER TYPES FOUND IN *IMPATIENS*

A. Relatively actinomorphic, lepidoptera pollinated species, *I. walleriana* Hk.f.

B. Zygomorphic lepidoptera-pollinated species, *I. clavicornu* Turcz.

C. Melittophilous species, *I. repens* Moon.

D. Ornithophilous species, *I. niamniamensis* Gilg.



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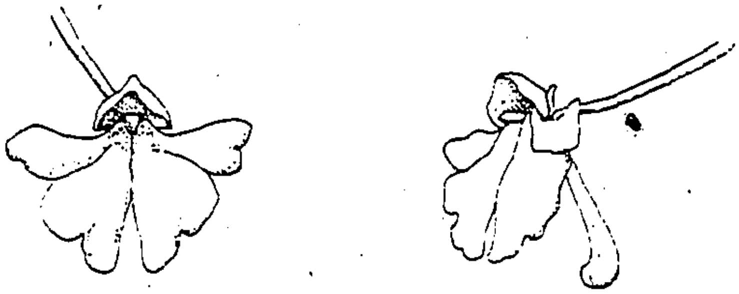

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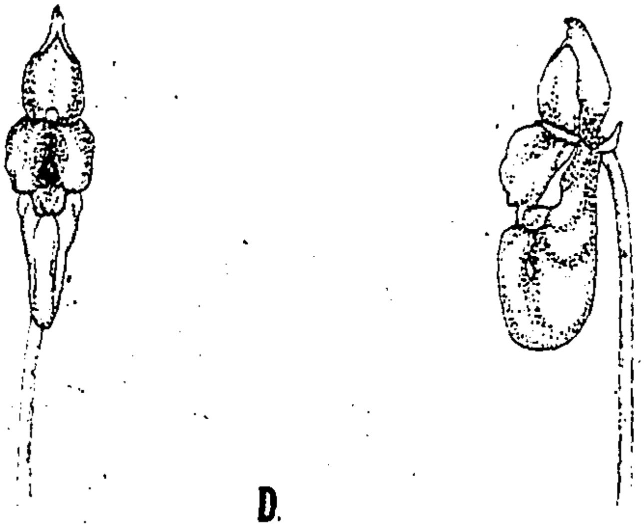

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resupination was absent.

2. The dorsal sepal became gibbose. In this position its bulk was awkward which was resolved by resupination of the flower during ontogeny so that at maturity the spur has come to lie in an abaxial position.
3. Once resupination had evolved, the antivexillar sepal became more pronounced, resulting in a shift of the lateral sepals toward the vexillum and the eventual disappearance of the anticous (or vexillar pair). Concurrently, the alae became connate and the antivexillar petals became differentiated into a labellum.
4. Simultaneously, the androecium developed into a fused structure which forced the pollinator to brush the anthers in order to reach the nectiferous tissue in the spur.

Grey-Wilson's explanation is on the surface extremely plausible, but it should be pointed out that in Vochysiaceae (Polygalales) there has been a parallel development of a gibbose spurred sepal on the dorsal surface which has not led to resupination (Chant, 1978).

BREEDING SYSTEMS

In many Impatiens species there are two types of flowers: a showy chasmogam which has been the subject of the foregoing discussion and an inconspicuous cleistogam. Having reviewed cleistogamy in detail elsewhere (Russell, 1976), I will not dwell on the subject except to point out that I am no longer convinced that cleistogams in Impatiens are either wholly apomictic or self-fertilized. Perrier (1933) reported observing small wingless insects in the Malagasy cleistogamous species, I. inaperta Perr. At the same time, he reported finding two other species which occasionally produce cleistogams (I. baroni Bak. and I. substerilis Perr.). In addition, two cleistogam species have been described from the Philippines: I. crytogama Hk.f. and I. cleistogama Hk.f. Hence, although cleistogamous flowers are rare in tropical Impatiens species, they are not wholly absent.

The chasmogamous flowers of Impatiens are as far as is known always protandrous, and this has led to the assumption that they are strictly out-crossing (Carroll, 1919; Valentine, 1978; Grey-Wilson, 1980g). In fact, in the absence of self-incompatibility, protandry will not insure cross-fertilization since geitonogamy (Baker, 1959) may lead to transfer of pollen to different flowers of the same plant. Absence of self-incompatibility was reported by Darwin (in Bennett, 1873) in I. noli-tangere L. and by Bhaskar (1975) in some of the annual South Indian Impatiens. On the other hand Arisumi (1980a,b) has reported very little success in artificial self-pollination of a large number of Impatiens species.

Initial attempts to carry out self-pollination met with failure. While examining the gynoecia of a number of species, it was found that, contrary to earlier reports, in many species the lobes of the stigma are well-developed at maturity. Further observations indicated that the stigma becomes receptive about 72 hours after the androecium has abscissed. Selfing was again carried out only using flowers with fully developed stigmas, and seed set was obtained in the following species: I. campanulata Wt., I. cinnabarina Grey-Wilson, I. clavicornu Turcz., I. cordata Wt., I. flaccida Arn., I. flanaganae Hemsl., I. hawkeri Bull, I. kleinii W.& A., I. leptopoda Arn., I. niamniamensis Gilg, I. oppositifolia L., I. platypetala Lindl., I. pseudoviola Gilg, and *I. usambarensis* Grey-Wilson. No seed set has been obtained in *I. coelopteris* Fisch., *I. parasitica* Bedd., and *I. repens* Moon. The first set of results confirms earlier observations that some *Impatiens* species are self-compatible, but it extends the phenomenon to include perennial species (only *I. kleinii*, *I. leptopoda* and *I. oppositifolia* are annual). It appears that some reports of failure to set seed following self-pollination may be due to pollinating stigmas whose surface is not yet mature.

CHAPTER V

THE FRUIT

THE FRUIT OF <u>IMPATIENS</u>

The fruit of <u>Impatiens</u> is a dehiscent capsule which when mature explodes at the slightest pressure. It is this characteristic which is the basis for the generic name (which is the Latin for "impatient") as well as for such vernacular epithets as "Springkraut", "Ruhr-mich-nicht-an", "Buzzy Lizzy", and "Touch-me-not". The capsule is not easily studied from herbarium specimens (being either immature or having dehisced during pressing), and fruit is often not produced by plants growing under artificial conditions such as found in greenhouses and botanical gardens (Hooker, 1874-75; Bhaskar, 1975; Grey-Wilson, 1980g). Consequently, few taxonomists have studied the fruit in any detail, it being assumed that the capsule is structurally quite uniform throughout the genus. Recently, many plants in my own collection have begun to bear fruit abundantly, which has given me the opportunity to examine fresh material of a number of species.

Previous Studies

Neither Linneaus (1753, 1754) nor his immediate successors refer to dehiscence in fruit of <u>Impatiens</u>, although this feature must have been known to them as it was to Gerard (1597). Modern taxonomic thinking on the diagnostic value of the fruit can be traced back to Hooker who divided the genus into two primary groups as follows:

1. Fruit capsule short and swollen in the middle (Series A)
2. Fruit capsule terete or clavate (Series B)

An enumeration of species which Hooker assigned to Series A is given in Table 1. There is a general decrease in the percentage of

Table 1

Impatiens species reported to belong to Series A (ellipsoid capsule, turgid in the middle). Data given only for those regions in which both series occur

Region	Species	Percent of balsam flora	Reference
Western Himalayan	1. I. balsamina[1]	4.0	Hooker, 1904-06
Eastern Himalayan	1. I. balsamina	15.9	Hooker, 1904-06
	2. I. bracteata[2]		
	3. I. exilis[3]		
	4. I. florigera[4]		
	5. I. infundibularis[3]		
	6. I. latiflora[5]		
	7. I. mishmiensis[3]		
	8. I. pulchra[5]		
	9. I. trilobata[2]		
	10. I. tripetala[6]		

Table cont'd.

Table 1 Cont'd.

Region	Species	Percent of balsam flora	Reference
Burmese	1. *I. acuminata*[7]	66.7	Hooker, 1904-06
	2. *I. andersoni*[3]		
	3. *I. annulifera*[3]		
	4. *I. balsamina*		
	5. *I. bracteata*[2]		
	6. *I. brandisii*[3]		
	7. *I. burmanica*[3]		
	8. *I. capillipes*[5]		
	9. *I. chinensis*		
	10. *I. circaesides*[8]		
	11. *I. craddockii*[3]		
	12. *I. curvipes*[3]		
	13. *I. cuspidifera*[3]		
	14. *I. florulenta*[3]		
	15. *I. formosa*[3]		

Table cont'd.

Table 1 Cont'd.

Region	Species	Percent of balsam flora	Reference
Burmese (cont'd.)	16. *I. helferi*[3]		
	17. *I. khasiana*[3]		
	18. *I. laevigata*[8]		
	19. *I. latiflora*[5]		
	20. *I. mannii*[9]		
	21. *I. marianae*[10]		
	22. *I. masoni*[3]		
	23. *I. micromeris*[3]		
	24. *I. mokimi*[3]		
	25. *I. nigrescens*[3]		
	26. *I. oppositifolia*		
	27. *I. parishii*[5]		
	28. *I. peguana*[3]		
	29. *I. porrecta*[8]		
	30. *I. pulchra*[5]		

Table cont'd.

Table 1 Cont'd.

Region	Species	Percent of balsam flora	Reference
Burmese (cont'd.)	31. *I. racemulosa*[8]		
	32. *I. radicans*[11]		
	33. *I. rangoonensis*[3]		
	34. *I. stricta*[4]		
	35. *I. strialata*[3]		
	36. *I. tavoyana*		
	37. *I. trilobata*[2]		
	38. *I. tripetala*[6]		
	39. *I. violaeflorae*[5]		
	40. *I. xanthina*[12]		Comber, 1934

[1] authority = L.

[2] Coleb.

[3] Hk.f.

Table cont'd.

Table 1 Cont'd.

[4] C.B. Clarke

[5] Hk.f. & T.

[6] Roxb.

[7] Benth.

[8] Wall.

[9] C.B. Clarke *ex* Hk.f. - nom. illeg.; first published in Hooker, 1904-06. Hooker earlier (1861) described an unrelated African species under the same specific epithet.

[10] Reich.f.

[11] Benth. *non* Zoll. *et* Mor.; the latter is a species from Java, description published in Systematisches Verzeichniss der im indischen Archipel in den Jahren 1842-1848 gesammelten so wie der aus Japan empfangenen Pflanzen. Zürich 1854-1855, 3 Hefte. The *Impatiens* species from Burma was first published in Wallich's Catalogue (no. 4763) in 1831 and is therefore valid.

[12] Comber

species belonging to this group as one proceeds in an arc from the African, Ceylonese and Deccan Regions (100%) to the Burmese (67%), to the eastern Himalayan (16%); and finally to the western Himalayan where only a single species occurs (*I. balsamina* L.); the Eurasian species were all placed in Series B. Recently, Bhaskar (1975) concurred with Hooker's diagnosis by assigning all the Deccan species to the same group. Other authors (e.g. Perrier, 1933; Shimizu, 1970) did not consider fruit characters in their treatments. Perhaps the most curious omission of all is that of Hooker himself in the publications which followed the "Epitome". This is particularly noticeable in his treatment of the *Impatiens* flora of Indo-China (1911) in which only passing mention is made to species with linear and ovate fruit.

Although Hooker was responsible for popularizing the idea that there are two classes of fruit capsule in *Impatiens*, he was not the originator of this idea, a frequent misconception which arises from his comments in the *Flora of British India* (p. 440). Rivinis (1691) used these two types of capsule to distinguish *Balsamina* (= Series A) and *Impatiens* (= Series B),but Linneaus (1754) did not consider the distinction significant enough to warrant the recognition of two genera. With the exception of Miller (1754) and De Candolle (1824), all later taxonomists followed Linneaus's treatment. When De Candolle resurrected the *Impatiens-Balsamina* dichotomy, he expanded the number of characters by which the fruit of the two genera differed:

1. Capsule ovate, puberulent, valves open inward from the apex (*Balsamina*)
2. Fruit terete, glabrous, valves open outward from the base (*Impatiens*)

The last feature (mode of dehiscence) is apparently a unique observation by De Candolle, noted by no previous or subsequent taxonomist.

It appears that only one study has been carried out on the mechanism underlying dehiscence (Warburg and Reiche, 1895). The capsule wall was found to consist of three layers, an epidermis, a middle, spongy layer, and an inner membranous layer. In contrast to the latter, the outer two layers are turgid and composed of very elastic cells which in early development are distended in a direction perpendicular to the valves. As turgor pressure increases, the cells begin to expand in the opposite direction (i.e. parallel to the valves) creating a stress which eventually leads the valves to rupture along the sutures.

The adaptive value of dehiscence has been discussed by several authors. It has been viewed as an evolutionary device for long-distance dispersal (Warburg and Reiche, 1895; Bhaskar, 1975). On the other hand, Stebbins (1974) has pointed out that the seed is scattered at most only a few meters, which suggested to him that its real evolutionary significance is to disperse the seed beyond the shading and rooting circumferences of the parental plant, thereby reducing competion.

Observations

In addition to herbarium material and published descriptions and drawings, fresh fruit capsules were studied when available. The latter included 25 taxa representing a diversity of forms and including the major phylogenetic lines (with respect to flower type) which are found in the genus.

The orientation of the fruit at maturity varies although usually it corresponds to that of the gynoecium. Thus in species with flat, relatively actinomorphic flowers the capsule is parallel to the pedicel with the apex directed in an upward direction, while in species with zygomorphic flowers (groups B-E in Table 2), the fruit is oriented at an oblique angle to the pedicel with the apex pointing outward away from the stem. In contrast, in the African ornithophilous species, I. niamniamensis Gilg, as the fruit ripens the pedicel reflexes so that the apex eventually faces inward toward the stem. The significance of this feature is unknown.

In all species examined, the fruit was found to be an elastically dehiscent capsule composed of five valves (or flaps) derived from the outer wall of the carpel and joined to adjacent valves by sutures.

In all species of Series A for which fresh capsules were available, the capsule was asymmetrical as a result of a swelling in the valve which occupies the antivexillar position. The gibbosity develops as the fruit matures. This feature has been omitted in a number of published illustrations, but is shown in Fig. 1, F and K. The outer surface of the capsule wall is convex while the inner is concave. In cross-section the capsule is circular with five slightly projecting lobes formed by the exterior surface of the valves. The lobing is somewhat more prominent in the species which Hooker assigned to Series A. The valve wall consists of an epidermis, a spongy layer, and a thin membranous layer which agrees with the observations of Warburg and Reiche (1895).

Contrary to earlier reports (Hooker, 1874-75; Bhaskar, 1975) the fruit is a septicidal capsule, not a loculicidal one. This was

Table 2

Distribution of two fruit capsule types in some *Impatiens* species

Flower type	Species	Native to
Capsule Type I		
A. Phalaenophilous, relatively actinomorphic = Series A (Grey-Wilson, 1980g)		
	1. *I. cinnabarina* Grey-Wilson	Africa
	2. *I. flaccida* Arn.	Ceylon
	3. *I. hawkeri* Bull	Papuasia
	4. *I. platypetala* spp. *platypetala* Lindl.	Indonesia
	5. *I. platypetala* spp. *nematoceras* (Mig.) Steen.	Indonesia
	6. *I. platypetala* spp. *aurantiaca* (Teysm. *ex* Kids) Steen.	Indonesia
	7. *I. pseudoviola* Gilg	Africa
	8. *I. pulcherrima* Dalz.	Deccan
	9. *I. walleriana* Hk.f.	Africa
B. Psychophilous or phalenophilous, zygomorphic = Series A (Hooker, 1874-75; Bhaskar, 1975)		
	1. *I. clavicornu* Bedd.	Deccan
	2. *I. cordata* Wt..	Deccan
	3. *I. cuspidata* W.& A.	Deccan
	4. *I. levingei* Hk.f.	Deccan
	5. *I. leptopoda* Arn.	Ceylon
	6. *I. viscida* Wt.	Deccan

Table cont'd.

Table 2 cont'd.

Flower type	Species	Native to
C. Ornithophilous, zygomorphic = Series A (Grey-Wilson, 1980g)		
	1. *I. niamniamensis* Gilg	Africa
D_1. Melittophilous, zygomorphic = Series A (Hooker, 1874-75; Bhaskar, 1975)		
	1. *I. balsamina* L.	Widespread
	2. *I. campanulata* Wt.	Deccan
	3. *I. kleinii* W.& A.	Deccan
	4. *I. leschenaultii* Wall.	Deccan
	5. *I. oppositifolia* L.	Deccan
Capsule Type II		
D_2. Melittophilous, zygomorphic = Series B (Hooker, 1874-75)		
	1. *I. capensis* Meerb.	North America
	2. *I. glandulifera* Royle	Himalayas
	3. *I. pallida* Nutt.	North America
	4. *I. parviflora* DC.	Himalayas and North Temperate Zone
	5. *I. scabrida* DC.	Himalayas
	6. *I. textori* Miq.	Japan

Figure 1

Fruit capsules of some *Impatiens* species arranged according to *Series A* (capsule short, turgid in the middle, ellipsoid or oblong) and *Series B* (capsule elongate, linear, or clavate).

Series A: A = *I. briartii* (Africa); B = *I. barbulata* (Africa); C = *I. gongolana* (Africa); D = *I. harmandi* (Vietnam); E = *I. indo-chinensis* (Cambodia); F= *I. kamerunensis* subsp. *obanensis* (Africa); G = *I. lanessani* (Vietnam); H = *I. makeyana* (Africa); I = *I. mazumbaiensis* (Africa); J = *I. nigeriensis* (Africa); K = *I. oreocallis* (Africa); L = *I. palpebrata* (Africa); M = *I. percordata* subsp. *percordata* (Africa); N = *I. pseudoviola* (Africa); O = *I. tinctoria* (Africa); P = *I. purpureo-violaceae* (Africa).

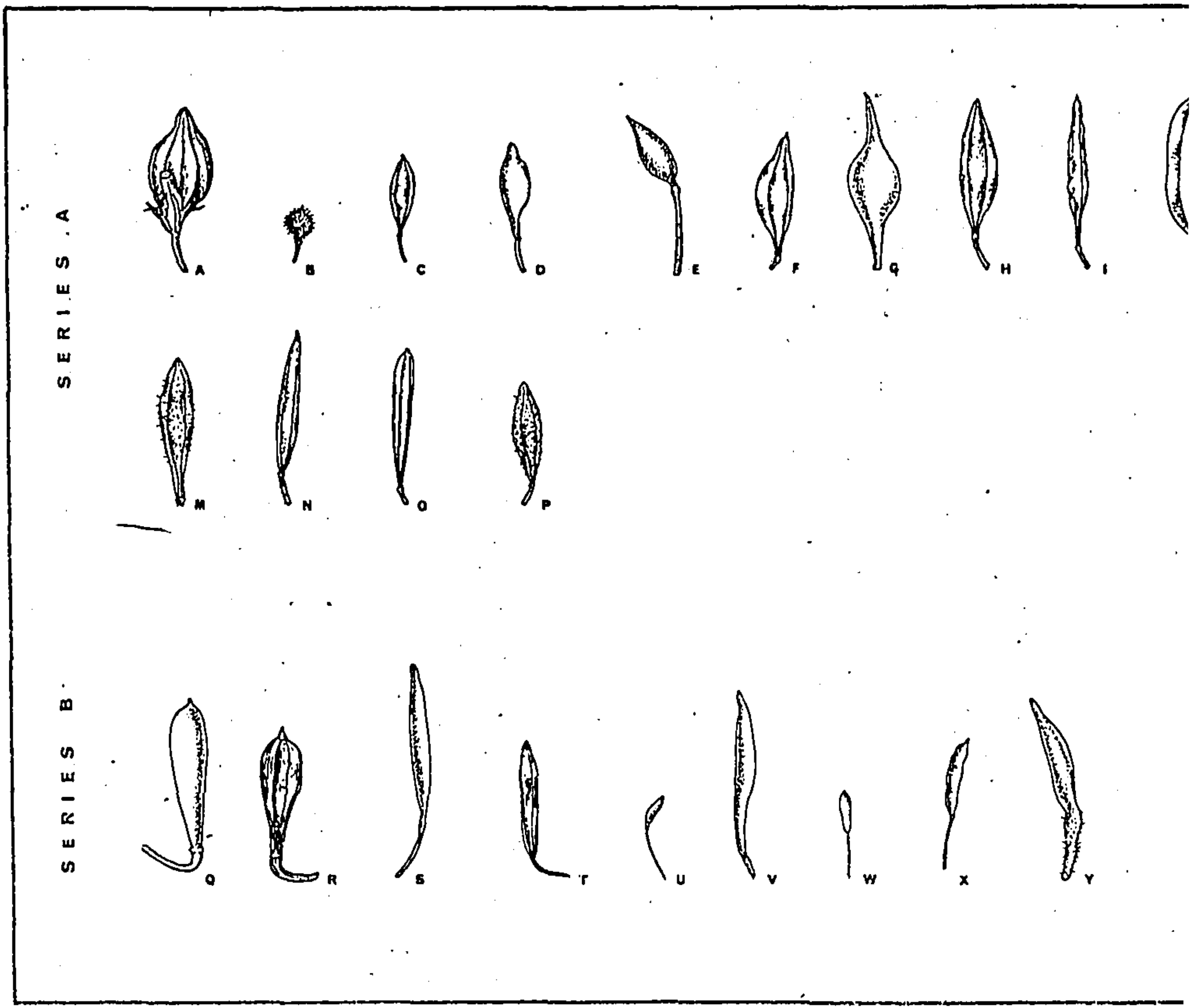
Series B: (all species are Western Himalayan except T, which is Eurasian). Q = *I. aitchisonii*; R = *I. glandulifera*; S = *I. langeana*; T = *I. parviflora*; U = *I. polysciadia*; V = *I. reidii*; W, X = *I. stoliczkia*, immature and mature fruit; Y = *I. vexillariana*.

D, E, and G based on Hooker (1908).

Q - Y (excepting R and T) based on Hooker (1910).

R and T from living material.

Remaining illustrations based on Grey-Wilson (1980g).



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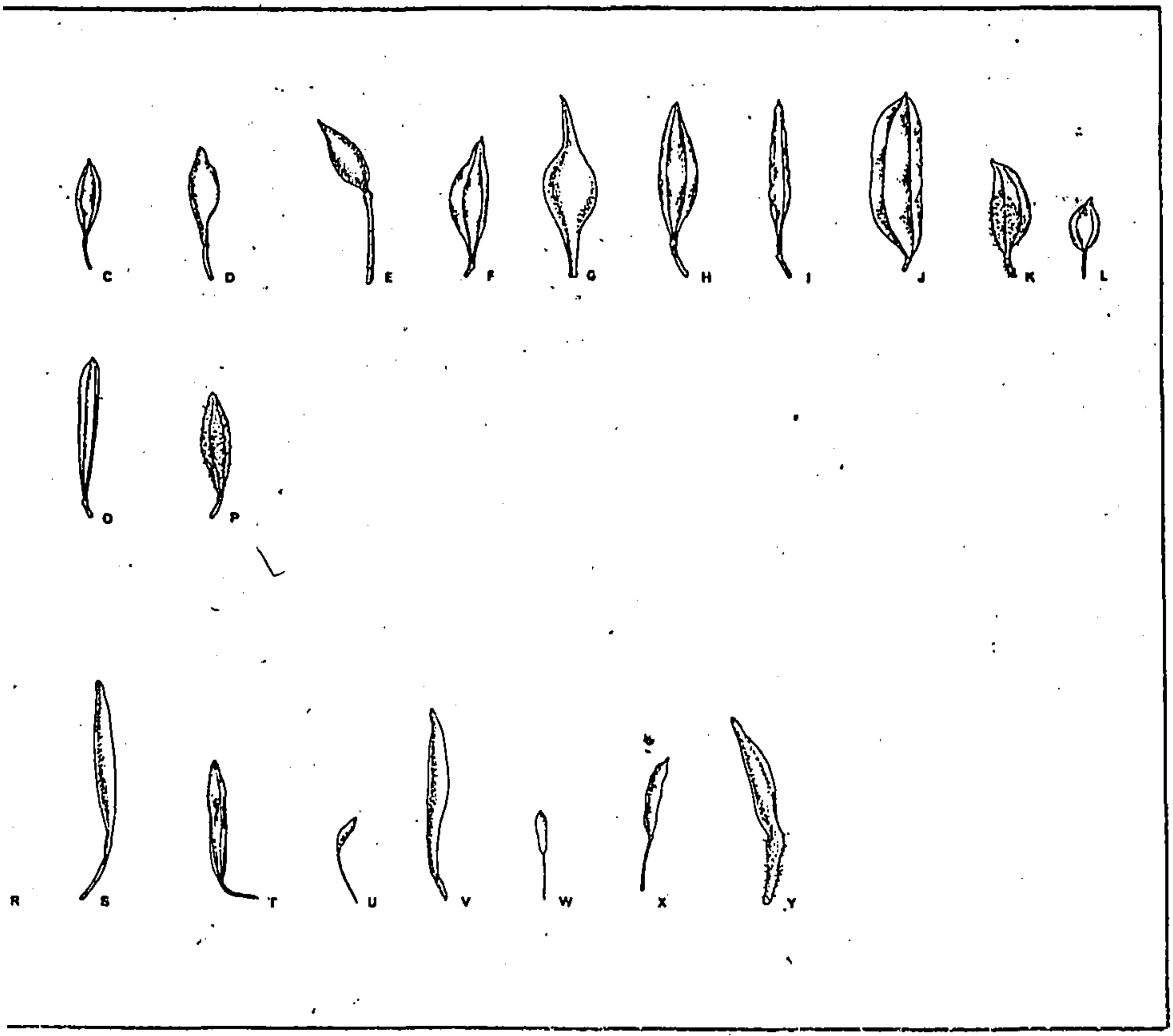


2 of 2

determined by making hand cross-sections of freshly harvested fruit capsules. The sutures are aligned with the septae not with the mid-rib of the locule. In all cases, the placentation was axile, but seed had developed only toward the apex of the placenta. The number of seed per capsule varied both inter- and infra-specifically. For example, I. parviflora DC. had an average of two seeds per capsule (this agrees with Coombe, 1956) while I. flaccida Arn. and I. walleriana Hk.f. averaged more than twenty. It was noted that seed size decreased as seed number increased.

Little evidence was found to support Hooker's two fruit capsule types. A number of specific examples are illustrated in Fig. 1. On the whole, Series B species do have fairly similarly shaped capsules. In constrast, Series A appears to be a heterogenous group with many differently shaped fruits. It is true that some of the species do indeed have a short ovate capsule as is illustrated by I. briartii De Wild. & Th. Dur., I. barbulata G.M. Schulze, and I. palpebrata Hk. f. This feature is also found in the two common ornamentals, I. balsamina L. and I. walleriana Hk.f. Some of the remaining types could have been derived from this basic type such as the beaked fruit in I. lanessani Hk.f., but it is very difficult to envision the fruit of I. mazumbaiensis Grey-Wilson, I. pseudoviola Gilg or I. tinctoria A. Rich. as being ovate rather than terete. On the other hand, it is evident that fruit shape may serve as a diagnostic feature separating closely related groups. For example, the I. tinctoria and I. stuhlmannii complexes of Africa are rather similar florally and vegetatively, but the former has elongated fruit while the latter has short ovate fruit (Grey-Wilson, 1980g).

Figure 2

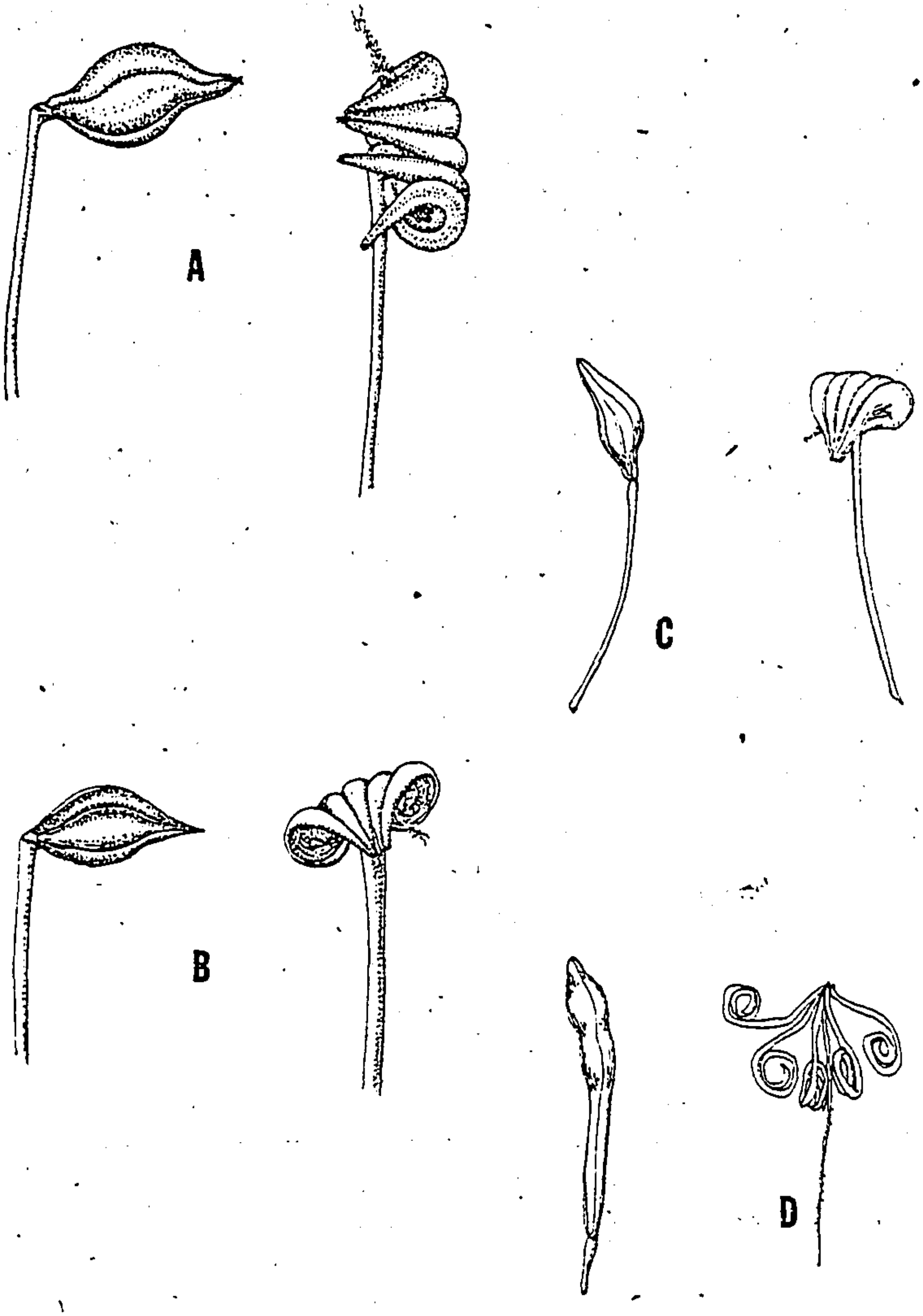
Mode of Dehiscence

A. _I_. _flaccida_ Arn., Type I capsule.

B. _I_. _niamniamensis_ Gilg, Type I capsule.

C. _I_. _kleinii_ W.& A., Type I capsule.

D. _I_. _parviflora_ DC. Type II capsule.


A
B
C
D

Contrary to De Candolle (1824), the Balsamina-type capsule may be puberulent (e.g. I. balsamina L.), or glabrous (e.g. I. leschenaultii Wall., I. chinensis L., I. flaccida Arn., I. oppositifolia L.). All the Impatiens-type capsules examined were glabrous.

While the species of Series A and Series B could not be distinguished on the basis of capsule shape, representatives of the two series which were available from live plants could be readily distinguished by their mode of dehiscence (Fig. 2). All Impatiens capsules do not burst into five segments scattering the seed as was previously thought. In all the species which have been assigned to Series A, the capsule is turgid and only one suture (which lies along the margin of the gibbose valve) ruptures completely. The rupture begins at the midpoint of the suture and progresses simultaneously toward the base and apex. As the suture ruptures, the capsule becomes flattened, and when the rupture reaches the apex, the deformation of the curved surface into a flat one causes the remaining four sutures to split slightly inward from the apex (except in the Annuae), which still leaves the valves adhering to each other as a single unit. (The one modification to this pattern was found in cultivars of I. balsamina L. The capsule is extremely turgid and when the valves fold a suture along the antivexillar surface splits. This often causes the capsule to break into two pieces. In the wild varieties of this species, the capsule is much less turgid and behaves like other Type I fruits.) The capsule wall immediately folds inward along the midline so that the apex and base meet. As this occurs the placenta and seeds are expelled. The folding action is so rapid that in many cases the placenta is not thrown clear, but remains trapped at its base between the folded capsule as if caught in a vise. The placenta with the still attached seed can often be observed protruding from the dehisced capsule. If the capsule is pried open, it will be seen that a number of seed have been trapped inside where they will remain until the capsule abscisses at the base (usually several days later).

In contrast, the Series B capsules are non-turgid and dehisce simultaneously along all five sutures, beginning at the base. The valves curl inward at the base (not outward as reported by De Candolle). Both the seeds and capsule are thrust explosively from the parent plant (the valves remain joined for a short distance at the apex). Consequently, the seed is liberated immediately following dehiscence.

Discussion

The division of <u>Impatiens</u> into two series on the basis of fruit shape appears simplistic as a phenetic marker. The species of Series B (terete or clavate capsule) appear to be a fairly cohesive group based on the examination of fresh capsules from 25 taxa as well as supplementary published evidence. In contrast, a variety of fruit shapes were found in Series A ranging from short and ovate to essentially linear. On the other hand, it was found that the fresh capsules could be divided into two categories based on mode of dehiscence.

1. Capsule dehisces along one suture, beginning at midpoint, folds inward, some seed trapped after dehiscence.
2. Capsule dehises along all five sutures beginning at the base, valves fold inward, seed thrown free of capsule, dehiscence and abscission simultaneous.

Except for the observations of Warburg and Reiche (1895) virtually nothing is known about the dehiscence mechanism in Impatiens. The present study confirmed the presence of a cell wall consisting of three tissues: epidermis, spongy layer, and inner membrane. It is now evident that more extensive studies are needed particularly of longitudinal sections of the two capsule types, focussing on structural differences in the sutures, bases and apices which would explain the different modes of dehiscence, and which would determine the degree of evolutionary divergence which has taken place in the fruit.

At first sight, it seems surprising that with the exception of De Candolle (1824) who was wrong in detail, no taxonomist has noted any difference between the dehiscence mechanism found in various groups of Impatiens, but it must be emphasized that very little material has been available for study. Most herbarium specimens do not include mature fruit, and when they do, it has been so damaged during pressing, that it is usually overlooked. Consequently, for many species of Impatiens there is no information on the capsule whatsoever. This becomes evident when one undertakes a detailed study of the fruit characters presented in Hooker's Flora of British India in which for many species no fruit was available and so only a tentative placement in Series A or Series B could be made. Finally, the weight of tradition cannot be ignored. The fact that Hooker studied the fruit, tends to make one believe that the fruit is well understood and offers no challenges. In fact, it was only a recent observation on greenhouse plants which convinced me that not all Impatiens dehisce in the same way. Earlier, I had spent months in the tropics prying seed out of folded capsules without a second thought to the fact that temperate species had not presented the same problem.

A correlation was found between the two types of capsules and the different flower types (Table 2). Type I capsules were widespread, occurring in species with relatively actinomorphic, phalenophilous flowers, in those with zygomorphic phalaenophilous or psychophilous flowers, in those with zygomorphic ornithophilous flowers (one species) and in some with zygomorphic, melittophilous flowers. Type II capsules were restricted to melittophilous species from the Himalayas and the North Temperate Zone, although it is likely that they also occur in Southern Asia. Thus there appears to be a correlation between primitive flower (Type A) and Type I capsule. Furthermore, based on its present taxonomic and geographic distribution, it seems that the Type II capsule is a relatively recent innovation in the evolutionary history of Impatiens, restricted to a single phylogenetic line in terms of floral evolution. Consequently, Hooker's primary division of the genus (or substituting mode of dehiscence for capsule shape) leads to a cladistic fallacy because the major flower types arose, proliferated, and dispersed before the fruit capsules diverged. This early floral evolution was accompanied by a concomitant elaboration of other phenetic characters (e.g. vegetative morphology) as well. If my hypothesis is correct, Hooker chose to give far more emphasis to Series B than it warrants, and in a more cladistic arrangement it should be treated as a sister group of the species with melittophilous flowers and Type I capsules (or some subgroup of them, should they prove to be paraphyletic).

As for the adaptive value of the two fruit types, little can be said at the present time, although it has been observed that Type II disperses the seed more efficiently. It may be that the seeds trapped within capsule Type I are more susceptible to predation (being a concentrated food source) or that once the capsule falls and decays, they germinate in a dense clump.

A hypothetical mechanism by which the Type II capsule could have arisen was suggested by observations on the androecium. Under normal conditions the filaments are ruptured at their base by the elongation of the gynoecium and slowly are pushed off. In preparation of material for pollen stainability, it was observed that when a drop of ethyl alcohol was placed on the androecium, the filaments ruptured violently at the base, coiling in a manner very reminiscent of that of the valves in Type II fruit and the androecium was violently thrust off. Now it is obvious that in the course of evolution the development of the androecium and gynoecium have become coordinated and this suggests linkage between the genes governing their ontogenies. Perhaps the Type I capsule gave rise to the Type II through a mutation utilizing certain duplicates of genes which control aspects of the androecium structure.

Finally it should be recognized that a number of additional variations may exist in the fruit of Impatiens. For example, a few species such as I. stoliczkai Hk.f. are dispermous with what appears to be apical and basal placentation. Such variations, once their distribution is better known may facilitate the delimiting of natural groups.

CHAPTER VI

CYTOTAXONOMY

INTRODUCTION

Karyological and cytogenetic studies for many years have played a central role in biosystematics. Probably the most influential work in this area was Babcock's (1947) monograph of the genus Crepis which served as a model in the application of cytotaxonomical techniques for a whole generation of biosystematists. Mention also should be made of the cytogenetic studies on Euoenothera by Cleland (1972) and on Clarkia by Lewis (1973).

Traditionally, the importance of chromosomes in cytotaxonomy has been two-fold: they have been used as a diagnostic tool in classification and as a means of providing insights into genetic phenomena and evolutionary processes leading to the differentiation of taxa. Three characteristics of chromosomes have been deemed to have especially high information content: chromosome number, chromosome morphology, and chromosome behavior at meiosis.

In recent years, techniques for detailed analysis have developed rapidly, and now in some groups each chromosome of the genome can be identified by its specific banding sequence. The earliest banding studies involved cold pretreatment (Darlington and La Cour, 1938, 1940; Callan, 1942; Wilson and Boothroyd, 1941, 1944) and mercuric nitrate prefixation (Levan, 1946). In 1968, Caspersson et al. demonstrated that the fluorochrome, quinacrine mustard, induces banding in several plant and animal species. A technically even more significant advance was the discovery by Pardue and Gall (1970) that Giemsa preferentially stains segments of the chromosome rich in repetitive DNA. Giemsa techniques were extended to plant chromosomes by Vosa and Marchi (1972). In contrast to quinacrine mustard, Giemsa does not require sophisticated equipment and is more permanent. Consequently, Giemsa soon dominated the field. The presence of Hy-bands in some taxa following acid hydrolysis of unfixed tissue was first reported by Yamasaki (1956). A modified method applicable to material fixed in Clarke's (usually referred to as Carnoy's) fixative was developed by Greilhuber (1973, 1974, 1975).

In the early stages of biosystematics, cytological characters were regarded as being of primary importance in delimiting taxa by some authors (Darlington, 1956; Stebbins, 1959; Löve, 1960). In recent years there has been a change in thinking (Davis and Heywood, 1963; Raven, 1974, 1976) and it is now recognized that cytological characters are only one of many types of data useful for classification. Cytological characters, especially chromosome number, suggest possible discontinuities. Studies have shown that they are often highly stable and show a correlation with natural groupings. On the other hand, they should not be used as the sole diagnostic criterion; they must be related to other phenetic evidence in a logical way as was stressed by Babcock (1947). For example, chromosome number is often subject to parallel evolution (as in Clarkia, Boronia, and Crepis). In such cases, there will be a discord between cytological and morphological data, and obviously the latter will be more information-rich.

A REVIEW OF THE CYTOTAXONOMY OF IMPATIENS

Chromosome Number in Impatiens

The first studies on the karyology of Impatiens were those by Smith (1934, 1935, 1938) and Warburg (1938a,b). Subsequent important communications include: Khoshoo (1955, 1956, 1957, 1966), Jones and Smith (1966), Chatterjee and Sharma (1970), Bhaskar and Razi (1972-73, 1974, 1976), Arisumi (1973a, 1980a), Bhaskar (1976, 1980), and Gill and Chinnappa (1977). Of particular significance was the discovery by Khoshoo (1956) that chromosome counts can be obtained from herbarium specimens. The generative nucleus remains in prometaphase until the pollen is shed, and the linear arrangement of chromosomes greatly facilitates the determination of chromosome number. Determinations have been carried out on material collected as early as 1900 (Khoshoo, 1956; Chinnappa and Gill, 1974). The technique involved has only proven successful in Impatiens (Solbrig, 1970).

Chromosome number determinations have been carried out for 112 species of Impatiens, which accounts for 10-25% of the genus, depending on which estimate of size is used. A complete list of published chromosome numbers is given in Appendix 1 to this Section which requires a brief explanation. For each species, the chromosome number is given under the correct name, based on the last major treatment (e.g. Shimizu, 1970 for Thailand; Bhaskar, 1975 for South India; Grey-Wilson, 1980g for Africa). Given the proliferation of synonyms in Impatiens, it is not surprising that in many cases, chromosome numbers have been reported for the same species under different specific epithets. Synonyms are included in Appendix 1 with a referral to the correct species name [e.g. Smith (1934) reports $2n = 16$ for *I. sultani* Hk.f. which is a synonym for *I. walleriana* Hk.f. according to Grey-Wilson (1980g). Consequently, Smith's actual count is given under the latter epithet]. The one exception to this is in the case of the New Guinea species *I. hawkeri* Bull, *I. linearifolia* Warb., *I. mooreana* Schltr. and *I. schlecteri* Warb. which Grey-Wilson (1980a) has treated as one aggregate (*I. hawkeri sensu lato*). This has been done to emphasize the ploidy levels. The present arrangement corrects for over-estimates of the number of species which have had their chromosome numbers determined (e.g. Bhaskar, 1975).

From Appendix 1, it is evident that *Impatiens* has undergone an extensive cytoevolution resulting in gametic numbers of n = 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 16, 17, 18, 20, 24, 32, and 33. The low haploid numbers appear rare. An $n = 3$ cytotype is only known to occur in the Deccan taxon, *I. leschenaultii* Wall., a suffrutescent species of the Northeast Monsoon Zone (Bhaskar and Razi, 1972-73; Rao, 1972). It also has been reported to have $n = 7$ (Krishnaswami *et al.*, 1969). The chromosome number $n = 4$ has been reported in *I. platypetala* Lindl. spp. *aurantiaca* (Teysm. *ex* Kds.) Steen., a native of the Celebes and in the cultivar 'Tangerine' which is apparently derived from it (Beck *et al.*, 1974). The African species *I. assurgens* Bak. has been reported to be $n = 5$ (Gill and Chinnappa, 1977). It is related to members of the Deccan Section Annuae, which are reported to have n = 6, 7, 8, and 13 (Rao, 1972, 1973a,b; Bhaskar, 1975). An $n = 5$ cytotype also occurs in *I. edgeworthii* Hk.f. (Khoshoo, 1957, 1966). The most common gametic number in this species is $n = 6$, but occasionally plants were found with chromosome numbers of n = 5 or n = 7.

The most frequent chromosome number in the genus appears to be n = 8, followed by n = 7 and n = 10 (Fig. 1). Cytotypes with n = 6, 9, and 16 are considerably more rare, and the remaining chromosome numbers only occur sporadically. Gametic chromosome numbers of n = 17 and n = 18 have been reported for several Malaysian species, but it has been suggested that these species are, in fact, dibasic polyploids based on lower chromosome numbers (Jones and Smith, 1966).

Thirty-five species are reported to contain dysploid series (these are preceeded by an asterisk in Appendix 1 of this section), that is, to have different basic chromosome numbers on the inter- or intra-population level (Rieger et al., 1968). Dysploidy appears most frequent in the Deccan and Himalayan species, but it does not appear to have much correlation with taxonomic groups. It has been proposed that dysploidy may lead to genotypic differentiation (Table 1).

Interspecific aneuploidy is also present in the genus (Table 2). The Scapigerae form an aneuploid series with n = 6, 7, 8, 9, and 10. The n = 16 and 20 cytotypes are probably euploids based on x = 8 and 10. Aneuploidy is also present in the Annuae with n = 6, 7, 8, while n = 13 may represent a dibasic polyploid of hybrid origin (Bhaskar, 1975). This series is further extended if one includes the African species *I. assurgens* Bak. with n = 5 (Gill and Chinnappa, 1977), which Grey-Wilson (1980g) has correctly recognized as belonging to the Annuae.

A number of groups are euploid. Authentic cases of autopoly-

Figure 1

Frequency of different chromosome numbers in *Impatiens*

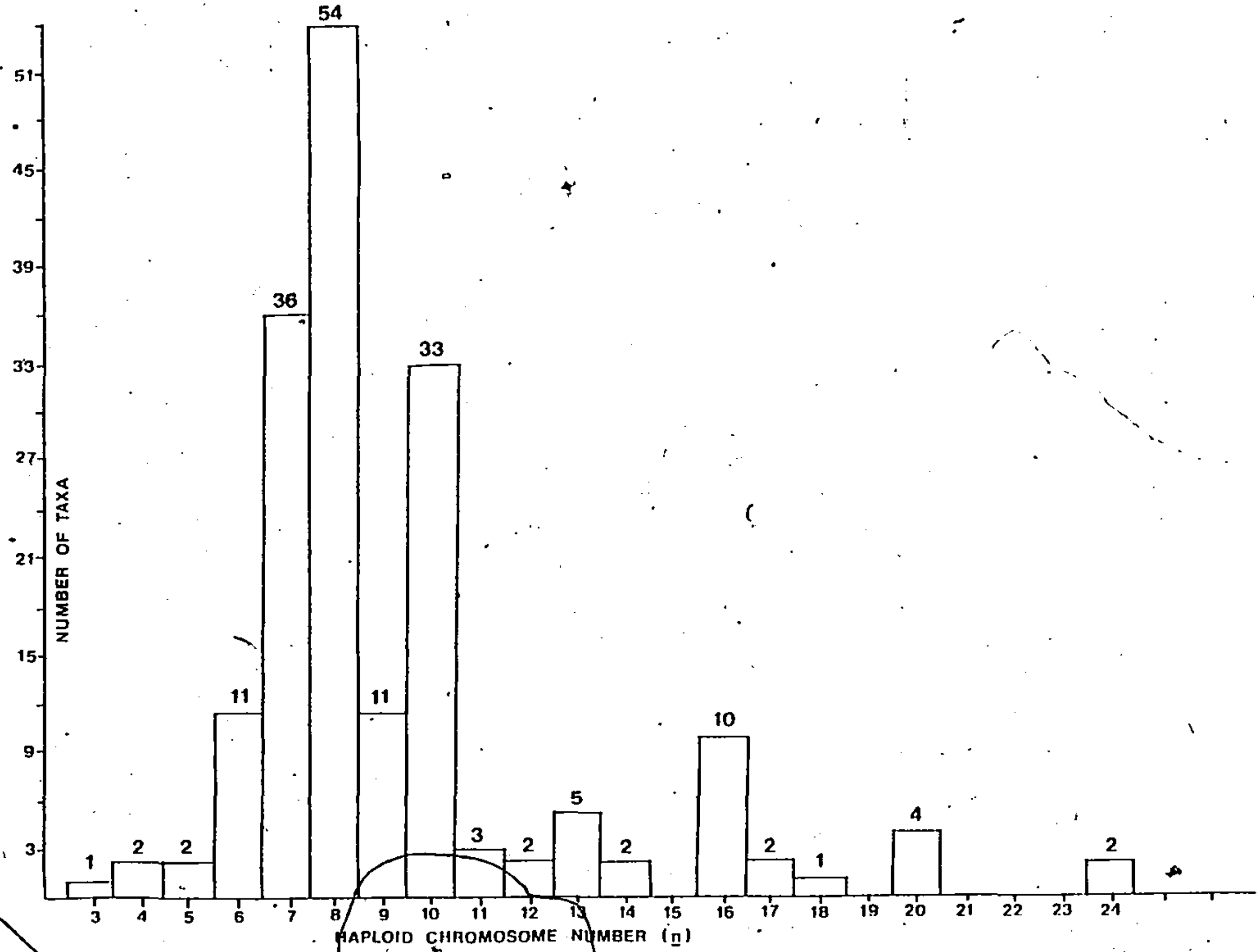

NUMBER OF TAXA
3
9
15
21
27
33
39
45
51
1
2
2
11
36
54
11
33
3
2
5
2
10
2
1
4
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
HAPLOID CHROMOSOME NUMBER (n)

Table 1

Possible character differences associated with some aneuploid changes in certain *Impatiens* species

Species	Cytotype *n*	Character	Reference
1. *I. acmanthera* L.	9	flowers yellow-white	Chatterjee and Sharma, 1970
	10	flowers violet	
2. *I. arguta* Hk.f.	6	flowers large	Chatterjee and Sharma, 1970
	9	flowers small	
3. *I. balsamina* Hk.f. & T.	7	single-flowered	Raghuvanshi and Joshi, 1968
	8	double-flowered	
4. *I. scapiflora* Heyne var. *scapiflora*	8	flowers July-September (monsoon season)	Bhaskar, 1975
	10	flowers October (post monsoon)	

Table 2

Chromosome numbers by sections (Hooker 1904-1906) of South Indian *Impatiens*[a]

Section	Chromosome numbers (*n*)
Scapigerae	6,7,8,9,10,16,20
Epiphyticae	9,10
Annuae	6,7,8,13
Microsepalae	3,6,7
Tomentosae	8
Subumbellatae	8,10,14,16,20
Racemosae	10

[a] Arrangement used by Bhaskar (1975).

ploidy occur in I. balsamina L. (Smith, 1938) and I. noli-tangere L. (Skalinska and Pogan, 1973); while Jones and Smith (1966) proposed that I. mirabilis Hk.f., with $n = 17$, is a dibasic allotetraploid with $x_2 = 8$ and 9 or 7 and 10. Polyploidy is clearly quite prevalent in African and Papuasian Impatiens. Jones and Smith (1966) postulated that the basic chromosome number for these groups was $x = 8$, which subsequently gave rise to tetraploids ($2n = 32$), hexaploids ($2n = 48$), and octoploids ($2n = 64$). In contrast, Beck et al. (1974) favored a basic chromosome number of $x = 4$, which then would have given rise to tetraploids ($2n = 16$), octaploids ($2n = 32$), duodecaploids ($2n = 48$), and 16-ploids ($2n = 64$). If any of the African or Papuasian taxa are autopolyploids they have undergone diploidization (Stebbins, 1971), there being no evidence of multivalent formation (Jones and Smith, 1966; Arisumi, 1973a,b; Beck et al., 1974).

Chromosome Morphology

There is almost no literature on karyotypes in Impatiens. The following observations have been made to date:

1. Chromosomes range from median to acrocentric and may vary on the infraspecific level (Khoshoo, 1957; Chatterjee and Sharma, 1970).
2. A complete examination of all published illustrations of metaphase plates (Table 3) shows that the number of chromosomes with satellites ranges from none to four and that there is no obvious correlation between the number of chromosomes and the number of satellite chromosomes.

Table 3

Species of *Impatiens* in which illustrations of metaphase plates have been published

Species	Chromosome number		Number of satellites	Reference
	n	2*n*		
* *I. acmanthera* (I)	–	20	2	Chatterjee and Sharma, 1970
* *I. acmanthera* (II)	–	18	2	Chatterjee and Sharma, 1970
I. amphorata	–	14	2	Khoshoo, 1957
I. balsamina	7	–	1	Raghavan *et al.*, 1939
I. balsamina	–	14	2	Smith, 1938
I. balsamina	–	21	3	Smith, 1938
* *I. balsamina* (II)	6	–	1	Chatterjee and Sharma, 1970.
* *I. balsamina* (III)	7	–	1	Chatterjee and Sharma, 1970
I. balsamina (IV)	7	–	0	Chatterjee and Sharma, 1970
I. capensis	–	20	4	Smith, 1938
I. edgeworthii	–	12	2	Khoshoo, 1957
I. flaccida	–	14	2	Jones and Smith, 1966
I. glandulifera[1]	–	20	2	Khoshoo, 1957

Table cont'd.

Table 3 cont'd.

Species	Chromosome number		Number of satellites	Reference
	n	2n		
I. hookeriana	–	40	0	Jones and Smith, 1966
I. insignis	9	–	1	Chatterjee and Sharma, 1970
I. leptoceras	–	18	2	Chatterjee and Sharma, 1970
I. mooreana	–	66	0	Jones and Smith, 1966
I. niamniamensis	16	32	0	Jones and Smith, 1966
I. pallida	–	20	4	Smith, 1934
I. pseudoviola	–	16	2	Jones and Smith, 1966
I. scabrida	–	14	2	Smith, 1934
I. scabrida	–	18	2	Chatterjee and Sharma, 1970
I. scapiflora var. scapiflora	10	–	3	Bhaskar, 1980
I. sulcata	–	20	2	Khoshoo, 1957
I. walleriana	–	16	2	Smith, 1934

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[*] Idiogram published. There is a discrepancy between TCL's and idiograms, which renders the analysis doubtful.

[1] Smith (1934) did not observe any satellites in a plant of this species with 2n = 18.

3. Chromocenters (prochromosomes in the older literature) are reported to occur in some species, but not others (Smith, 1934). Chromocenters are present in both mitotic and meiotic material, but in the last mitosis preceeding microsporogenesis, they are anomalously shaped and it has been suggested that this indicates pair-wise association (Chauhan and Abel, 1968).
4. It is a little known fact that Impatiens was the first plant group in which heterochromatin was reported (Heitz, 1929). Heterochromatin appears to be both proximal and intercalary (Bhattacharjya, 1954).

Mechanisms Giving Rise to Aneuploidy

From the foregoing review it is evident that Impatiens has undergone extensive changes in chromosome number. The literature suggests that several processes may be involved:

1. Whole arm translocation resulting in aneuploid decreases in chromosome number: The most convincing report of this is in *I. glandulifera* Royle. Khoshoo (1957) found that in the $n = 10$ cytotype there were ten small, metacentric chromosomes. In contrast, he observed that in the published figure of an $n = 9$ cytotype (Smith, 1934) the genome consisted of eight small, metacentrics and a ninth, large acrocentric.
2. Unequal segregation leading to aneuploid increases: Pollen grains with aberrant aneuploid chromosome numbers have been reported in a number of species including *I. balsamina* L.

(Khoshoo, 1955, 1966; Raghuvanshi and Joshi, 1968), I. acaulis Arn. (Bhaskar and Razi, 1974), I. acmanthera Hk.f. (Chatterjee and Sharma, 1970), I. arguta Hk.f.& T. (Chatterjee and Sharma, 1970), I. edgeworthii Hk.f. (Khoshoo, 1955, 1957), I. modesta Wt. (Bhaskar and Razi, 1974; Bhaskar, 1975, 1976, 1980), and I. parviflora DC. (Khoshoo, 1966). A special case of this was reported by Smith (1938) who found that spontaneous triploids of I. balsamina L.(2n = 21) when backcrossed to their diploid progenitors yielded trisomic offspring.

Primitive Basic Chromosome Number

The extensive cytoevolution in Impatiens (n = 3 to 33) has led to conjectures as to which of these numbers was the original basic chromosome number of the genus. The most frequent hypothesis has been x = 7 (Warburg, 1938a,b; Khoshoo, 1955, 1957; Jones and Smith, 1966; Chatterjee and Sharma, 1970), although x = 10 was proposed by Bhaskar (1975). All of these conjectures are based on three lines of argument:

1. The Balsaminaceae is a geranialian family and that the original chromosome number of the Geraniales was x = 7;
2. n = 7 is the most frequent chromosome number in Impatiens; and
3. n = 7 is the lowest chromosome number which occurs with any significant frequency in Impatiens.

Obviously, the second point has not withstood the test of time. With many more chromosome counts, n = 8 has been found to be more frequent than n = 7. More recently, Raven (1975) in a review of the cytotaxonomy of the Angiosperms, suggested that _x_ = 8 may have been the primitive basic chromosome number of _Impatiens_ because _n_ = 8 has been reported in _Hydrocera_ Blume, another genus of the Balsaminaceae, which he thought was perhaps more primitive than _Impatiens_.

Only 25% of the species have at least one chromosome number determination and therefore, it is premature to discuss most frequent or lowest chromosome number. Moreover, the question of the original chromosome number in _Impatiens_ will have to await a more extensive survey of chromosome numbers in the genus, "accompanied by a phylogenetic sequence based on morphological characters" as was pointed out by Khoshoo (1957). With respect to this last point, it must be emphasized that, with the exception of Bhaskar (1975), no author has even attempted to discuss chromosome numbers in the context of taxonomic categories above the species level. Bhaskar's results in terms of numbers of species for which he determined the chromosome number represents an enormous advance in our knowledge of chromosome numbers in _Impatiens_. Without detracting from his achievements, it should be noted that even among the Deccan species nearly half still have not had their chromosome numbers determined and in several groups only a few species have been counted (Table 4 and Appendix 2 to this Section).

Cytogeography

Jones and Smith (1966) proposed a relatively straightforward pattern to the cytogeography of _Impatiens_ based on the data available to them (Fig. 2). In the Himalayas were found species with _n_ = 7 and _n_ = 10. North of the Himalayas all the native species are

Table 4

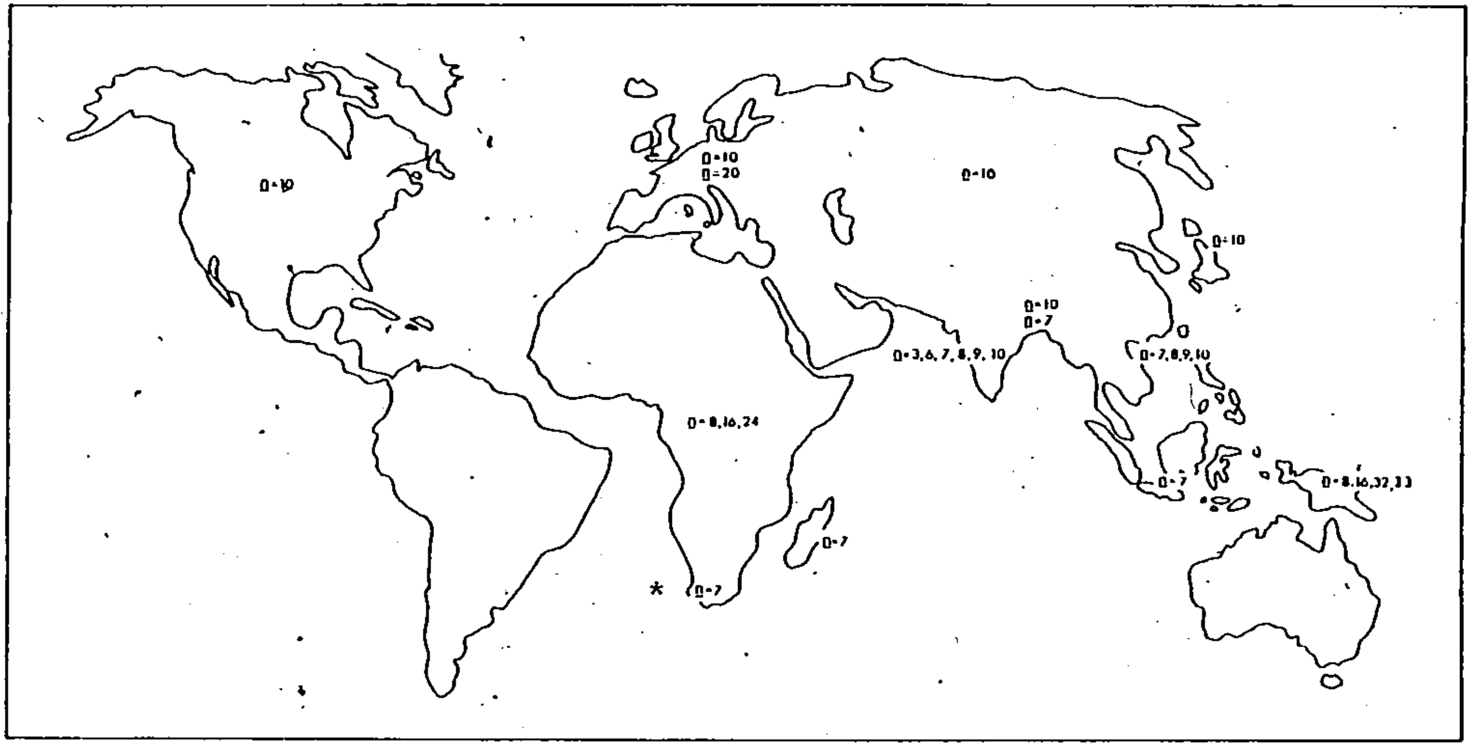
Percent of the taxa in South India on which chromosome number determinations have been carried out

Section	Total[a]	Number of taxa with at least one chromosome number determination	Percent of total
Scapigerae	20	12	60.0
Epiphyticae	7	1	14.3
Annuae	30	13	43.3
Microsepulae	24	10	41.7
Tomentosae	3	1	33.3
Subumbellatae	19	13	68.4
Racemosae	4	2	50.0
TOTAL	105	54	51.4

[a] Number of taxa = species, hybrids, and varieties recognized by Bhaskar (1975), plus _I. ureolata_ Bhask. (mss!) and _I. nairii_ Bose (mss!).

Figure 2

Cytogeography of Impatiens as proposed by Jones and Smith (1966)



*n = 7 in South Africa was ignored in the discussion by Jones and Smith (1966) as being anomalous, and therefore, outside the normal range for this cytotype.

based on x = 10. To the south, the Indian subcontinent contained species with haploid chromosome numbers of n = 7, 10 and 20. They postulated that the species of Southeast Asia were based on x = 7, 8, 9 or 10, and that the x = 7 species reached their eastern limits on Java and their western limits on Madagascar. The African and Papuasian species were all based on x = 8, but included many polyploids at the geographic limits for the genus. Thus only in Southern Asia was there a mixture of basic chromosome numbers. Unfortunately this pattern has not withstood the test of time as more chromosome number determinations have been carried out (Fig. 3). In terms of basic chromosome numbers, the only regions which appear to be relatively stable are Papuasia, the western Himalayas and the North Temperate Zone.

From a cytogeographic point of view the only regions which have been well studied are the Deccan Peninsula, Papuasia, and the North Temperate Zone (Table 5). Of the 105 South Indian Impatiens taxa recognized at present, 54 (51.4%) have had at least one chromosome number determination. The high percentages for Papuasia and the North Temperate regions are a reflection of the small numbers of species found in these regions. In contrast, less than 20% of the species native to Africa, Sri Lanka, and the eastern and western Himalaya have had their chromosome number determined. And finally, virtually nothing is still known about the distribution of chromosome numbers for the Impatiens species of southern Asia exclusive of New Guinea.

Figure 3

Revised cytogeography based on additional chromosome number determinations since Jones and Smith (1966)

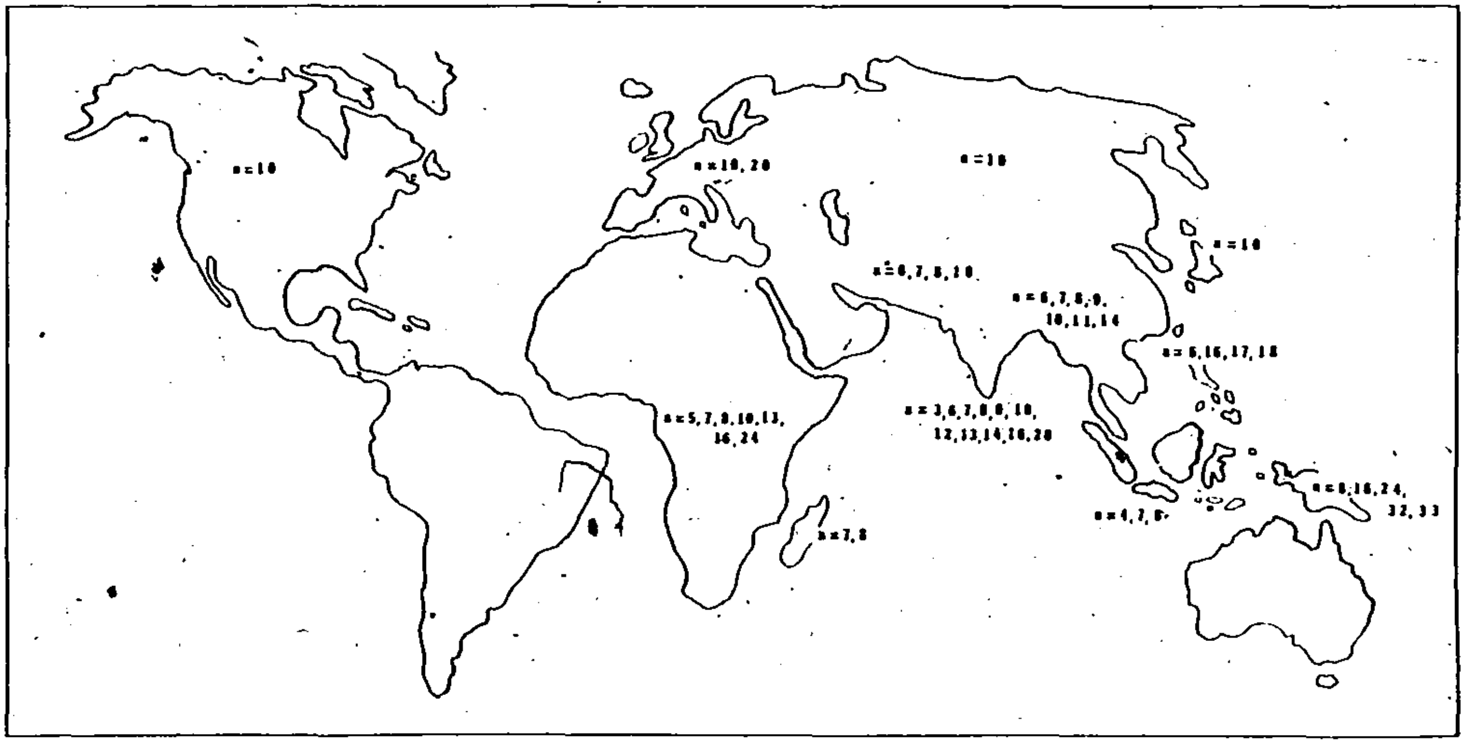


Table 5

Percent Chromosome Number Determinations of *Impatiens* Species by Region

Region	Number of taxa[a]	Percent of total
African	15	13.6
Ceylonese	1	4.8
Deccan	54	51.4
Eastern Himalayan	12	19.0
Western Himalayan	16	59.3
Papuasia	4	100.0
North Temperate	10	83.3

[a] With at least one chromosome number determination.

KARYOLOGICAL STUDIES

Very little is known concerning karyotypes in Impatiens; the majority of studies have dealt only with chromosome number determinations. After examining the distribution of chromosome numbers, it soon became evident that ~~the~~ various cytotypes were not uniquely derived; that is, all the $\underline{n} = 8$ cytotypes do not represent a single clade, nor do the $\underline{n} = 9$, and so on. Each cytotype appears to have arisen several times independently, a fact which has escaped most cytotaxonomists who have chosen to ignore the morpho-phenetic aspects of Impatiens. If this hypothesis concerning parallel cytoevolution is correct, cytological data only become fully meaningful if each chromosome of the complement can be identified. For this reason, the main goal of the present study was to explore techniques for identifying individual Impatiens chromosomes. Examination of other karyological aspects (chromosome number, gametogenesis, chromocenters) was somewhat secondary.

Cytological Techniques Used in the Present Study

Somatic chromosomes were mainly studied from root tips although chromosomes in apical meristems and tapetal cells were also observed. From the beginning it was evident that root tips from potted plants were too poor in quality and showed too little activity. After several procedures were tried, it was found that the best results were obtained by the following technique:

1. Cuttings 8 to 10 cm in length were dipped in rooting hormone ("Seradix 1").
2. Treated cuttings were inserted into a "Promix" substrate

in a mist frame (with misting regulated to one minute every ten minutes) and bottom heat supplied by heating coils beneath the substrate.

3. When initiation of root growth was observed, the material was transferred to glass containers which were filled with half-strength Hoagland's solution (Hoagland and Arnon, 1938). Full-strength Hoagland's was not used because it was found to cause an apparent disintegration of the chromonemata. No such effect was observed with a more dilute solution.
4. The solution was aerated by means of flexible plastic tubing, and air flow was regulated by means of laboratory clamps (Fig. 4). It was later found that by using fine-bore flexible plastic tubing with a bore size of 0.794 mm and a wall thickness of 2.38 mm, the clamps were unnecessary.
5. Initially, rooted cuttings were placed on fine-mesh plastic screening which was stapled to a wooden frame for support. The resulting tray was filled with vermiculite, the plants were inserted in the substrate, and the roots allowed to grow through the mesh. It was found that during periods of high temperatures, the water level often fell unpredictably exposing the roots to dessication. Subsequently, the cuttings were floated on the surface by means of styrofoam disks (50 to 55 mm in diameter) prepared from large sheets 0.5 cm in thickness. The rooted cuttings were inserted into the holes cut in the center of each ring. This technique resulted in improved root growth. This set-up is

Figure 4

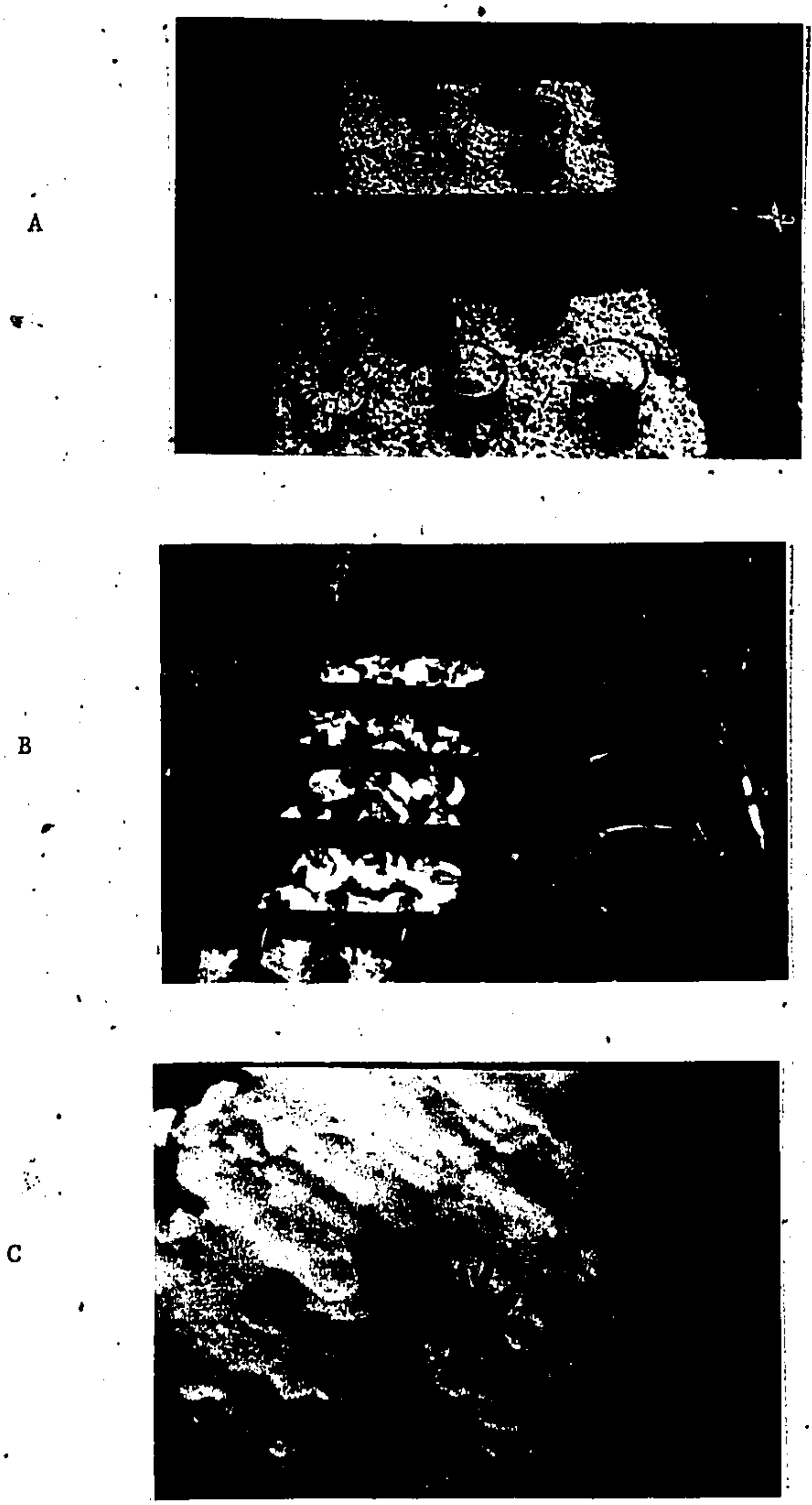
ROOT CULTURE OF <u>IMPATIENS</u>

1. Original apparatus in which cuttings were on a screened frame filled with vermiculite.

2. Modified apparatus, using styrofoam disks.

3. Roots ready for harvesting. Note anthocyanins in root cap. This characterizes all <u>Impatiens</u> species which do not have an albino flower.

Figure 4



illustrated in Fig. 4.

After a series of preliminary experiments involving varying concentrations, temperatures, and times, the following schedule was used for making preparations of somatic material:

1. Pre-fixation in 0.003 M 8-hydroxyquinoline at 12-16°C for 1.5 hours in the dark.

Two mitotic arrest agents were tested as pretreatments for increasing the number of prometaphase and metaphase figures. At first 0.075-0.02% colchicine was used for one to two hours. Even at the lowest concentrations, and the shortest time periods, metaphase chromosomes clumped. According to Dustin (1978), colchicine inhibits spindle movement without destroying the spindle fibers. Consequently, it was suspected that the spindle fibers perhaps were interfering with chromosome spreading. Furthermore, it was found that Sharma and Sharma (1972) reported that colchicine may cause unequal contraction of chromosome arms. Therefore, it was decided to replace colchicine with 8-hydroxyquinoline which had been reported to be a successful mitotic arrest agent for _Impatiens_ chromosomes (Khoshoo, 1955, 1958; Jones and Smith, 1966). It was found that if 8-hydroxyquinoline was used for periods longer than 2 hours, the resulting metaphases were so contracted as to be only suitable for determining the chromosome number and revealed little chromosome morphology.

Two agents were tested on _I. leschenaultii_ (2_n_ = 6) in order to enhance Hy-banding. Treatment with trichloroacetic acid following the schedule of Sharma and Sharma (1972) did not result in improved differentiation. Cold pretreatment carried out as outlined by

Sharma and Sharma (1972) resulted in the appearance of so large a number of bands that at this stage it was impossible to analyze the pattern. It is thought that this may prove a useful technique once the chromosome morphology is better understood.

2. Root tips were washed in running water for 15 minutes at room temperature and immediately transferred to Carnoy's fluid (3:1, 95% ethanol: glacial acetic acid) for 16 hours, and then rinsed again in running water for 15 minutes.
3. Root tips were placed in 0.1 N HCl for 1 minute at room temperature and then hydrolyzed at 60°C for 10 minutes. For times less than six minutes no staining was observed; for times of more than 15 minutes the chromosomes stained uniformly and no Hy-bands were observed.
4. Root tips were washed for 5 minutes at room temperature.
5. Staining was carried out in basic fuchsin (Feulgen's reagent) which is DNA specific (Darlington and La Cour, 1976) for 2 hours at room temperature in the dark.
6. Material was washed in running water for 15 minutes followed by three changes of SO_2 water (Löve and Löve, 1975) for 5 minutes each and then again distilled running water for 15 minutes and stored in distilled water for up to 24 hours. If maintained longer, it was stored in 70% ethanol at 0° to 3°C.
7. Root tips were macerated and cleared in a drop of 45% acetic acid by heating over an alcohol lamp. Uncleared cytoplasm was found to be extremely granular. Several clearing agents were used including BB-4½, clove oil, lactic

acid, IKI-4½, PP-4½, and PPBB-4½ (Radford *et al.*, 1974). BB-4½ was the most successful as a cytoplasmic clearing agent, but left a translucent film on the chromosomes which obscured the Hy-bands. Acetic acid was found not to have this drawback and the clearing was quite satisfactory as long as the chromosomes were heated for at least 15 seconds. The meristematic tissue was then carefully teased with an insect pin, and the resulting suspension aspirated with a 10 μl syringe to further facilitate separation of the cells. Pectinase was not used as a macerating agent because it has been implicated in loss of chromosome banding (Darlington and La Cour, 1976; Shankland, 1975). Preliminary studies using 4% Pectinase for 1 to 2 hours at 20°C indicated that this is the case in *Impatiens*.

8. The preparation was mounted with a coverslip. As an aid to spreading and flattening the chromosomes, the slide was placed in a Ikonen micro-press set for a pressure of "9", which was just below the breaking point of the slide.
9. The preparation was examined under a microscope and if staining was found to be inadequate aceto-orcein was added and gently heated over an alcohol lamp.

It was often difficult to obtain good staining of the chromosomes using basic fuchsin alone. Various procedural modifications for improving staining with basic fuchsin have been proposed by Löve and Löve (1975). None were found successful in the present study.

10. The preparation was again squashed in the micro-press and the coverslip was sealed with gum arabic mixture.

11. Examination of the slides was carried out immediately and photographs taken of the figures with a Zeiss photomicroscope using phase contrast optics.

12. In addition to photomicrographs, a drawing apparatus, was used to prepare karyotypes of the somatic chromosomes of a number of species. Somatic chromosomes were observed in tapetal cells, but karyotype analyses were made only from root tip cells. For the construction of idiograms, measurements of the entire chromosome complements were made for ten representative species on up to 15 cells for each species. The chromosomes are drawn to scale as percentage of total complement length (TCL) and the total complement length is represented by the ordinate in the idiograms which follow. The chromosomes are drawn in decreasing size with the long arm towards the abcissa. The centromere region is represented by a clear-central region which is given equal spacing for each chromosome. The measurements for each chromosome include the centromere region but not the satellite for those chromosomes possessing satellites. The percentage TCL was calculated by dividing the total length of each chromosome pair by the total length of the chromosome complement and multiplying the quotient by 100. The ratio of the long to short arm of a chromosome (L/S) was calculated by dividing the average of the two short arms of one pair into the average of the

two long arms. The L/S calculation gives a ratio which indicates the shape of the chromosome (metacentric or submetacentric). Lengths of the chromosomes in micrometers were calculated from actual measurements of the chromosomes. The bar drawn below each karyotype represents ten micrometers.

In addition, Giemsa banding of somatic chromosomes was attempted using the schedule of Darlington and La Cour (1976) and Shankland and Grant (1976), and staining for NORs following the silver nitrate technique of Berardino _et al._ (1979). These techniques were not successful.

For studies of meiosis and pollen mitoses only the following modifications were required.

1. No pretreatment was used since it was found that cold and 8-hydroxyquinoline did not increase the number of metaphases.
2. Hydrolysis was carried out for 20 minutes rather than 10 minutes.
3. Anthers were dissected out, the pollen squeezed out of the sacs and all the vegetative tissues were discarded.
4. Slides were examined to determine the stage. If it was a stage earlier than quartets, the material was gently tapped to improve spreading. If later, no pressure was applied because this often shattered the exine and interfered with observation of the chromosomes. The first and second pollen mitoses were viewed under light rather than phase contrast optics because under the latter the reflect-

ance from the exine hindered a clear image of the cell content. Since the fully developed exine in Impatiens is highly sculptured at maturity, it is never possible to make chromosome number determinations for all or even a majority of generative nuclei in a specific sample. Khoshoo (1956) attempted to solve the difficulty using the enzymes Pectinase and Clarase without success. In the present study, Dirsolase also failed to achieve the desired results.

RESULTS

Chromosomes of Impatiens species were observed in both mitotic and meiotic tissue. Figure 5 illustrates a typical mitotic division while Fig. 6 is a representative meiotic cycle. In both cases, the species used is I. leschenaultii Wall. (2n = 6) from material collected from Dodabetta Peak in the Nilgri Hills of South India.

Chromocenters

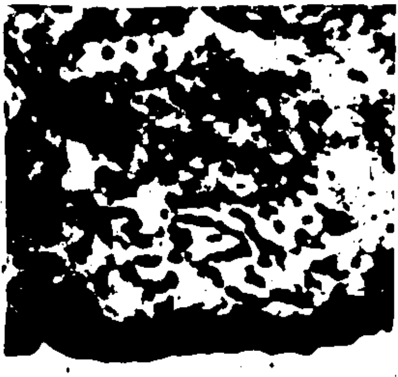
Chromocenters were observed in both mitotic and meiotic interphases of all species examined. A sample of these is illustrated in Fig. 7. In general, the chromocenters are very large, deep-staining bodies which to the untrained eye resemble highly contracted metaphase chromosomes. They are, in fact, so prominent that root tips not undergoing division stain strongly with basic fuchsin. Occasionally, in a specific preparation, chromocenters show poor resolution. It was not possible to determine what physiological or technical factors were responsible. It was evident that the number of chromocenters was greater than the number of chromosomes. Attempts to relate the number of chromocenters to the number of apycnotic blocks observed in prophases and metaphases of I. leschenaultti Wall. (2n = 6) were unsuccessful. This species was selected for this particular analysis because the number of chromosomes and heterochromatic segments is relatively small in comparison with the other species studied.

Chromocenters in the last interphase preceeding microsporogenesis appear different from those of other somatic and meiotic divisions,

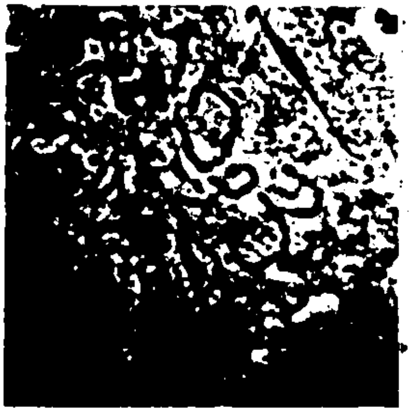
Figure 5

Mitotic cycle in *Impatiens leschenaultii* Wall. (2*n* = 6)

INTERPHASE, X 1900



EARLY PROPHASE, X 3400



PROPHASE, X 410

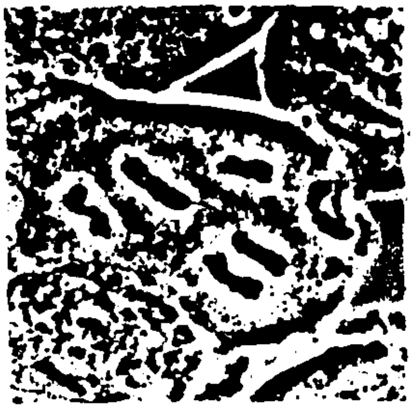
PROPHASE, X 1125

LATE PROPHASE, X 975

PROMETAPHASE, X 1200

PROMETAPHASE, X 600

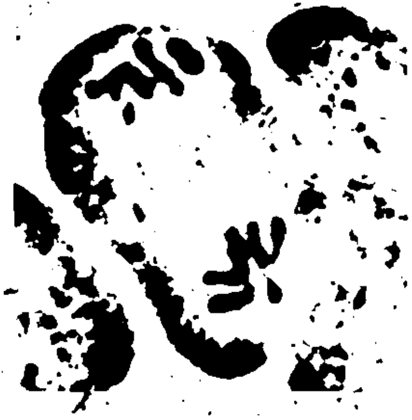
EARLY METAPHASE, X 725



METAPHASE, X 1325

METAPHASE, X 1200

EARLY ANAPHASE, X 1450



TELOPHASE, X 2100

Figure 6

Representative Stages of Meiosis in *Impatiens leschenaultii* Wall.

In the prophase stages (zygotene - pachytene) one chromosome may be seen associated with the nucleolus. The dark swelling at the point of attachment to the nucleolus is the nucleolus organizer of the two synapsed homologues. In the second pachytene picture, the chromosomes are clearly double-stranded and chromomeres are prominent along the chromosomes.

In diakinesis, five to six chiasmata are present.

In interkinesis a complete breakdown of the chromosomes between the two meiotic divisions does not occur.

In the quartets, chromocenters may be observed.

In the prophase of the first pollen mitosis, there is some evidence of banding.

LATE ZYGOTENE, X 975

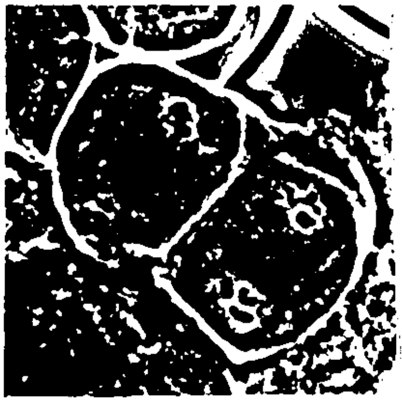
PACHYTENE, X 1060

PACHYTENE, X 840

DIAKINESIS, X 1150

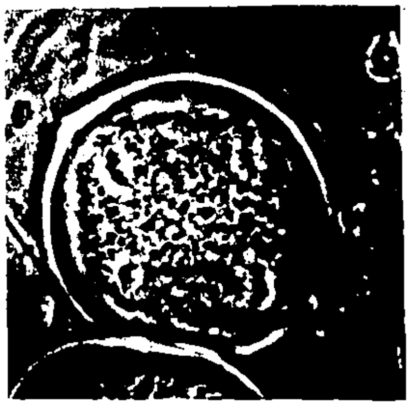
METAPHASE I, X 1575

LATE ANAPHASE I, X 940



TELOPHASE I, × 690

INTERKINESIS, × 1340



LATE TELOPHASE II, × 910

QUARTETS, × 820

PROPHASE, FIRST POLLEN MITOSIS, × 1135

METAPHASE, FIRST POLLEN MITOSIS, × 1260

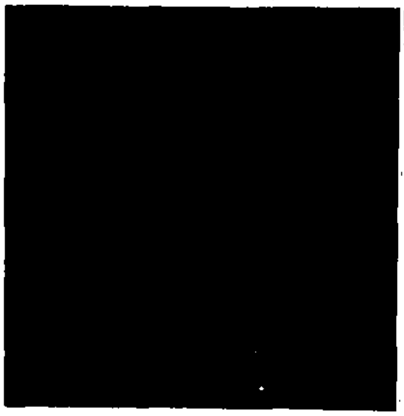
Figure 7

Chromocenters in some species of *Impatiens*

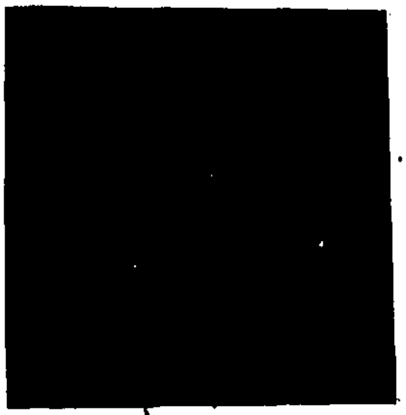
These appear as dark staining bodies in interphase. Note that in some figures they are more distinct than in others.

Figures

1. and 2. *I. clavicornu* (Scapigerae), tapetal cells.
3. *I. modesta* (Scapigerae), tapetal cells.
4. and 5. *I. leschenaultii*; 4, tapetal cells; 5, somatic cells, root tip.
6. *I. repens*, somatic cells, root tip.
7. *I. parasitica*, quartet cell.
8. *I. niamniamensis* (*Impatiens gomophylla* aggregate), cell in last premeiotic interphase.
9. *I. flaccida*, interphase at beginning of meiosis.
10. *I. platypetala*, somatic cells, root tip.
11. *I. sodeni* (*Impatiens walleriana* aggregate), quartet cells.
12. *I. walleriana*, somatic cells, root tip.



1. I. clavicornu



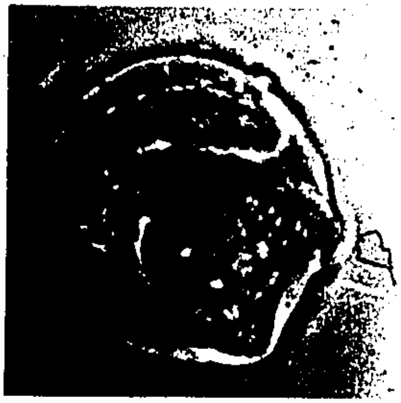
2. I. clavicornu

3. I. modesta

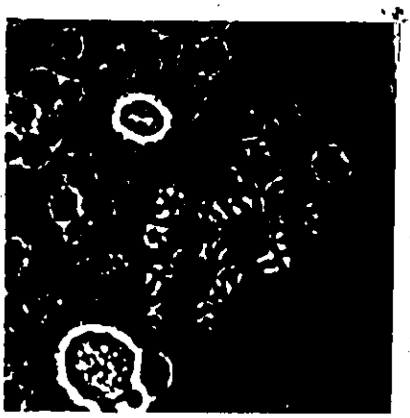
4. I. leschenaultii

5. I. leschenaultii

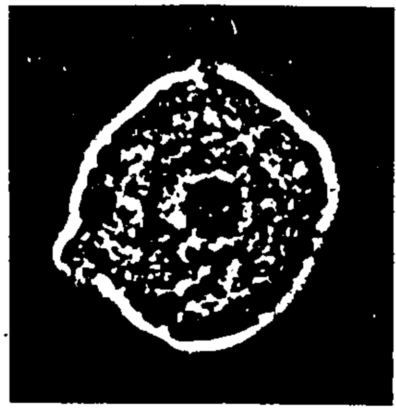
6. I. repens



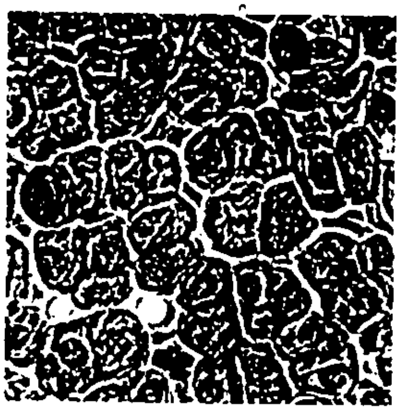
7. I. parasitica



8. I. niamniamensis

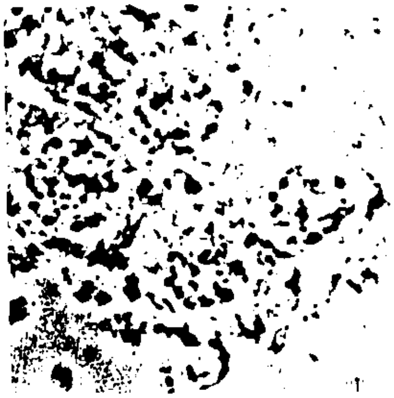


9. I. flaccida



10. I. platypetala

11. I. sodeni



12. I. walleriana

in that they are differentiated into short strands. Occasionally, several threads arise from a single locus forming a stellar configuration. This is seen in I. niamniamensis in Fig. 7, No. 8.

Chromosome Number Determinations

These are given in Table 6; selected examples of meiotic metaphases are shown in Fig. 8. Metaphases in somatic tissues of some Impatiens species are shown in Figs. 9, 10, 11 and 14. The following observations should be noted:

1. Chromosome numbers are reported for the first time in I. cinnabarina Grey-Wilson (n = 8, $2n$ = 16), I. coelotropis Fisch. ($2n$ = 34), I. dalzellii Hk.f. and T. ($2n$ = 16) I. flanaganae Hemsl. ($2n$ = 16), I. gordoni Horne (n = 8, $2n$ = 16), I. pulcherrima Dalz. (n = 6, $2n$ = 12) and I. usambarensis ($2n$ = 16).
2. New chromosome numbers were found in some species for which chromosome numbers have been reported previously.
    a. I. goughii Wt., $2n$ = 40; previously reported to have n = 10 (Jayarama Reddy, 1941; Bhaskar and Razi, 1972-73, 1974; Bhaskar, 1975, 1976), and $2n$ = 16 (Rao, 1973b).
    b. I. parasitica Bedd., n = 7 (in addition to n = 9, 10) which was previously reported as having the latter numbers by Bhaskar (1975, 1976).
    c. I. viscosa Bedd. $2n$ = 32, whereas Rao (1973b) reported $2n$ = 16; and Jayarama Reddy (1941), Bhaskar and Razi (1972-73), and Bhaskar (1975) reported n = 10.
3. Both I. balsamina var. azaleiflora and I. balsamina var. camilliflora were found to be $2n$ = 14, in contrast to the

Table 6

Chromosome numbers determined for *Impatiens* species

Species	n	2n	Source
I. balfourii Hk.f.	7	14	Botanic Garden, Besançon, France
I. balsamina L. var. *rosea* Hk.f.	7	14,28	Khandala, Maharashtra
var. *balsamina* L.	7	14	Mahableshwar, Maharashtra
var. *coccinea* Hk.f.	7	14	Ootacamund, Tamil Nadu
var. '*azaleiflora*'	–	14	cultivar, Pocha's Seed Farm, Pune, Maharashtra
var. '*camelliflora*'	–	14	cultivar, Pocha's Seed Farm, Pune, Maharashtra
I. cinnabarina Grey-Wilson	8	16	Royal Botanic Gardens, Kew (Africa[1])
I. coelotropis Fisch.	–	34	Rajmalai, Kerala
I. cordata Wt.	–	20	Munnar, Kerala
I. cuspidata W.& A.	7	14,42,56,98	Lamb's Rock, Coonoor, Tamil Nadu
I. dalzellii Hk.f.& T.	–	16	Mahableshwar, Maharashtra
I. flaccida Arn. var. *flaccida*	7	14	Kandy, Sri Lanka
I. flaccida Arn. cv. '*alba*'	7	14	University of Ottawa (S.E. Asia)
I. flanaganae Hemsl.	–	16	Royal Botanic Gardens, Kew (Africa)
I. gardneriana Wt.	–	16	Calicut Dt., Kerala

Table cont,d.

Table 6 cont'd.

Species	n	2n	Source
I. gordoni Horne	8	16	Royal Botanic Gardens, Kew (Seychelles)
I. goughii Wt.	-	40	Kodaikanal, Tamil Nadu
I. hawkeri Bull	24	-	Royal Botanic Gardens, Kew (Papuasia)
I. hookeriana Arn.	-	40	Royal Botanic Gardens, Kew (Sri Lanka and Deccan Pen.)
	-	18	Coonoor, Tamil Nadu
I. kleinii W.& A.	-	16	Khandala, Maharashtra
I. leschenaultii Wall.	3	6	Dodabetta Peak, Ootacamund, Tamil Nadu
	3	6	Woodhouse, Ootacamund, Tamil Nadu
I. levingei Hk.f.	-	16	Lamb's Rock, Coonoor, Tamil Nadu
I. maculata Wt.	-	20	Upper Vagavurai, Kerala
Impatiens cv. 'Miss Swiss'	-	16	Ottawa Research Station
I. niamniamensis Gilg.	16	32	Royal Botanic Gardens, Kew (Source: Entebbe Bot. Garden)
I. oppositifolia L.	-	16,32	Mahableshwar, Maharashtra
I. parasitica Bedd.	7,9,10	20	Rajmalai, Kerala

Table cont'd.

Table 6 cont'd.

Species	n	2n	Source
I. parviflora DC.	13	–	Montreal, Staynor Park
I. platypetala Lindl.	8	16	Univ. of Ottawa (Indonesia)
I. pseudoviola Gilg.	–	16	Royal Botanic Gardens, Kew (Africa)
I. pulcherrima Dalz.	6	12	Fritzgerald Ghat, Maharashtra
I. repens Moon	7	14	Ottawa Research Station (Sri Lanka)
	7	14	Royal Botanic Gardens, Kew (Sri Lanka)
I. scabrida DC.	7	14	Botanic Garden, Besançon, France
I. sodeni Eng.& Warb. ex. Engl.			
(flowers white)	8	16	Royal Botanic Gardens, Kew (Teita Hills, Kenya)
(flowers lavender)	8	16	Royal Botanic Gardens, Kew (Africa)
I. usambarensis Grey-Wilson	–	16	Royal Botanic Gardens, Kew (Africa)
I. viscida Wt.	8	16	Silver Cascade, Kodaikanal, Tamil Nadu
I. viscosa Bedd.	–	32	Calicut Dt., Kerala

Table cont'd.

Table 6 cont'd.

Species	n	2n	Source
I. walleriana Hk.f.			
(single-flowered)	8	16	cultivar, Atwater Market, Montreal
(double-flowered)	–	16	cultivar, Sheridan's Nursery, Montreal

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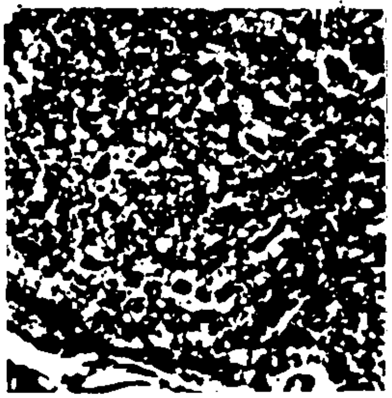
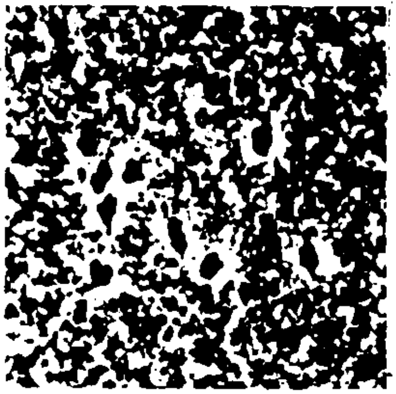
[1] Region in parenthesis indicates area where species is autochthonous.

FIGURE 8

MEIOTIC METAPHASES IN _IMPATIENS_ SPECIES

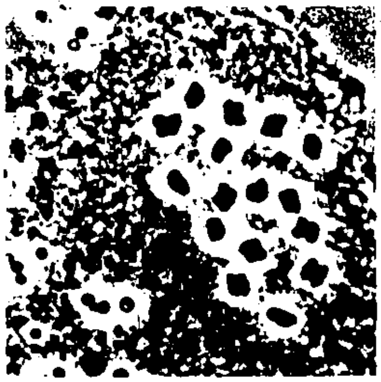


I. *parasitica*, MI, *n* = 10
X 750



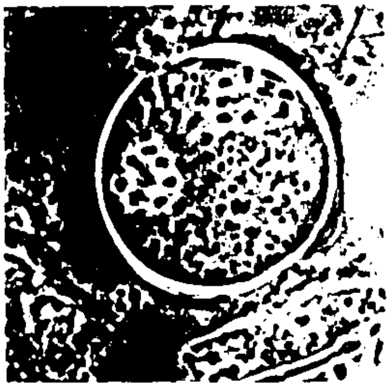
I. *gordoni*, MI, *n* = 8
X 1340

I. *cuspidata*, MI, *n* = 7
X 890



I. *niamniamensis*, MI, *n* = 16
X 1060

I. *pulcherrima*, MII, *n* = 6
X 900

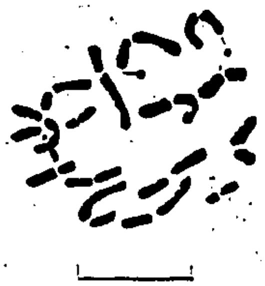


I. *flaccida*, MII, *n* = 7
X 785

Figure 9

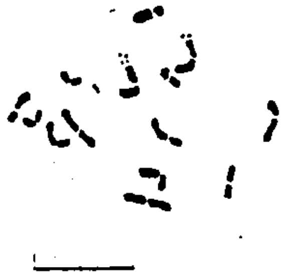
SOMATIC METAPHASES OF VARIOUS *IMPATIENS* SPECIES

I. CINNABARINA



X3537

I. FLACCIDA

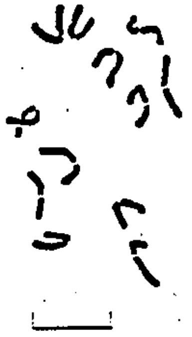


X3000

I. PLATYPETALA

X3306

I. PULCHERRIMA

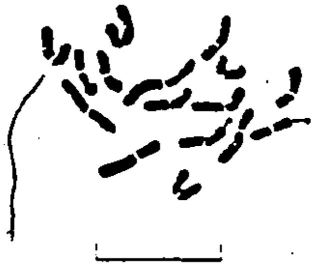


X2300

I. SODENI

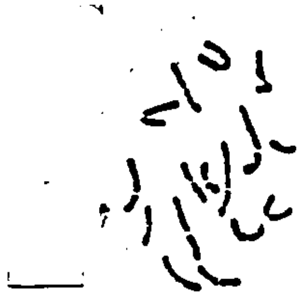
X3000

I. USAMBARENSIS



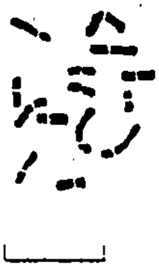
X3900

I. WALLERIANA



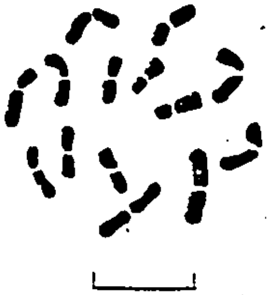
X2415

I. CUSPIDATA



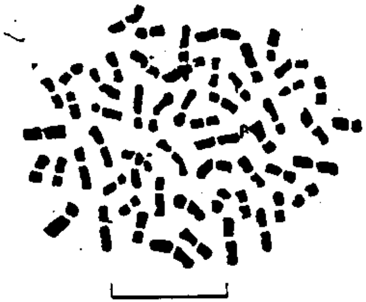
X3000

I. CUSPIDATA.



X3110

I. CUSPIDATA

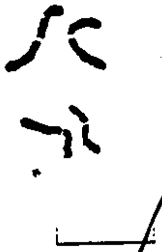


X3570

I. HOOKERIANA

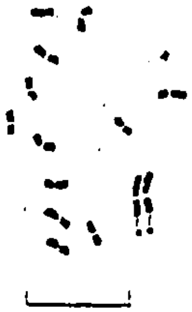
X7800

I. LESCHENAULTII



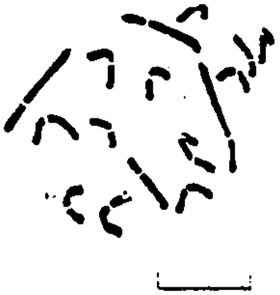
X3053

I. BALSAMINA



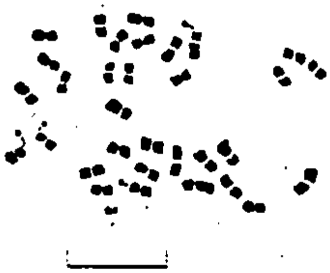
X3158

I. GORDONI



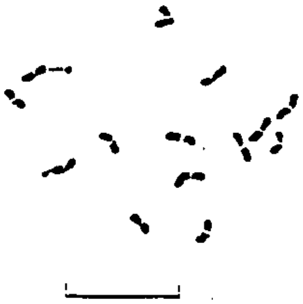
X2833

I. NIAMNIAMENSIS



X3046

I. REPENS



X3482

Figure 10

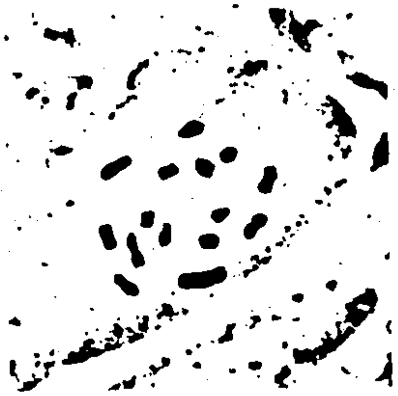
VARIOUS IMPATIENS SPECIES

SHOWING CHROMOSOME COMPLEMENTS

I. gordoni, 2n = 16, X 1380

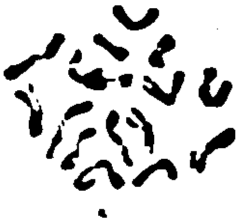
I. maculata, 2n = 20, X 1670

Miss Swiss, 2n = 16, X 1430



I. oppositifolia, 2n = 16, X 1330

I. pulcherrima, 2n = 12, X 585



I. walleriana, 2n = 16, X 1030

Figure 11

SATELLITE CHROMOSOMES IN SOME *IMPATIENS* SPECIES

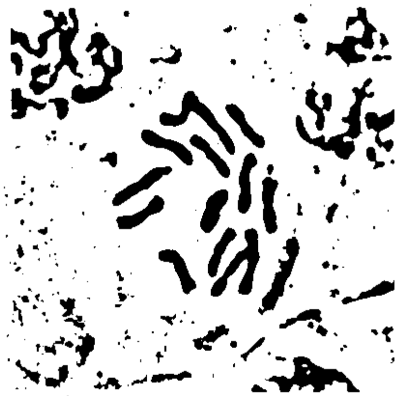
I. flaccida , 2 satellite chromosomes

I. repens, 2 satellite chromosomes

I. niamniamensis, 4 satellite chromosomes

I. sodeni, 2 satellite chromosomes

I. usambarensis, 2 satellite chromosomes

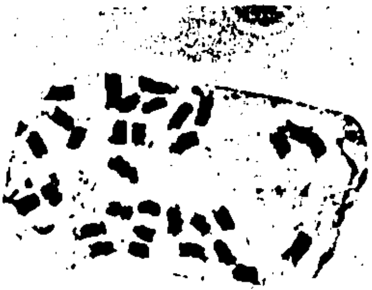


I. flaccida, 2n = 14, X 1225

I. repens, 2n = 14, X 1085

I. sodeni, 2n = 16, X 1740

I. niamniamensis, 2n = 32, X 850



I. niamniamensis, 2n = 32, X 1225

I. usambarensis, 2n = 16, X 1800

report of Raghuvanshi and Joshi (1968) that the latter has a somatic chromosome number of 2_n_ = 16.

4. Mixoploid counts are discussed under a later section (Endopolyploidy).

KARYOTYPES

Satellites

Satellites were observed in 11 species of _Impatiens_ and these are enumerated in Table 7 and illustrated in Figs. 9 and 11. The following results should be noted:

1. In seven of these species, the report of satellites is made for the first time.
2. The presence of two satellites in _I. balsamina_ L. and _I. flaccida_ Arn. are in agreement with previous reports (Smith, 1938; Chatterjee and Sharma, 1970; Jones and Smith, 1966).
3. In one species, _I. niamniamensis_ Gilg, four satellites were observed (Fig. 11), whereas the only previously published karyotype (Jones and Smith, 1966) showed none.
4. In four species, _I. cuspidata_ W.& A., _I. leschenaultii_ Wall., _I. pulcherrima_ Dalz., and _I. walleriana_ Hk.f., no satellites were observed. In the last species, Smith (1934) reported seeing two.
5. The specific chromosome of the genome possessing a satellite was found to vary between species (Table 7 and Fig. 12).
6. Presence or absence of satellites was not correlated with any particular cytotype, although one species, _I. niamniamensis_

Table 7

Number of satellite chromosomes observed in *Impatiens* species

Species	Chromosome number (2*n*)	Number of satellite chromosomes	Previous report	Number of chromosome containing satellite [2]
1. *I. balsamina*[1]	14	2	2	-
2. *I. cinnabarina*	16	2	-	3
3. *I. cuspidata*	14	0	-	-
4. *I. flaccida*	14	2	2	3
5. *I. gordoni*	16	2	-	3
6. *I. leschenaultii*	6	0	-	-
7. *I. niamniamensis*	32	4	0	-
8. *I. pulcherrima*	12	0	-	-
9. *I. repens*	14	2	-	5
10. *I. sodeni*	16	2	-	7
11. *I. usambarensis*	16	2	-	7
12. *I. walleriana*	16	0	2	-

[1] var. *vulgaris*.

[2] Chromosomes numbered according to length; chromosome number 1 is the longest chromosome in the complement.

Gilg with a high chromosome number ($2n = 32$) was found to have two pairs of chromosomes with satellites which suggests that it is a euploid taxon.

General Morphology

For ten species of Impatiens there were a sufficient number of good metaphases to permit analyses of karyotypes and preparation of idiograms (Fig. 12). Additional karyotypes are illustrated in Figs. 9, 10, 11 and 14. The data which were used in the preparation of the idiograms are given in Table 8, and a comparison of the total length of the complement vs. chromosome number is given in Fig. 13. The following taxonomic relationships have been proposed for the taxa under discussion:

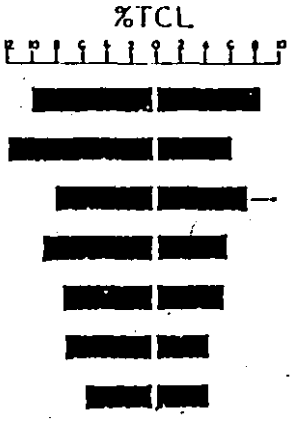
1. I. cinnabarina, I. usambarensis, I. walleriana and I. sodeni are all members of the I. walleriana aggregate. I. walleriana and I. usambarensis are sibling species, and I. cinnabarina is of hybrid origin derived from I. walleriana and I. hamata (of which no material was available) according to Grey-Wilson (1980g).
2. I. cuspidata and I. flaccida are sibling species (Hooker, 1874-75).
3. On the contrary, I. cuspidata and I. leschenaultii are sibling species (Bhaskar, 1975).
4. The remaining species, I. pulcherrima, I. gordoni, and I. repens are not thought to be related to each other or to any of the foregoing species.

The results of the karyotypic analyses can be summarized as

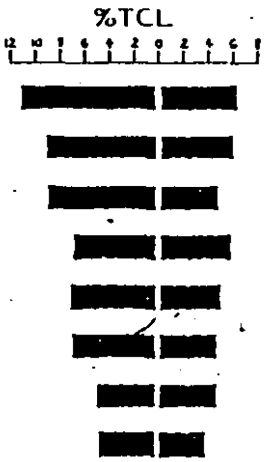
Figure 12

IDIOGRAMS OF TEN SPECIES OF IMPATIENS

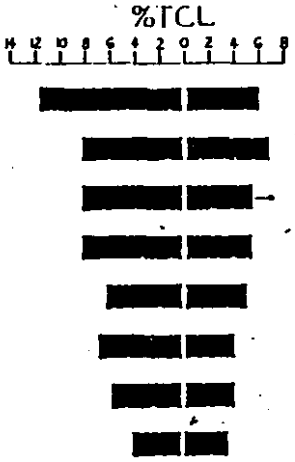
I FLACCIDA



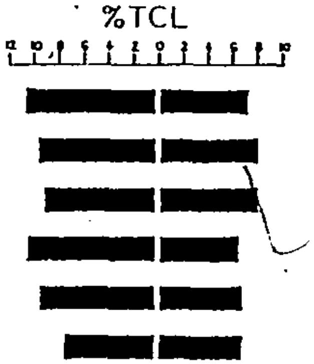
I.WALLERIANA



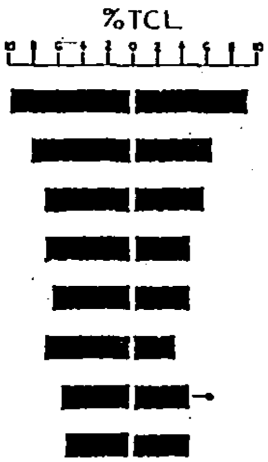
I.CINNABARINA



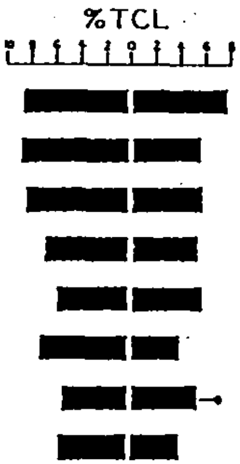
I.PULCHERRIMA



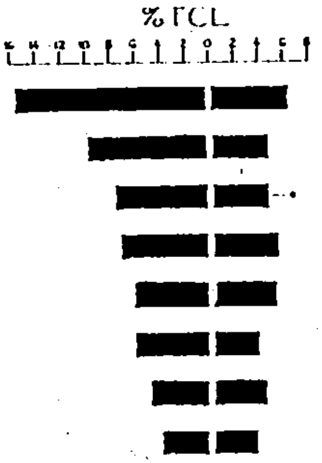
I SODENI



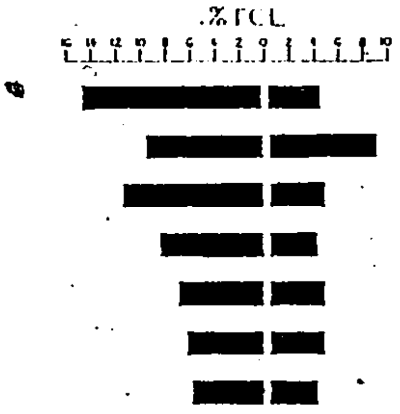
I.USAMBARENSIS



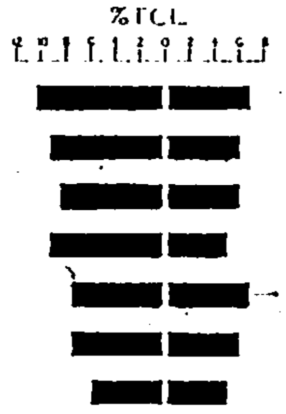
E GORDONII



E CUSPIDATA



E REPENS



E LESCHENAULTII

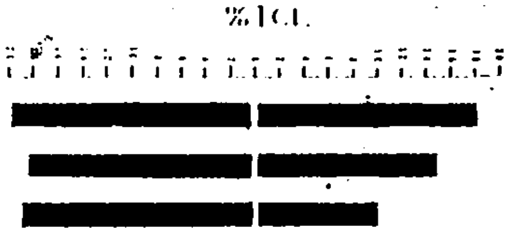
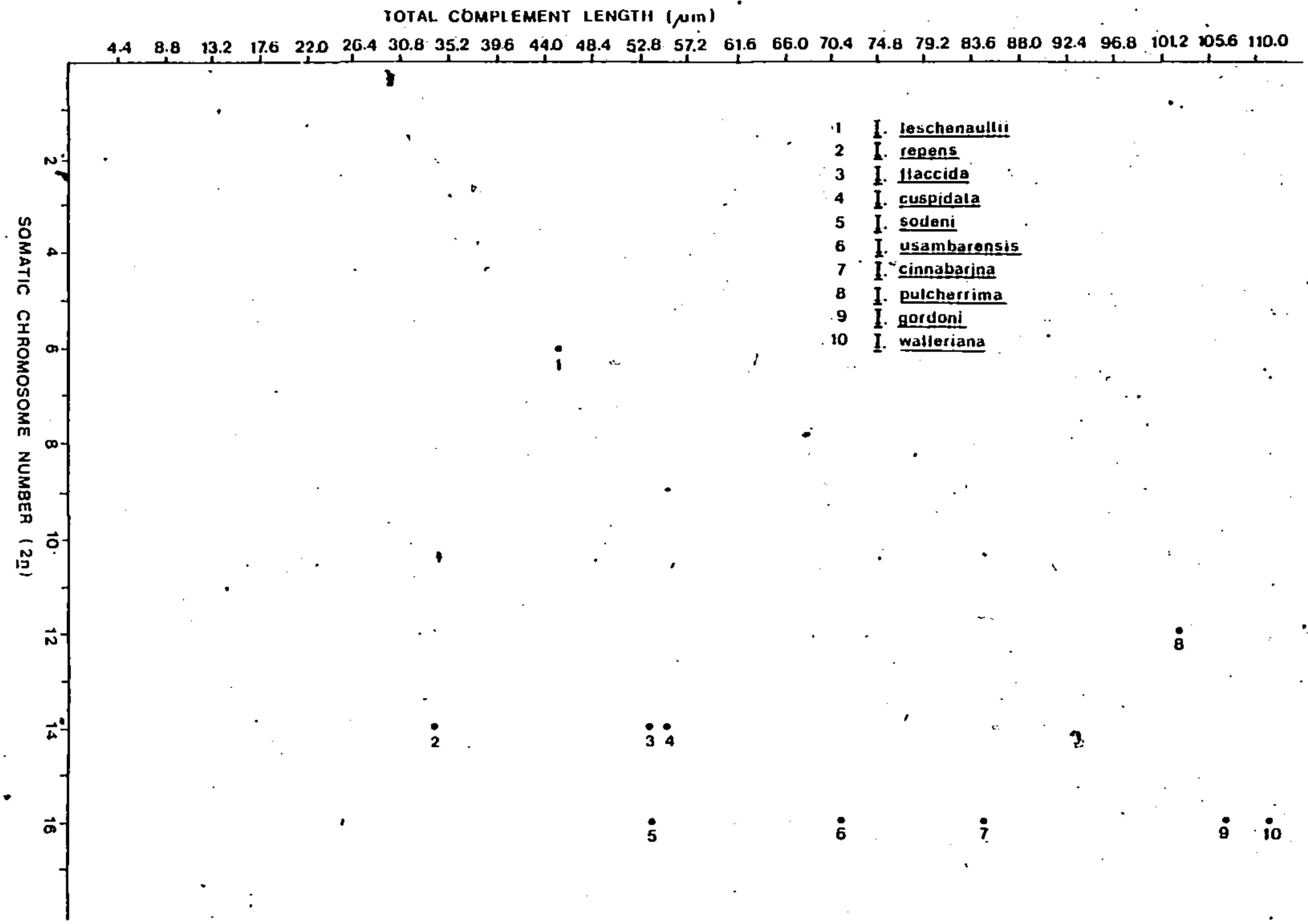


Figure 13

COMPLEMENT AS A FUNCTION
OF CHROMOSOME NUMBER


TOTAL COMPLEMENT LENGTH (μm)
4.4
8.8
13.2
17.6
22.0
26.4
30.8
35.2
39.6
44.0
48.4
52.8
57.2
61.6
66.0
70.4
74.8
79.2
83.6
88.0
92.4
96.8
101.2
105.6
110.0
SOMATIC CHROMOSOME NUMBER (2n)
2
4
6
8
10
12
14
16
1 I. leschenaultii
2 I. repens
3 I. flaccida
4 I. cuspidata
5 I. sodeni
6 I. usambarensis
7 I. cinnabarina
8 I. pulcherrima
9 I. gordoni
10 I. walleriana
1
2
3
4
5
6
7
8
9
10

follows:

1. No karyotype was wholly symmetric. Based on the arm ratio, L/S (Table 8), the chromosomes ranged from metacentric to submetacentric [on the scale provided in Levan *et al.* (1964)].

2. Sufficient karyotypic differences were observed between individual species to suggest that chromosome morphology can be developed into a useful cytotaxonomic tool.

3. No distinct affinities in karyotype were observed between the taxa which are supposedly closely related, but the following points were noted:

   a. There is a general similarity of karyotypes in the *I. walleriana* aggregate. On the other hand, it does not appear that the karyotypes of *I. cinnabarina*, *I. usambarensis*, and *I. walleriana* are more similar to each other than they are to the supposedly less closely related *I. sodeni*. The analysis was complicated by failure to observe satellites in *I. walleriana* as was reported by Smith (1934).

   b. *Impatiens cuspidata* and *I. flaccida* show some similarity in karyotype particularly if it could be shown that chromosome 1 of *I. flaccida* is homeologous to chromosome 2 of *I. cuspidata* and that chromosome 1 of *I. flaccida* and chromosome 2 of *I. cuspidata* differ by a translocation, although this still would not explain the absence of a satellite in the latter.

   c. No similarity was found between the karyotypes of

Table 8

Karyotype analyses for ten *Impatiens* species. TCL = total complement length; L/S - long/short arm ratio

Species	Chromosome pair	% TCL	L/S (Nomenclature)[1]	Chromosome length (μm)	TCL (μm)
I. cinnabarina					84.52
	1	17.61	1.97 (sm)	7.44	
	2	14.99	1.25 (m)	6.33	
	3	13.74	1.47 (m)	5.81	
	4	13.46	1.53 (m)	5.69	
	5	11.32	1.26 (m)	4.78	
	6	11.04	1.66 (m)	4.67	
	7	9.95	1.39 (m)	4.20	
	8	7.89	1.22 (m)	3.33	
I. usambarensis					71.28
	1	16.37	1.12 (m)	5.83	
	2	14.39	1.58 (m)	5.13	
	3	14.03	1.44 (m)	5.00	
	4	12.23	1.27 (m)	4.36	
	5	11.51	1.00 (m)	4.10	
	6	11.15	1.82 (sm)	3.97	
	7	10.79	1.00 (m)	3.85	
	8	9.53	1.41 (m)	3.40	

Table cont'd.

Table 8 cont'd.

Species	Chromosome pair	% TCL	L/S (Nomenclature)	Chromosome length (μm)	TCL (μm)
I. walleriana					111.98
	1	17.34	1.76 (sm)	9.71	
	2	14.76	1.50 (m)	8.27	
	3	13.65	1.85 (sm)	7.65	
	4	12.55	1.13 (m)	7.03	
	5	12.18	1.36 (m)	6.82	
	6	11.44	1.39 (m)	6.41	
	7	9.59	1.00 (m)	5.37	
	8	8.48	1.09 (m)	4.75	
I. sodeni					53.34
	1	19.19	1.06 (m)	5.50	
	2	14.53	1.27 (m)	4.17	
	3	12.79	1.20 (m)	3.67	
	4	11.63	1.50 (m)	3.33	
	5	11.05	1.38 (m)	3.17	
	6	10.47	2.00 (sm)	3.00	
	7	10.47	1.25 (m)	3.00	
	8	9.88	1.13 (m)	2.83	

Table cont'd.

Table 8 cont'd.

Species	Chromosome pair	% TCL	L/S (Nomenclature)	Chromosome length (µm)	TCL (µm)
I. flaccida					54.00
	1	18.52	1.14(m)	5.00	
	2	16.98	1.75(sm)	4.58	
	3	15.43	1.08(m)	4.17	
	4	14.81	1.53(m)	4.00	
	5	12.96	1.33(m)	3.50	
	6	11.42	1.64(m)	3.08	
	7	9.88	1.29(m)	2.67	
I. pulcherrima					102.32
	1	17.83	1.47(m)	9.10	
	2	17.62	1.18(m)	9.02	
	3	17.20	1.13(m)	8.80	
	4	16.99	1.58(m)	8.70	
	5	16.14	1.38(m)	8.36	
	6	14.23	1.09(m)	7.28	

Table cont'd.

Table 8 cont'd.

Species	Chromosome pair	% TCL	L/S (Nomenclature)	Chromosome length (μm)	TCL (μm)
I. cuspidata					55.17
	1	19.34	3.00 (sm - st)	5.33	
	2	18.73	1.07 (m)	5.17	
	3	16.31	2.38 (sm)	4.50	
	4	12.69	2.00 (sm)	3.50	
	5	11.78	1.44 (m)	3.25	
	6	11.18	1.31 (m)	3.08	
	7	9.97	1.36 (m)	2.75	
I. leschenaultii					45.64
	1	37.81	1.10 (m)	8.63	
	2	33.22	1.24 (m)	7.58	
	3	28.98	1.93 (sm)	6.61	

Table cont'd.

Table 8 cont'd.

Species	Chromosome pair	% TCL	L/S (Nomenclature)	Chromosome length (μm)	TCL (μm)
I. gordoni					108.30
	1	21.86	2.44(sm)	11.84	
	2	14.52	2.07(sm)	7.86	
	3	12.56	1.66(m)	6.80	
	4	12.56	1.33(m)	6.80	
	5	11.42	1.19(m)	6.18	
	6	9.95	1.65(m)	5.39	
	7	9.30	1.11(m)	5.04	
	8	7.83	1.09(m)	4.24	
I. repens					33.91
	1	16.95	1.50(m)	2.87	
	2	15.25	1.57(m)	2.59	
	3	14.41	1.43(m)	2.44	
	4	14.41	1.83(sm)	2.44	
	5	14.41	1.13(m)	2.44	
	6	13.56	1.29(m)	2.30	
	7	11.02	1.17(m)	1.87	

[1] m = metacentric; sm = submetacentric; st = acrocentric.

I. cuspidata and I. flaccida to support the hypothesis that these are closely related taxa.

4. TCLs varied widely ranging from 33.91 to 111.98 μm (Table 8). No trend was observed with respect to chromosome number. Within the I. walleriana aggregate all the species studied were $2n = 16$, but TCLs varied from 53.34 to 111.98 μm (Fig. 13).

Chromosome Banding

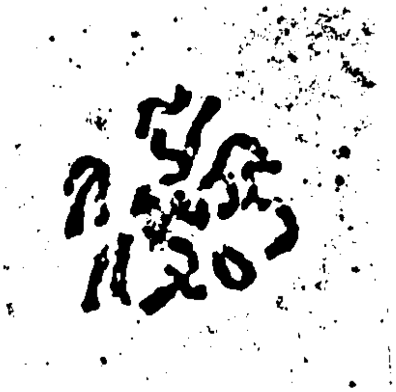
Following a standard technique for staining chromosomes with basic fuchsin, it was noted that the chromosomes differentiated into pycnotic and apycnotic regions. It is evident that the pycnotic segments are euchromatic and the apycnotic one are heterochromatic. The pycnotic regions are diffuse and bead-like in early prophase, gradually coalescing until at prometaphase they form distinct blocks (which agrees with the coiling theory; Ris, 1945; Gall, 1956; Swanson et al., 1981, p. 144). Highly contracted chromosomes at metaphase do not exhibit banding (Fig. 5). In late telophase, the banding of the chromonemata is again evident. These Hy-bands were described earlier by Grielhuber (1973, 1975) in Allium, Fritillaria, Scilla and Vicia. The Hy-bands in a number of Impatiens species are illustrated in Fig. 14. As is evident from the photographs they were observed in both mitotic and meiotic material.

It was found that Hy-bands varied in different chromosomes of the complement. This is illustrated using I. leschenaultii Wall. ($2n = 6$) as an example. In Fig. 15, prometaphases from three different plants of the same population are shown. In each cell, the three pairs of homologues have been identified, and it is evident that the same general banding pattern occurs in the corresponding chromosomes of all

FIGURE 14

CHROMOSOME BANDING IN SOME IMPATIENS SPECIES

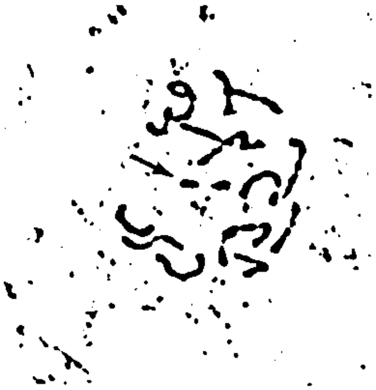
Note that the complement of 'Miss Swiss' is incomplete. Arrows indicate a small dumbell-shaped chromosome seen in African, but not in Asian *Impatiens* species.



I. cuspidata,
tapetal cell

I. cuspidata,
tapetal cell

I. flaccida,
root tip.



I. gordoni,
root tip

'Miss Swiss',
root tip

I. walleriana,
root tip

Figure 15

BANDED METAPHASES IN THREE PLANTS
OF *I*. *LESCHENAULTII* WALL.
FROM DODABETTA PEAK IN THE
NILGRIS

I. leschenaultii, $2n = 6$, homologues of three different plants. A, X 2070; B, X 1650; C, X 3400.

three individuals.

On the other hand, at this stage, the quality of banding is highly variable. In a certain number of cells from the same plant or from plants of the same species the pattern was identical, in other cases differences were observed, and occasionally no banding was evident. These problems will have to be overcome before Hy-banding can be fully exploited as a phenetic character in _Impatiens_.

A PHOTOGRAPHIC TECHNIQUE FOR IMPROVED RESOLUTION OF HY-BANDS

Recently, while preparing prints of somatic chromosomes, it was observed that with exposure times suitable for ordinary metaphases Hy-bands, which were distinct in the original preparation and in the negative, did not appear on the final print. This is the result of a reduction in contrast between the light and dark regions of a chromosome with increasing exposure. To illustrate, a series of photographs of a prometaphase of _I. leschenaultii_ Wall. (2_n_ = 6) have been printed using a single negative, but varying the exposure times (Fig. 16).

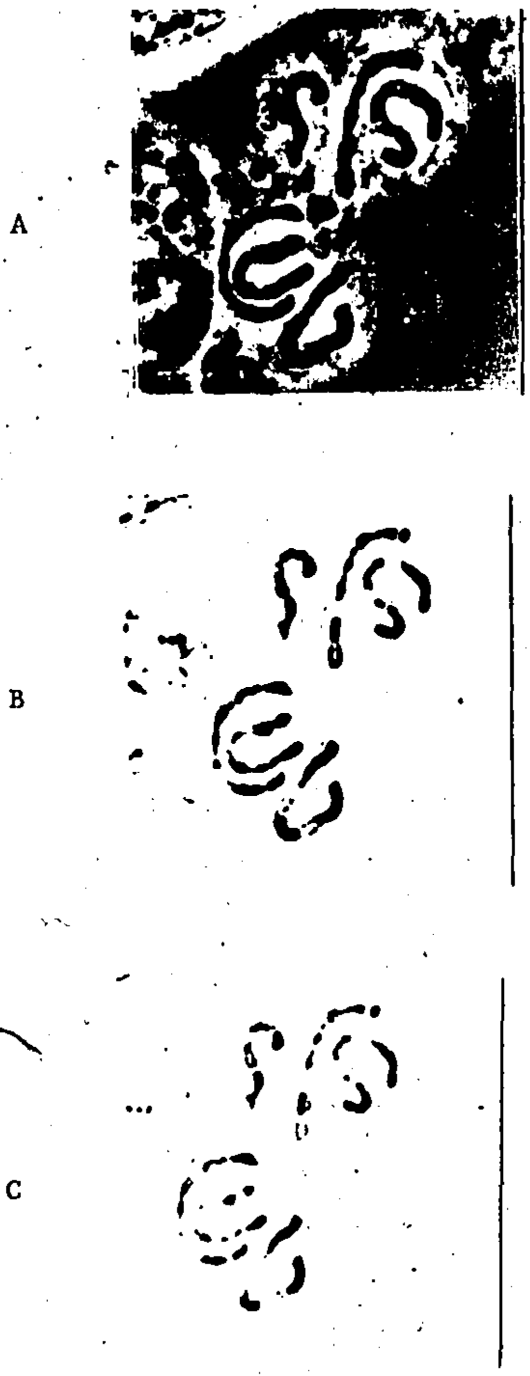
Figure 16 shows a prometaphase printed at a series of decreasing exposures. Homologues have been numbered to correspond with those at metaphase (Fig. 15; note that in _I. leschenaultii_ Wall. chromosome 2 undergoes greater condensation between late prophase and metaphase than does chromosome 1). All photographs were printed at a constant aperture setting of f 4.0, with the exposure time varied as follows:

1. Fig. 16A was printed at 12 seconds,
2. Fig. 16B, at 6 seconds, and
3. Fig. 16C, at 3 seconds.

Figures 16 and 17

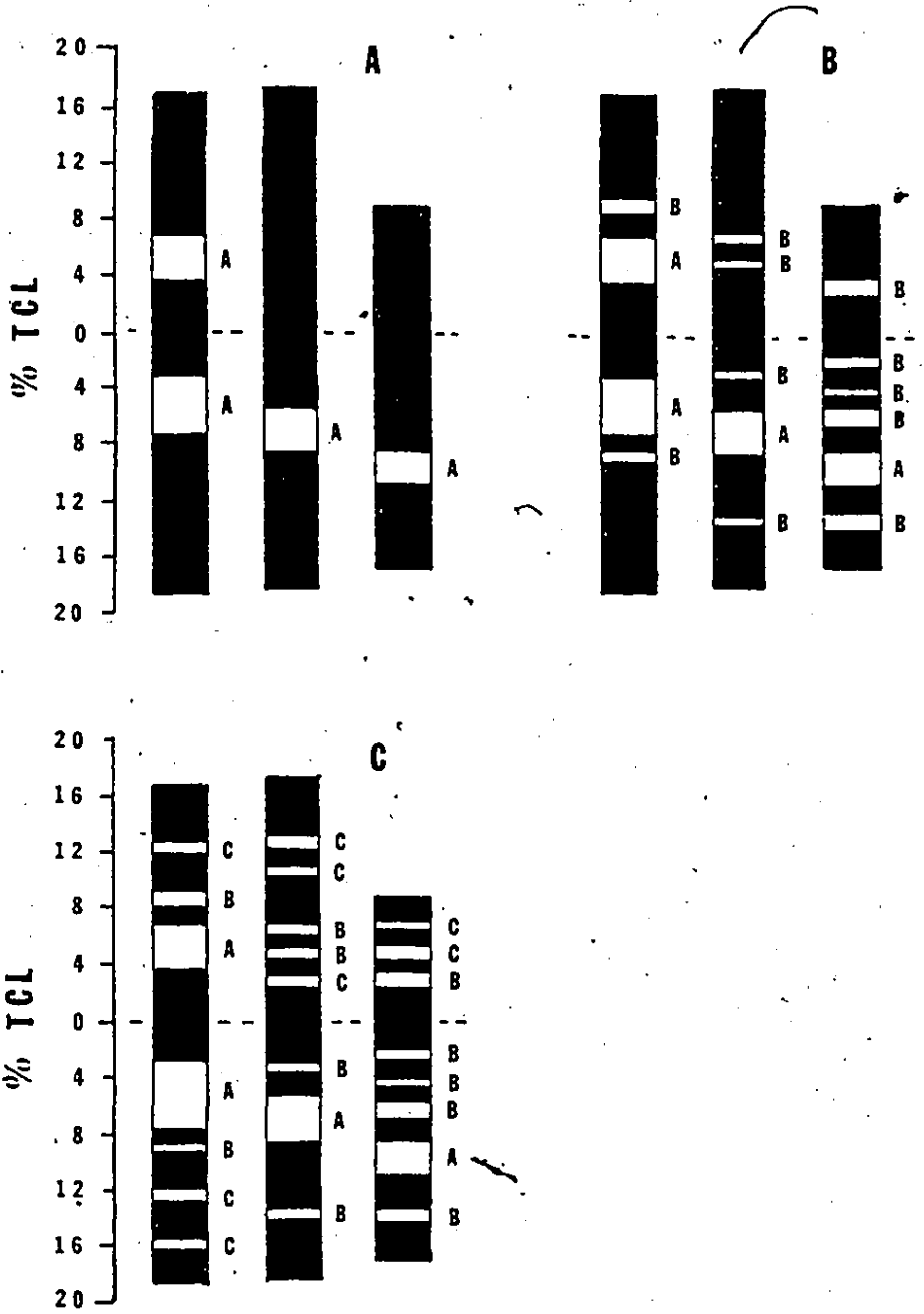
THE EFFECT OF PRINTING EXPOSURE TIMES ON THE RESOLUTION OF HY-BANDS

Figure 16



Prometaphase of Impatiens leschenaultii printed at three different exposure times at an aperature setting of f 4.0. Figure A, 12 seconds; Fig. B, 6 seconds; and Fig. C, 3 seconds. Magnification X 1245.

Figure 17



Banded idiograms corresponding to photographs in Fig. 16. Letters A, B, and C correspond to photograph in which band first appeared.

Figure 17 is the corresponding idiogram of the chromosomes drawn to scale as a percentage of the total complement length (TCL) by the technique described earlier, that is:

1. Fig. 17A = idiogram illustrating the Hy-bands seen in photograph 16A.
2. Fig. 17B, the same of Fig. 16B;
3. Fig. 17C, the same of Fig. 16C.

The letters adjacent to each band correspond to the photographic figure in which the particular band was first observed (i.e. A = Fig. 16A, B = Fig. 16B, and C = Fig. 16C). At the longest exposure time (12 seconds) only the largest heterochromatic blocks are visible (Figs. 16A and 17A). At six seconds, narrow bands were first visible, and at three seconds additional heterochromatic bands could be distinguished from the adjacent euchromatic blocks, but these were not narrower than those resolved at six seconds. With exposure times less than three seconds no additional bands were noted.

This recent discovery should facilitate greatly the analysis of Hy-banding. Naturally, the printing times will have to be determined for each photograph independently. Furthermore, having subsequently examined a number of negatives of banded chromosomes, it is evident that even in a single frame, the ideal exposure time will not be the same for all chromosomes. Despite these complications, it is obvious that the usefulness of Hy-banding in cytotaxonomic studies can be enhanced by this technique.

Diakinesis

Very few cells were observed at this stage and it is postulated that it is extremely short in duration. Consequently, there was little opportunity to search for multivalent formation. Figure 18 shows representative samples of diakinesis in a number of species of Impatiens. In general, bivalent formation occurred. Possible exceptions are illustrated for I. cuspidata W.& A. and I. flaccida Arn.

Chromosome Aberrations

Endopolyploidy: This phenomenon has not been reported previously in Impatiens. It was observed in somatic tissue (root meristems) of three species (Table 6):

1. I. balsamina L. var. rosea Hk.f., 2n = 14, 28 (2x, 4x), in only one population. The aberrant chromosome numbers have persisted for three years in plants grown in the greenhouse.
2. I. cuspidata W.& A., 2n = 14, ~ 42, ~ 56, and ~ 98 (2x, 6x, 8x, 14x). These are illustrated in Fig. 19.
3. I. oppositifolia L., 2n = 16, 32 (2x, 4x). Tetraploid cells are illustrated in Fig. 19.

The aberrant tissues were always mixoploid. In the two species (I. balsamina L., I. cuspidata W.& A.) in which it was possible to study microsporogenesis, there was no evidence of endopolyploidy in the pollen mother cells.

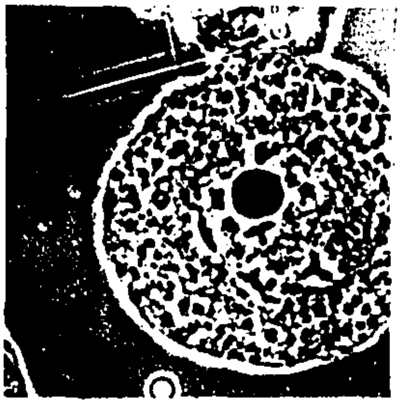
Other somatic anomalies: A ring chromosome was occasionally seen in I. flaccida var. alba. No significance in evolutionary terms is attached to this phenomenon unless such a chromosome should become lost (Swanson, 1957).

Meiotic abnormalities: A number of aberrations were observed in

Figure 18

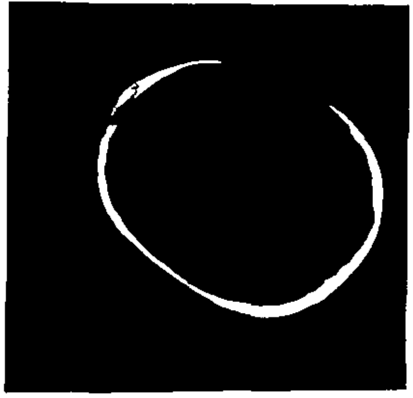
DIAKINESIS

I. cuspidata, X 925

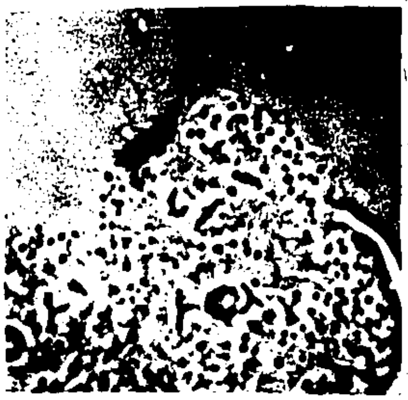


I. cuspidata, X 750

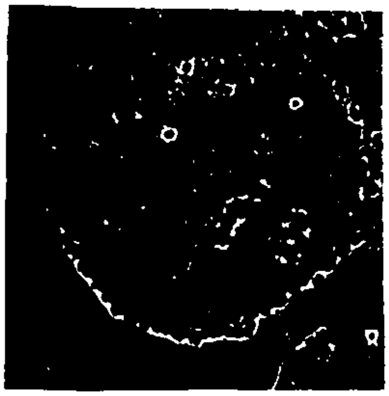
I. cuspidata, X 675



I. cuspidata, X 940



I. cuspidata, X 915

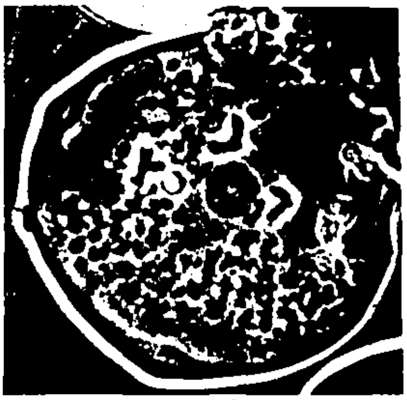


I. cuspidata, X 560

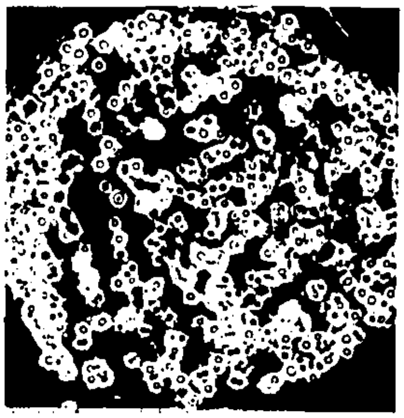
I. flaccida var.
flaccida, X 1135

I. flaccida var.
alba, X 1208

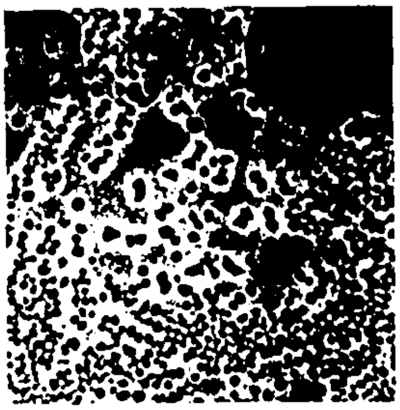
I. leschenaultii, X 1050



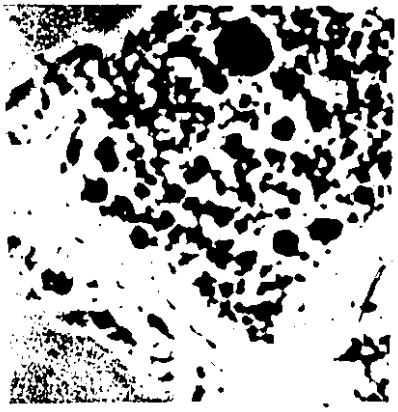
I. leschenaultii, X 895



I. niamniamensis, X 665



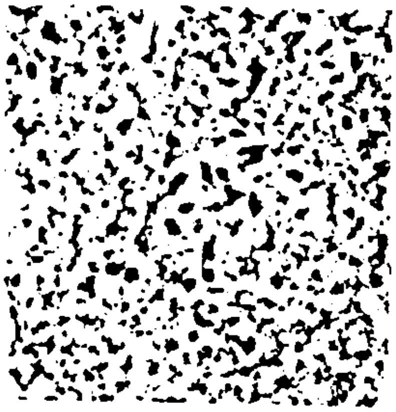
I. niamniamensis, X 785



I. *parasitica*, X 1170

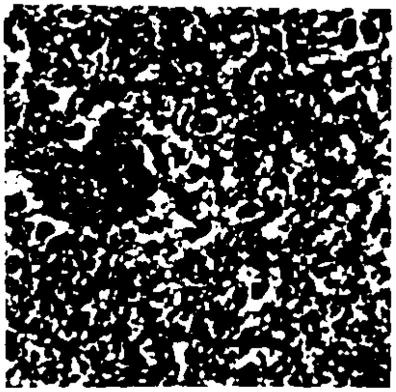
I. *parasitica*, X 796

I. *parasitica*, X 1295



I. *repens*, X 885

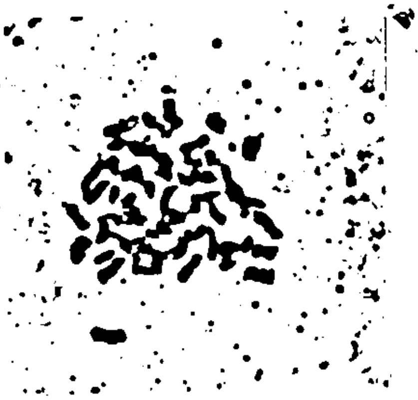
I. *repens*, X 1050



I. *repens*, X 975

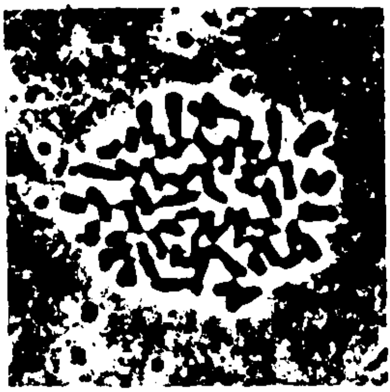
Figure 19

ENDOPOLYPLOIDY



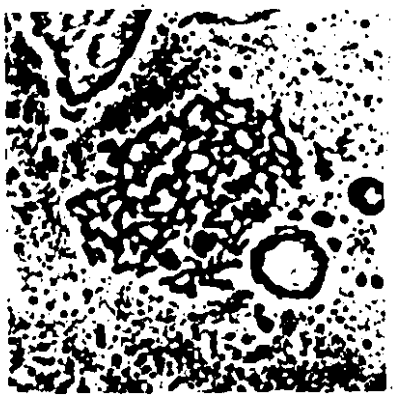
I. cuspidata,
2n = 6x = ca. 42
X 1290

I. oppositifolia,
2n = 4x = ca. 32
X 1210

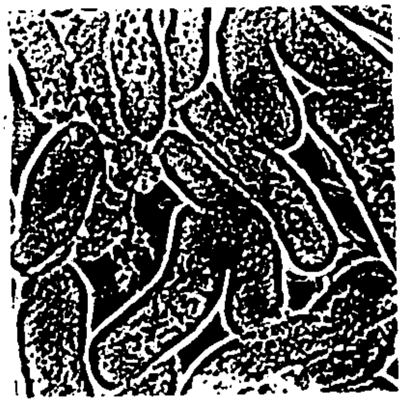


I. cuspidata,
2n = 8x = ca. 56
X1260

I. oppositifolia,
2n = 4x = ca. 32
X1200



I. cuspidata,
2n = 14x = ca. 98
X1340



I. oppositifolia,
2n = 4x = ca. 32
X 465

gametogenesis (examples are illustrated in Fig. 20). These included lagging chromosomes, bridges, secondary associations, micronuclei, additional cells at the quartet stage, and pollen grains varying in size. This last phenomenon was of particular interest because it was noted in all species in which pollen was examined. Furthermore, micropollen stained as consistently with cotton blue as did the large grains, suggesting that the former are not sterile.

DISCUSSION

Chromocenters

Chromocenters were observed in all species of *Impatiens* studied. Thus the observations of Heitz (1926) and Smith (1934) that chromocenters are absent in *I. sultani* Hk.f. and *I. holstii* Warb.& Eng. (= *I. walleriana* Hk.f.) were not confirmed. Since chromocenters are more prominent in some preparations than others, it is hypothesized that some physiological or technical factors caused the chromocenters in their preparations to lack clarity.

No correlation was found between chromosome number and number of chromocenters although, in both mitotic and meiotic material, it was found that there are more chromocenters than chromosomes. The two only could be expected to coincide if each chromosome contained a single block of heterochromatin. On the contrary, as the present study has shown, heterochromatin is both centromeric and intercalary in *Impatiens* (Fig. 15). This confirms and extends Bhattacharjya's (1954) observations on heterochromatin in *I. balsamina* L.

The anomalous structure of chromocenters in the last interphase preceeding meiosis as reported in *I. balsamina* by Chauhan and Abel

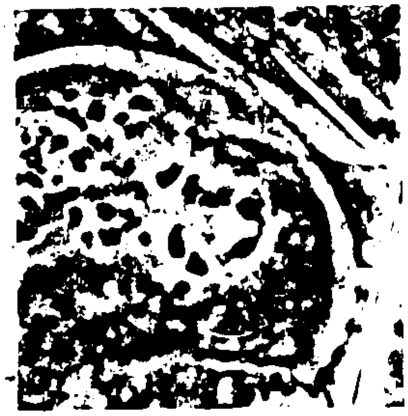
Figure 20

ABERRATIONS IN MICROSPOROGENESIS

I. pulcherrima
Bridge, Telophase I

I. viscida
Bridge, Telophase I

I. cuspidata
Lagging chromosomes, AI



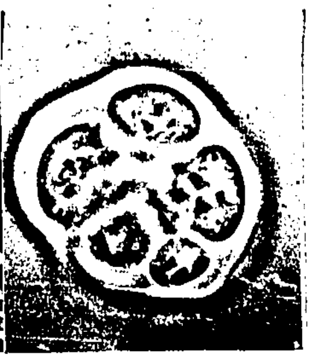
I. flaccida
2 chromosomes connected,
MII

I. pulcherrima
Bridge, Telophase II

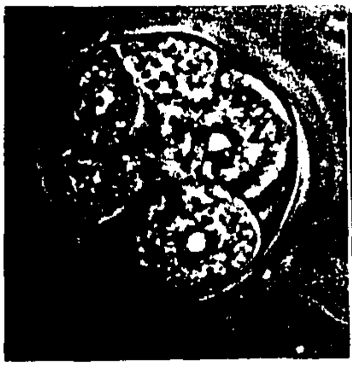
I. pulcherrima
Lagging chromosomes, TII

I. coelopteris
Quartet, 6 nuclei

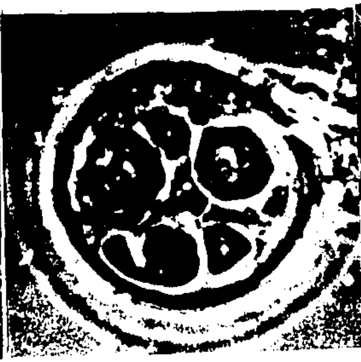
I. flaccida
Quartet, micronuclei



I. leschenaultii
Quartet, 5 nuclei



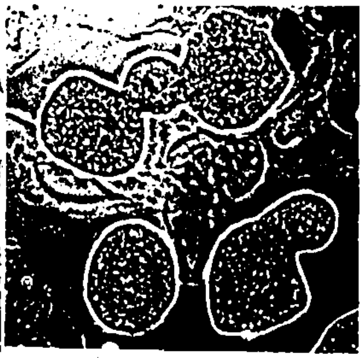
I. platypetala
Quartet, 5 nuclei



I. sodeni
Quartet, micronuclei

I. sodeni
Quartet, 2 micronuclei

I.cuspidata
Quartet, micronuclei



I. cuspidata
Quartet, micronuclei

I. flaccida
Quartet, 5 nucleoli

(1968) was confirmed, but no unequivocal evidence of paired chromocenters was observed. Their camera lucida drawing is not entirely convincing. This aspect of chromocenters needs a careful reevaluation probably using material which has not been squashed and with photomicrographs taken on a series of focal planes.

Chromosome Numbers

A wide range of chromosome numbers was observed in the Impatiens species studied. Seven species have their chromosome numbers reported for the first time. The chromosome numbers of $2n = 16$ in I. cinnabarina and I. usambarensis confirms the preponderance of species with $n = 8$ cytotypes in the I. walleriana aggregate. New chromosome counts are reported for five other species. No evidence was found that double-flowered forms are associated with supernumerary chromosomes as was previously reported for I. balsamina (Raghuvanshi and Joshi, 1968).

Original Chromosome Number

Perhaps the most frequent question one is asked concerning the karyology of Impatiens is "What was the primitive basic chromosome number?" In the last two years, I have come to realize that this is a problem which cannot be easily resolved. I have found that Keith Jones (Kew; personal communication) is in agreement with my position, and I believe it is worthwhile discussing the various theories in detail.

It was immediately apparent in reviewing the karyological literature, that all recent cytotaxonomists have ultimately based their assumption that $x = 7$ was the original chromosome number in Impatiens on Warburg's (1938a,b) early very limited data. Actually, Warburg merely suggested that $x = 7$ was possibly the original chromosome number, being the lowest one he had found in his cytological studies on eleven species (actually nine since I. rosea Lindl. = I. balsamina L., and I. sultani Hk.f. = I. holstii Engl.& Warb.). Consequently, he believed it premature to do more than speculate on the subject.

A number of authors in addition to Warburg, have equated the lowest or most frequent chromosome number ipso facto with the oldest number. In the first place there have been too few chromosome number determination in Impatiens (only about 25% of the species) to permit valid statements concerning the mean distribution of chromosome numbers. For example, Jones and Smith (1966) favored $n = 7$ as the original chromosome number in Impatiens, arguing that it was the lowest number in the genus which occurred with any frequency (only two $n = 6$ cytotypes were known). Subsequent research brought to light cytotypes with $n = 3$ (Bhaskar and Razi, 1972-73; Bhaskar, 1975), $n = 4$ (Beck et al., 1974; Arisumi, 1978, 1980a), and $n = 5$ (Gill and Chinnappa, 1977), as well as a number of additional species with $n = 6$ (Raghuvanshi and Joshi, 1968; Shimizu, 1971; Bhaskar and Razi, 1972-73, 1974; Bhaskar, 1975, 1976, 1980). It also has become evident that in addition to $n = 7$ cytotypes, $n = 8$, and $n = 10$ cytotypes are frequent and widespread in Impatiens. In the second place, it is by no means certain that either low or frequent chromosome numbers per se are indicative of primitiveness. For example, it has been found in Crepis (Babcock et al., 1942; Tobgy, 1943; Sherman, 1946; Babcock, 1947) and Clarkia (Lewis, 1958) that the species which are the most morphologically and ecologically primitive are not those with either the lowest or most frequent chromosome number.' Numerous other examples of reduction in chromosome number in the course of evolution are reviewed by Raven (1975). Obviously, the most reliable index of original chromosome number would be the number(s) associated with the most primitive Balsaminacae. As was earlier discussed, these primitive species may have included the following features: A regular perianth with five sepals one of which was modified into a nectary, five free and relatively equal petals, absence of resupination, probably an androecium with some degree of connation, and 3-colpate pollen. If this hypothesis is true, then the highly zygomorphic *I. leschenaultii* Wall. *n* = 3 and *I. assurgens* Bak.(*n* = 5) are relatively advanced and are probably examples of chromosome reduction. No extant species combine all these hypothetical primitive features. Those which appear to be relatively primitive are the actinomorphic, psychophilous species. The chromosome numbers which have been reported for this group of taxa are given in Table 9. As can be seen, these are based on *n* = 4, *n* = 7 and *n* = 8. It should be emphasized that within this group considerable evolution may have taken place and that only 30% of the species have had their chromosome numbers determined. It should be noted that the *n* = 7 species enumerated here do not include any of the *n* = 7 Himalayan taxa which Khoshoo (1957) and Jones and Smith (1966) postulated were primitive and which on morphological grounds appear to be relatively advanced groups. There is no reason, at present, to believe that there is any direct ancestor-descendant relationship between species with *n* = 7 cytotypes in Africa and southern Asia on the one hand, and those of the Himalayas on the other. Considering the degree of aneuploidy within the various groups, it is likely that these are examples of parallel evolution.

Among the species listed in Table 9, the higher numbers are obviously polyploid, leaving two hypotheses as to the original chromosome number:

1. $\underline{x} = 4$, with $\underline{n} = 7$ and $\underline{n} = 8$ being tetraploids (Beck et al., 1974).
2. $\underline{x} = 7$ or 8, with $\underline{n} = 4$ being a reduction in chromosome number. Although the presence of a primitive cytotype in Indonesia is very difficult to reconcile with the evidence for the origin of Impatiens in Gondwanaland, it is not grounds for dismissing it. More suggestive is the report by Arisumi (1980a) of reduced fertility in this species. Obviously, the problem can only be resolved by a careful study.

With respect to the primitive basic chromosome number, one also must consider Hydrocera triflora (L.) W.& A. which alone among the Balsaminaceae is reported to have free petals. The gametic chromosome number is $\underline{n} = 8$ (Darlington and Wylie, 1955) and this led Raven (1975) to suggest that $\underline{n} = 8$ was the original chromosome number of the family. While Hydrocera apparently has some primitive characters, in other ways it appears quite advanced (as is discussed in the final chapter), and may represent a case of heterobathmy or reversal. This taxon needs further study to clarify its evolutionary position.

Thus it is evident that there is no one species or group of

Table 9

Chromosome numbers which have been reported in species of *Impatiens* with relatively actinomorphic corollas

Species	Chromosome number	
	n	2*n*
African		
1. *I. cinnabarina*	8	16
2. *I. hamata*	7	–
3. *I. pseudoviola*	8	16
4. *I. sodenii*	8	16
5. *I. walleriana*	8,10	16
Asian		
1. *I. flaccida*	7	14
2. *I. gardneriana*	8	16
3. *I. hawkeri*	24	48
4. *I. henslowiana*	8	16
5. *I. herzogii*	–	32
6. *I. linearifolia*	–	32
7. *I. mooreana*	32	66
8. *I. platypetala*		
var. *platypetala*	7	14
var. *aurentica*	4,7	8
var. *nematoceras*	8	16
9. *I. pulcherrima*	6	12
10. *I. schlecteri*	–	32

species in the Balsaminaceae which can be described as truly primitive. This is not really surprising in a taxon which had already undergone major diversification before the break up of Gondwanaland 100 m. y. B. P. (Raven and Axelrod, 1974). Consequently, there is no reason to assume that the original chromosome number of the Balsaminaceae can ever be known with certainty. The best one can say is that certain chromosome numbers are associated with the more primitive of the extant taxa.

A Note on n = 7 and n = 10 Cytotypes

It has been suggested (Khoshoo, 1957; Jones and Smith, 1966) that the ancestors of the temperate Impatiens were Western Himalayan species (where all the species for which chromosome numbers are available have $n = 7$ or $n = 10$ cytotypes.) All the autochthonous species in the temperate zone have a gametic chromosome number of $n = 10$ except for two tetraploid ($2n = 40$) populations of I. noli-tangere L. (Skalinska et al., 1959). Furthermore, I. glandulifera Royle, an introduced species into this region from the Himalayas, is thought to have had a primitive cytotype of $n = 10$. A second successful introduction, I. parviflora DC., is known to have gametic numbers of $n = 10$, 12, and 13 (Appendix 1), and so may be based on $x = 10$. After collecting Impatiens in both the tropics and the temperate zone, I noticed that in southern Asia, the annual species have a growth cycle which coincides with the monsoon; whereas in contrast, the temperate species germinate immediately following spring thaw. Since according to Mani (1974) the Himalayas experience both a winter with snow (until early April) and a monsoon season (beginning in August), it was thought that perhaps the species with n = 10 cytotypes have some seed germination cue which is associated with spring thaw, while the n = 7 cytotypes have a dormancy breaking factor associated with the onset of the monsoon, and consequently the latter could not successfully colonize the temperate zone in the absence of a monsoonal climate. This hypothesis could not be tested experimentally because of the difficulty of recreating a complete climatological scenerio under artificial circumstances. A review of the literature led to the discovery that all ten species known to occur in Kashmir had their chromosome numbers determined, but, of course, no germination data were available. Eventually, it was found that Blatter (1927) gives the flowering period, and this was used as a relative index of germination date. The species were then arranged from earliest to latest to coincide with the initiation of flowering (Table 10). As can be seen, the species with n = 7 cytotypes are both the earliest and latest to begin blooming, and so in Kashmir are not associated exclusively with the onset of the monsoon.

This exercise had one interesting outcome. By looking at these species carefully it became evident that while they bear some morphological similarity to the temperate species, they may not be as closely related as the hypothesis at the beginning of this section suggested. Further studies now suggest that it is likely that the ancestors of the temperate species originated in eastern Asia.

KARYOLOGY

Satellites

Satellites were not seen in every metaphase plate, but in four

Table 10

Comparison of flowering period and chromosome numbers of *Impatiens* species in extreme west of the Himalayas

Species	Flowering period[1]					Chromosome number (n)
	M	J	J	A	S	
1. *I. brachycentra* Kar. & Kir.	—	—	—			7
2. *I. balfourii* Hk.f.		—				7
3. *I. sulcata* Wall.		—				10
4. *I. thomsoni* Hk.f.		—	—			7
5. *I. glandulifera* Royle		—	—	—		10
6. *I. amplexicaulis* Edgew.			—			10
7. *I. edgeworthii* Hk.f.			—			5,6,7
8. *I. scabrida* DC.			—	—		7
9. *I. balsamina* L.				—		7
10. *I. amphorata* Edgew.					—	7

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[1] Based on Blatter (1927); species arranged from earliest to latest initiation of flowering.

species there was no evidence of their presence whatsoever. There is a knob-like structure on chromosome 2 in I. leschenaultii Wall. (Fig. 16), but no evidence of satellites was found in metaphases (Fig. 5 and Fig. 9). Based on an analysis of the idiograms, the satellites are not always found on the same chromosome. For example, in the species of the I. walleriana aggregate which Grey-Wilson (1980g) considers a group of closely related taxa, one species had no satellites (I. walleriana Hk.f.), one had a satellite on chromosome 3 (I. cinnabarina Grey-Wilson) and two had a satellite on chromosome 7 (I. sodeni Eng.& Warb. and I. usambarensis Grey-Wilson). Now according to Grey-Wilson (1980g), I. cinnabarina, I. usambarensis and I. walleriana are very closely related. Having examined all these species myself, I find no evidence that his treatment is wrong, and I cannot see that I. usambarensis is more closely related to I. sodeni than to the other two species. An attempt to match up the satellite chromosomes of the various species was unsuccessful. In I. cinnabarina and I. usambarensis, the short arms of chromosomes 3 and 7 respectively (which are those with the satellites) match up suggesting that these arms are perhaps homologous. On the other hand, the long arm of chromosome 7 in I. usambarensis is considerably shorter than the long arm of chromosome 3 in I. cinnabarina. If the satellite chromosomes are homeologous, it is impossible to say whether this is the result of a translocation, duplication or deletion. This again underlines the importance that banded karyotypes must play in cytoevolutionary studies of Impatiens.

General Morphology

In the ten species for which sufficient material was available for karyotype analyses, the following observations were made:

1. Chromosomes ranged from metacentric to acrocentric and this confirms, in general, previous reports (Khoshoo, 1957; Chatterjee and Sharma, 1970) and suggests that karyotypes can be used as a taxonomic character.
2. Some karyotypic evidence was found to support various taxonomic treatments:
   a. The species of the _I._ _walleriana_ aggregate have somewhat similar karyotypes supporting Grey-Wilson (1980g).
   b. _I._ _cuspidata_ and _I._ _flaccida_ also have somewhat similar chromosomes supporting Hooker (1874-75).
   c. _I._ _cuspidata_ and _I._ _leschenaultii_ karyotypes are very dissimilar. It is very difficult to find any evidence in living or herbarium specimens for the affinity of these two species as was postulated by Bhaskar (1975) whose conclusions may well have been based on a misinterpretation of the text in Hooker (1874-75).
3. TCLs varied greatly between the species for which data were available. No correlation was found between chromosome number and TCL values. Of particular interest was the finding that in the _n_ = 8 species of the _I._ _walleriana_ aggregate there was a considerable range in TCLs (53.34 μm to 111.98 μm) which suggests that in addition to aneuploidy

and euploidy as reported by earlier authors, cryptopolyploidy has been a factor in the cytoevolution of Impatiens. This phenomenon is not evident from mere chromosome number determinations, and so emphasizes the importance of karyotype analysis.

Banded Karyotypes

Hy-bands were observed in a number of Impatiens species. Hy-bands have been reported in several angiosperm genera, but not in Impatiens. In one species, I. leschenaultii Wall., each pair of homologues showed a distinct banding pattern. In other species it was observed that certain homologues of the complement could readily be matched on the basis of their banding pattern.

At present the results are not wholly consistant. There are several factors to consider. In the first place a greater control of the growing conditions previous to fixation may result in more consistant results. Secondly, rather than emphasizing exact matching of bands for all the plants of a single species as was attempted in this study, an effort should be made, at least initially, to identify certain very distinct chromosomes and map their distribution. Examples of such "marker" chromosomes are chromosome 2 in I. leschenaultii Wall. (Fig. 16) and the small dumbell-shaped chromosome indicated in Fig. 14 which was observed in a number of African taxa, but not the Asian species. A third such chromosome with one heterochromatic arm and one euchromatic arm was observed in I. balsamina L., I. repens Moon and a number of Asian taxa. Such an approach may prove to be more valuable cytotaxonomically than detailed mapping of all bands which severely limits the number of species which can be studied.

Karyology as a Basis for Affinities

Two comparative studies have been carried out on the karyology of families purportedly belonging to the Geraniales (Warburg, 1938a,b; Chatterjee and Sharma, 1970). The first of these has been extensively cited as a basis for treating the Balsaminaceae as a geranialian taxon. In the first place, Warburg reached no such conclusion, but proposed instead that two hypotheses were possible:

1. The Geraniales of Hutchinson (1926) were a natural group which included the Limnanthaceae, Balsaminaceae, Geraniaceae, Oxalidaceae, Tropaeolaceae, Linaceae, and Zygophyllaceae. In that case, based on chromosome numbers *per se*, *Limanthus* (x = 5) was the oldest genus perhaps followed by *Impatiens* (x = 7?).
2. The Limnanthaceae and Balsaminaceae did not belong in the Geraniales at all, and rightly should be placed in the Sapindales as Engler had done.

Secondly, a major objection to these studies carried out on the cytotaxonomic affinities of the Balsaminaceae involves their exclusive reliance on in-group comparisons. Both Warburg (1938a,b) and Chatterjee and Sharma (1970) studied only those families assigned to the Geraniales by Hutchinson (1926). As a consequence, they have no real basis on which to judge the cytological closeness of these taxa.

Finally, the criteria on which they based their conclusions are the following:

1. The Balsaminaceae differs from the core families of the Geraniales in having better marked constrictions and incomplete terminalization of the chromosomes in meiotic metaphase (Warburg, 1938a,b).
2. The Geraniales (excepting _Averrhoa_ L.) is a natural cytotaxonomic group on the basis of both inter- and intraspecific aneuploidy and euploidy, and the presence of acrocentric, metacentric, and submetacentric chromosomes.

The criteria as spelled out are sufficient commentary on the value of any conclusions which were reached on the basis of these studies. On the other hand, they do lead one to consider an important point. Given the enormous amount of karyotypic evolution which is found even within a genus (Stebbins, 1971) what is the value of cytotaxonomic studies at higher levels? In our present state of knowledge, I find it difficult to envision what cytological characters could possibly serve as markers for delimiting families and orders.

Chromosome Aberrations

Endopolyploidy: Mixoploid somatic tissue was observed in three species: _I. balsamina_ L., _I. cuspidata_ W.& A., and _I. oppositifolia_ L. This has not been previously reported in _Impatiens_. No evidence was found of polyploid pollen mother cells. It is evident that mixoploidy is often found in root meristems, and in most cases has no evolutionary significance.

Meiotic abnormalities: Lagging chromosomes, bridges, secondary associations, micronuclei, and additional cells at the quartet stage were observed. Of particular interest were pollen grains which distinctly varied in size and were found in all the species in which the pollen was studied. There was no evidence that the small grains are sterile since they stained as consistently with cotton blue as did the large grains. It is not possible at present to conclude whether this observation indicates that pollen dimorphism occurs in the genus.

Since in many species of Impatiens the very sculptured exine interferes with chromosome number determinations in the generative nucleus, it is proposed that Feulgen's cytophotometry may be of assistance in determining (albeit indirectly) whether the small grains contain fewer chromosomes than the normal haploid complement. More extensive germination tests (preliminary ones indicated that micropollen grains do germinate) would be useful. Such observations may facilitate understanding aneuploidy and dysploidy in Impatiens.

APPENDIX 1

Chromosome Numbers Reported in the Literature for *Impatiens* species

Species	Region	n	2n	Reference
* *I. acaulis* Arn. var. *acaulis*	D	8,10,16		Bhaskar & Razi, 1974
		10		Bhaskar, 1975, 1976, 1980
* *I. acaulis* Arn. var. *granulata* Bhask.	D	9,10		Bhaskar & Razi, 1972-73
		8,9		Bhaskar, 1975, 1980
* *I. acmanthera* Hk. f.	EH	8,9,10	18,20	Chatterjee & Sharma, 1970
I. agumbeyana Bhask.	D	8		Bhaskar, 1975, 1976, 1980
I. aliciae Fisch. var. *bababudensis* Bhask.	D	8		Bhaskar, 1975, 1976
I. amphorata Edgew.	WH	7		Khoshoo, 1955, 1966; Lee, 1967
		7	14	Khoshoo, 1957
			14	Wulff (T. 1935, 36); Warburg, 1938a,b

Table cont'd.

Species	Region	n	2n	Reference
I. amplexicaulis Edgew.	WH	10		Khoshoo, 1955, 1957, 1966; Lee, 1967
* *I. arguta* HK.f. & T.	EH	6,9	12	Chatterjee & Sharma, 1970
I. assurgens Bak.	A	5		Gill & Chinnappa, 1977
I. auricoma Baill.	CI		16	Arisumi, 1980 a
I. balfourii Hk.f.	WH		14	Wulff, 1937
		7		Khoshoo, 1955, 1957, 1966; Vazart, 1958; Lee, 1967
	WNA			Chinnappa & Gill, 1974
* *I. balsamina* L.	C	7		Kanna, 1926
			14	Kakhidze (in Tischler, 1927)
			14	Heitz, 1929

Table cont'd.

Species	Region	n	2n	Reference
* I. balsamina L. (cont'd)			14	Souza-Violante, 1929
			14	Margadant (in Tischler, 1931)
			14	Gregoire, 1932
			14	Yung, 1932
			14	Doutreligne, 1933
			14	Kanna, 1934, 1935
			14	Smith, 1934
			14	Nakamura, 1935, 1936
			14	Schaede, 1935
			14	Heitz, E. and Resende, 1936
			14	Yamaha and Seumatsu, 1936
		7	14	Warburg, 1938a,b
		7	14	Raghavan *et al.*, 1939
			14	Delay, 1947
			14	Hoevermann, 1951
			14	Bhattacharjya 1954, 1958

Table cont'd.

Species	Region	n	2n	Reference
* I. balsamina (cont'd.)		7	14	Khoshoo, 1957
			14	Vazart, 1957
		7	14	Lee, 1967
			14	Chauhan & Abel, 1968
		6,7,8	14,14 + 28	Raghuvanshi & Joshi, 1968
			14,16	Chatterjee & Sharma, 1970
		7		Chinnappa & Gill, 1974
		7		Terasaka & Tanaka, 1974
		7		Gill & Chinnappa, 1977
			14	Arisumi, 1980a
			21	Smith, 1938
I. balsamina L. (WT)	WH	7,11,12,13,14		Khoshoo, 1955,1966
	D		14	Rao, 1972
	D	7	14	Bhaskar & Razi, 1972-73
	WH		14	Koul & Gohil, 1973

Table cont'd.

Species	Region	n	2n	Reference
I. balsamina L. var. arcuata Hk.f.	D	7	14	Bhaskar, 1975
I. balsamina L. var. azaleiflora	C		14	Rao, 1973a
I. balsamina L. var. camelliflora	C		14	Rao, 1973a
I. balsamina L. var. coccinea Hk.f.	D		14	Rao, 1973a
		7	14	Bhaskar, 1975
I. balsamina L. var. vulgaris	D		14	Rao, 1973a
I. barberi Hk.f.	D	8		Bhaskar & Razi, 1974; Bhaskar, 1975, 1976, 1980
I. beddomei Hk.f.	D	8		Bhaskar & Razi, 1972-73; Bhaskar, 1975

Table cont'd.

Species	Region	*n*	2*n*	Reference
I. bella Hk.f. & T.	WH	7		Khoshoo, 1966; Lee, 1967
I. bicornuta Wall.	WH	8		Malla *et al.*, 1978
I. biflora Nutt. = *I. capensis* Meerb.				
I. brachycentra Kar. & Kir.	WH	7		Khoshoo, 1955, 1956, 1957, 1966; Lee, 1967
	WH		14	Koul & Gohil, 1973
I. burtonii Hk.f.	A	8	16	Jones & Smith, 1966
			20	Rao, 1973b[1]
* *I. campanulata* Wt.	D	10	20	Jones & Smith, 1966
		10		Bhaskar, 1975
			18	Arisumi, 1980a,b

Table cont'd.

Species	Region	n	2n	Reference
* I. campanulata Wt. (cont'd.)			20	Rao, 1973b
I. canariensis[2] Arn. = I. hookeriana				
I. capensis Meerb.	ENA, WNA		20	Smith, 1934
		10	20	Chinnappa & Gill, 1974
		10		De Lisle, 1965; Lee, 1967
		10		Khoshoo, 1955, 1957, 1966
			20	Russell, 1976
		10		Bostick, 1965
			14	Wulff, 1936[3]
I. capensis Thunb. = I. hochstetteri Warb.				
I. chiangdaoensis T. Shimizu	SEA	6	12	Shimizu, 1971
I. chinensis L.	D	8	16	Bhaskar & Razi, 1972-73; Bhaskar,1975
			16	Rao, 1972

Table cont'd.

Species	Region	n	2n	Reference
I. chinensis L. var. brevicornis Barnes	D	8		Bhaskar & Razi, 1972-73
		8	16	Bhaskar, 1975
I. chinensis L. var. intermedia Bhask.	D	8		Bhaskar & Razi, 1972-73
		8	16	Bhaskar, 1975
I. chinensis var. intermedia X I. tomentosa Heyne	D	8		Bhaskar, 1975
* I. clavicornu Turcz.	D		14	Rao, 1972
		8		Bhaskar, 1980
I. congolensis Schulze et Wilczek	A		48	Arisumi, 1980a,b
I. congolensis var. longicalcarata Schulze & Wilczek	A	24	48	Jones & Smith, 1966

Table cont'd.

Species	Region	n	2n	Reference
* I. *cordata* Wt.	D	10		Bhaskar & Razi, 1972-73; Bhaskar, 1975, 1976
		20		Rao, 1973b
I. *cuspidata* W.& A.	D	7	14	Bhaskar & Razi, 1972-73; Bhaskar, 1975
			14	Rao, 1973b
I. *dendricola* Fisch.	D	7		Bhaskar, 1976, 1980
I. *digitata* Warb.	A	10		Gill & Chinnappa, 1977
I. *diversifolia* Wall.	D	8		Bhaskar & Razi, 1972-73; Bhaskar, 1975
I. *drepanophora* Hk.f.	EH	10		Krusheva, 1975
		10		Sarkar *et al*., 1975

Table cont'd.

Species	Region	n	2n	Reference
I. ecalcarata Blank.	WNA	10		Chinnappa & Gill, 1974
* I. edgeworthii Hk.f.	WH	6		Khoshoo, 1956, 1966; Baquar & Abid Askari, 1970; Lee, 1967
		5,6,7	12	Khoshoo, 1955, 1957
I. epiphytica G.M. Schulze = I. keilli Gilg				
I. fimbriata Hk.f.	EH	8		Chatterjee & Sharma, 1970
I. firmula Bak.	M		14	Wulff (T. 1935,36); Heitz & Resende, 1936
I. flaccida Arn.	D,S,Mt	7		Bhaskar & Razi, 1972-73; Bhaskar, 1975; Sokolovskaya, 1966
		7	14	Jones & Smith, 1966
			14	Rao, 1973b

Table cont'd.

Species	Region	*n*	2*n*	Reference
I. flaccida var. *alba*	C		14	Arisumi, 1980a
* *I. fruticosa* DC.	D		16	Rao, 1973b
		10		Bhaskar, 1975
		10	20	Krishnaswami *et al.*, 1969
I. furcillata Hemsley			20	Sokolovskaya, 1966
I. gardneriana Wt.	D	8	16	Bhaskar & Raz[illegible] 1972-73; Bhaskar, 1975
* *I. glandulifera* Royle	WH	10		Khoshoo, 1955
		10	20	Khoshoo, 1957
	NTZ	9,10		Jones & Smith, 1966
		9	18	Smith, 1934
			18	Valentine, 1971
			18	Javurkova, 1979

Table cont'd.

Species	Region	n	2n	Reference
* I. glandulifera Royle (cont'd)			18	Majovsky et al., 1974
			18	Jackson (Darlington & Wylie, 1955)
			18	Steffen, 1951
		10		Chinnappa & Gill, 1974
		10		Lee, 1967
			20	Warburg, 1938b
* I. goughii Wt.	D	10		Bhaskar & Razi, 1972-73, 1974
		10		Bhaskar, 1975, 1976
		10		Jayarama Reddy, 1941
			16	Rao, 1973b
I. grandis Heyne	D		20	Rao, 1973b
		20		Bhaskar, 1975, 1976
I. hamata Warb.	A	7		Gill & Chinnappa, 1977

Table cont'd.

Species	Region	n	2n	Reference
I. hawkeri Bull (*sensu stricto*)	NG	24	48	Jones & Smith, 1966
I. henslowiana Arn.	D	8	16	Krishnaswami *et al.*, 1969
		8		Bhaskar, 1975,1976
I. herbicola Hk.f.	D	7		Bhaskar, 1975, 1976
I. herzogii K. Schum.	NG		32	Arisumi, 1978a, 1980a
I. hochstetteri Warb.	A		16	Jones & Smith, 1966
		7		Heitz (in Darlington & Wylie, 1955)
I. holstii Engl. & Warb. = *I. walleriana* Hk.f.				
* *I. hookeriana* Arn.	D,S		40	Jones & Smith, 1966
		10	20	Bhaskar & Razi, 1972-73; Bhaskar, 1975

Table cont'd.

Species	Region	n	2n	Reference
* I. hookeriana Arn. (cont'd.)	D,S		36	Arisumi, 1980 a,b
			16	Rao, 1972
I. insignis DC.	D		18	Chatterjee & Sharma, 1970
* I. keilli Gilg	A	7		Gill & Chinnappa, 1977
			16	Arisumi, 1980 a
I. kilimanjari Oliv.	A	13		Gill & Chinnappa, 1977
I. kleinii W.& A.	D	8		Bhaskar & Razi, 1972-73; Bhaskar, 1975
I. lawii Hk.f. & T.		8		Bhaskar & Razi, 1974; Bhaskar, 1975
I. lawsonii Hk.f.	D	10		Bhaskar, 1975, 1976, 1980

Table cont'd.

Species	Region	n	2n	Reference
I. lenta Hk.f.	D	8		Bhaskar, 1976
I. leptoceras DC.	EH		18	Chatterjee & Sharma, 1970
* I. leschenaultii Wall.	D	3	6	Bhaskar & Razi, 1972-73; Bhaskar, 1975
			6	Rao, 1972
		7	14	Krishnaswami et al., 1969
I. levingei Hk.f.	D		16	Rao, 1973b
I. ligulata Bedd.	D	8		Bhaskar & Razi, 1974
I. linearifolia Warb.	NG		32	Arisumi, 1973a, 1975, 1978a,b
I. lucida Heyne	D	7		Bhaskar, 1975

Table cont'd.

Species	Region	n	2n	Reference
I. maculata Wt.	D	10		Bhaskar & Razi, 1972-73; Bhaskar, 1975, 1976
			20	Rao, 1973b
I. marianae Reichb.	EH[4]		16	Arisumi, 1980a
I. mathildae Chiov.	WH		14	Heitz, 1929
I. mirabilis Hk.f.	SEA	17		Jones & Smith, 1966
* *I. modesta* Wt.	D	8,9		Bhaskar & Razi, 1974; Bhaskar, 1975
		8,9,16		Bhaskar, 1976
		8,9,8+9,16		Bhaskar, 1980
* *I. mooreana* Schltr.	NG	32		Arisumi, 1973a, 1975, 1978a,b, 1980a
			66	Jones & Smith, 1966

Table cont'd.

Species	Region	*n*	2*n*	Reference
I. mysorensis Roth.	D	7		Bhaskar, 1975, 1976
I. niamniamensis Gilg	A	16	32	Jones & Smith, 1966
			32	Arisumi, 1980a,b
* *I. noli-tangere* L.	NTZ		20	Winge, 1925
			20	Tischler, 1931
			20	Packer, 1964
			20	Gadella and Kliphuis, 1966
			20	Rao, 1973b
			20	Majovsky *et al.*, 1973, 1974
		10		Chinnappa & Gill, 1974
		10		Ishikawa, 1960
		10		Laane, [illegible]1
			20,40	Skalinska & Pogan, 1973
			20,40	Skalinska *et al.*, 1959

Table cont'd.

Species	Region	n	2n	Reference
* I. noli-tangere L. (cont'd.)		20		Sokolovskaya, 1963, 1965
I. olivieri C.H. Wright ex W. Watson = I. sodenii Engl. & Warb. ex Engl.				
* I. omissa Hk.f.	D		28	Rao, 1973b
		10		Bhaskar, 1975
* I. oppositifolia L.	D	6,7,8		Bhaskar & Razi, 1972-73; Bhaskar, 1975
I. pallida Nutt.	ENA	10		De Lisle, 1965
		10		Chinnappa & Gill, 1974
		10		Smith, 1934
			20	Russell, 1976

Table cont'd.

Species	Region	n	2n	Reference
* I. pallidiflora Hk.f.	D	13		Bhaskar, 1976; Khoshoo, 1966
			16	Rao, 1973b
* I. parasitica Bedd.	D	9,10		Bhaskar, 1975, 1976
* I. parviflora DC.	NTZ	10,12,13		Khoshoo, 1966
		12		Wulff, 1934a,b
		13		Chinnappa & Gill, 1974; Lee, 1967
			20	Heitz, 1926
			24	Tischler, 1934; Wulff, 1934a,b
			24	Löve & Löve, 1942
			26	Heitz & Resende, 1936
			26	Ehrenberg, 1945
			26	Polya, 1949
			26	Skalinska et al., 1959; Skalinska & Pogan, 1973

Table cont'd.

Species	Region	n	2n	Reference
* I. parviflora (cont'd.)			26	Holub et al., 1971
			26	Majovsky et al., 1973
		10	20	Schurhoff, 1926, 1931
I. parvifolia Bedd.	D	10		Bhaskar, 1975
I. petersiana Rehd. = I. walleriana Hk.f.				
* I. phoenicea Bedd.	D	9,10		Bhaskar, 1975, 1976
* I. platypetala Lindl.	I	7		Lee, 1967
			16	Beck et al., 1974
			16	Arisumi, 1975, 1978a, 1980a
* I. platypetala Lindl. var. aurentiaca	I	7		Khoshoo, 1955, 1957
		4	8	Arisumi, 1975, 1978a; Beck et al., 1974

Table cont'd.

Species	Region	n	2n	Reference
I. pseudoviola Gilg	A		16	Jones & Smith, 1966; Arisumi, 1980a
I. psychadelphiodes Launert	A		32	Jones & Smith, 1966
I. puberula DC.	EH	14		Malla *et al.*, 1977
I. pusilla Heyne	D	8		Bhaskar, 1976
			16	Rao, 1972
I. pusilla Heyne var. inconspicua Bhask.		8		Bhaskar, 1975, 1976
I. pusilla Heyne X I. aliciae Fisch.		8		Bhaskar, 1975
* I. racemosa DC.	EH	9		Chatterjee & Sharma, 1970
		10		Malla *et al.*, 1977

Table cont'd.

Species	Region	n	2n	Reference
I. radiata Hk.f.	EH	10		Sarkar *et al.*, 1974
I. raziana Bhask.	D	8		Bhaskar, 1975
I. repens Moon	S,D	7	14	Bhaskar & Razi, 1972-73; Bhaskar, 1975
			14	Jones & Smith, 1966; Arisumi, 1980a,b
I. ridleyi Hk.f.	SEA	17	34	Shimizu, 1973
I. roylei Walp. = I. glandulifera Royle				
I. rubromaculata Warb.	A		16	Jones & Smith, 1966
I. salicifolia Hk.f. & T.	EH	8		Chatterjee & Sharma, 1970

Table cont'd

Species	Region	n	2n	Reference
* I. scabrida DC	WH	6,7		Jones & Smith, 1966
		6,7,8		Khoshoo, 1955
		7		Khoshoo, 1957, 1966
		7		Huynh, 1967
		9	18	Chatterjee & Sharma, 1970
			14	Smith, 1934
I. scabriuscula Heyne	D	7		Bhaskar & Razi, 1972-73, Bhaskar, 1975
* I. scapiflora Heyne var. scapiflora	D	6		Bhaskar & Razi, 1974
		6,8,10		Bhaskar, 1976
		8,10		Bhaskar & Razi, 1972-73
		10		Krishnaswami *et al*., 1969
		6,7,8,10		Bhaskar, 1975, 1980

Table cont'd.

Species	Region	n	2n	Reference
I. scapiflora Heyne var. pseudo-acaulis Bhask.	D	10,16,20	10+20, > 20	Bhaskar, 1976, 1980
		10,16		Bhaskar, 1975
		10,16,20		Bhaskar, 1976
I. schlecteri Warb.	NG		32	Jones & Smith, 1966; Arisumi, 1973, 1975, 1978a,b, 1980a
I. serrata Benth.	WH	7		Khoshoo, 1966
I. sodenii Engl. & Warb. ex Engl.	A		16	Wulff, 1933
			16	Rao, 1973b
I. spp.	NG		32	Jones & Smith, 1966
	–		14	Wulff, 1937
	SEA		36 + 2f	Jones & Smith, 1966
	SEA		32	Jones & Smith, 1966
	NG		32	Arisumi, 1978b

Table cont'd.

Species	Region	*n*	2*n*	Reference
I. spp. (cont'd.)	NG		64	Arisumi, 1978a
	I	4		Arisumi, 1978
	I		8	Arisumi, 1980a
I. stenantha Hk.f.	EH	11		Chatterjee & Sharma, 1970
I. stocksii Hk.f.	D	10		Bhaskar & Razi, 1972-73
		7		Bhaskar & Razi, 1974; Bhaskar, 1975, 1980
I. sulcata Wall.	WH	10		Khoshoo, 1955, 1956, 1966
		10	20	Khoshoo, 1957
I. sultani Hk.f. = *I. walleriana* Hk.f.				
I. talbotii Hk.f.	D	6	12	Bhaskar, 1975

Table cont'd.

Species	Region	n	2n	Reference
I. talbotii Hk.f. (cont'd.)		6		Bhaskar, 1976
* I. tenella Heyne	D	8	16	Bhaskar & Razi, 1972-73; Bhaskar, 1975
			14	Rao, 1972
I. textori Miquel	EA		20	Lee, 1967
		10		Ishikawa, 1960
I. thomasetti Hk.f.	Se		16	Arisumi, 1980a
I. thomsoni Hk.f.[5]	WH	7,10		Khoshoo, 1955, 1957, 1966
			14	Koul & Gohil, 1973
* I. tomentosa Heyne	D		16	Rao, 1972
		13		Bhaskar, 1975

Table cont'd.

Species	Region	n	2n	Reference
I. trichocarpa Hk.f.	D	6		Bhaskar & Razi, 1972-73
I. tripetala Roxb.	EH	7		Khoshoo, 1966
		8		Sarkar et al., 1973, 1980
I. tuberifera Humbert	M		16	Arisumi, 1980
			16	Jones & Smith, 1966; Arisumi, 1980a
I. ulugurensis Warb.	A	8		Gill & Chinnappa, 1977
I. umbellata Heyne			20	Rao, 1973b
I. uncinata Wt.	D	8		Bhaskar, 1975, 1976
			14	Rao, 1973b

Table cont'd.

Species	Region	n	2n	Reference
I. verticillata W.	D	8		Bhaskar & Razi, 1972-73; Bhaskar, 1975
			16	Rao, 1973b
I. viscida Wt.	D	8	16	Krishnaswami et al., 1969
		8		Bhaskar, 1975
			16	Rao, 1972
I. viscosa Bedd.	D	10		Jayarama Reddy, 1941; Bhaskar & Razi, 1972-73; Bhaskar, 1975
			16	Rao, 1973b
* I. walleriana Hk.f. (WT)	A	10		Gill & Chinnappa, 1977
I. walleriana Hk.f.	C	8		Wulff, 1933, 1934
		8	16	Suguira, 1935-36
		8	16	Warburg, 1938a,b

Table cont'd.

Species	Region	n	2n	Reference
I. walleriana Hk.f. (cont'd.)		8	16	Bhaskar & Razi, 1972-73
		8	16	Tara and Namboodiri, 1974
		8	16	Bhaskar, 1975
			16	Heitz, 1929
			16	Smith, 1934
			16	Bhattacharjya, 1954a, b
			16	Jones & Smith, 1966
			16	Rao, 1972
			16	Beck *et al*., 1974
			16	Arisumi, 1975, 1980 a,b

*Species which contain a dysploid series.

A = Africa, C = Cultivar, CI = Comoro Is, D = Deccan Peninsula, EA = Eastern Asia, EH = Eastern Himalayas, ENA = Eastern North America, I = Indonesian Archipelago, M = Madagascar, Mt = Mauritius, NG = New Guinea, NTZ =

Table cont'd.

North Temperate Zone, S = Ceylon, Se = Seychelles, SEA = Southeast Asia, WH = Western Hamalayas, WNA = Western North America, WT = Wild Type.

[1] The identification of the material is doubtful.

[2] Rao gives no authority for _I. canariensis_ which is not listed in the _Index Kewensis_ and supplements. The present author was supplied material from the same population which proved to be _I. hookeriana_.

[3] Identification is doubtful; _I. hochstetteri_ which is often incorrectly referred to as _I. capensis_ Thunb. is reported to be $2n = 16$.

[4] Arisumi mistakenly assumed the material was of East African origin.

[5] Khoshoo expressed doubt as to the identification of the material.

APPENDIX 2

Distribution of chromosome numbers in Deccan Species of *Impatiens* by Sections as recognized by Hooker (1904-1906)

Region	Section	Chromosome no. n	Chromosome no. 2n	Species	Author
S. India	Scapigerae				
		10	–[a]	*I. acaulis* var. *acaulis*[b]	Bhaskar, 1975
		8,9	–	*I. acaulis* var. *granulata*	Bhaskar, 1976
		8	–	*I. agumbeana*	Bhaskar, 1976
		8	–	*I. barberi*	Bhaskar, 1976
		8	–	*I. beddomei*	Bhaskar, 1975
		–	–	*I. crenata*	–
		7	–	*I. dendricola*	Bhaskar, 1976
		–	–	*I. denisonii*	–
		–	–	*I. laticornis*	–
		10	–	*I. lawsonii*	Bhaskar, 1976
		16	–	*I. levingei*	Bhaskar, 1975
		8,9,16		*I. modesta*	Bhaskar, 1976
		–	–	*I. neo-barnesii*	–

Table cont'd...

Region	Section	Chromosome no.		Species	Author
		n	2n		
		-	-	I. niligrica	-
		-	-	I. orchiodes	-
		-	-	I. pandata	-
		6,7,8,10	-	I. scapiflora var. scapiflora	Bhaskar, 1976; Krishnaswami et al., 1969
		10,16,20	-	I. scapiflora var. pseudo-acaulis	Bhaskar, 1976
		7	-	I. stocksii	Bhaskar, 1975
	Epiphyticae				
		-	-	I. auriculata	-
		-	-	I. coelopteris	-
		-	-	I. jerdoniae	-
		9,10	-	I. parasitica var. parasitica	Bhaskar, 1975
		-	-	I. parasitica var. moniliformis	-
		-	-	I. urceolata	-

Table Cont'd...

Region	Section	Chromosome no. n	2n	Species	Author
	Annuae				
		–	–	I. aliciae var. aliciae	–
		8	–	I. aliciae var. bababudensis	Bhaskar, 1975
		–	–	I. aliciae var. pandavaramalyensis	–
		8	–	I. aliciae X pusilla	Bhaskar, 1975
		8	16	I. chinensis var. chinensis	Rao, 1972; Bhaskar, 1975
		8	16	I. chinensis var. intermedia	Bhaskar, 1975
		–	–	I. chinensis var. rupicola	–
		8	–	I. chinensis X tomentosa	Bhaskar, 1975
		8	–	I. dalzielli	Bhaskar, 1975
		–	–	I. debilis	–
		8	–	I. diversifolia	Bhaskar, 1975
		8	16	I. gardneriana	Bhaskar, 1975
		7	–	I. herbicola	Bhaskar, 1976
		–	–	I. kleiniformis	–

Table Cont'd...

Region	Section	Chromosome no.		Species	Author
		n	2n		
		8	–	*I. kleinii*	Bhaskar, 1975
		–	–	*I. lawii*	–
		8	–	*I. lenta*	Bhaskar, 1976
		–	–	*I. ligulata*	–
		–	–	*I. munnarensis*	–
		6,7,8,	–	*I. oppositifolia* var. *oppositifolia*	Bhaskar, 1975
		–	–	*I. oppositifolia* var. *nataliae*	–
		13	16	*I. pallidiflora*	Rao, 1973b; Bhaskar, 1976
		8	16	*I. pusilla* var. *pusilla*	Rao, 1973b
		8	16	*I. pusilla* var. *inconspicua*	Bhaskar, 1975
		8	–	*I. raziana*	Bhaskar, 1975
		–	–	*I. rivulicola*	–
		8	16	*I. tenella*	Bhaskar, 1975
		13	–	*I. tomentosa* var. *tomentosa*	Bhaskar, 1975
		–	–	*I. tomentosa* var. *rufescens*	–

Table Cont'd...

Region	Section	Chromosome no. n	Chromosome no. 2n	Species	Author
		–	–	I. tomentosa var. agastyamalayensis	–
		–	–	I. tomentosa var. nataliae	–
	Microsepalae				
		–	–	I. balsamina var. balsamina	–
		7	14	I. balsamina var. arcuata	Bhaskar, 1975
		7	14	I. balsamina var. azaleiflora	Rao, 1973a
		7	14	I. balsamina var. camelliflora	Rao, 1973a
		7	14	I. balsamina var. coccinea	Bhaskar, 1975, Rao, 1973a
		–	–	I. balsamina var. parasnathica	–
				I. balsamina var. rosea	–
				I. balsamina var. vulgaris	Rao, 1973a
		–	–	I. cochinica	–
		7	14	I. cuspidata	Rao, 1973b; Bhaskar, 1975
				I. dasysperma	–
		7	14	I. flaccida	Jones and Smith, 1966, Rao, 1973b; Bhaskar, 1975

Table Cont'd...

Region	Section	Chromosome no.		Species	Author
		n	2n		
		–	–	*I. floribunda*	–
		3	–	*I. latifolia*	Rao, 1975
		3,7	6,14	*I. leschenaultii*	Rao, 1972; Bhaskar, 1975; Krishnaswami *et al.*, 1969
		7	–	*I. lucida*	Bhaskar, 1975
		–	–	*I. macrocarpa*	–
		7	–	*I. mysorensis*	Bhaskar, 1976
		–	–	*I. penudula*	–
		–	–	*I. pulcherrima*	–
		7	14	*I. repens*	Bhaskar, 1975
		7	–	*I. scabriuscula*	Bhaskar, 1975
		6	12	*I. talbottii*	Bhaskar, 1975
		–	–	*I. trichocarpa*	–
S. India, Sri Lanka	Tomentosae				
		8	16	*I. henslowiana*	Krishnaswami *et al.*, 1969
		–	–	*I. johnii*	–

Table Cont'd...

Region	Section	Chromosome no.		Species	Author
		n	2n		
		–	–	*I. munronii*	–
	Subumbellatae				
		–	–	*I. anaimudica*	–
		10	20	*I. campanulata*	Rao, 1973b; Bhaskar, 1975
		10	20	*I. cordata*	Bhaskar, 1976; Rao, 1973b
		–	–	*I. disotis*	–
		–	–	*I. elegans*	–
		10,16	20	*I. fruticosa*	Krishnaswami *et al.*,1969 Rao, 1973b; Bhaskar, 1975
		10	16	*I. goughii*	Rao, 1973b; Bhaskar, 1976
		10	20	*I. grandis*	Rao, 1973b; Bhaskar, 1976
		10,20	16,20,40	*I. hookeriana*	Bhaskar, 1975; Jones and Smith, 1969; Rao, 1973b
		–	–	*I. leptura*	–
		10	28	*I. omissa*	Bhaskar, 1975; Rao, 1973b
		10	–	*I. parvifolia*	Bhaskar, 1976
		–	–	*I. travancorica*	–

Table Cont'd..

Region	Section	Chromosome no. n	Chromosome no. 2n	Species	Author
		–	20	*I. umbellata*	Rao, 1973b
		–	14	*I. uncinata*	Rao, 1973b
		–	–	*I. verecunda*	–
		8	–	*I. verticillata*	Bhaskar, 1975
		8	16	*I. viscida*	Krishnaswami *et al*., 1969
		10	16	*I. viscosa*	Bhaskar, 1975; Rao, 1973b
	Racemosae				
		10	20	*I. maculata*	Bhaskar, 1976; Rao, 1973b
		10	–	*I. phoenicea*	Bhaskar, 1976
		–	–	*I. platydena*	–
		–	–	*I. tanagachee*	–
Sri Lanka		–	–	*I. walkerii*	–

[a] No chromosome number determination has been reported.

[b] Varieties and hybrids following Bhaskar, 1975.

CHAPTER VII

TAXONOMIC TREATMENTS

OF

THE GENUS *IMPATIENS*

TAXONOMIC TREATMENTS OF THE GENUS IMPATIENS

Historical Review

The genus Impatiens is a Linnaean taxon. Species Plantarum (1753) includes descriptions of six Indian taxa (I. balsamina, I. chinensis, I. cornuta = I. balsamina L. var. coccinea Hk.f., I. latifolia, I. oppositifolia, and I. triflora = Hydrocera triflora (L.) W.& A.) and the Eurasian I. noli-tangere (which, as discussed in the next chapter, includes the endemic North American species, I. capensis Meerb.). De Candolle (1824) divided the genus into two genera, Impatiens L. and Balsamina Mill. ex Scop. Within each genus the species were grouped on the basis of inflorescence type (solitary vs. not solitary). Hooker and Thomson (1859) recognized only one genus, Impatiens, which was divided into a number of sections using phyllotaxy, inflorescence, habit and to some extent seed characters, as diagnostic features. In contrast to De Candolle, Hooker recognized subdivisions within the category of "compound inflorescence" (subumbellate, subcapitate, and racemous). This classification, in a modified version, served as the basis for the conspectus of Impatiens in the Flora of British India (Hooker, 1874-75). The proposed alteration was to make the primary division of the genus into two Series based on the shape of the fruit capsule. The sections used in the earlier treatment (1859) were retained. As a consequence, most of the sections in Series A were duplicated in Series B. Presumably, it is this parallel ordering which inspired the adoption of the term "Series" for the two major divisions. In An Epitome of the

British Indian Species of Impatiens (1904-06.) Hooker added a further refinement by dividing the genus on a geographic basis so that Series A and B were now treated separately for the Western and Eastern Himalayan, Deccan, Burmese, Ceylonese, and Malayan regions. Hooker justified this approach on the basis of his observation that most of the Impatiens species were endemic to only one of these regions. He later expanded on this point and proposed that the Impatiens species in each of these areas formed a distinct group, which evolved in situ from a relatively small number of colonizing ancestors (1909b). His publications following the Epitome (Hooker, 1908b, 1909a,b,c, 1910a, 1911a,b,c) keep to this scheme of treating the genus on a regional basis.

One important difficulty with Hooker's major efforts at classifying Impatiens (1874-75; 1904-06) was the restriction of the datum base to a portion of southern Asia which was rationalized by invoking endemism. Hence the divisions were based on within-group comparisons, and no effort was made to relate the resulting groups to the Impatiens species found elsewhere. In this sense, neither the treatment in the Flora of British India nor the Epitome constitutes a monograph of the genus as a whole. On the surface it appears that Warburg and Reiche (1895) in their treatment of the Balsaminaceae in Engler and Prantl's Natürliche Pflanzenfamilien did attempt to achieve precisely this goal. Their scheme was based on species from the entire range of the genus. Two subgenera were recognized: Acaulimpatiens Warb. (composed only of the Section Scapigerae of Hooker, a group which is restricted to the Deccan and Ceylonese regions) and Caulimpatiens which included all the other species. Thus, the primary division of the genus was based on a dichotomy in stem characters rather than fruit characters. Otherwise, it is evident that the system is merely a reworking of Hooker's original proposal (Hooker and Thomson, 1859) and in fact most of the sections used in that publication are retained (e.g. Uniflorae, Latiflorae, Subumbellatae, Racemoseae, and so on), although now they are elevated to the rank of "supersection". In contrast to Hooker who did not attempt to subdivide his sections (but merely noted that certain species appeared closely related), Warburg and Reiche subdivided their supersections into sections, grouping the species together which had long or short spurs. Implicit in this treatment is a rejection of perhaps the most awkward aspect of Hooker's classification, the numerous parallel sections within each series; but the resulting system is equally cumbersome since the subgenus Acaulimpatiens contained 19 species and subgenus Caulimpatiens several hundred (by conservative estimate) with parallel long and short-spurred groups within each section. Despite the fact that we often speak of the merits of Hooker's system *versus* Warburg and Reiche's system, there is really very little to recommend one over the other.

The difficulty with both the foregoing treatments is that neither has proven wholly satisfactory as a framework for systematic studies because both are essentially phenetic except in a few highly specialized and localized groups. For example, following an extensive palynological survey of the Balsaminaceae, Huynh (1968a,b) concluded that it was impossible to interpret his observations in keeping with the scheme provided by Warburg and Reiche (1895) and that reorganization of the genus was very much needed. While basically conservative in his revision of the South Indian Impatiens, Bhaskar (1975) did note that certain species (e.g. *I. fruticosa* DC. and *I. henslowiana* Arn.), which were assigned to totally unrelated sections in Hooker's scheme, are in fact closely related.

THE ENDEMISM PROBLEM IN IMPATIENS

The emphasis placed by Hooker on the endemism found in *Impatiens* has had an overwhelming influence on our perception of the genus. His observations were very much the outgrowth of his long years of study on the balsam flora of India which culminated in the *Epitome* (1904-06). The basis for his conclusions are to be found in Tables 1 and 2, which give the world distribution of *Impatiens* on a regional basis and the number of endemic species in southern Asia (the region on which Hooker almost exclusively concentrated). As Table 1 demonstrates, in the Old World Tropics and Subtropics, a high percentage of the species are restricted to a single phytogeographic region, and as Table 2 indicates only two species, *I. balsamina* L. and *I. chinensis* L. occur in more than two of these regions. Furthermore, an observation in the Introduction to the *Epitome* particularly attracted the attention of later taxonomists, namely that there is a major discontinuity between the Indian subcontinent and "adjacent" portions of the Himalayas. This was illustrated by his noting the absence of species with Series B type fruit capsules from the Deccan region, and indicating that this region and the Eastern Himalayas share only one or two species in common (Table 2, footnote a). This theme was taken up by Chatterjee (1939, 1962) in two extremely influential communications in which he concluded that the genus has three "separate and independent areas of development" (the Himalayas,

Table 1

World Distribution of *Impatiens* Species

Region	Number of species	Number of endemics	Reference
African	110	109	Grey-Wilson, 1980g
Madagascaran	83	83	Perrier, 1933
Ceylonese	21	16[1]	Hooker, 1904-06
Deccan[a]	89[2]	83	Bhaskar, 1975
W. Himalayan[b]	27[3]	18	Hooker, 1904-06, 1910a
E. Himalayan[c]	63	48	Hooker, 1904-06
Burmese[d]	62	40	Hooker, 1904-06, 1910a; Comber, 1934
Thai	50[4]	15	Shimizu, 1970
Malay	7	6	Ridley, 1922; Shimizu, 1970
Indochinese	25	21 (?)	Hooker, 1911a
Indonesian	8[5]	5	Backer & van den Brink, 1963
Phillipine	25	24	Merrill, 1923
Papuasian	1	1	Grey-Wilson, 1980a
Chinese	183	–	Hooker, 1908, 1910b; Comber, 1934

Table cont'd.

Table 1 Cont'd.

Region	Number of species	Number of endemics	Reference
Japanese	4	2	Ohwi, 1965
Eurasian	6	0	Tutin *et al.*, 1968
W.N. American	4	2	Russell, 1976
E.N. American	2	1	Russell, 1976
Mexican	1	1	Rydberg, 1910
Central American	1	1	Smith, 1897

[a] Central India to Cape Comorin.

[b] Chitrâl to Nepal frontier.

[c] Katmandu Valley to Mishmi Hills (Upper Assam) and Chumbi Valley (Tibet).

[d] Assam to Tenasserim.

[1] Hooker considers only 15 species as endemic; but in the present author's opinion the Indian and Ceylonese populations assigned to *I. acaulis* Arn. unquestionably belong to two very distint species.

Table cont'd.

Table 1 Cont'd.

[2] Bhaskar (1975) gives 87 species. He has since found a distinct new member of the "Epiphyticae" and Chandra Bose of the Botanical Survey of India (Coimbatore) has discovered a remarkable new species belonging to the "Scapigerae". This would make at least 89 species for this region.

[3] Chatterjee (1939) gives the total number of Impatiens species for the Eastern and Western Himalayas as 112, but does not include a regional breakdown.

[4] Shimizu's list of 48 does not include the Deccan species I. gardneriana and I. kleinii which occur in northwestern Thailand and vouchers of which (unidentified) are deposited at BKF where they were discovered by the present author.

[5] The authors treat I. holstii and I. sultani as separate species. Impatiens oncidioides which occurs on the slopes of Mt. Gede (pers. obs.) has been added.

Table 2

Species which occur in more than one phytogeographical region

Regions	Species	Total number of species in two regions	Percent in common
Ceylonese - Deccan:		105	4.8
	1. *I. balsamina*[1]		
	2. *I. flaccida*[2]		
	3. *I. grandis*[3]		
	4. *I. henslowiana*[2]		
	5. *I. oppositifolia*[1]		
Deccan - E. Himalayan:		149	1.3
	1. *I. balsamina*[1]		
	2. *I. chinensis*[1,a]		
E. Himalayan - W. Himalayan:		80	12.5
	1. *I. balsamina*[1]		
	2. *I. bicolor*[4]		
	3. *I. bicornuta*[5]		

Table cont'd.

Table 2 Cont'd.

Regions	Species	Total number of species in two regions	Percent in common
E. Himalayan - W. Himalayan: (cont'd.)	4. *I. cristata*[5]		
	5. *I. laxiflora*[6]		
	6. *I. racemosa*[7]		
	7. *I. serrata*[8]		
	8. *I. sulcata*[5]		
	9. *I. tigens*[6]		
	10. *I. thomsoni*[9]		
Deccan - W. Himalayan:	1. *I. balsamina*[1]		
E. Himalayan - Burmese:		111	12.6
	1. *I. arguta*[12]		
	2. *I. balsamina*[1]		
	3. *I. bracteata*[10]		
	4. *I. chinensis*[1,a]		
	5. *I. drephanophylla*[9]		
	6. *I. drepanophora*[9]		
	7. *I. juripa*[11]		
	8. *I. latiflora*[12]		

Table cont'd.

Table 2 Cont'd.

Regions	Species	Total number of species in two regions	Percent in common
E. Himalayan - Burmese: (cont'd.)	9. *I. pulchra*[12]		
	10. *I. racemosa*[7]		
	11. *I. radiata*[12]		
	12. *I. stenantha*[9]		
	13. *I. trilobata*[10]		
	14. *I. tripetala*[13]		
Burmese - Chinese:		248	2.8
	1. *I. balsamina*[1]		
	2. *I. ceratophora*[1]		
	3. *I. chinensis*[1]		
	4. *I. clavicuspis*[9]		
	5. *I. forrestii*[9]		
	6. *I. stenantha*[9]		
	7. *I. xanthina*[14]		

Table cont'd.

Table 2 Cont'd.

Regions	Species	Total number of species in two regions	Percent in common
Burmese - Indochinese:		80	8.8
	1. *I. aureliana*[9]		
	2. *I. balsamina*[1]		
	3. *I. chinensis*[1]		
	4. *I. harmandi*[9]		
	5. *I. inops*[9]		
	6. *I. kerriae*[15]		
	7. *I. purpurata*[16]		

[a] Hooker (1904-06) lists only one Deccan species as occurring in the Eastern Himalaya (i.e. *I. balsamina*), but in 1874-76 gives the two species cited here.

[1] authority = L.
[2] Arn.
[3] Heyne
[4] Royle
[5] Wall.
[6] Edgew.
[7] DC.
[8] Benth.
[9] Hk.f.
[10] Coleb.
[11] Ham.
[12] Hk.f. & T.
[13] Roxb.
[14] Comber
[15] Craib
[16] Tardieu

Assam, and the Deccan-Ceylon Region). As a result, the endemic aspects of Impatiens have been stressed by every subsequent author and became a rationale for regional treatments of the genus. Lost from sight was Perrier's (1933) communication in which he observed that although all the Malagasy species are endemic to the island, the groups to which they belong are clearly related to species found elsewhere. Specifically, he found that Section Humblotianae was allied to the African bucciniform species such as I. digitata Warb. and I. russorensis Warb., while many of the Vulgares group had relatives in southern Asia. Recently, in a revision of the African Impatiens, Grey-Wilson (1980g) suggested that there are at least three groups which are common to Africa and Southern India.

OBSERVATIONS

For several years, I have had the opportunity to evaluate the merits of the classifications of Hooker (1874-75; 1904-06) and of Warburg and Reiche (1895) as frameworks within which to carry out my own systematic studies. Both proved totally inadequate and only compounded my confusion about relationships within the genus. From my own experience, in Hooker's classification the sections Annuae, (excluding I. gardneriana Wt.), Epiphyticae, and Scapigerae are natural groups, whereas the Tomentosae, Microsepalae, Subumbellatae, and Racemosae are taxonomical "dustbins". The last of these, I recognized as being totally bizarre during my year of study in India (1976-77) because, particularly in the field, the included taxa bear no resemblance to each other whatsoever. The only link between these species appeared to be "all Deccan species with racemes which are not in section Epiphyticae" except that I was fairly certain that one species, I. phoenicea Bedd., was allied to the Epiphyticae. Once I had the opportunity to observe living plants of I. mirabilis Hk.f., I was convinced that Hooker's regional approach was incorrect. Next I turned to Warburg and Reiche (1895) which initially seemed to offer a more natural system. I was gratified to discover that they had recognized the affinity between I. mirabilis and some Deccan and Ceylonese Epiphyticae, but I. phoenicea was still allied with other species of the Racemosae and with a number of species with white or pink flowers and long spurs to which it bore no similarity.

More recently I discovered Perrier's excellent monograph which, as I have discussed in Chapter IV, took a radically different approach from previous classifications, and which seemed to offer a rational and biologically sound basis for approaching the classification in Impatiens. In this context, Grey-Wilson's (1980g) publication on the Impatiens of Africa has been of enormous assistance, especially because of its many illustrations and the colored photographic plates. This induced me to search the literature for other illustrations in order to supplement field and herbarium studies in Southern Asia and to work out a classification of my own. Although my revision is only in its initial stages, it is surprising to see how groups organized along the lines suggested by Perrier and Grey-Wilson begin to fall into place, and how often other types of data [for example, Huynh's (1968a,b) pollen studies] become meaningful. At the same time, one must be aware that the task of reclassifying Impatiens will by no means be easy. Some groups are very obvious, others are not. One major problem with using flower types is the phenomenon of convergence. As Grey-Wilson has pointed out, certain species may have made the transition from one major group of pollinators to another and will most likely combine floral features of both types of flowers. This problem which brings ecology and phylogeny into conflict has been discussed by Gould (1981), and is one of the difficulties which will have to be considered in proposing a new classification so as to arrive at results which will satisfy a fairly broad clientele.

The following section summarizes some of the groups, which I believe are natural lines:

GROUP I

Diagnostic characters

Type A flower with petals of alae large; vexillum non-cucullate; shallow, navicular antivexillar sepal with long filliform spur. Pollinated by Lepidoptera.

Chromosome number: *n* = 4,7,8 and euploid taxa in Papuasia based on *n* = 8.

Included Taxa

Africa

A. *I. walleriana* aggregate: 1. *I. cinnabarina* Grey-Wilson, 2. *I. hamata* Warb., 3. *I. messumbaensis* G.M. Schulze, 4. *I. pseudohamata* Grey-Wilson, 5. *I. pseudoviola* Gilg, 6. *I. serpens* Grey-Wilson, 7. *I. sodeni* Engl.& Warb. *ex* Engl., 8. *I. thamniodea* G.M. Schulze, 9. *I. usambarensis* Grey-Wilson, 10. *I. walleriana* Hk.f.

B. *I. rubromaculata* aggregate: 1. *I. cecilli* N.E. Br., 2. *I. eryaleia* Launert, 3. *I. hoehnelii* T.C.E. Fries, 4. *I. hydrogetonoides* Launert, 5. *I. kentrodonta* Gilg, 6. *I. lukwangulensis* Grey-Wilson, 7. *I. mazumbaiensis* Grey-Wilson, 8. *I. meruensis* Gilg, 9. *I. nana* Engl.& Warb. *ex* Engl., 10. *I. oreocallis* Laurent, 11. *I. pallide-rosea* Gilg, 12. *I. pseudozombensis* Grey-Wilson, 13. *I. psychaedelphoides* Launert, 14. *I. raphidothrix* Warb., 15. *I. rubrumaculata* Warb., 16. *I. saliensis* G.M. Schulze, 17. *I. sylvicola* Burtt Davy and Greenway, 18. *I. zombensis* Bak.f.

Sri Lanka

1. *I. flaccida* Arn., 2. *I. henslowiana* Arn., (omitted *I. bipartita* Arn. = *I. cuspidata* var. *bipartita* Arn. which according to the illustration in Fernando (1954) has an actinomorphic corolla. Discussion in Hooker (1874-75; 457) suggests that this is correct, but Hooker (1904-06) gives lobes of alae as very unequal).

India

1. *I. gardneriana* Wt., 2. *I. fruticosa* DC., 3. *I. henslowiana* Arn. 4. *I. pulcherrima* Dalz.

Malaysia

1. *I. sarcantha* Hk.f. *ex* Ridley.

Indonesia

1. *I. blumei* Zoll.& Mor., 2. *I. celebica* Miq., 3. *I. hubertii* Hk.f., 4. *I. javensis* (Bl.) Steud., 5. *I. lancifolia* Hk.f., 6. *I. motleyi* Hk.f. *ined.*, 7. *I. platypetala* Lindl., 8. *I. radicans* Zoll.& Miq.,

9. I. zollingeri O.K.

Philippines

1. I. burkei Hk.f., 2. I. hutchinsonii Hk.f., 3. I. merrillii Hk.f., 4. I. montalbana Hk.f., 5. I. quercetorum Hk.f.

Papuasia

1. I. hawkeri Bull, 2. I. herzogii K. Schum. 3. I. linearifolia Warb., 4. I. mooreana Schltr., 5. I. schlecteri Warb.

Comments

As a whole this is probably the oldest extant (or at least most primitive morphologically) group of Impatiens species, and it was recognized by both Perrier (1933) and Grey-Wilson (1980g). Hooker (1874-75) and Warburg and Reiche (1895) distributed the species included here among several sections of the genus, invariably allied to bucciniform taxa. The Deccan species, I. gardneriana Wt., finds its true affinities here,not in the section Annuae as was postulated by Hooker and by Bhaskar (1975), since in addition to floral characters, it shares the brown and rugose seed testa with Group I, as also do I. henslowiana Arn. and I. fruticosa DC.

The latter species introduces a special problem posed by the corolla in Group I, namely that the petals in a number of the species have become modified. This can be seen in Appendix 2 of Chapter III in I. flaccida Arn. (Microsepalae; in which the vexillar petals are reduced) and I. fruticosa DC. (Subumbellatae, in which they are twisted), but on the basis of vegetative, palynological, and seed character these are related to I. platypetala Lindl. and

I. henslowiana Arn., respectively. In the I. walleriana aggregate, I. pseudoviola Gilg and I. cinnabarina Grey-Wilson pose a similar problem. The best characters which identify taxa belonging to Group I are the overall flatness of the flower, the non-cucullate vexillum, and the shallow antivexillar sepal with a long filliform spur. Given the probable age of the group, there undoubtedly has been considerable diversification.

GROUP II

Diagnostic Characters

Type B flower, petals of alae often leathery and much reduced; vexillum deeply cucullate to form a hood; antivexillar sepal bucciniform; spur, short and often recurved; flowers, red, yellow, or green, often in combination. Pollinated by bees or birds.

Chromosome number: n = 7,8,9,10,13,16,17 and 24, euploid species present throughout the range.

Pollen: 4-colpate, long rectangular.

Included Taxa

Africa

I. kilimanjari aggregate: 1. I. bururiensis Grey-Wilson, 2. I gesneroidea Gilg, 3. I. kilimanjari Oliv. 4. I. quadrisepala R. Wilczek & G.M. Schulze, 5. I. russoriensis Warb., 6. I. ulugurensis Warb.

I. gomophylla aggregate: 1. I. austrotanzanica Grey-Wilson, 2. I. congolensis G.M. Schulze, 3. I. densifolia (Schulze & Wilczek) Grey-Wilson, 4. I. digatata Warb., 5. I. flammea Gilg, 6. I. gomophylla Bak., 7. I. iteberoensis R. Wilczek & G.M. Schulze, 8. I. keilii Gilg, 9. I. miniata Grey-Wilson, 10. I. niamniamensis Gilg, 11. I. paucidentata Wild. 12. I. salpinx Schulze & Launert, 13. I. tricaudata G.M. Schulze,

14. I. tweediae E.A. Bruce, 15. I. ukagurensis Grey-Wilson.

Madagascar

Section Preimpatiens, Group Humblotianae: 1. I. amoena H. Perr., 2. I. antongiliana H. Perr. 3. I. bicaudata H. Perr., 4. I. catati Drake, 5. I. danguyana H. Perr., 6. I. eriosperma H. Perr., 7. I. fuchsioides H. Perr., 8. I. fulgens H. Perr., 9. I. humblotiana Baill.

Sri Lanka

1. I. walkeri Hk.f.

India

1. I. auriculata Wt., 2. I. coelotropis Fisch., 3. I. jerdoniae Wt., 4. I. munronii Wt., 5. I. parasitica Bedd., 6. I. phoenicea Bedd., 7. I. urceolata Bhask., 8. I. viridiflora Wt.

Malaysia

1. I. mirabilis Hk.f.

Comments

This group represents the second major phylogenetic line. The Asian species I. auriculata Wt., I. jerdoniae Wt., I. parasitica Bedd., I. viridiflora Wt. and I. walkeri Hk.f. were recognized as a natural group by Hooker (1874-75; 1904-06) and by Warburg and Reiche (1895). Fischer (1930) placed I. coelotropis in the Racemosae, but Bhaskar (1975) correctly included it in the Epiphyticae. Perrier (1933) was the first to recognize the affinities between the African and Malagasy bucinniform species. Grey-Wilson (1980g) grouped together all the foregoing species and added *I. munronii* Wt. I have no doubt that *I. phoenicea* Bedd. (see Chapter III, Appendix 2) belongs here rather than in the Racemosae, and it is surprising that Bhaskar failed to see this. Perhaps this was because it does differ in habit from the other Deccan members of group II in having a weak, sometimes prostrate stem; but it is very definitely allied to such African taxa as *I. ukagruensis* Grey-Wilson and *I. digitata* Warb., which are subepiphytes. In addition, it shares with the latter species a common gametic chromosome number of $n = 10$. Bhaskar (1975) concluded that the Racemosae (minus *I. coeloptropis*) was a natural group because all the species had a haploid chromosome number of $n = 10$. As the photographs in Appendix 2 of Chapter III demonstrated, the Racemosae is clearly a "dustbin" taxon, and this again underlines the dangers of using chromosome numbers *per se* to draw taxonomic conclusions in *Impatiens*. There is no hesitancy on my part to ally *I. mirabilis* Hk.f. to the Epiphyticae. This taxon has puzzled taxonomists for a long time (Hooker, 1909a; Ridley, 1922) because under natural conditions it reaches a height of about two meters. In the garden of the Forest Herbarium in Bangkok there is a dwarf potted plant, which immediately made me recognize its affinity to *I. parasitica* Bedd. which I had been collecting in the Travancore High Range just a few weeks before. Subsequently, I found that Warburg and Reiche (1895) arrived at a similar conclusion.

It is interesting that among the African members of Group II, there is only one true epiphyte (Grey-Wilson, 1980g and Table 3) whereas in the Ceylonese and Deccan regions all the species of

Table 3

Epiphytes in Group II

Region	Species	Type of epiphyte[1]
African	1. *I. digatata* Warb.	subepiphyte
	2. *I. keilli* Gilg	typical
	3. *I. niamniamensis* Gilg	occasional
	4. *I. paucidentata* De Wild.	typical (prostrate)
Ceylonese	1. *I. walkeri* Hk.f.	typical
Deccan	1. *I. auriculata* Wt.	typical (prostrate)
	2. *I. jerdoniae* Wt.	typical (erect)
	3. *I. parasitica* Bedd.	typical (erect)
	4. *I. urceolata* Bhask.	typical (erect)
	5. *I. viridiflora* Wt.	typical (erect)

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[1] Using classification of Oliver (1930).

section Epiphyticae are epiphytes except I. coelotropis Fisch. which is a large shrub. In this connection, the growth habit of the African and Indian species differs, the former being sparingly branched while the Indian ones usually have a simple, unbranched stem. Furthermore, in collecting I. parasitica Bedd., I discovered that this species has a moniliform tuberous root, contrary to earlier reports (Hooker, 1874-75; 1904-06; Bhaskar, 1975). I have never observed this feature in herbarium specimens, but this is not surprising since the stem is very succulent and easily snaps off at ground level. Cuttings do not appear to readily regenerate this type of root system. It may well be that this is an adaptation to epiphytism only found in the Indian species for, according to Grey-Wilson (1980g), all of the African taxa of Group II have a fibrous root system. The prevalence and distribution of moniliform roots in the Epiphyticae needs further clarification.

GROUP III

Diagnostic Characters

Type A flowers, alae deeply lobed and with conspicuous throat markings; antivexillar sepal shallowly navicular with long filliform spur; flowers pink, purple or white. Pollinated by lepidoptera. Seeds, minute with long spiral hairs which uncoil when wet and fasten to the substrate.

Chromosome numbers: n = 6,7,8,9,10; n = 16 and 20 are thought to be euploid counts. Chromosome determinations have been carried out only in Scapigerae.

Pollen: 3-colpate with triangular equator.

Included Taxa

Africa

1. *I. ethiopica* Grey-Wilson, 2. *I. filicornu* Hk.f., 3. *I. congolana* N. Hallé, 4. *I. kamerunensis* Warb., 5. *I. nigeriensis* Grey-Wilson, 6. *I. oumina* N. Hallé, 7. *I. palpebrata* Hk.f. 8. *I. percordata* Grey-Wilson.

Sri Lanka

1. *I. acaulis* Arn.

India

1. *I. agumbeana* Bhask., 2. *I. barberi* Hk.f., 3. *I. clavicornu* Turz. 4. *I. crenata* Bedd., 5. *I. dendricola* Fisch., 6. *I. densonii* Bedd., 7. *I. gracilis* Bedd., 8. *I. laticornis* Fisch., 9. *I. lawsonii* Hk.f., 10. *I. levingei* Wt., 11. *I. modesta* Wt., 12. *I. nairii* Bose, 13. *I. neo-barnesii* Fisch., 14. *I. niligrica* Fisch., 15. *I. orchoides* Bedd., 16. *I. pandata* Barnès, 17. *I. scapiflora* (incl. *I. rivalis* Wt.), 18. *I. stocksii* Hk.f.& T.

Comments

Hooker (1974-75; 1904-06), Warburg and Reiche (1895), and Bhaskar (1975) recognized the Indian species as a natural group. Grey-Wilson (1980g) treated all the African species of Group III as a single complex, the *I. filicornu* aggregate, but had some hesitancy in treating the African and Asian taxa as allied because in the former, the stem is caulescent; in the latter, acaulescent. In the first place, the seeds are unlike any found elsewhere in the genus.

Secondly, most of the Indian taxa (excepting *I. clavicornu* Turz.) are epiphytes and the acaulescent stem is obviously a modification of life-form to an aerial environment; one can see the transition in the African species *I. ethiopica* Grey-Wilson which has a very short stem with only one or two nodes. In addition, all the Indian species have a tuberous rootstock, whereas the African ones are rhizomatous. As far as I have been able to ascertain, none of the species of the *I. filicornu* aggregate are subjected to seasonal drought, whereas many of the Scapigerae are. For example, at Materan and Mahableshwar in Maharashtra, *I. acaulis* Arn. (*I. gracilis* Bedd.) has a four month growing season (during the southwest monsoon). For the remainder of the year, the substrate is dry and hard. Consequently, the tubers are dormant for most of the year. Plants of several scapigerous species grown in the greenhouse at Macdonald College have for the last two years exhibited a phenological cycle exactly the same as the one they undergo in India even though the two environments are very different (Table 4). This suggests that dormancy is under strict genetic control. Since the monsoon is very regular (Mani, 1974) this poses no great hazard.

Warburg and Reiche (1895) recognized two sections in the subgenus *Acaulimpatiens*: section Scapimpatiens (*I. acaulis* Arn., *I. denisonii* Bedd., *I. rivalis* Wt., and *I. scapiflora* Heyne) and Orchimpatiens (all small-flowered and having a spur shorter than the flower). The flower in the Scapimpatiens is indistinguishable from that of the *I. filicornu* aggregate. In this context, it is interesting to note that Grey-Wilson reports that the species of the *I. filicornu* aggregate occupy rocks in waterfall zones. Similarly the Scapimpatiens

Table 4

Comparison of the phenology of some scapigerous *Impatiens* in natural and greenhouse populations

Species	Active growth period (Months)	
	Herbarium and field	Greenhouse
I. acaulis Arn.	VI - X[1]	VI - X[2]
I. clavicornu Turz.	II - XI	II - XI
I. levingei Hk.f.	I - XI	I - XI
I. modesta Wt.	V - X	V - X
I. niligrica Fisch.	VI - X	VI - X
I. scapiflora Heyne var. *pseudo-acaulis* Bhask.	V - IX	V - X

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[1] This is a record for Maharashtra. In North Kanara at the southern limit of the range, the dates are V - XII.

[2] Has produced leaves, but not flowered.

are found growing on the vertical faces of rocks within seasonal waterfalls, whereas the Orchidimpatiens are found on trees in sholas (a high elevation humid and subtemperate forest formation which characterizes the Western Ghats of Southern India). This suggests that the Scapimpatiens are older than the Orchidimpatiens. The one Ceylonese member of this group (_I. acaulis_ Arn.) has all the characteristics of the Scapimpatiens. In my opinion, it is morphologically not equivalent to the _I. acaulis_ Arn. which is found in Goa and Maharashtra. All the herbarium specimens collected from South Kanara to the Niligris are referable to _I. scapiflora_ var. _pseudo-acaulis_. Since the types of _I. acaulis_ Arn. (Arnott, 1836) are referable to the Ceylonese taxon, the correct name for the Indian material is _I. gracilis_ Bedd. (Beddome, 1859).

GROUP IV

Diagnostic Characters

Leaves opposite, sessile or subsessile, linear; flowers small to minute; modified Type A; vexillum deeply cucullate with prominent costa; vexillar petal of alae reduced, antivexillar petal ovate; antivexillar sepal deeply navicular, with short, straight filiform spur. Flowers white, yellow or purple. Pollinated by bees. Seed globose, black and shiny.

Chromosome number: _n_ = 5,6,7,8, and 13.

Pollen: 4-colpate with square equator.

Included Taxa

Africa

1. I. assurgens Bak.

Ceylon

1. I. oppositifolia L.

India

Annuae: 1. I. alicia Fisch., 2. I. chinensis L., 3. I. coccinea Hk.f., 4. I. dalzelli Hk.f.& T., 5. I. debilis Turcz., 6. I. diversifolia Wt., 7. I. herbicola Hk.f., 8. I. inconspicua Benth.(= I. pusilla var. inconspicua in Bhaskar, 1975), 9. I. kleiniformis Sedw., 10. I. kleinii W.& A., 11. I. lawii Hk.f. & T., 12. I. lenta Hk.f., 13. I. ligulata Bedd., 14. I. munnarensis Barnes, 15. I. oppositifolia L., 16. I. pallidiflora Hk.f., 17. I. pusilla Heyne, 18. I. raziana Bhask., 19. I. rheedii W.& A., 20. I. tenella Heyne, 21. I. tomentosa Heyne.

Burma

1. I. chinensis L., 2. I. craddockii, 3. I. ecalcarata Coll. & Hemsl., 4. I. helferi Hk.f., 5. I. masonii Hk.f., 6. I. oppositifolia L., 7. I. reticulata Wall.

Thailand

1. I. chinensis L., 2. I. pseudochinensis Shimizu.

Indo-China

1. I. chinensis L.

Comments

The Annuae of Hooker (1904-06) constitute a natural group if one removes I. gardneriana Wt. which has verticillate leaves, relatively actinomorphic petals, a non-cucullate vexillum, and brown rigose seed. In order to accommodate this species in the Annuae, Bhaskar (1975) was forced to erect a separate monotypic subsection (Verticillatae), whereas it obviously is better accommodated in Group I.

Only one species of Group IV occurs in Africa, and I have found no evidence of its presence in Madagascar. In India and adjacent portions of Asia, I have observed that the group is restricted to a growing season which corresponds to the period of the southwest monsoon, which suggests that it is a relatively late line in the evolution of Impatiens. From my observation of the various species under natural conditions, the group appears to be more tolerant of open and dry conditions than any other group of South Asian Impatiens. The plants of all the taxa are small, weedy and have very reduced, often leathery leaves.

The species in this group are among the most difficult of all Impatiens to distinguish. Bhaskar (1975) attributes this to extensive hybridization and considers I. tenella, I. diversifolia, I. oppositifolia, I. lawii, I. lenta, and I. debilis to be species of hybrid origin. On the other hand, I find after working with herbarium and field material that the group has been splintered on the basis of minute and taxonomically doubtful variation. For example, I. rheedii W.& A. is distinguished from I. kleinii W.& A. by having larger leaves and fruit, while the latter species is in turn distinguished from I. kleiniformis Sedgewick by having glabrous pedicels, presence of small extra-floral nectaries at the base of the leaves, and a short spur. Impatiens kleiniformis is reported to occur only at the type locality (Castle Rock, Goa), but plants which I have collected at Khandala showed a marked variation in size of the nectaries (including their absence) and some plants had pubescent pedicels and so approach I. kleiniformis. There has been a tendency in India to collect and recollect at the same localities because so few places are readily accessible to botanists. Consequently, we know very little about variation over the entire range of most taxa. There is no doubt in my mind that many of the species which have been described are merely local variants. While I am not sure that much can be done to improve the situation in terms of coverage, I do think that this problem should influence the weight one gives to minor variations.

GROUP V

Diagnostic Characters

Flowers epedunculate and usually in fascicles of two or more in the leaf axils; flower modified Type A; vexillum deeply cucullate; antivexillar petal obovate; vexillar, less than half as large and bilobed; antivexillar sepal deeply navicular and abruptly constricted into filliform spur. Bee or bird pollinated.

Chromosome numbers: Unknown.

Included Taxa

Africa

1. I. burtonii Hk.f., 2. I. glandulisepala Grey-Wilson,

3. I. leedalii Grey-Wilson, 4. I. polyantha Gilg, 5. I. quisqualis Laurent, 6. I. rosulata Grey-Wilson, 7. I. shirensis Bak.f., 8. I. volkensii Warb.

Sri Lanka

1. I. taprobanica Hiern.

Comments

Morphologically, if one is acquainted with the species, this is a very distinctive group. Impatiens volkensii Warb. is the only species which is known to be ornithophilous. Group V is probably represented on Madagascar (Section Preimpatiens, Group Vulgares Perrier, 1933) but this must await confirmation using herbarium specimens. I have found no evidence that this group extends to the Asian mainland.

GROUP VI

Diagnostic Characters

Perennials with scrambling or upright pubescent stems; leaves ovate, membranous and pubescent; inflorescences subumbellate racemes or true racemes; flowers modified Type A; vexillum cucullate; antivexillar petal of alae large and ovate; vexillar, narrow oblong and much reduced; antivexillar sepal shallowly navicular, abruptly constricted into filliform spur; flowers bright pink or mauve. Lepidoptera pollinated.

Chromosome number: n = 10 (only I. maculata Wt.)

Included Taxa

Africa

1. I. apiculata De Wild., 2. I. masisiensis De Wild., 3. I. stuhlmannii Warb., 4. I. warburgiana Schulze & Wilczek.

Madagascar

1. I. longipedunculata Perr.

India

1. I. maculata Wt.

Comments

This group, like the preceeding one appears small. In the Deccan Region, I. maculata Wt. (Appendix 2, Chapter III) is totally isolated taxonomically whereas it shares a number of diagnostic characters in common with the African and Malagasy species enumerated above.

The Origin of Impatiens

The distribution of the groups which have been described in the foregoing section, together with the absence of the genus from South America, suggests that Impatiens evolved after the separation of Western and Eastern Gondwanaland (100 m. y. B. P.), but before the separation of Africa, Madagascar, and India [63 m. y. B. P.; according to Raven and Axelrod, 1974)]. There is no evidence to support Khoshoo's hypothesis that Impatiens originated in the Himalayas "because the species there appear more primitive morphologically." The Himalayan species have a highly evolved Type B flower and it is difficult to imagine their having given rise to species with relatively actinomorphic corollas such as found in Group I. It is true that the vegetative parts of the Himalayan species are quite simple compared to those of many tropical taxa, but this is clearly associated with the evolution of an annual habit which permitted these species to overwinter as seed in an environment which otherwise would be unsuited for Impatiens with its extremely succulent stems.

Endemic Species

It still remains to be explained why the Impatiens species of lower latitudes tend to have very restricted ranges. It was first pointed out by Beddome (1855) that in the tropics, Impatiens is almost exclusively a montane genus, but with the exception of Bhaskar (1975) no subsequent botanist has considered the implications of this observation. In Appendix 1, ranges are given for Deccan, Burmese and Himalayan species of Impatiens. It is evident that a majority of the species are found at elevations above 1000 m; and some species occur at elevations up to 4,000 m (e.g. I. sulcata Wall. and I. urticifolia Wall.). Furthermore, according to Hooker (1904-06) and Comber (1934) there is an extensive and taxonomically difficult subalpine balsam flora in the Himalayas and Burma which barely has been collected, much less described and classified. Grey-Wilson (1980g) reported very similar data for Africa. Although elevations in Southeast Asia are lower, it is evident that the same general pattern is found in this region. A majority of the Thai (Shimizu, 1970), Indonesian (Backer and van den Brink, 1963) and Papuasian (Winters, 1973) taxa are orophytes. As Cain (1944), Razi

(1955), Mani (1974), and Bhaskar (1975) have pointed out the climate and vegetation in the tropical mountains is essentially subtemperate. For example, the highest temperature recorded at Ootacamund in the Nilgris is 24°C, and the average is 15°C. Since the mountain systems of the Tropics are isolated from each other, they are analogous to islands in a phytogeographic sense. In contrast, temperate species of Impatiens all occur at low elevations (Russell, 1976), and these taxa are all wide ranging (Table 1).

PHYTOGEOGRAPHY RECONSIDERED

From the foregoing observations, it is evident that we must distinguish between two phenomena in Impatiens in the Old World Tropics and Subtropics. On one hand, we have the individual species which for the most part are highly endemic. On the other hand, we have the natural sections (phylogenetic lines) which in many cases cut across regional boundaries. It is one thing to prepare a balsam flora of Thailand as Shimizu (1970) has done, it is quite a different one to make a comparative study of the cytoevolution of the genus in South India as Bhaskar (1975) has done and which I initially planned, when in most cases the nearest relatives of each group are not the other species in South India, but species in Africa and Madagascar. The whole concept of cytogeography (based on chromosome number per se) is meaningless in Impatiens because over most of its range, evolution has followed from numerous phylogenetic lines each with more than one cytotype.

It is not astonishing to find few links between the Impatiens flora of the Deccan and "adjacent" portions of the Himalayas.

These two areas happen to be included in a single political unit (India), but phytogeographically they form two very distinct provinces with markedly different floras and faunas (Mani, 1974). What is surprising is the number of authors who have confused these two entities (Hooker, 1904-06; Chatterjee, 1939, 1962; Jones and Smith, 1966; Bhaskar, 1975; Grey-Wilson, 1980g). Based on the concept of phytogeographic provinces one can expect the Deccan species to be allied to those of the Ceylonese and Malayan regions and those of the Himalayas to the Impatiens of Assam and Burma (Shan States).

APPENDIX 1

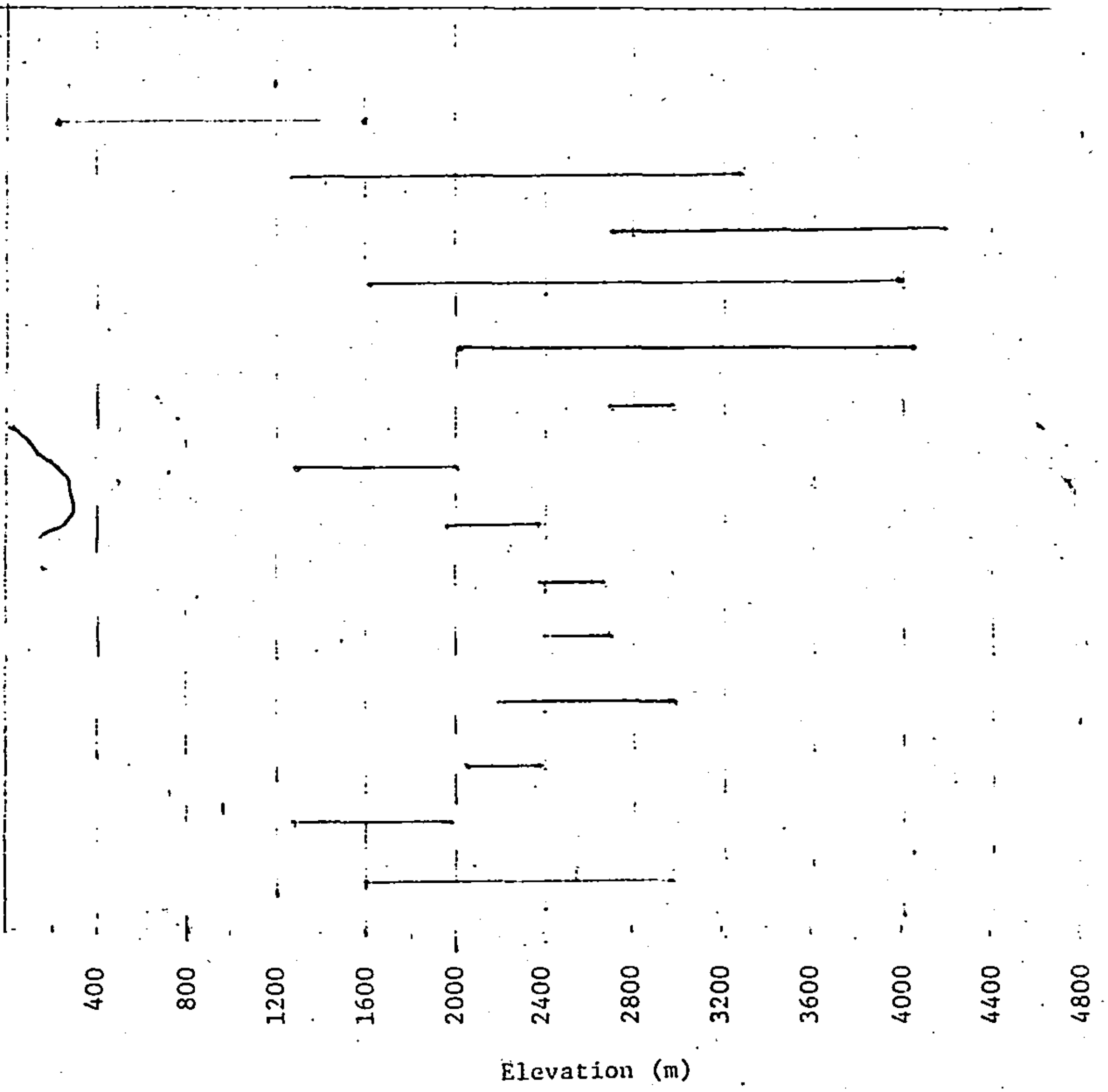
APPENDIX 1. Elevations at which some Asian species of *Impatiens* are found based on herbarium collections

Region Species

W. Himalayan[a]

1. *I. balsamina*[1]
2. *I. glandulifera*[2]
3. *I. sulcata*[3]
4. *I. thomsoni*[4]
5. *I. amplexicaulis*[5]
6. *I. bicornuta*[3]
7. *I. bicolor*[2]
8. *I. lemanni*[6]
9. *I. violoides*[5]
10. *I. aitchinsoni*[4]
11. *I. balfouri*[4]
12. *I. flemingii*[4]
13. *I. edgeworthii*[4]
14. *I. tingens*[5]

Table cont'd.



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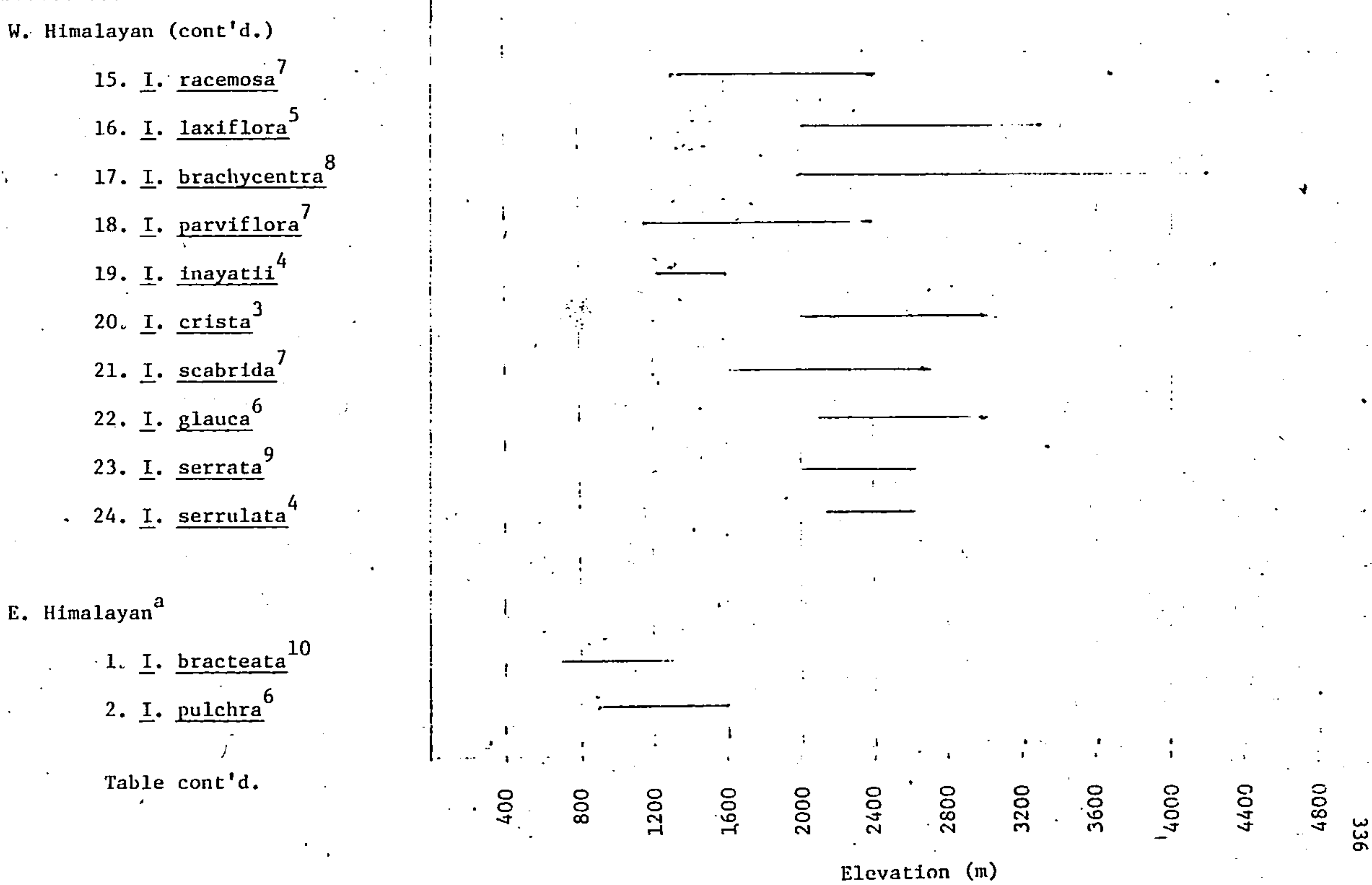

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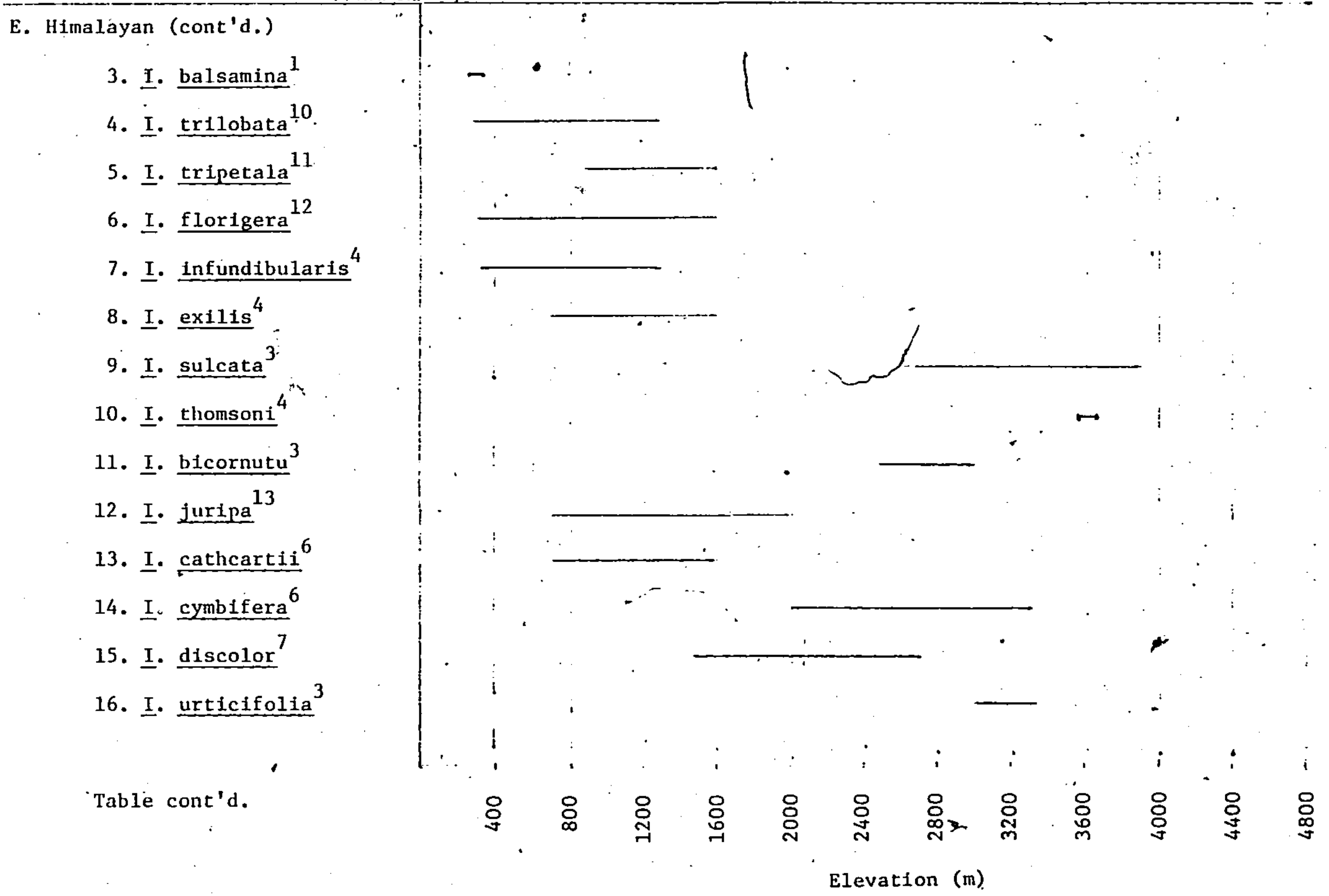

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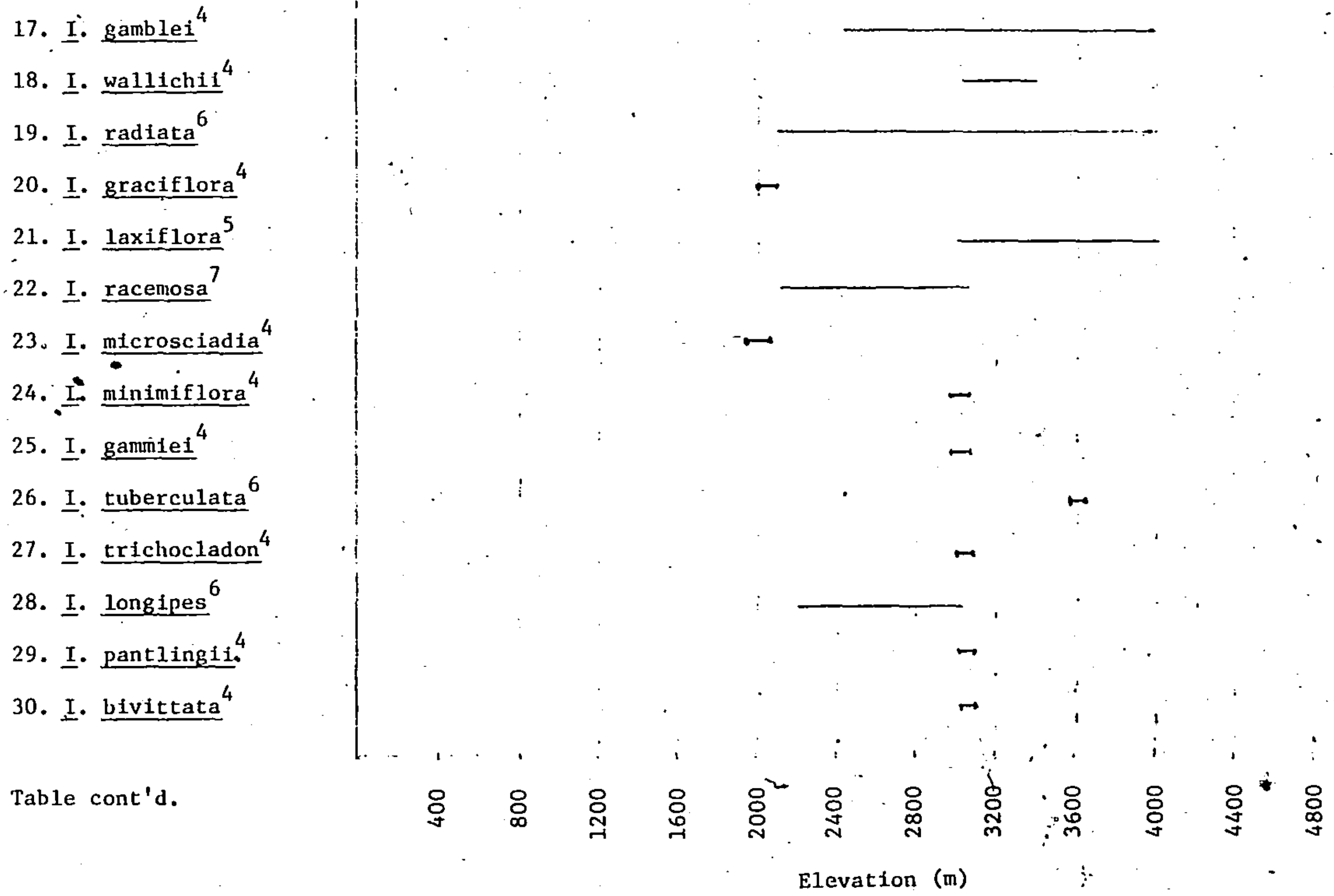
APPENDIX 1. Cont'd.

E. Himalayan (cont'd.)



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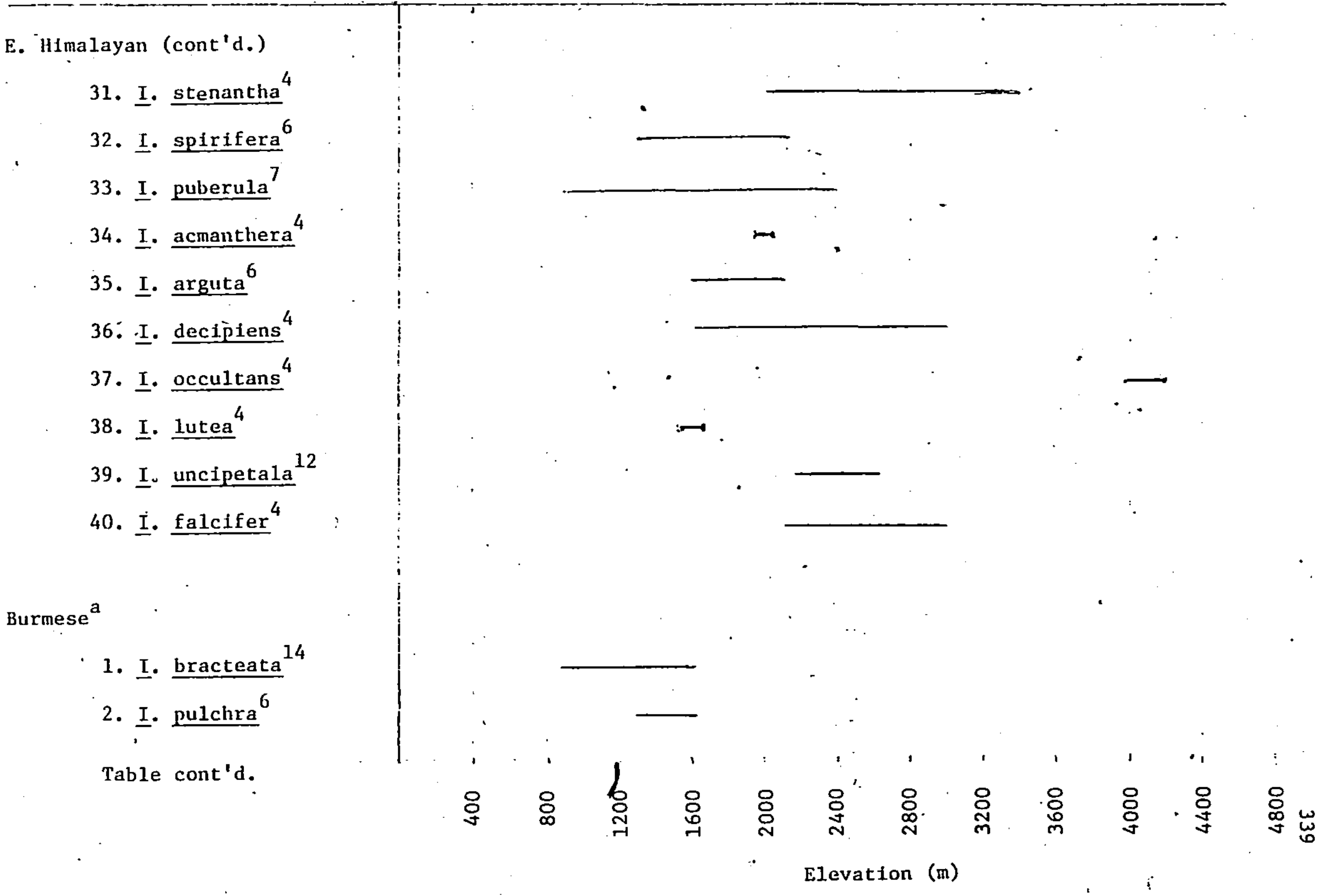

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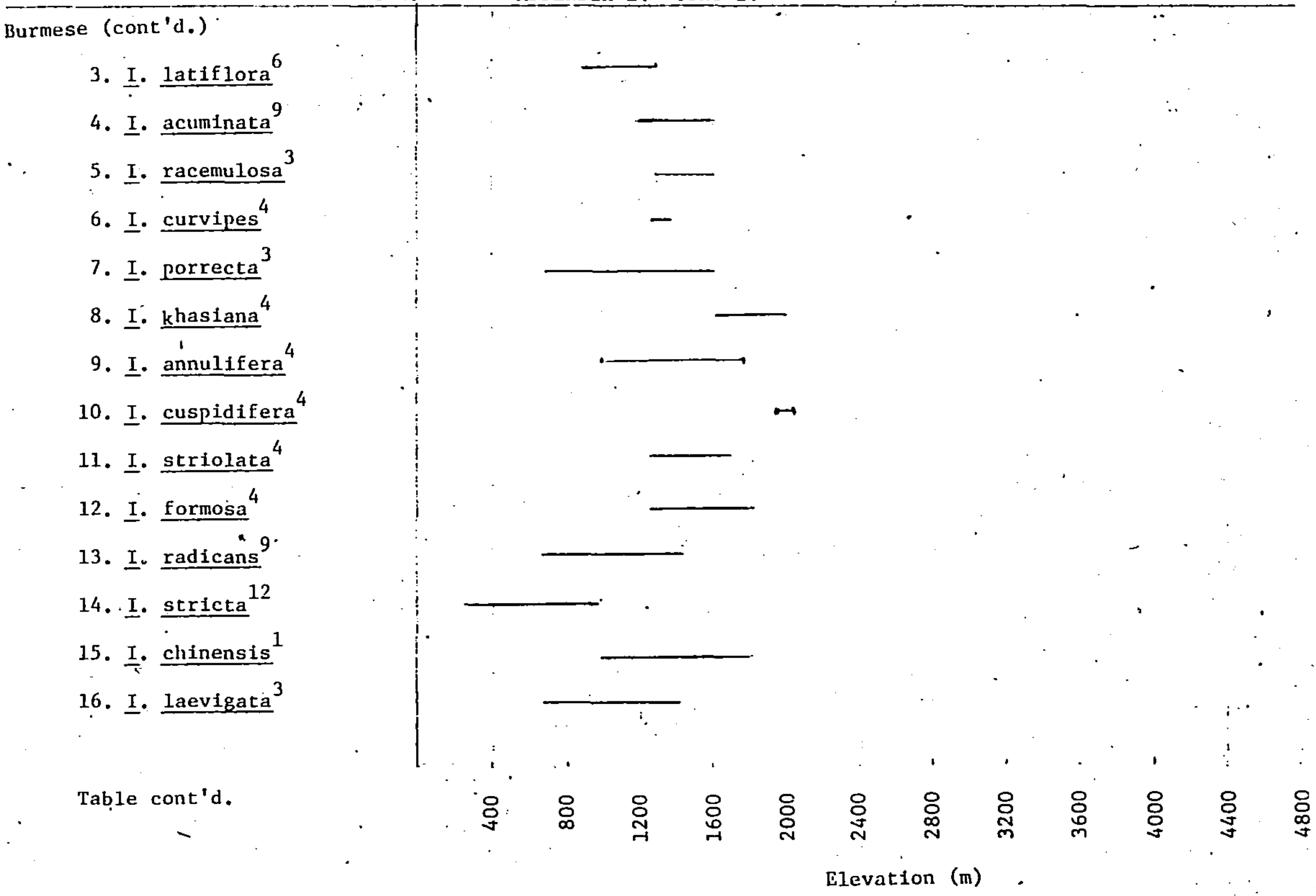

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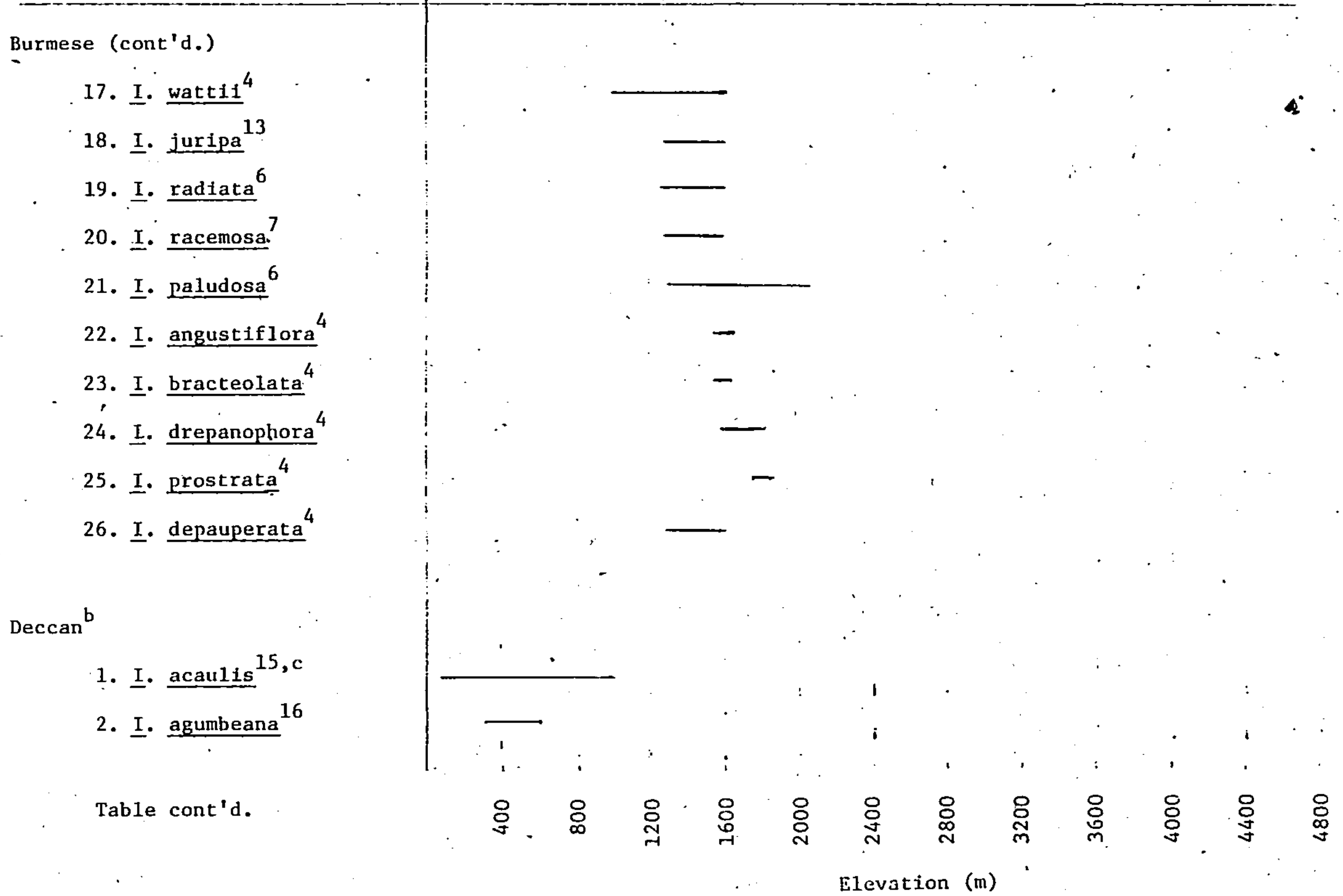

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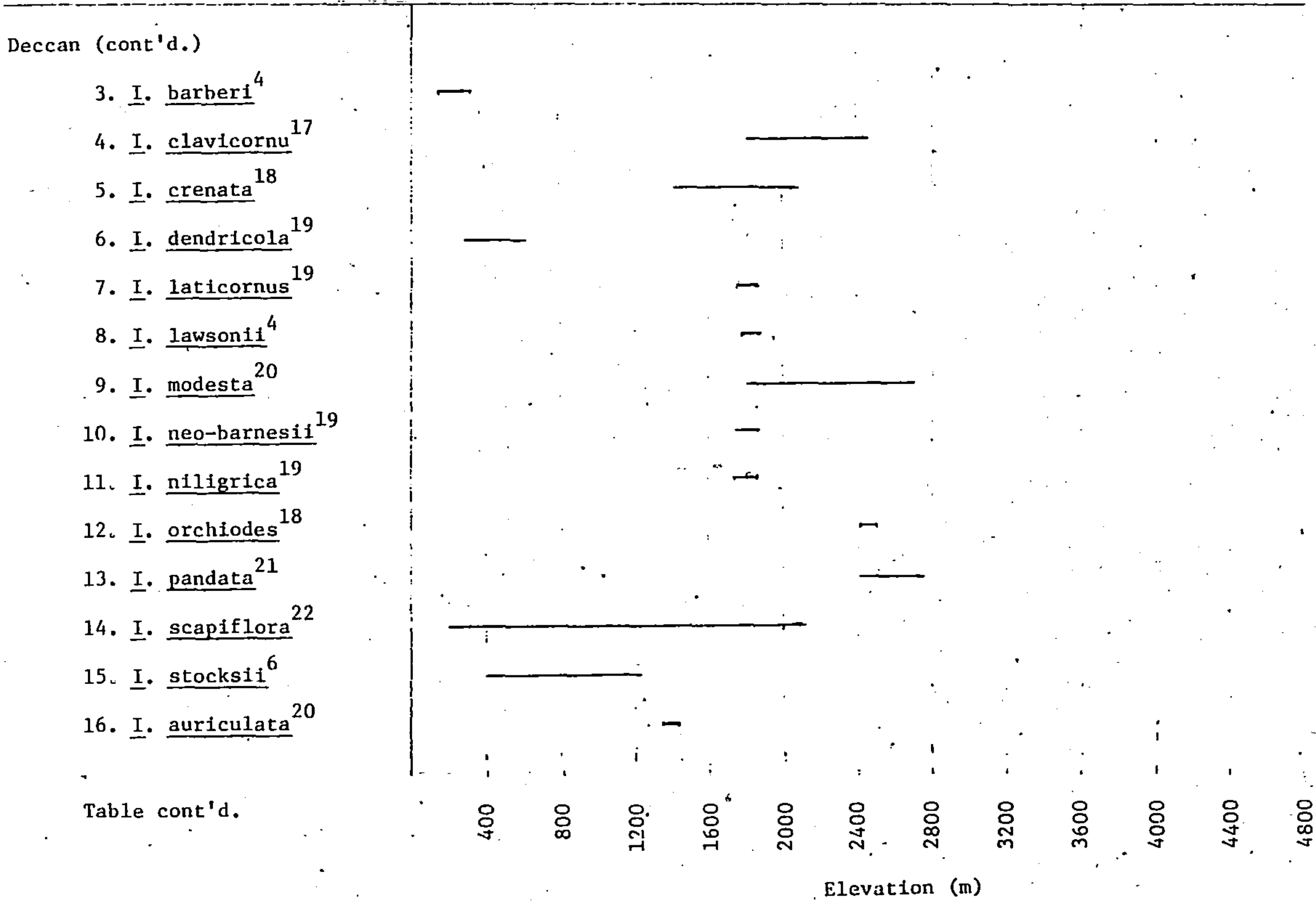

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Deccan (cont'd.)

17. *I.* *coelotropis*[19]
18. *I.* *jerdoniae*[20]
19. *I.* *munronii*[20]
20. *I.* *parasitica*[18]
21. *I.* *phoenicea*[18]
22. *I.* *urceolata*[16]
23. *I.* *viridiflora*[20]
24. *I.* *aliciae*[19]
25. *I.* *chinensis*[1]
26. *I.* *dalzellii*[6]
27. *I.* *diversifolia*[3]
28. *I.* *herbicola*[4]
29. *I.* *kleiniformis*[23]
30. *I.* *kleinii*[24]

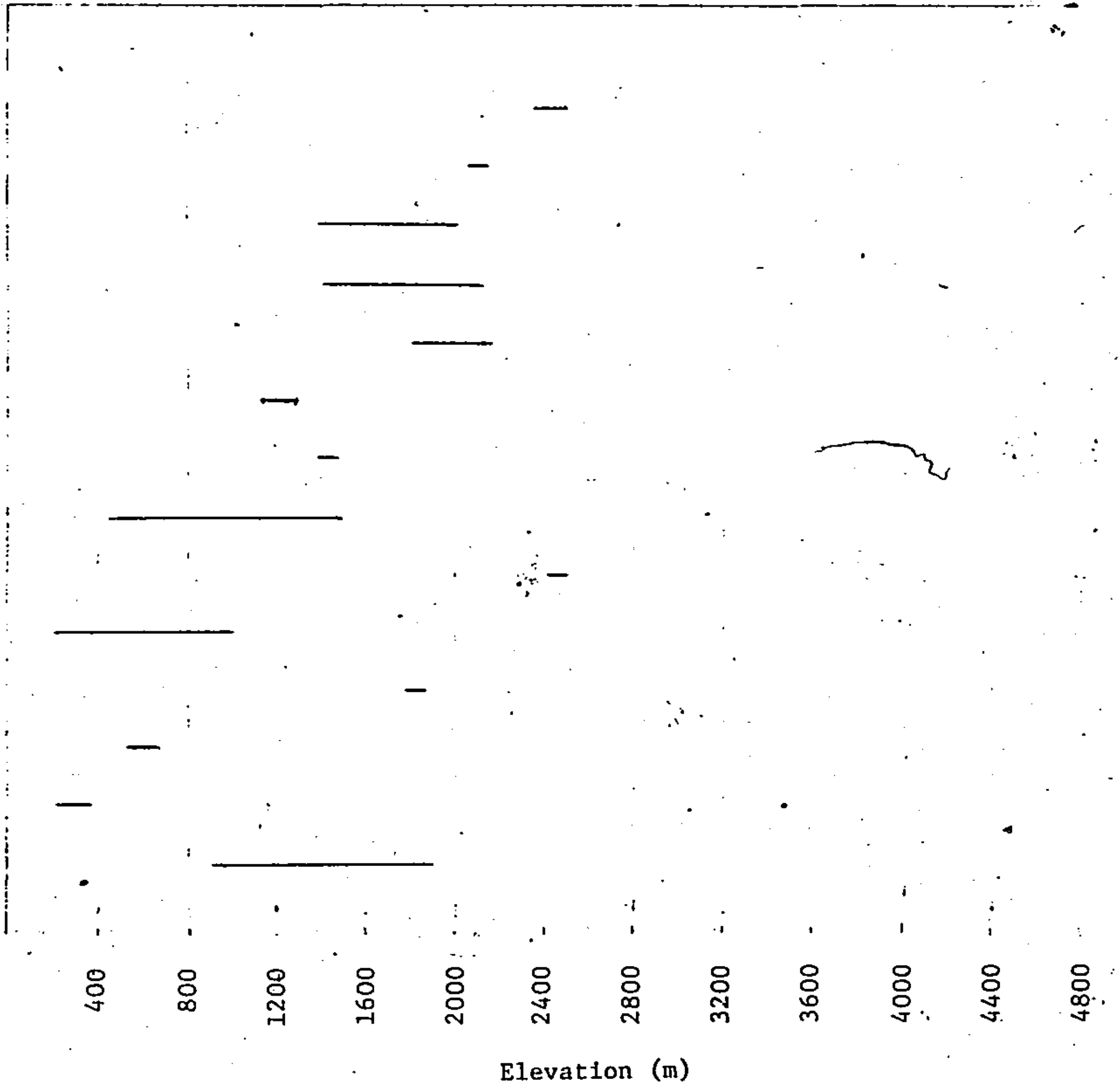
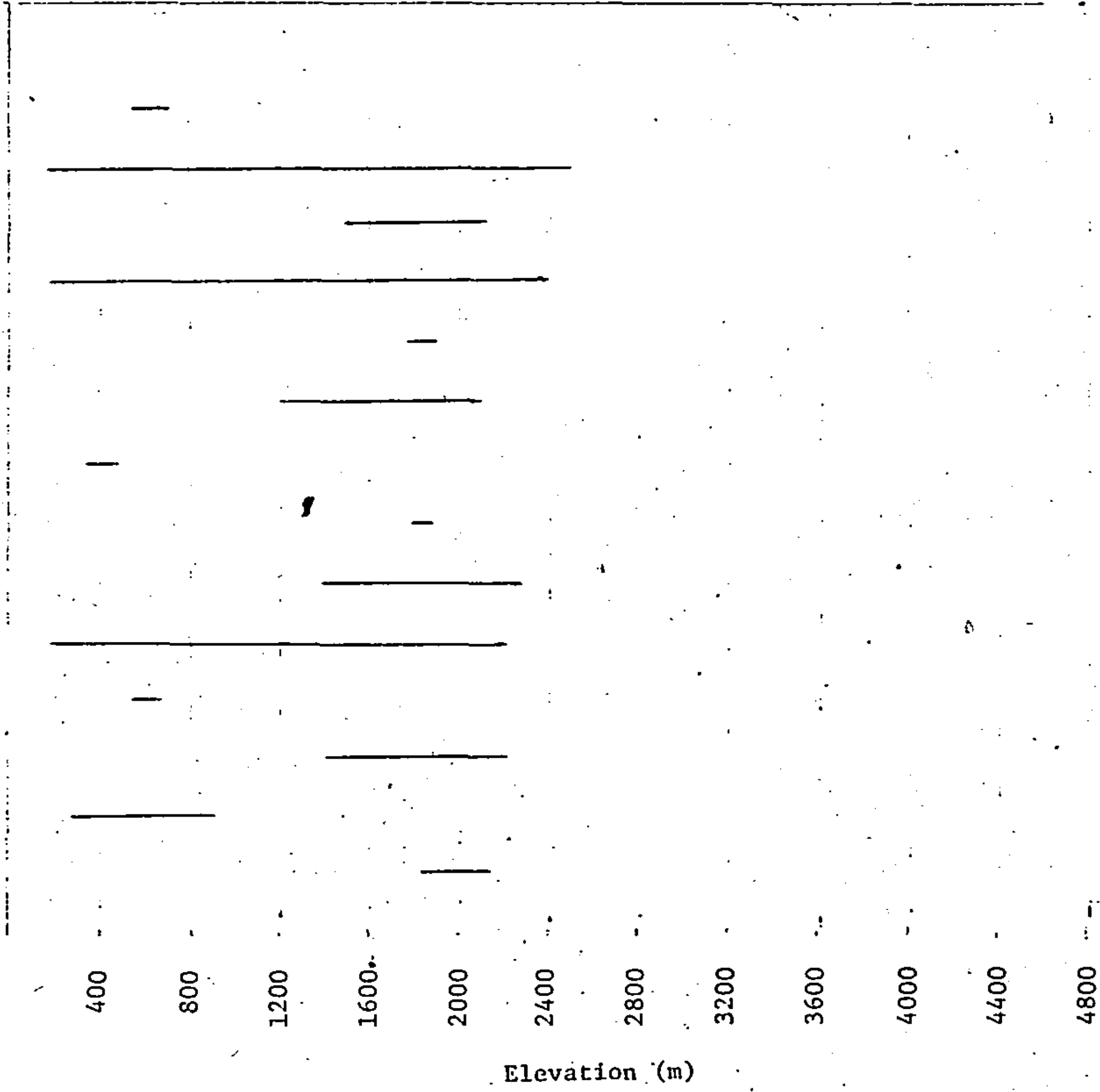


Table cont'd.

APPENDIX 1. Cont'd.

Deccan (cont'd.)

31. *I. lenta*[4]
32. *I. ligulata*[18]
33. *I. munnarensis*[21]
34. *I. oppositifolia*[1]
35. *I. pallidiflora*[4]
36. *I. pusilla*[22]
37. *I. raziana*[16]
38. *I. tenella*[22]
39. *I. tomentosa*[22]
40. *I. balsamina*[1]
41. *I. cochinica*[4]
42. *I. cuspidata*[24]
43. *I. flaccida*[15]
44. *I. floribunda*[20]



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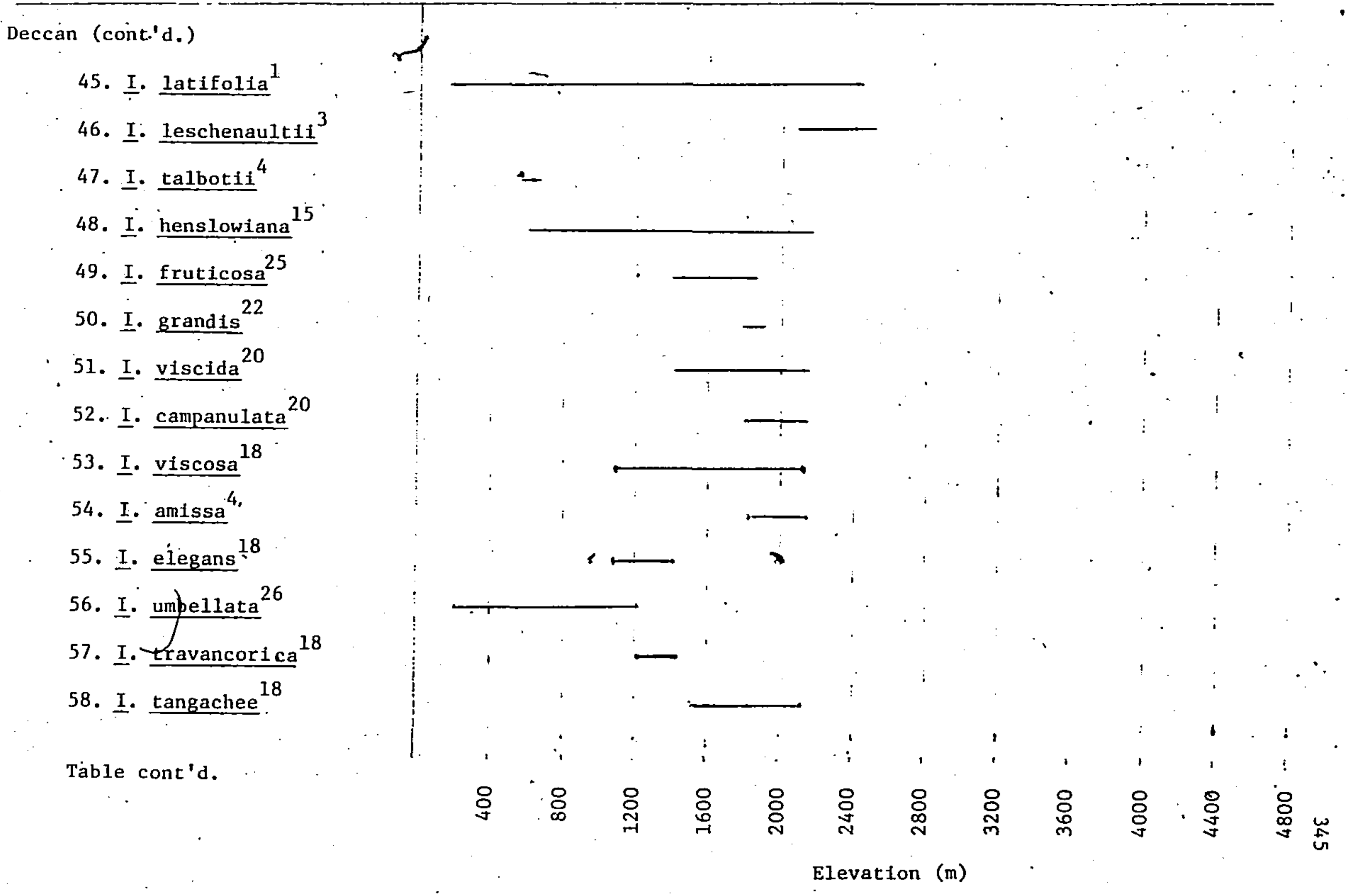

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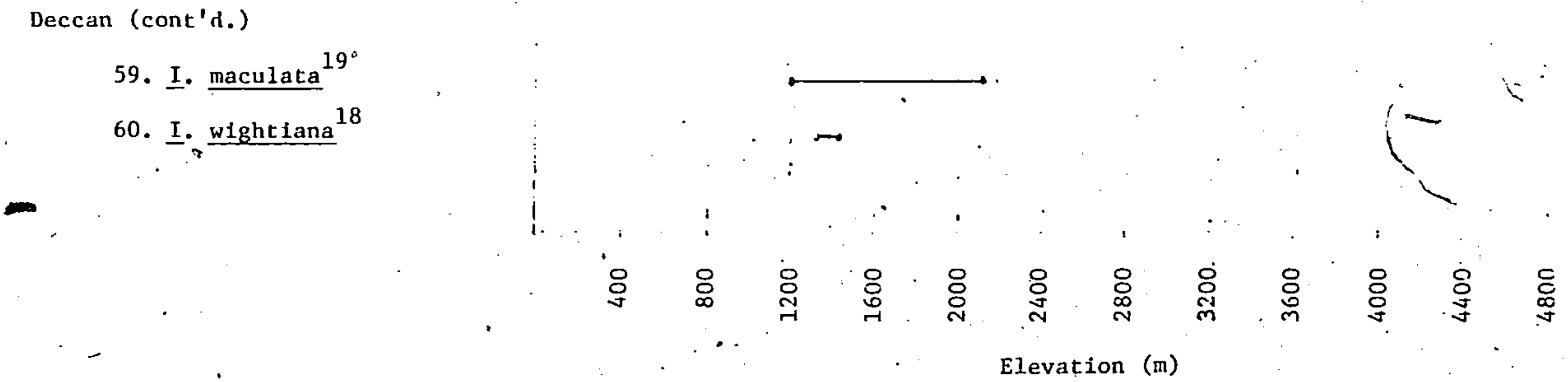

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[a] Based on Hooker, 1904-06.

[b] Based on herbarium specimens at BLATT, BSI, MH and the present author's modification of sections in in Bhaskar (1975).

[c] Properly I. gracilis Bedd.

[1] authority = L.
[2] Royle
[3] Wall.
[4] Hk.f.
[5] Edgew.
[6] Hk.f. & T.
[7] DC.
[8] Kar. & Kir.
[9] Benth.
[10] Coleb.
[11] Roxb.
[12] C.B. Clarke
[13] Ham.
[14] Coleb.
[15] Arn.
[16] Bhask.
[17] Turcz.
[18] Bedd.
[19] Fisch.
[20] Wt.
[21] Barnes
[22] Heyne
[23] Sedgw.
[24] W. & A.
[25] Lesch.
[26] Heyne & Roxb.

CHAPTER VIII

TAXONOMY OF THE BALSAMINACEAE

INTRODUCTION

The family Balsaminaceae A. Rich. is both coherent and distinct; consequently, there has been virtually no disagreement (except Blume, 1825) as to its boundaries. On the other hand, the Balsaminaceae has long been the subject of controversy as to its rank (i.e. tribe, family, order), its affinities to other dicotyledonous families (specifically the Tropaeolaceae and certain families of the Polygales or Sapindales), and to the number of genera which should be recognized. For example, two recent works on Impatiens (Bhaskar, 1975; Grey-Wilson, 1980g) have assumed that the Balsaminaceae are a geranalian family. These same authors together with Airy-Shaw (1973) have enumerated valid and invalid genera which are more the product of tradition than a major reorganization of the family reflecting the main phylogenetic lines. A review of the literature clearly indicates that many of the inter- and infra-familial relationships which have been postulated are based on extremely weak evidence and consequently should not be considered as resolved. To lend support to this contention the following review is undertaken.

DIAGNOSIS OF THE FAMILY

Balsaminaceae A. Rich. in Dict. Class. Hist. Nat. ii: 173 (1822); De Candolle in Prod. i: 685(1824); Wight and Arnott in Prod. Fl. Pen. Ind. Orient.: 140(1834); Arnott in Hook. Comp. Bot. Mag. i: 321(1835); Beddome in Madr. J. n. s. iv: 66(1858); Miquel in Fl. v. Nederl. Ind. i: 130(1859) and iv: 161, 396(1860); Hooker and Thomson in Praecursiones ad Fl. Indic., "Balsamineae", J. Linn. Soc. iv: 106(1860); Bentham and Hooker in Gen. Pl. i: 277(1862); Hooker in Oliver, Fl. Trop Afr. i: 298(1869); Baillon in Hist. Pl.: 17(1874); Warburg and

Reiche in Prantl and Engler in Nat. Pflanzenf. iii(5): 383(1895); Gilg in Bot. Jahrb. 43: 97(1909); Blatter in J. Bombay Nat. Hist. Soc. 36(2): 307(1933); Bailey in Man. Cult. Pl.: 643(1949); Hutchinson in Fam. Fl. Pl. I: 499(1959); Backer and van den Brink in Fl. Java I: 248(1963).

Nomenclature

The Balsaminaceae was first treated as a family by A. Richard (1822). Although his actual designation was "Ordo Balsamineae", under Article 18.2 of the International Code of Botanical Nomenclature (Stafleu et al., 1978) names intended as family names, but preceded by "ordo" or "ordo natural" are considered as having been published as family names. At first sight, a subsequent difficulty arises because the typus of the family is the genus Impatiens L. (in accordance with the strictures of Article 13.1), and "Balsaminaceae" was derived from Balsamina P. Mill ex Riv. (Miller, 1754) which is a nomen illegitimatum (declared so in Appendix II of the Code). Despite this, the name "Balsaminaceae" is a nomen conservandum by Article 14.1 because family names derived from genera (whether themselves legitimate or not) used by Jussieu (1789) are retained.

Blume (1825) described a new monotypic family, the Hydroceraceae, which contained a single species Hydrocera angustifolia. In contrast to the Balsaminaceae, the Hydroceraceae was typified by having five sepals, five free petals, and a drupaceous fruit. The family was merged with the Balsaminaceae in 1834 by Wight and Arnott. No subsequent taxonomist has suggested that the Hydroceraceae be reinstated.

General Features of the Family

The Balsaminaceae consists mostly of herbs (some species of Impatiens sensu lato are suffrutescent) with succulent and caulescent stems (excepting section Scapigerae in Impatiens). The phyllotaxy is opposite, alternate, or verticillate. The leaves are always simple, usually exstipulate, the margins never entire (except occasionally in Hydrocera), and the venation pinnate (except in section Scapigerae). Extra-floral nectaries are frequent and diverse. The flowers are perfect, basically pentamerous, and to varying degrees zygomorphic. They usually resupinate during ontogeny. The lateral sepals are foliaceous and imbricate; the odd or antivexillar sepal is modified into a gibbose, petaloid structure which usually terminates in a spur (excepting Section Trimorphopetalum of Impatiens). There are five petals, one of which is always free, while the remaining four are free or connate to varying degrees. The stamens are monadelphous or syngenesious, forming a cap over the gynoecium; a few didymous exceptions are known. The ovary is superior. The fruit is a dehiscent capsule (except perhaps in the genus Hydrocera). The seeds lack endosperm, and the embryo is straight.

Rank

Taxonomists subsequent to Richard have assigned various ranks to the Balsaminaceae which reflect the author's opinions as to the distinctness of the taxon:

1. Order (Balsaminales): Huynh (1970).
2. Family (Balsaminaceae, Balsamineae): De Candolle (1824), Warburg and Reiche (1895), Gilg (1909), Hallier (1912),

Bessey (1915), Hutchinson (1959), Melchior (1964), Cronquist (1968), Thorne (1968, 1976), Dahlgren (1975), Soo (1975), Takhtajan (1980).

3. Tribe (Balsaminae): Hooker and Thomson (1860), Bentham and Hooker (1862), Hooker (1874-75).

GENERA OF THE BALSAMINACEAE

A review of the literature indicates that seven genera have been recognized in the Balsaminaceae: Balsamina Miller, Hydrocera Blume, Impatiens L., Impatientella Perrier, Petalomena Peter, Semeiocardium Zollinger, and Trimorphopetalum Baker (Table 1). Airy-Shaw (1973) in the latest addition of Willis' "Flowering Plants and Ferns" accepts the validity of four of these genera (Hydrocera, Impatiens, Impatientella, and Semeiocardium), and places the remaining taxa in synonymy with Impatiens. Bhaskar (1975) recognizes three genera (Hydrocera, Impatiens, and Semeiocardium), while Grey-Wilson (1980e,g) concludes that only two are valid (Impatiens and Hydrocera).

There is no monograph treating the genera of the Balsaminaceae. With the exception of Balsamina, each genus was established on the basis of a single species which was thought to deviate significantly from Impatiens, usually by botanists not well-versed with the enormous variation to be found in the latter genus. Consequently, genera often have been split off in an entirely arbitrary manner. The following discussion does not constitute a monographic treatment of the included genera of the Balsaminaceae. It is merely a preliminary survey bringing together for the first time data from many scattered sources, and includes an evaluation and discussion of the criteria

Table 1

Genera which have been recognized in the Balsaminaceae

Genus	No. species	Distribution	Habit
1. Balsamina	37[1]	Old World Tropics and Subtropics, North Temperate Zone	herbaceous to suffrutescent
2. Hydrocera	1-3[2]	Southern Asia (India to Indonesia)	herbaceous
3. Impatiens	400-1000[3]	Old World Tropics and Subtropics, Temperate Zones	herbaceous to suffrutescent
4. Impatientella	1[4]	Madagascar	herbaceous
5. Petalomena	1-2[5]	Africa	herbaceous
6. Semeiocardium	1[6]	Sunda Islands	herbaceous
7. Trimorphopetalum	39[4]	Madagascar	herbaceous

[1] 51 specific epithets are listed under Balsamina in the Index Kewensis + Suppls. Of these, eight are synonymous with I. balsamina L., three with I. chinensis L., and one each with I. glandulifera Royle, I. noli-tangere L., and I. scabrida DC.

[2] Depending on the taxonomic status of I. natans Willd., I. madagascarensis DC. and I. triflora (L.) W.& A.

[3] 400 (Mani, 1974); 500-600 (Chatterjee, 1939); 1000 (Grey-Wilson, 1980e); 900 (Grey-Wilson, 1980b).

[4] Perrier (1933).

[5] (1, Grey-Wilson, 1980g); (2, Peter, 1928).

[6] Backer and van den Brink (1963).

which have been used to distinguish the various genera. Finally, there is a brief discussion of the consequences, in the context of nomenclature, cladistics and phylogenetics, of recognizing any genus other than Impatiens.

Note on Typification: In the succeeding sections, the subject of typification of various taxa is discussed in some detail. For this reason, the subject will be briefly reviewed here. Typification as now practiced by taxonomists is historically a product of the first half of this century, and it is only from January 1, 1958, that the nomenclature type or typus must be designated in order for a new taxon to be validly published (International Code of Botanical Nomenclature, 1978 (Stafleu et al., 1978); Article 35.1; henceforth the Code will be abbreviated to I.C.B.N.). The following points should be noted:

1. The typus rules apply at the rank of family or lower (I.C.B.N., Article 71.). The typus is the element to which the correct name of the taxon is permanently attached, whether as the correct name or as a synonym. The typus need not be the most representative element of a taxon (Article 7.2).

2. The element which is the typus need not be a specimen; it may be a description or figure (Article 9.3).

3. Effective publication is that which conforms to Articles 29-31, concerning distribution to the botanical community.

4. Valid publication is in accordance with Articles 32-45, governing the components of a proper diagnosis or protologue (= first discourse).

5. A legitimate name or epithet (correct name) is one which complies with Article 11. It must be used in scientific publications (Article 6.5).

6. An illegitimate name is one that does not comply with Article 18.3 (for families) or Articles 63-67 (for taxa below the rank of family). An illegitimate name may be effectively and validly published in which case it is a synonym of the correct name.

Before about 1890, botanists rarely designated a typus for their new taxa, and as a consequence many taxa are without holotypes (the specimen or other element designated by the original author as the typus; I.C.B.N., Article 7.3). A competent botanist may wish to select a lectotype (a specimen or other element from the material on which the protologue was based to serve as the typus when one was not designated at the time of the original publication; I.C.B.N., Article 7.5). Since this is a highly subjective task and one requiring critical judgement, it is very important to know which element the original author had solely or primarily in mind. For this one must be familiar with his intent and methodology (Stearn, 1957). Since the nomenclature problems in the Balsaminaceae, for the most part, historically fall into the period before widespread and systematic typification, there is often no direct evidence for the specific elements which formed the basis of the protologue. In many cases, the search for a suitable lectotype can be narrowed down by the use of secondary evidence. The main sources which have been used for this task are Stearn (1957) and Stafleu et al. (1967).

DIAGNOSIS OF THE GENERA

1. Balsamina P. Miller ex Rivinis in Gard. Dict. Abr. ed. 4 (1754); Rivinis in Irr. Tetr. Ic. (1691); Scopili in Fl. Carn. ed. 2, ii: 183(1772); Tournefort in Inst. Rei Herb.: 418, t. 235 (1700); Antoine de Jussieu in Gen. Pl. : 270(1789); J. Gaertner in Fruct. et Sem. Pl. 2, p. 151, t. 113 (1791); De Candolle in Prod. i: 685 (1824); Druce in Rep. Bot. Exch. Cl. Brit. Is. iii: 429 (1913).

Impatiens L.

Nomenclature: Balsamina Mill. is effectively and validly published. Since Species Plantarum (Linnaeus, 1753) is the official starting point for taxonomic nomenclature, Miller's publication is the protologue for Balsamina not the earlier references which have been cited. The name was declared synonymous with Impatiens L. (and therefore a nomen illegitimatum) in Appendix II of the I.C.B.N. (1978).

Illustrations: Rheede in Hort. Mal. ix, t. 47, 48 (1689).

Typus: Balsamina femina P. Miller (= I. balsamina L.). The lectotype should be based on a specimen in Miller's Herbarium which is in the general collection and the Sloan Herbarium at BM.

Distribution: Old World Tropics and Subtropics.

Diagnostic Characters: These are given in Table 2. The earliest reference I have found to Balsamina is that of Rivinus (1691) who treated this genus as distinct from Impatiens on the basis of fruit shape (ovate vs. linear). This dicotomy was maintained by subsequent taxonomists until Linnaeus (1753, 1754) who noted the two types of capsules, but considered the flower characters (zygomorphy, structure of the antivexillar sepal, fused anthers) to be a stronger

Table 2

Characters used by De Candolle to distinguish *Balsamina* and *Impatiens* and species used to reevaluate the two genera

	Diagnostic feature					
Genus	Anthers	Stigma	Fruit	Cotyledons	Inflorescence	Species examined
Balsamina	5 bilocular	5 free	a. ovate b. puberulent c. valves open inward from apex	fleshy	solitary	1. *I. balsamina* L.[1] 2. *I. chinensis* L.[2] 3. *I. flaccida* Arn.[3] 4. *I. latifolia* L.[4] 5. *I. leschenaultii* Wall. 6. *I. oppositifolia* L.

Table cont'd.

Table 2 cont'd.

	Diagnostic feature					
Genus	Anthers	Stigma	Fruit	Cotyledons	Inflorescence	Species examined
Impatiens	3 bilocular 2 unilocular	5 fused	a. terete b. glabrous c. valves open outward from base	membranous	many-flowered	1. *I. capensis* L.[5] 2. *I. fruticosa* DC. 3. *I. noli-tangere* L. 4. *I. pallida* Nutt. 5. *I. parviflora* DC. 6. *I. scabrida* DC.

[1] As *B. hortensis*, *B. coccinea* , *B. cornutu*

[2] As *B. fasciculata* and *B. chinensis*

[3] As *B. bifida*

[4] As *B. leschenaultii*

[5] As *I. fulva*

unifying factor than was fruit shape a divisive one. Consequently, he recognized only one genus Impatiens. Miller (1754) retained both Balsamina and Impatiens. With few exceptions (Jussieu, 1789; Gaertner, 1791), later taxonomists chose to follow Linnaeus's treatment. De Candolle (1824), in retaining the Impatiens--Balsamina dichotomy, enumerated a number of additional characters not described by previous authors (Table 2). He assigned seventeen "species" to Balsamina and fourteen to Impatiens, but suggested that I. natans Willd. and Balsamina madagascariensis DC. may form a separate genus (this is discussed in detail under Hydrocera). Hooker (1874-75) divided Impatiens into two primary categories: Series A (capsule short and ovate) and Series B (capsule terete or clavate). Although he does not refer to earlier treatments as the basis for his series, it is obvious that Series A is equivalent to Balsamina and Series B to Impatiens. Since Hooker, all major taxonomists have considered Balsamina as synonymous with Impatiens.

Observations

A number of the taxa enumerated by De Candolle were available (Table 2), so it was possible to evaluate the validity of his observations. The following technique proved satisfactory and rapid for examining anther structure. The stamens were dissected from unopened buds and mounted on an insect pin inserted perpendicular to the long axis of the stamens. A razor blade was used to make a transverse cut through the anthers a quarter of the way below the apex, and the top portion was discarded. The remaining section was dipped in a drop of cotton blue and then rinsed in 70% ethyl alcohol. The specimens were then viewed under a dissecting microscope at a magnification of 4X. The microsporangial wall takes on a deep blue color while the cavity and pollen are barely stained. The results are given in Table 3; these can be summarized as follows:

1. In all flowers examined, there were five anthers each with four microsporangia; this was true not only for De Candolle's species, but for all taxa which were studied. One anther (in the antivexillar position) was always smaller than the remaining four. This anther produced abundant pollen and the pollen stainability did not differ from that of the other four anthers. Hence it is not a staminodium.

2. All stigmas were basically terete and lobed at the apex. In some species the stigmatal lobes were very prominent (_I. flaccida_ Arn., _I. fruticosa_ DC., _I. parviflora_ DC.), while in the remaining species they were reduced to minute protuberances. While the stigmas may prove of taxonomic value in distinguishing various interspecific taxa, they are not useful in distinguishing the species of _Balsamina_ and _Impatiens_.

3. The fruit characters have been discussed in detail elsewhere. The only species in De Candolle's enumeration with puberulent fruit was _I. balsamina_ L. With respect to fruit shape and mode of dehiscence, the six species of the _Balsamina_ type plus _I. fruticosa_ DC. were ovate and dehisced along one of the vexillar sutures (cultivated forms of _I. balsamina_ also dehisced along an antivexillar suture). The _Impatiens_ species dehisced along all five sutures.

4. Cotyledons of young seedlings did not vary in thickness (fleshy _vs._ membranous), but they did have a waxy or non-waxy epidermis which was correlated with the equivalent character state in

Table 3

Results of character state studies of some species of Balsamina and Impatiens (De Candolle)

Taxon	Anthers	Stigma	Fruit	Cotyledons	Number of flowers in inflorescence
	Diagnostic feature				
Balsamina					
1. I. balsamina	5(2)	TR	OvI	NW	1
2. I. chinensis	5(2)	TR	OvI	W	1
3. I. flaccida	5(2)	TD	OvI	W	1
4. I. latifolia	5(2)	TR	OvI	W	1
5. I. leschenaultii	5(2)	TR	OvI	W	1
Impatiens					
1. I. capensis	5(2)	TR	LnII	NW	2-3
2. I. fruticosa	5(2)	TD	OvI	?	2
3. I. noli-tangere	5(2)	TR	LnII	NW	2-5
4. I. pallida	5(2)	TR	LnII	NW	2-3
5. I. parviflora	5(2)	TD	LnII	NW	3-4
6. I. scabrida	5(2)	TR	LnII	NW	3-4

5(2) = 5 bilocular anthers; LnII = linear capsule, rupturing along all five sutures; NW = non-waxy epidermis; OvI = ovate capsule, rupturing along vexillar suture; W = waxy epidermis; TD = terete with well developed stigmatal lobes; TR = terete with stigmatal lobes reduced to protuberances.

the adult leaves rather than with the *Balsamina* and *Impatiens* species. Of the six *Balsamina* species, five had a waxy epidermis and one (*I. balsamina* L.), a non-waxy epidermis. Five of the *Impatiens* species had a non-waxy epidermis. No seedlings of *I. fruticosa* DC. were available for study, but the cotyledons may well be non-waxy (and perhaps tomentose) as are the leaves in adult plants. Further support for this relationship comes from observations on the seedlings of *I. clavicornu* Bedd. It appears that the Scapigerae is the only group in the Balsaminaceae with leathery leaves, and the cotyledons of this species were distinctly leathery in contrast to those of all other species which were observed.

5. The number of flowers in the inflorescence agreed with De Candolle's data, but it must be remembered that only a small number of species were available to him compared to the number now known. It happens to be that the species which he placed in *Balsamina* all belong to groups with solitary inflorescences (Hooker's Annuae and Microsepalae). If a greater number of species had been available, the correlation between fruit and inflorescence types would not have held up.

The present observations indicate that only one character used by De Candolle to distinguish *Balsamina* and *Impatiens* is valid, namely the fruit characters (if *I. fruticosa* DC. is included in the former taxon). *Balsamina* is then equivalent to Hooker's Series A and *Impatiens* to Series B.

2. *Hydrocera* Blume in Bijdr.: 241 (1825); Hooker in Fl. B. I. i: 483(1874-75) and in Leconte, Fl. Indochin.: 628(1911); Warburg and Reiche in Prantl and Engler Nat. Pflanzenf. iii(5): 392(1895);

Backer and van den Brink in Fl. Java I: 251(1963); Grey-Wilson in Kew Bull. 35(1): 213(1980).

Hydroceras, Hooker and Thomson in J. Linn. Soc. iv: 156(1860), *lapsu* = *praec.*

Tytonia G. Don in Gen. Syst. i: 749(1831).

a. *Hydrocera triflora* (L.) Wight and Arnott in Prod. Fl. Pen. Ind. Orient.: 140(1834); Hooker in Fl. B. I. i: 483(1874-75) and in Leconte, Fl. Indoch.: 629(1911); Backer and van den Brink in Fl. Java i: 251(1963), Grey-Wilson in Kew Bull. 35(1): 213(1980).

Impatiens triflora Linnaeus in Sp. Pl.: 938(1753) and in Fl. Zeyl.: 315(1747); Willdenow in Sp. Pl. i: 1175(1798); De Candolle in Prod. i: 687(1924).

I. angustifolia Blume in Cat. Buitenz.: 49(1823) and in Index Kew. I: 1183(1895).

Balsamina angustifolia Burman in Zeyl. 41, t.16, f.2(1737).

B. erecta Hermann in Par. Bot. 105, t. 105(1698).

Hydrocera angustifolia Blume in Bijdr.: 241(1825).

b. *Impatiens natans* Willdenow in Sp. Pl.: 1175(1798); Roxburg Fl. Ind. i: 652(1820).

I. (?) *natans* De Candolle in Prod. i: 687(1824).

Tytonia natans (Willd.) G. Don in Gen. Syst. i: 749(1831).

Hydrocera triflora in Index Kew. I: 1210(1895).

c. *Hydrocera madagascariensis* Endl. ex Walp. in Rep. Bot. Syst. i: 477(1842) and in Index Kew. I: 1183(1895) -- description not seen.

Balsamina? madagascariensis De Candolle in Prod. i: 686(1824) = *I. madagascariensis* W.& A. in Index Kew. I: 266(1895).

d. *Impatiens madagascariensis* Wight and Arnott in Prod. Fl. Pen. Ind. Orient.: 140(1834) and in Index Kew. I: 1210(1895).

Nomenclature: Although "Hydrocera" is the generic name which almost exclusively has been used for this taxon for the last 150 years, it is invalidly published. Blume (1823) merely lists I. angustifolia (nom. nov.) and later (1825) he transferred it to a new genus Hydrocera of which it became the sole species. The family Hydroceraceae was given a protologue, but the genus Hydrocera and the species H. angustifolia Blume were not. Article 42.1 of the I.C.B.N. provides that for a monotypic genus a combined generic and specific description (descriptio generico-specifica) is permitted. The first valid protologue for Hydrocera is that of Wight and Arnott (1834), but by then Don (1831) had validly and effectively described the same genus under the name Tytonia, which is the correct name for this genus.

Illustrations: Warburg and Reiche in Prantl and Engler Nat. Pflanzenf. iii(5): 392(1895); Venkateswarlu and Dutt in J. Bom. Nat. Hist. Soc.: 547(1961); Grey-Wilson in Kew Bull. 35(1): 217(1980).

Typus: The typus for Hydrocera is the species H. triflora (L.) W.&.A. Grey-Wilson (1980e) has selected as a lectotype a specimen from the Hermann Herbarium (3:35) at BM. The lectotypification is correct since Linnaeus is known to have used the material in Hermann's collection for the preparation of the Flora Zeylonica (1747) and the description given there was the basis for the protologue in Species Plantarum (1753) which in turn was the basis for Wight and Arnott's (1834) diagnosis.

Don (1831) included Impatiens natans Willd. and Balsamina madagascariensis DC. in the genus Tytonia.
All the names which have been assigned to taxa in what is now Hydrocera (or Tytonia) are given in Table 4. As can be seen,

Table 4

A comparison of some diagnostic characters of certain taxa which have been referred to *Hydrocera*

Author	*Impatiens triflora*	*Impatiens natans*	*Balsamina madagascariensis*	*Hydrocera triflora*	*Hydrocera angustifolia* var. *angustifolia*	*Hydrocera angustifolia* var. *latifolia*
Linnaeus (1753)	1. peduncles solitary, 3-flowered 2. - 3. leaves linear-lanceolate 4. Ceylon (marshes) 5. -	-	-	-	-	-
Willdenow (1798)	1. peduncles solitary 3-flowered, 2. nectary[a] longer than flower, curved 3. leaves linear-lanceolate 4. Ceylon (marshes) 5. = *I. triflora* (Linnaeus, 1753)	1. peduncles solitary, 3-flowered 2. nectary very short 3. leaves lanceolate 4. Eastern India[b] 5. = sp. nov.	-	-	-	-
De Candolle (1824)	1. peduncles very short, 3-flowered 2. spur long, reflexed 3. leaves linear-lanceolate 4. Ceylon 5. = *I. triflora* (Linnaeus, 1753)	1. peduncles 3-flowered 2. spur very short, swollen 3. leaves lanceolate 4. Eastern India 5. = *I. natans* (Willdenow, 1798)	1. pedicels solitary 2. spur swollen near tip 3. leaves ovate 4. Madagascar 5. forms new genus with *I. natans*]	-	-	-
Wight and Arnott (1831)				1. peduncles short, 1 to 2 flowered 2. spur short 3. leaves, lanceolate 4. - 5. = *Comb. nov.* (Linnaeus, 1753; Blume, 1825)		
Ridley (1922)					1. - 2. Spur short 3. Leaves, (3.5-13.8) x (0.5-0.7) cm 4. Thailand, Indo-China, Java (paddy and shallow water 5. Blume (1825)	1. - 2. Spur short 3. Leaves, (3.5-11.0) x (1.5) cm 4. India (common), Malacca (rare) 5. = *Hydrocera triflora* (Wight and Arnott, 1834)

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[a] For the Linnaeans, nectary = spur.

[b] Linnaeus' Indian material was mainly from the Malabar and Coromandel coasts (Stearn, 1957). In South India, *Hydrocera* only occurs in the latter region. In addition, it is said to occur in Bengal (Hooker, 1874-75).

Linnaeus (1753) described one species, *I. triflora*, and Willdenow (1798) added a second, *I. natans*, which supposedly differed in three characters (spur length and shape, leaf shape, and distribution). De Candolle (1824) described an additional species which differed from the first two in inflorescence type, leaf shape and distribution, but it was suggested that *Balsamina madagascariensis* and *I. natans* may form a separate genus of taxa with swollen spurs (subsequently many *Impatiens* species with swollen spurs have been described). *Balsamina madagascariensis* then disappeared (except for a single reference in *Index Kewensis* which is incomplete). It was not treated by Perrier (1933) either as a correct name or as a synonym. Hooker (1874-75) considered *I. natans* Willd. to be synonymous with *H. triflora* (L.) W.& A. Ridley (1922) used the name *Hydrocera angustifolia* which he considered to include two varieties, var. *angustifolia* Blume with very narrow leaves and a distribution throughout southeast Asia, and var. *latifolia* Ridley with broader leaves and occurring mainly in India. It would make the taxonomic relationships relatively simple if var. *angustifolia* could be equated with Linnaeus's *I. triflora* and var. *latifolia* with Willdenow's *I. natans*, but unfortunately this is not the case. In the first place, both varieties are short-spurred. In the second place, Linnaeus does not describe spur length in his protologue for *I. triflora*, but the specimens in Hermann's Herbarium are all narrow-leaved, with a short swollen spur which is recurved. Hence the description of *I. triflora* in Willdenow is incorrect, whereas his description of *I. natans* suggests var. *latifolia* as does that of Wight and Arnott. Unfortunately, the few Deccan specimens of *Hydrocera* which I have seen at MH are both very narrow-leaved as is the drawing in Venkateswarlu and Dutt (1961) and in no way differ from Hermann's material, which suggests that the linear-leaved and lanceolate plants are not geographically segregated as Ridley believed. If this proves to be the case, then the _typus_ for _Tytonia_ becomes _I. triflora_ L. under the designation _Tytonia triflora_ (L.) G. Don.

Distribution: Bengal, Deccan (east of the Eastern Ghats), Sri Lanka, Burma (?), Thailand, Malaysia, Indo-China, Indonesia.

Diagnostic Characters: 1. Sepals 5. 2. Petals 5, free. 3. Fruit, a pentagonal fleshy pseudo-berry which is indehiscent. 4. Semi-aquatic growing in ponds and paddies, but also marshes.

Discussion

The species _Hydrocera triflora_ (L.) W.& A. bears a strong overall resemblance to _Impatiens balsamina_ L. which was also noted by Grey-Wilson (1980e); however it can be distinguished on the basis of several characters. There are five rather than three sepals; but as was discussed earlier at least sixty species of _Impatiens_ also have this feature, and often closely related species have the alternative states. In _Hydrocera_, the outer sepals are very large and enclose the antivexillar sepal, while the inner ones are much smaller (Fig. 1). Corresponding size differences are found in most _Impatiens_ with a full complement of sepals.

On the other hand, the presence of five free petals (Fig. 1) has not been found in _Impatiens_. This character state warrants confirmation. While I would not be surprised to find that the petals are

Figure 1

Three taxonomists impressions of
Hydrocera triflora (L.) W.& A.

A. Warburg and Reiche (1895)

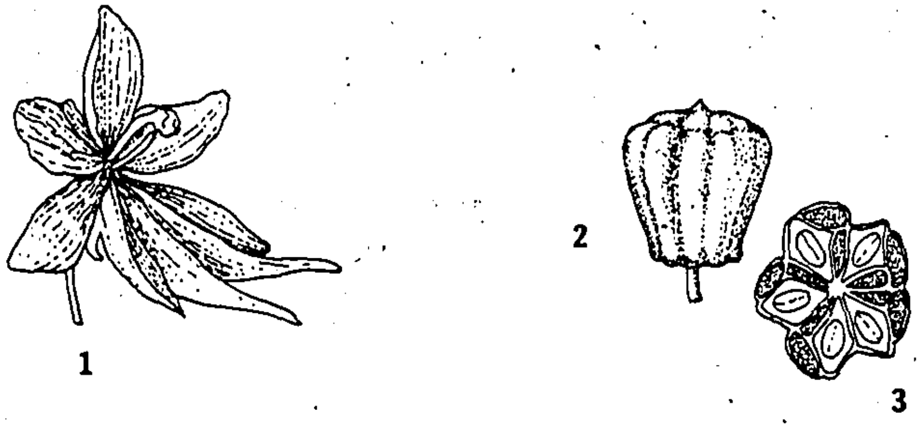
1. Flower (based on the herbarium specimens seen by the present author, the illustration is inaccurate)
2. Fruit
3. Cross-section of fruit

B. Venkateswarlu and Dutt (1961)

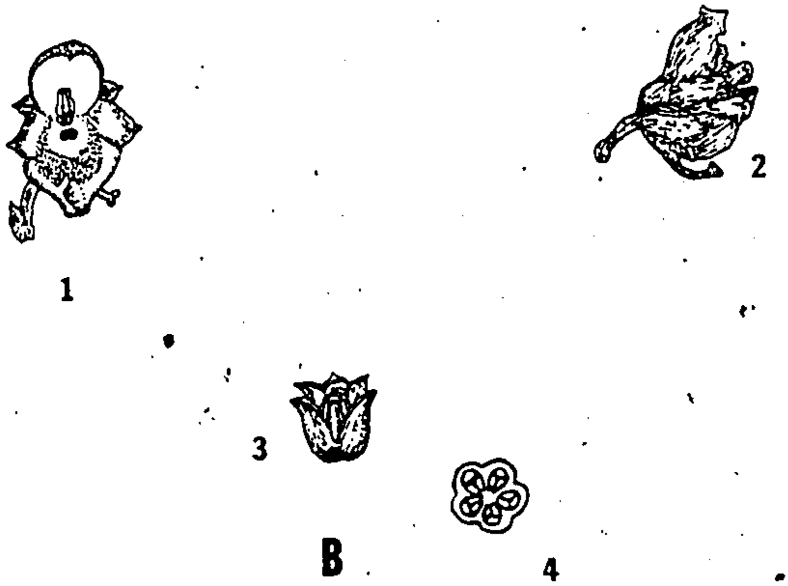
1. Flower (front view)
2. Flower (side view)
3. Mature fruit (note mode of dehiscence)
4. Cross-section of fruit (note three chambers)

C. Grey-Wilson (1980e)

1. Flower (front view)
2. Flower (side view)
3. Antivexillar sepal
4. Nearly mature fruit
5. Cross-section fruit (note air chambers)



A



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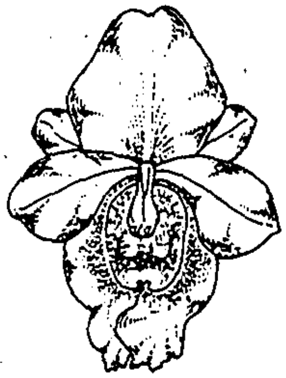
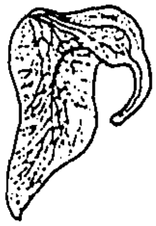


1

2



3

4

5

C

free given the number of other floral anomalies present in the family, I feel that, if in *Hydrocera* the alae are fused at the base for only a short distance, the petals could easily become separated during dissection. I have experienced precisely this situation in the African species *I. niamniamensis* Gilg. While dissecting the flowers, I became aware of a tear which was always associated with the removal of the alae and which upon investigation led to the discovery that these are in fact a single unit resulting from the fusion of the antivexillar petals along their inner margins. This feature did not correspond to my recollection of published descriptions, and in fact it has been omitted. In Grey-Wilson (1980g) none of the illustrations or accompanying descriptions indicate that some of the African *Impatiens* species have fused alae although this phenomenon is referred to once in the text (p. 17). Consequently, I believe that a study of the *Hydrocera* perianth throughout ontogeny is by no means superfluous.

The fruit of *Hydrocera* has been described as a non-dehiscent berry, pseudo-berry, or drupe (Wight and Arnott, 1834; Hooker, 1874-75, 1911; Backer and van den Brink, 1963; Bhaskar, 1975; Grey-Wilson, 1980e). The last author after examining nearly mature capsules on living plants, as well as those on herbarium specimens, concluded that the fruit abscisses without dehiscing and because of its weight sinks below the surface of the water. Subsequently, the epicarp and mesocarp either rot or are digested by aquatic fauna, leaving the endocarp in five separate pieces. This scenario is somewhat complicated by his observation that each carpel has one ovule and two hollow compartments (Fig. 1) which he believes serve as flotation chambers or air sacs and contribute to dispersal. In contrast, earlier Venkateswarlu and Dutt (1961) reported that the fruit is in fact a fleshy capsule which dehisces septicidally. The seed remains attached to the placenta initially, but later falls away. Their conclusion was that Hydrocera is much closer to Impatiens than was previously thought. The latter results are more in keeping with my own observations that the fruit is a septicidal, not a loculicidal capsule. Furthermore, the dehiscence along one suture with some separation of the valves along the apex (Fig. 1) is very similar to the situation I have found in the Type I capsules of Impatiens. Since the mesocarp is fleshy, one would not expect the valves to fold over.

In maintaining the generic distinction between Hydrocera and Impatiens, Grey-Wilson (1980e) considered the habitat preference of the former to be significant because in his experience Impatiens species were never semi-aquatic. In the first place, it is not correct that there are no semi-aquatic Impatiens since I know of at least two -- I. tangachee Bedd. in the Deccan Region and I. amphibia Perr. in Madagascar. Several of the Scapigerous species are commonly found in waterfalls (e.g. I. acaulis Arn. and I. scapiflora Heyne), while others are crenophilous (e.g. I. levingei Hk.f.). Furthermore in contrast to Grey-Wilson (1980e), Backer and van den Brink (1963) maintained that Hydrocera is found in marshes in addition to ponds and ditches, which suggests that it is only a facultative aquatic.

Although the resolution of the taxonomic status of Hydrocera can only be determined once all these problems have been resolved, I would like to make the following observation. Grey-Wilson (1980e) says:

"Why then should Impatiens have diverged into so many species whereas Hydrocera appears to have stagnated? It may be that floral development or some other factor of the biology in Impatiens offers a much broader scope for variation. Certainly in this genus the fruit structure and development has led to a more efficient dispersal mechanism, with the production of very many more seeds. However, I feel that habitat has possibly had an over-riding effect, an aquatic environment being more inhibiting, leaving less room for divergence and resultant speciation. Impatiens are mainly plants of upland forest, the montane environment with its numerous rivers, deep valleys and isolate peaks serving to isolate various elements. Impatiens is notable for its high numbers of local endemics. Hydrocera on the other hand is restricted to a lowland habitat, rarely being found much above 100 m altitude."

Without contesting the details of this statement, I would like to point out that Grey-Wilson (1980e) himself noted the morphological similarity between I. balsamina L. and H. triflora (L.) W.& A. The two species have, for tropical members of the Balsaminaceae, a very extensive and for the most part sympatric distribution. If the two indeed are closely allied then perhaps the meaningful comparison to be made is one between these two species and not between H. triflora and the whole of Impatiens. Finally, I will end this discussion with an ethnobotanical note: In Malay, the word "Inai" is used both for Hydrocera and for Impatiens.

3. Impatiens Linnaeus in Sp. Pl.: 937(1753) and in Gen. Pl. ed. 5: 403(1754); Rivinus in Irr. Tetn. Ic. (1691); Miller in Gard. Dict. Abr. ed. 4(1754); Jussieu in Gen. Pl.: 270(1789); Willdenow in Sp. Pl. i: 1175(1798); De Candolle in Prod. i: 687; Bentham and Hooker in Gen. Pl. i: 277(1862); Hooker in Oliver, Fl. Trop. Afr. i: 298(1868) and in Fl. Bl. I. i: 440(1874-75) and in Leconte, Fl. Indochin.: 611(1911); Perrier in Arch. Bot. t. vii, Mem. 1: 3(1933); Backer and van den Brink in Fl. Java: 249(1963); Grey-Wilson in Impatiens of Afr.: 3 (1980).

Balsamina P. Miller.

Nomenclature: *Impatiens* L. was validly and effectively published. It has priority over *Balsamina* Riv. *ex* Scop. nomenclaturally.

Illustrations: List in Index Lond. II: 492(1929) and Worsdell in Suppl. to Index Lond.: 2(1941).

Typus: *Impatiens noli-tangere* L. has been designated as a lectotype by Britton and Brown in Illus. Fl. ed. 2, ii: 512(1913); by Hitchcock and Green in Int. Bot. Cong., Cambridge, England, *Nom. Prop.*, III: 111-199; by Phillips, in Gen. So. Afr. Fl. Plants, ed. 2 (1951); by Rydberg in N.Y. Bot. Gard., Fl. N. Am., 25(2): 93(1910).

Thus in a revision of the genus, the subgenus and section in which *I. noli-tangere* is placed should be designated subgenus and section " Impatiens" (without citation of an author's name) in compliance with Article 22.1 of the I.C.B.N. (1978). Hence Warburg and Reiche's (1895) Subgenus *Caulimpatiens* and Section (IX) "Microcentron" are *nomenclaturally* invalid.

Impatiens noli-tangere is a Linnaen taxon and as a consequence its typification presents certain problems. To facilitate the discussion the original page from Sp.Pl. is reproduced in Fig. 2. In the first place it should be noted that the distribution is given as Europe and Canada. This strongly suggests that Linnaeus's *I. noli-tangere* not only includes *I. noli-tangere sensu stricto*, but also *I. capensis* Meerb. (Afbeel. Gew. t. 10; 1775), the common *Impatiens* species of eastern North America which was recognized as being distinct from the European species (under the binomial *I. biflora*) by Walter (1788) and by Willdenow (1798), but not by Michaux (1803). The North American material studied by Lineaus is known to have been

Figure 2

IMPATIENS.

* *Pedunculis unifloris.*

1\. IMPATIENS pedunculis unifloris ſolitariis, foliis oppoſitis ovatis, nectariis arcuatis. *chinenſis.*
Habitat in China. ⊙
Caulis *alternatim ramoſus, ruber.* Folia *oppoſita, ſeſſilia, ovata, ſubſerrata.* Pedunculi *axillares, ſolitarii, folio longiores, uniflori.* Flos *purpureus.* Nectarium *valde arcuatum, craſſum.*

2\. IMPATIENS pedunculis unifloris ſolitariis, foliis ovatis: ſerraturis lanceolatis, nectariis flore longioribus. *latifolia.*
Valli-onapu. *Rheed. mal.* 9. *p.* 91. *t.* 48.
Habitat in India. ⊙
Folia *lanceolata, alterna, crenata, e ſingula crena mucrone prominente.* Pedunculi *ſolitarii, uniflori, longitudine fere foliorum.* Flos *magnitudine J. Balſaminæ, at Calcar ſubulatum, longitudine fere pedunculi.*

3\. IMPATIENS pedunculis unifloris aggregatis, foliis oppoſitis linearibus. *Fl. zeyl.* 314. * *oppoſitifolia.*
Kondam-paliu. *Rheed. mal.* 9. *p.* 57. *t.* 31?
Habitat in Zeylonæ *arenoſis.*

4\. IMPATIENS pedunculis unifloris aggregatis, foliis lanceolatis, nectariis flore longioribus *Fl. zeyl.* 316.* *cornuta.*
Balſamina latifolia, floris calcari longiſſimo. *Burm. zeyl.* 41. *t.* 16. *f.* 1.
Habitat in Zeylona ⊙

Nuus

Balſamina. 5. IMPATIENS pedunculis unifloris aggregatis, foliis lanceolatis, nectariis flore brevioribus. *Hort. upſ.* 276.
Impatiens pedunculis confertis unifloris. *Hort. cliff.* 428.
Balſamina femina. *Bauh. pin.* 306.
Balſamina. *Dod. pempt.* 671.
Habitat in India. ⊙

* *Pedunculis multifloris.*

triflora. 6. IMPATIENS pedunculis trifloris ſolitariis, foliis anguſto-lanceolatis, *Fl. zeyl.* 315.*
Balſamina anguſtifolia, floribus ternis communi pedunculo ortis. *Burm. zeyl.* 41. *t.* 16. *f.* 2.
Balſamina erecta ſ. femina, perſicæ anguſto folio, zeylanica. *Herm. par.* 105. *t.* 105.
Habitat in Zeylonæ *paludoſis.*

noli tangere. 7. IMPATIENS pedunculis multifloris ſolitariis, foliis ovatis, geniculis caulinis tumentibus. *Fl. ſuec.* 722. *Dalib. pariſ.* 270.
Impatiens pedunculis ſolitariis multifloris. *Hort. cliff.* 428. *Roy. lugdb.* 431. *Hall. helv.* 405. caule angulato. *Gort. gelr.* 502.
Balſamina lutea ſ. Noli me tangere. *Bauh. pin.* 306.
Noli me tangere. *Col. ecphr.* 1. *p.* 149. *t.* 150.
Habitat in Europæ, Canadæ *nemoribus.* ⊙

collected by Pehr Kalm (Stearn, 1957; Stafleu et al., 1967) who visited eastern, but not western North America (I. noli-tangere sensu stricto is only found from Alaska to British Columbia on this continent). Since the elements upon which Linnaeus based the name "I. noli-tangere" were heterogeneous (i.e. I. noli-tangere sensu stricto plus I. capensis Meerb.), the lectotype should be selected so as to conform with current usage (that is a specimen of I. noli-tangere sensu stricto) in accordance with Article 7B.1 of the I.C.B.N. (1978). Since Linnaeus cites his own Hortus Ciffortianus (1737), a suitable lectotype for I. noli-tangere can be chosen (and consequently as a typus for the genus Impatiens) from specimens in the Clifford Herbarium at BM.

Distribution: Nearly subcosmopolitan, excluding South America, Australia, and Oceania (except as cultivated ornamentals). The main center of diversity is in the Old World Tropics and Subtropics.

Diagnostic characters: These have been discussed in detail in preceeding chapters.

4. Impatientella Perrier in Bull. Acad. Malagache, n.s. x: 22 (1927) and in Arch. Bot. t. vii, mém. 1: 110(1933).

a. Impatientella inaperta Perrier in Bull. Acad. Malagache, n.s. x: 22(1927).

Impatiens inaperta Perrier comb. nov. in Arch. Bot. t. vii., mém. 1: 110(1933).

Illustrations: Impatientella inaperta Perrier in Bull. Acad. Malagache n.s. x: 36(1927).

Typus: Impatientella inaperta var. typica Perrier (later changed to Impatiens inaperta Perr.); Madagascar: Mandraka, east of Tananarive, at about 1200 meters in vestigial elfin forest, no collection date (Perrier no. 18.309), at P. (M.G. Aymonin, pers. comm.).

Nomenclature: Both Impatientella and Impatiens inaperta are validly and effectively published. In 1933, Perrier reduced Impatientella inaperta to Impatiens inaperta in the monotypic Section Impatientella, thus effectively abolishing this monotypic genus.

Distribution: Only on Madagascar at Mandrake, Analabe, and Manerinerina from 1200-1600 meters.

Diagnostic characters: 1. Antivexillar sepal spurless. 2. Flowers always cleistogamous, minute and green. 3. Anthers without intralocular septae. 4. Anthers and filaments fused entirely; former extrorse and dehisce longitudinally. 5. Plants grass-like.

Discussion

Perrier described the monotypic genus, Impatientella, in 1927, but in his revision of the Malagasy Impatiens flora (1933) he united it with Impatiens, designating a separate section Impatientella for the one included species. He noted that species of Impatiens which bear cleistogams are rare, but not unknown in Madagascar. For example, in the section Preimpatiens (perhaps an unfortunate designation since it includes all of the types which we normally associate with the genus), one species, I. baroni Perr., occasionally produces cleistogamous flowers, but only under abnormal conditions such as are found late in the growing season or at elevations above its usual limits. In section Trimorphopetalum, I. substerilis Perr. is the only species known with certainty to produce cleistogams. In I. inaperta cleistogamy does not appear to be a strictly phenotypic character because plants of variety typica which were cultivated in the Tananarive Botanic Garden produced no chasmogams. Perrier noted that in I. inaperta there is a discordance between the perianth parts which are modified for self-fertilization and the androecium which is modified for outcrossing. He suggested that the small wingless insects which are frequently found inside the flowers are needed to effect both types of pollination. In addition to the presence of species which produce cleistogams in Malagasy sections of the genus, Perrier felt that there was sufficient continuity of characters between the species of Section Trimorphopetalum and I. inaperta to warrant the inclusion of the latter in Impatiens.

While I agree with Perrier that there is little basis for separating Impatientella from Impatiens, there are a number of questions specifically related to I. inaperta which require further study, including its pollination biology and the factors underlying cleistogamy (I. inaperta yet may prove to be merely a cleistogamous form of some other or even several Malagasy Impatiens species). Finally, I am very dubious of his designation of five varieties, which are based on minor differences in vegetative characters. Several of the varieties were found at the same localities, but obviously in different microhabitats. In my own experience (Russell, 1976), the vegetative characters in Impatiens vary greatly as a result of differences in such parameters as soil moisture and illumination even on the microscale. One cannot help but suspect that in the absence of conspicuous flowers, Perrier was led to overemphasize vegetative variability which may be ecologically interesting, but is taxonomically unimportant.

5. Petalonema Peter in Abh. Ges. Wiss. Göttingen, n.f. xiii; II: 84(1928).

a. P. fissibracteum Peter in Abh. Ges. Wiss. Göttingen, n.f. xiii, II: 84(1928); G.M. Schulze in Feddes Repert. 39: 21(1935).

I. briartii De Wild. & Th. Dur. in Bull. Soc. Roy. Bot. Belg. 38(2): 185(1899); E. Gilg in Engl., Bot. Jahrb. 43: 104(1909); Th. & H. Dur., Syll. 79(1909); De Wild. in Ann. Soc. Sci. Brux., Ser. B. 38, 2: 18(1914) and in Contr. Fl. Katanga 119(1921); G.M. Schulze in Consp. Fl. Angol. 2: 56(1954), in Bol. Soc. Brot., Ser. 2, 29: 12 (1955); Lauhert in Fl. Zamb. 2,1: 164 t 26(1963); Grey-Wilson in Impatiens of Afr.: 77(1980).

I. bagshawei Bak.f. in J. Linn. Soc. 37: 129(1905).

I. fissibractea (Peter) G.M. Schulze in Feddes Repert. 39: 21(1935).

I. exellii G.M. Schulze in Bol. Soc. Brot. Ser. 2,29: 6(1955) and in Consp. Fl. Angol. 2: 156, t. 35(1954).

b. P. racemosum Peter in Abh. Ges. Wiss. Göttingen, n.f. xiii. II: 84(1928).

I. racemosa DC. Index Kew. Suppl. viii (1926-30).

Illustrations: Launert in F. Zamb. 2, 1: 64, t. 26, fig. 18 (1963); Grey-Wilson in Impatiens of Afr.: 78, fig. 18 (1980).

Typus: Petalonema fissibracteum Peter; Tanzania: Buha Dt. Ujiji (Peter 27322) at B.

I. briartii De Wild. & Th. Dur.; Zaire: Shaba, Nzilo, Briart s.n. (BR, holotype; B, isotype); (Grey-Wilson, 1980)

Nomenclature: Petalonema Peter is invalidly published. Grey-Wilson (1980g) pointed out that the name was used earlier for different genera:

1. by Correns (1889) in the Cyanophyceae.

2. by Gilg (1897) in the Melastomataceae (= Neopetalonema Bren.). In addition Schlechter (1915) applied the name to a genus in the Asclepiadaceae (nomenclature not corrected). Grey-Wilson (1980g) has treated P. fissibracteum as synonymous with I. briartii De Wild. & Th. Dur. which was first described in 1899.

Distribution: Africa, Angola to Uganda (P. fissibracteum); Himalayas (P. racemosum).

Diagnostic characters: 1. Bracts and lateral sepals glandular. 2. Margins of bracts and lateral sepals with long, branch-like projections toward the base. Lateral sepals persistent. 3. Alae with long filliform appendages (Fig. 3).

Discussion

The diagnostic characters used to distinguish Petalonema from Impatiens are found in a number of species in the latter genus though rarely in combination (Fig. 3 and Table 5). Filliform appendages although rare occur in at least 15 species of Impatiens. As would be expected many of the species are phalenophilous or psychophilous. There is no doubt that taken as a whole these taxa are a paraphyletic group. The two African species are not related to each other or to the two species of Petalonema. Among the Deccan species filliform appendages developed in three different groups: the Scapigerae (I. agumbeana Bhask., I. barberi Hk.f., I. denisonii Bedd., and I. lawsonii Hk.f., the I. parvifolia aggregate) which also includes I. goughii Wt., I. omissa Hk.f., and I. viscosa Bedd., and in I. ligulata Bedd. which is in the Section Annuae. The two Himalayan

Figure 3

Diagnostic characters of *Petalonema* and some *Impatiens* species which share them in common

---

A-D: *Petalonema fissibracteum* Peter (*I. briartii* De Wild. & Th. Dur. (Africa).

A. Ala with filliform appendage.

B. Lateral sepals, showing blunt glandular apex and long teeth on margins.

C. Bracts with teeth.

D. Fruit with persistent sepals.

E. *I. glandusepala* Grey-Wilson showing toothed sepals with glands. (Africa)

F. *I. mackeyana* Hk.f. with toothed and glandular sepals. (Africa)

G. *I. joachimii* G.M. Schulze, ala with filliform appendage (Africa)

H. *I. microtheca* Hk.f., ala with filliform appendage (Deccan).

A - G, based in Grey-Wilson (1980); H, on Hooker in Ic.Pl. Ser. 4, x(1), t. 2910.


A
B
C
D
E
F
G
H

Table 5

Impatiens species which share some of the diagnostic characters of *Petalonema* Peter

Character	Region	Species
1. Filliform appendages	African	1. *I. joachimii* G.M. Schulze
		2. *I. pallida-rosea* Gilg
	Deccan	1. *I. agumbeana* Bhask.
		2. *I. barberi* Hk.f.
		3. *I. denisonii* Bedd[a]
		4. *I. goughii* Wt.[b]
		5. *I. lawsonii* Hk.f.
		6. *I. ligulata* Bedd.
		7. *I. omissa* Hk.f.[c]
		8. *I. parvifolia* Bedd.
		9. *I. viscosa* Bedd.
	Himalayan	1. *I. racemosa* DC.
		2. *I. tigens* Edgew.[d]
	Chinese	1. *I. imbecilla* Hk.f.
		2. *I. faberi* Hk.f.

Table cont'd.

Table 5 cont'd.

Character	Region	Species
2. Glandular sepals	African	1. I. glandusepala Grey-Wilson 2. I. mackeyana Hk.f.
	Himalayan	1. I. bicornuta Wall. 2. I. gamblei Hk.f. 3. I. hobsoni Hk.f. 4. I. urticifolia Wall. 5. I. racemosa DC. 6. I. wallichii Hk.f.
3. Sepals aristate	Burmese	1. I. drepanophora Hk.f.
	Himalayan	1. I. bicornuta Wall. 2. I. leptocarpa Hk.f. 3. I. pantlingii Hk.f. 4. I. racemosa DC.

Table cont'd.

Table 5 cont'd.

Character	Region	Species
4. Persistent sepals	Deccan	1. I. clavicornu Turcz.[e]

[a] Acc. no. 7340, MH(!) has very prominent appendage not seen in Hooker's accompanying sketch.

[b] I. microtheca Hk.f. (1910).

[c] Not present in all varieties.

[d] Hooker (1874-75) states that I. racemosa DC. (Prod. i:688,1824) and I. tigens Edgew. (Trans. Linn. Soc. xx: 41,1846; not seen by present author) are identical and so adopts the former epithet. Both species appear in Hooker (1904-06), but in I. racemosa DC. the appendages are short or absent. This contradicts De Candolle's protologue.

[e] Only occasionally.

and the two Chinese taxa are sister species, but have no close affinities to other groups with filliform appendages. Glandular sepals are present in at least eight Impatiens, but again it is obvious that they form parallel groups. The two African species have no relatives with this character as is also true for the Himalayan I. bicornuta Wall. and I. racemosa DC. The remaining four species form a single group.

In his revision of the African Impatiens, Grey-Wilson (1980g) noted that while persistent sepals may be a unique feature of P. fissibracteum Peter, glandular and toothed sepals occur in two other African Impatiens species. Consequently, he merged Petalonema with Impatiens.

This leaves unresolved the second species which Peter (1928) assigned to Petalonema, the Himalayan I. racemosa DC. It is not clear whether this species has filliform appendages (see footnote d, Table 5). The sepals are glandular, but aristate rather than toothed. Aristate sepals occur sporadically in Asian species of Impatiens, but these taxa are not related to the African species with toothed sepals. Finally, I find that Peter mistook the persistent bracts of certain species in Section 7 (which includes I. racemosa DC.) of the eastern Himalayan Impatiens to mean persistent sepals. Obviously, these are two very different characters. The only species in which I have observed persistent sepals is I. clavicornu Bedd. in the Scapigerae. Hence, there is no evidence to warrant relating I. briartii De Wild. and I. racemosa DC., nor in maintaining the genus Petalonema.

6. Semeiocardium Zollinger in Tijdschr. Nederl. Ind. xvii: 245 (1858); Backer in Gard. Bull. Straits Settlements, ix: 71(1935), descr. emend; Backer and van den Brink in Fl. Java: 251(1963).

Polygala L. in Index Kew. II: 867(1895).

a. S. arriensii Zoll. in Tijdschr. Nederl. Ind. xvii: 245(1858); Backer in Gard. Bull. Straits Settlements, ix: 72(1935); descr. emend.; Backer and van den Brink in Fl. Java: 251(1963).

S. glaucescens Hasskarl in Miquel Ann. Mus. Bot. Lugd. Bat. i: 151(1863).

S. hamiltoni Hassk. in Miq. Ann. Mus. Bot. Lugd. Bat. i: 151(1863).

S. hyalinum Hassk. in Miq. Ann. Mus. Bot. Lugd. Bat. i: 151(1863).

Polygala triphyllum Buch.-Ham. ex G. Don (Prod. Fl. Nep.: 200, 1825) in Index Kew. II: 867(1895).

Illustrations: None.

Typus: S. arriensii Zoll., not located. Zollinger collections at P; these were used by Miquel (their correspondence is at Univ. Lib. Utrecht, and may include additional observations). Zollinger's material was also sold privately and is at many herbaria (Stafleu et al., 1967). Backer's collections are at BO and PAS, with duplicates at P. There is no material of Semeiocardium at BO(!)

Nomenclature: Semeiocardium Zoll. is validly published. Semeiocardium (Polygalaceae) in Index Kew. II: 867(1895) is synonymous with Semeiocardium (Balsaminaceae).

Distribution: Madura (Sunda Islands) of the Indonesian Archipelago; stony or rocky habitats; calciphile.

Diagnostic characters: 1. sepals 3, lateral ones largely connate; costa carinate. 2. spur bifid. 3. wings connate. 4. stamens free.

Discussion

The characters used to diagnose Semeiocardium are found in a number of tropical Impatiens. For example, connate wings are found in a number of African ornithophilous or melittophilous species including I. keilii Gilg, I. niamniamensis Gilg, I. volkensii Warb., as well as a number of Asian phalenophilous or psychophilous species. Bifid (or even multifurcate) spurs are also widespread, occurring in such African species as I. tricaudata G.M. Schulze and I. digitata Warb. (Grey-Wilson, 1980g), as well as in the Chinese I. crassicornu Hk.f., and a number of southeast Asian species including I. pygmae Hk.f., and I. harmandi Hk.f. and I. scortechnii Hk.f. These characters have undoubtedly arisen several times independently. With specific reference to Semeiocardium Zoll., the most interesting group of Impatiens occurs in southeast Asia and adjacent portions of China (Table 6 and Fig. 4). These share to varying degrees the characters of Semeiocardium. The greatest similarity is found in I. harmandi Hk.f. and I. zygosepala Hk.f., which differ from Semeiocardium in only one character, the degree of fusion in the stamens. Those of S. arriensii Zoll. are free, those of I. harmandii Hk.f. are didymous, and those of I. zygosepala are connate. It has been overlooked by virtually all taxonomists except Hooker that not all Impatiens have connate anthers. Aside from species enumerated in Table 6, additional didymous species are listed in Table 7. Taken as a whole, the didymous species clearly

Table 6

Some *Impatiens* of Southeast Asia which resemble *Semeiocardium*

Species	Character					
	Lateral sepals connate	Spur bifid	Costa carinate	Wings connate	Androecium	Habitat preference
1. *I. boni*[1]	-	+/-[2]	+	+/-[3]	c/d[4]	Ca
2. *I. harmandi*	+	+	+	+	d	Ca
3. *I. lanessiani*	-	+	+	+	d	Ca
4. *I. macrosepala*	-	+	+	+	d	Ca
5. *I. musyana*	-	-	-	+	c	Ca
6. *I. pygmaea*	-	+	-	+	c	Ca
7. *I. spireana*	-	+	+	+	c	?
8. *I. zygosepala*	+	+	+	+	c	Ca

[1] Authority for all species = Hk.f.; + = character present; - = character absent; [2] two lobes are very attenuated (Hooker, 1910c); [3] alae connate or very rarely free (Hooker, 1910c); [4] connate or didymous; Hooker (1910c) queries the character state of the anthers; the legend accompanying the diagram is clearly mislabeled with anthers as gynoecium, gynoecium as fruit, capsule as seed; the illustration shows both didymous and connate anthers; obviously, this species must be reexamined; c = connate; d = didymous; Ca = calciphile; ? = character state not known.

Figure 4

Some *Impatiens* species which resemble
Semeiocardium arriensii Zoll.

A – C, *I. harmandii* Hk.f.

A. Fused lateral sepals

B. Fused alae

C. Bifid spur

D – F, *I. zygosepala* Hk.f.

D. Fused lateral sepals

E. Fused alae

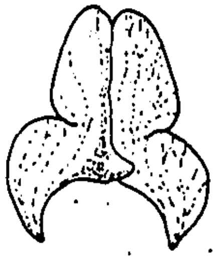
F. Bifid spur

G – H, *I. lanessani* Hk.f.

G. Fused alae

H. Bifid spur

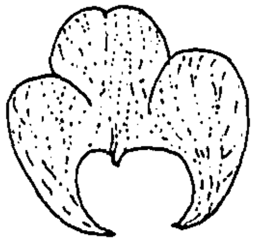
A



B

C

D



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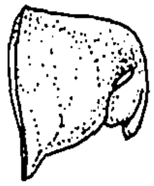

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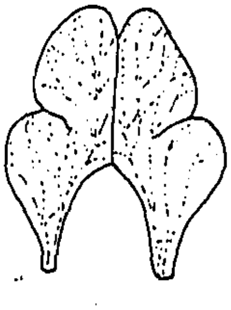

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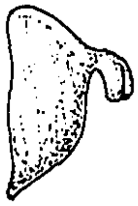


H

Table 7

Additional species of Impatiens with didymous anthers

Region	Species
Western Himalayan	1. *I. coriosepala* Hk.f.[a]
	2. *I. langeana* Hk.f.
	3. *I. reidii* Hk.f.
	4. *I. stoliczkai* Hk.f.
	5. *I. vesillaria* Hk.f.
Deccan	1. *I. debilis* Turcz.
	2. *I. perrottetii* Turcz.
China	1. *I. imbecillia* Hk.f.

[a] It is not clear whether this species has connate or didymous anthers.

represent a paraphyletic group. The Western Himalayan species probably represent a single evolutionary line. The two Deccan species (which belong to Section Annuae) are not closely allied to the preceeding group. The southeast Asian species (Table 6) form a third assemblage. The Chinese calciphile species I. imbeccillia Hk.f. (Table 7) may be related to this group since it displays some vegetative and floral similarities, but this cannot be said with certainty at the present time.

The presence of species of Impatiens in Southeast Asia which share in varying degrees a set of characters approaching that of Semeiocardium, suggests that the one species of the latter genus is probably an evolutionary endpoint of a group of calciphile Impatiens species. Obviously, this group of balsam species needs a very critical reevaluation, especially I. bonii Hk.f. for which I feel the protologue is very unsatisfactory. Furthermore, the Sunda Islands to which S. arriensii Zoll. is native are botanically poorly known. It may well be that there are additional species which would shed more light on the Semeiocardium problem, but even with the data at hand, it is evident that S. arriensii shows definite affinities to certain Impatiens species and it is highly misleading to isolate it as a monotypic genus.

7. Trimorphopetalum Baker in J. Linn. Soc.xxii: 454(1887); Perrier in Arch. Bot. t. vii, mém. 1: 64(1933).

a. T. dorstenioides Bak. in J. Linn. Soc.xxii: 455(1887).

I. dorstenioides (Bak.) Warburg in Prantl and Engler, Nat. Pflanzenf. iii(5): 391(1895); Hooker in Ic. Pl. xxix, t. 2828(1907). Perrier in Arch Bot. t. vii, mém. 1: 79(1933).

Nomenclature: Hooker (1907) is not strictly correct in stating that Baker (1887) described the genus incorrectly. The Latin protologue for Trimorphopetalum is correct, but the English protologue for T. dorsteniodes contains an erroneous reference to the upper "sepal" rather than the vexillum, an understandable confusion since the vexillum and antivexillar sepals are very similar. Hence, Trimorphopetalum is validly and effectively published in my opinion.

Illustrations: Hooker in Ic. Pl. xxix, t. 2828(1907).

Typus: T. dorstenioides Bak.: Madagascar, no locality given (Rev. R. Baron, no. 4476). Location of type unknown.

Distribution: Madagascar; Perrier did not find the type species while collecting. The remaining species of section Trimorphopetalum are confined to the eastern and central portions of the island (Perrier, 1933).

Diagnostic characters: 1. Antivexillar sepal galeate lacking any gibbosity, and spurless. 2. Flowers small, inconspicuous and colored green, yellow, or reddish.

Discussion

This genus which Baker described on the basis of a single species, is in fact a large group of forty-six species (Perrier, 1933) confined to Madagascar. The most remarkable feature, which Hooker (1907) failed to appreciate, is the antivexillar sepal which does not display the peculiar morphology so characteristic of Impatiens. The odd sepal and vexillum are rigid and veined with brown in a manner not seen in other Balsaminaceae (Fig. 5). This is to be expected since the

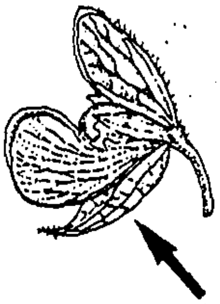
Figure 5

Trimorphopetalum dorstenioides Baker

A. Side view (arrow indicates galeate antivexillar sepal).

B. Front view (arrow indicates vexillum).

Based on Hooker (1907).



A

B

markings in species with gibbose antivexillar sepals are arranged as guides to the floral nectary which is located in the tip of the spur.

Except for the standard and antivexillar sepal Trimorphopetalum species do not differ from the Humblotianae (bucciniform-spurred) and Vulgares (navicular-spurred) species which make up the other two major groups found on Madagascar. For this reason Perrier (1933) combined Trimorphopetalum with Impatiens, but as a separate section intermediate between Preimpatiens and Impatientella.

One can speculate as to whether the galeate spur is a plesiomorphic or apomorphic character: The perianth as a whole is highly zygomorphic and obviously apomorphic. Furthermore, the absence of truly galeate-spurred species of Balsaminaceae except on Madagascar suggests that Trimorphopetalum arose after the breakup of Gondwanaland and is therefore not as ancient as the groups of Impatiens which are shared by Africa, Madagascar, and southern Asia. [I cannot accept Hooker's contention that I. dorstenioides Bak. (or I. dorstenioides (Bak.) Warb.) is related to I. balsamina L. merely because both have a solitary inflorescence; otherwise they are entirely different]. On the other hand, it cannot be said with certainty that this is not an example of heterobathomy and that Trimorphopetalum has survived in isolation on Madagascar while its relatives became extinct elsewhere.

Concluding Remarks

Seven genera have been recognized in the Balsaminaceae. Their taxonomic validity has for the most part been the subject of the individual perferences of various authors, who usually confined themselves to a relatively small group of taxa without a thorough grounding in the enormous variability which exists in the Balsaminaceae as a whole.

It would be premature at this stage to propose any major reorganization of the family. From the preceeding review I am left with the following impressions:

1. Balsamina which includes most of the tropical species is a highly heterogenous group. The various evolutionary lines may share a common character (Type I fruit capsule), but this must be verified by a study of many more taxa.

2. Hydrocera is a monotypic genus which in many ways resembles I. balsamina. If one does recognize Hydrocera as a distinct genus, then one may be led to making comparisons with Impatiens as a whole (as Grey-Wilson has done), and it is not at all clear that we are in fact discussing comparable evolutionary units. The free petals have suggested to at least one author that Hydrocera is more primitive than Impatiens (Raven, 1975). Since the perianth is in most other ways highly modified, it is more likely that this feature represents an instance of heterobathmy or even reversion to a primitive character state.

3. Impatiens sensu stricto (species with Type II fruit capsules) may well prove to be a fairly homogeneous group. Impatiens sensu lato, by including species with Type I capsules, leaves us with the same problems as encountered in Balsamina.

4. Impatientella is so poorly understood that one hesitates to discuss its status, but it clearly is not an evolutionary unit comparable to Impatiens or Balsamina.

5. Petalonema appears to be a taxon which has merely developed

certain anomalous structures. It is difficult to imagine that it represents an adaptive peak.

6. Semeiocardium shares a number of critical characters with certain calcophile Impatiens species in adjacent portions of Southeast Asia. Since there is no radical discontinuity, it is difficult to justify conferring generic states on the single included species.

7. Trimorphopetalum is a distinct group distinguished by one character (a galeate antivexillar sepal) which is apparently not found elsewhere in the family. Furthermore, it is confined to Madagascar. It has perhaps of all the genera the greatest authenticity, but again it does not appear to be an evolutionary unit comparable to Balsamina or Impatiens sensu lato.

The resolution of the generic problem can only follow a thorough examination of all the species in the family, using many more characters than has been the case in the past. Serious consideration should be given to biotic and historic factors which have led to evolutionary divergence, and to the significance of the various phenetic groups in terms of evolutionary peaks. Perhaps this will be a better basis for judging taxonomic rank than the previous haphazard methods. At the same time the effect of any proposed scheme on nomenclature should be considered. A major problem is that Impatiens as now accepted is a very heterogeneous taxon. For example, it may well be that there is a greater difference between the relatively actinomorphic species and the red-or orange-flowered bucciniform species than there is between Impatiens and the remaining genera. Dividing Impatiens into several genera will lead to a nightmare in terms of the nomenclature. Perhaps a better solution, which would conserve names but at the same time reflect natural groupings, would be to treat the Balsaminaceae as a monotypic family, in which the major evolutionary units would be organized as subgenera, series, and sections within Impatiens.

AFFINITIES

The majority of taxonomists have seen the Balsaminaceae as allied to the Geraniales. Linnaeus (1753, 1754) dealt only with the genus Impatiens which he placed (in his admittedly artificial system) last in the class "Syngenesia Monogamia", following Viola. Neither Jussieu (1789) nor De Candolle (1824) organized their "natural orders" (the modern equivalent of which is the family) into higher categories specifically, but they did arrange them in a sequence in which one can see the germ of the modern orders. In both treatments the Balsaminaceae, Ordo 48, Class 13 (Dicotyledones, Polypetalae, Hypogenae), is placed between the Tropaeolaceae and Oxalidaceae. Bentham and Hooker (1862) treated the Balsaminaceae as a tribe of the Geraniaceae, a scheme which Hooker retained in the Flora of British India (1874-75). Most subsequent taxonomists (including Bessey, 1915; Hutchinson, 1926, 1973; Cronquist, 1968; Dahlgren, 1975, 1978; Thorne, 1976 and Takhtajan, 1980) in outlining natural (i.e. phylogenetic) schemes have treated the Balsaminaceae as a distinct family in the Geraniales. This treatment was accepted by Bhaskar (1975) and Grey-Wilson (1980g) in their respective studies on the Deccan and African Impatiens.

A minority school of thought has allied the Balsaminaceae with the Polygales or the Sapindales (depending on which of these two Orders was thought to include the families Tremandraceae, Trigoniaceae, and Vochysiaceae). This arrangement has been subscribed to by Warburg and Reiche (1895), Melchior (1964) and Gibbs (1974). Finally, Hallier (1912) proposed that the Balsaminaceae (which included four tribes: the Balsamineae, Tropaeoleae, Limnantheae, and Parnassieae) was a member of the Passiflorales, and was descended from the Malvales. This final somewhat astonishing hypothesis seems to bring us back to Linnaeus's observation of the superficial resemblance between Impatiens and Viola, but is perhaps no more bizarre than other similarities which have been suggested.

Cronquist (1968) alone has discussed the problem in some detail:

> "On a purely morphological basis, the Balsaminaceae might be accommodated in either the Geraniales or the Polygales as here conceived. They would be wholly isolated in the Polygales, however, whereas they do have certain similarities to the Tropaeolaceae in the Geraniales. The most obvious of these is the conspicuous retrose spur on one of the sepals. The two families also have very similar pollen. On the other hand, they differ in so many other ways that one is tempted to treat the similarities as accidental."

As the preceeding quotation indicates, it is the presence of a spur both in the Balsaminaceae and Tropaeolaceae that has been the main criterion for placing the former family in the Geraniales. The pollen similarities referred to by Cronquist were not seen by Huynh (1968a,b, 1970) who proposed that the Balsaminaceae be elevated to ordinal rank. In view of these diverse opinions, it was decided to make a preliminary survey of the Tropaeolaceae and the Vochysiaceae (which was judged among the Polygales to bear the closest resemblance to the Balsaminaceae).

Materials and Methods

Herbarium specimens of the Tropaeolaceae were borrowed from GH and of the Tremandraceae, Trigoniaceae and Vochysiaceae from DAO. The species which were examined are given in Table 8. In addition, fresh material of a number of Impatiens species and of Tropaeolum majus L. was examined.

Observations

A comparison of selected character states is given in Table 9 (the Trigoniaceae and Tremandraceae bore no resemblance to the other three families and hence are excluded from the discussion). As can be seen the Tropaeolaceae and Vochysiaceae differ from the Balsaminaceae in approximately an equal number of characters. This preliminary survey yielded two particularly interesting observations:

1. The spur in the Tropaeolaceae is not derived from the calyx, but from the receptacle. This was readily seen in fresh material of T. majus L. when one looked down the perianth. The spur arises below a faint ridge (Fig. 6) which is clearly a lateral extension of the receptacle. The same phenomenon was observed in herbarium specimens of the Tropaeolaceae although the ridge was less evident than in fresh material. Specimens in which it was clearly evident included: T. azureum Miers (Wagnerknecht, no. 4294), T. leptophyllum G. Don (Aravena, no. 33336), T. moritziana Klotzsch (Morazán, no. 13758), T. tricolorum Sweet (Montero, no. 138), T. warmingianum Rohrb. (Williams, no. 6771), and T. weberbaueri Loesn. (Plowman & Davis, no. 4892). The ridge has been omitted from most of published illustrations of the Tropaeolaceae, and consequently, one is left with the impression

Table 8

Species of Tremandraceae, Trigoniaceae, Tropaeolaceae and Vochysiaceae of which herbarium specimens were examined

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A. Tremandraceae

Tetratheca: *T. ciliata* Lindl., *T. denticulata*, *T. ericifolia* Sm., *T. glandulosa* Lab., *T. gunnii* Hk.f., *T. hirsuta* Lindl., and *T. juncea* R. Br.

B. Trigoniaceae

Trigonia: *Trigonia floribunda* Oerst.

C. Tropaeolaceae

Magallana: *M. hialata* Buchn., and *M. porifolia* Cav.

Tropaeoleum: *T. argentinum* Buchen., *T. azureum* Meirs, *T. benthii* Klotzsch, *T. brachyceras* Hk.f.& Arn., *T. capillares* Buch., *T. cochabambae* Buch., *T. crenatiflorum* Hk.f., *T. dipetalum* R.& P., *T. haynianum* Bernh., *T. hookeriana* Barn., *T. huigrense* Killip, *T. incisum* (Speg.) Sparre, *T. kingii* Phil., *T. lepidum* Phil., *T. leptophyllum* G. Don, *T. looseri* Sparre, *T. majus* L., *T. meyeri* Sparre, *T. moritziana* Klotzsch, *T. myriophyllum* (P.& E.) Sparre, *T. papillosum* Hughes, *T. peltophorum* Benth., *T. pentaphyllum* Lam., *T. peregrinum* L., *T. polyphyllum* Cav., *T. pubesens* H.B.& K., *T. seemanni* Buch., *T. sessifolium* Poepp.& Endl., *T. smithii* DC., *T. speciosum* Poepp.& Endl., *T. tricolorum* Sweet, *T. tuberosum* R.& P., *T. umbellata* Hk.f., *T. warmingianum* Rohrb. and *T. weberbaueri* Loesn.

D. Vochysiaceae

Erisma: *E. calcartum* (Link.) Warm.

Vochysia: *V. guatamalensis* Sm., *V. hondurensis* Sprague, and *V. thyrsoidea* Pohl.

Table 9

A comparison of the families Balsaminaceae, Tropaeolaceae, and Vochysiaceae

Character	Family		
	Balsaminaceae	Tropaeolaceae	Vochysiaceae
habit	herbaceous to suffrutescent	herbaceous lianas	lianas; suffrutescent to small arborescent
phyllotaxy + petiole insertion	opposite alternate verticillate never peltate	alternate peltate	opposite alternate verticillate never peltate
leaf margins	toothed	lobed or dissected	entire
stipules	absent or reduced to glands	absent	absent or reduced
inflorescence	varied	solitary	compound racemes
resupination	some species	absent	absent
flowers	perfect zygomorphic	perfect zygomorphic	perfect zygomorphic
sepals	2-5 (free or connate) 1 spurred	5 (free) 1 spurred[a]	5 (connate) 1 spurred
petals	5 (connate)	5 (free)	1-5 (free)

Table cont d.

Table 9 cont'd.

	Family		
Character	Balsaminaceae	Tropaeolaceae	Vochysiaceae
stamens	5 (connate)	8 (free)	1 + 2-4 staminodes (free)
ovary	superior 5 fused carpels (1 locule/carpel)	superior 3 fused carpels[1] (1 locule/carpel)[1]	usually superior 1-3 (fused) carpels[3] (1 locule/carpel)[3]
placentation	axile	axile[1]	axile[3]
ovules	numerous	1[1]	1-numerous[3]
stigmas	1-5	3	1
fruit	dehiscent capsule or berry	schizocarp or samara	capsule or samara[3]
endosperm	none	none[1]	usually none[3]
embryo	straight	straight[1]	straight[3]
chromosome number (*n*)	3-33	12,13,14[2]	unknown

[1] Jury (1978).

[2] Raven (1975).

[3] Chant (1978).

[a] According to literature.

Figure 6

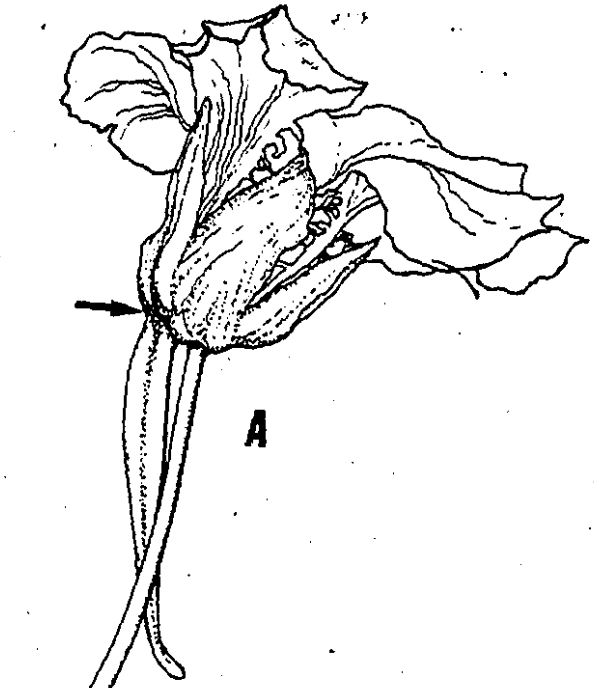
The spurs of _Tropaeolum_ and _Impatiens_

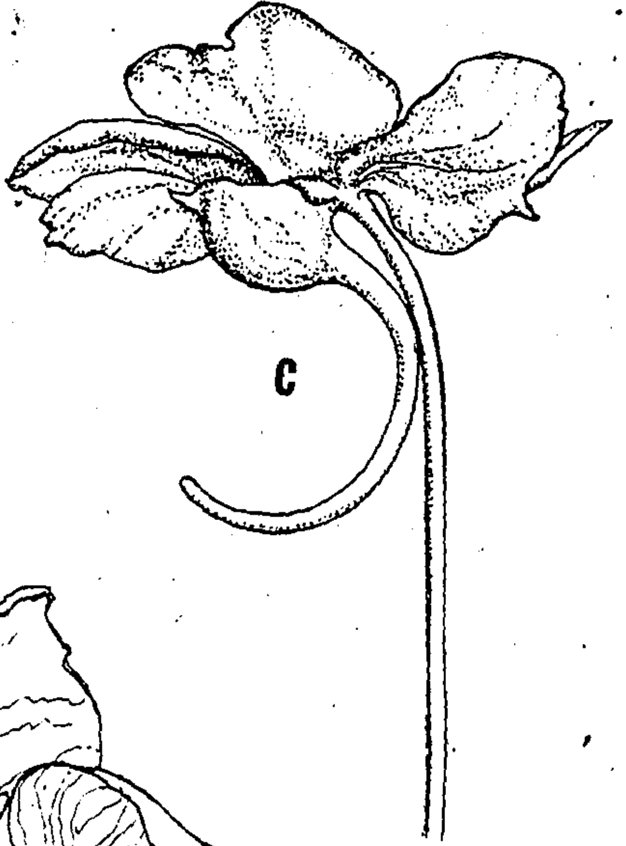
A - B, _Tropaeolum majus_ L.

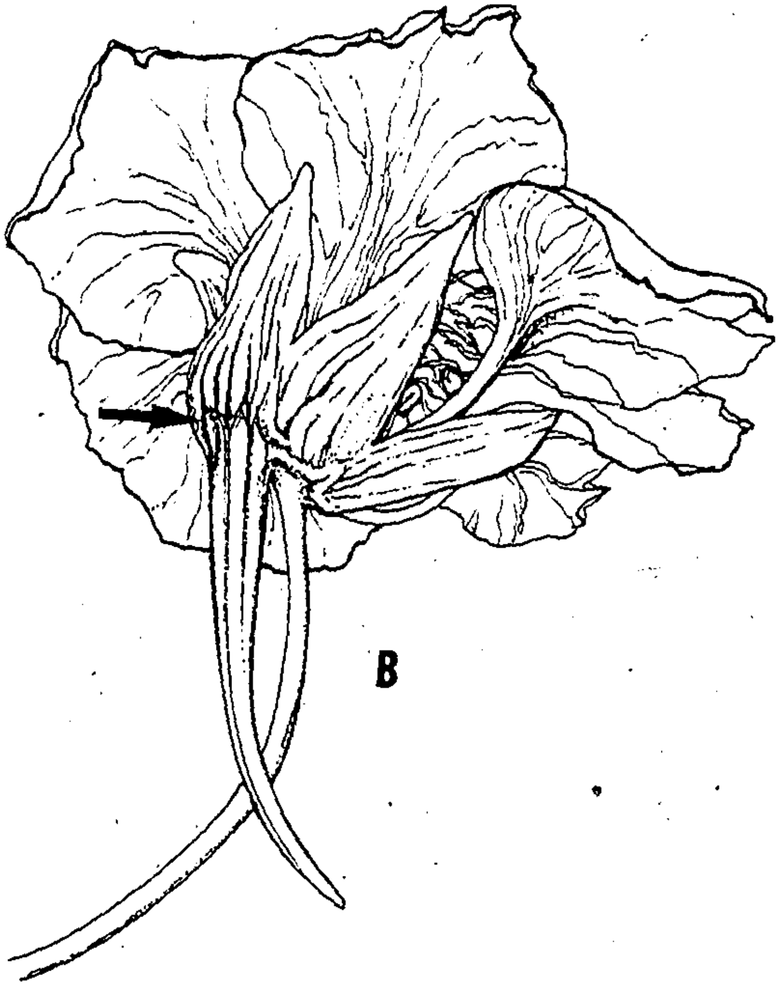
A. Lateral view showing faint ridge which is an extension of the receptacle (arrow) and spur arising from the ridge.

B. Posterior view (arrow indicates ridge).

C. _Impatiens hawkeri_ Bull with spur arising from sepal.


A


C


B

that the spur arises directly and smoothly from one of the sepals. This may help explain the erroneous assumptions which have been made concerning its origin. In contrast, it was found that in the Balsaminaceae and Vochysiaceae the spur was found to be derived wholly from sepalar tissue (Figs. 6). Support for these observations was later found in Payer (1857). As can be seen (Fig. 7), during development the receptacle in Tropaeolum expands asymmetrically and the spur arises from the resulting swelling. This is a very different situation than is found in Impatiens (Payer did not study the Vochysiaceae). Thus there is good evidence for stating that the spurs are nonhomologous and merely a parallel development. Obviously, a thorough study of the flower development in the families of the Geraniales and Polygalales might yield valuable insights into their true relationships.

2. It was found that neither in the Tropaeolaceae nor the Vochysiaceae was the presence of a spur associated with resupination. This lends further support to my earlier thesis that the development of resupination in the Balsaminaceae was not a necessary consequence of the evolution of a spur as was earlier postulated by Grey-Wilson (1980g).

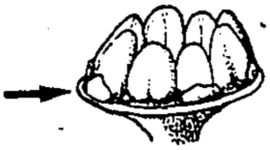
I found the genus Erismadelphus Mildbraed, which appears to be a relatively primitive member of the Vochysiaceae Mildbraed, of particular interest to the question of affinities. This genus (with three species) is the only African representative of the family, and is restricted to a small area in Cameroon. The species E. exsul Mildbraed is illustrated in Fig. 8. In many ways, this species resembles what I imagine to have been the ancestor of the Balsaminaceae.

Figure 7

The development of the spur during floral ontogenesis as reported by Payer (1857)

A. Early development showing anther, petal initials, and receptacle (arrow). Sepals have been removed to facilitate observation.

B. Later development showing lateral bulging of receptacle (thick arrow) with spur (thin arrow) arising below.



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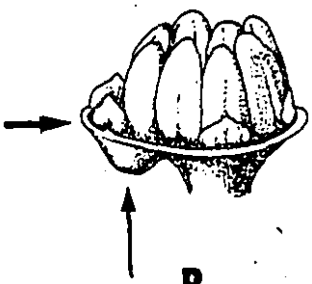


B

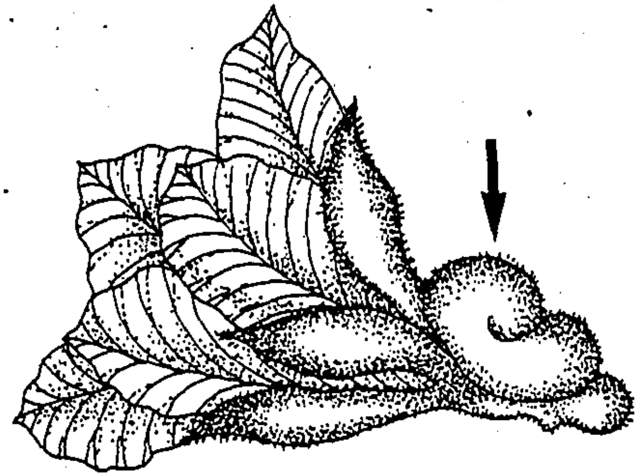
Figure 8

Erismadelphus exsul Mildbraed (Vochysiaceae)

A. Flower (arrow indicates nectary).

B. Longitudinal section showing ovary, fertile stamen, and staminodes.

Based on Chant (1978).



A

B

A gibbose nectary develops on one of the sepals, and there are five free petals. The ovary is reported to be inferior (Chant, 1978), whereas in Balsaminaceae it is superior. It is quite evident in cross-section (Fig. 7) that the inferior ovary could well be a secondary modification associated with the development of a gibbose nectary and the subsequent displacement of the gynoecium and androecium. It should be stressed that these comments are not an endorsement of Warburg and Reiche's (1895) hypothesis that the Balsaminaceae is more nearly related to the Polygalales than to the Geraniales, but merely an indication of the limited and often uncritical data bases which have been used in generating phylogenies.

CONCLUSIONS AND SUMMARY

1. The genus Impatiens in the family Balsaminaceae has the reputation of being one of the most taxonomically difficult genera in the angiosperms. Its classification has been impeded by the poor quality of herbarium specimens, and an overly regional and phenetic approach to its taxonomy. As a consequence, in the present studies herbarium and literature work was supplemented by field studies in peninsular India, Sri Lanka, Malaysia and Indonesia. Seeds were collected whenever available, but those of many species failed to germinate, necessitating a second trip to India to obtain sufficient material for study. Plants were collected and imported into North America as sterile-rooted cuttings. Additional cuttings were obtained from several institutions. Live plants have been an enormous aid in understanding the genus.

2. Neither the classification developed by Hooker (1874-75; 1904-06) nor by Warburg and Reiche (1895) was found adequate. Hooker was unable to interpret the flower itself in a meaningful way, and so he turned to the inflorescence as the basis for his classification. Warburg and Reiche only made minor modifications in this system. A very different approach was used by Perrier (1933) in his study on the balsam flora of Madagascar. He recognized two major flower types: one in which the corolla was relatively flat and the spur long and filliform; and a second with a much reduced corolla, a deeply cucullate vexillum, and a short-spurred, funnel-shaped antivexillar sepal. In terms of modern concepts of pollination biology, the former is a

butterfly-pollinated flower; the latter, a bee-pollinated one. Grey-Wilson (1980g) has made effective use of this pattern in his revision of the African Impatiens, contributing subclasses of flowers that are based on additional pollinator groups.

The flower of Impatiens is highly zygomorphic, and this has led to varying interpretations of the perianth segments. Knuth postulated that the vexillum consists of two fused sepals which were absent in all Impatiens then known. Later Thomson and Hooker (1859) reported that there were species with four lateral sepals, and they concluded that the vexillum is merely a modified petal. In the present study, it was shown that there are at least three types of flowers which can be distinguished on the basis of the number of calyx segments; those which always have five sepals, those which always have three, and those which may have five or three. A survey was made of all species in the genus, and the number of sepals was recorded. It was found that the condition is by no means as rare as was thought; but it was not found that this character state was associated with species which have the classical butterfly-pollinated flower and which are presumably primitive. Furthermore, studies (Payer, 1857; Grey-Wilson, 1980e) purporting to observe traces of the missing sepals were carried out on a single species, I. glandulifera Royle. According to the present study this species has at times three sepals, at others five. The problem is underscored by Grey-Wilson's earlier (1977) report that he was unable to find any rudimentary vascular traces in I. walleriana Hk.f. a species with a primitive flower which always has two sepals. Studies must be made using species in each of the three categories outlined above.

Living material of only one species with four lateral sepals was available for observation. The inner pair were found to be smaller and more membranous than the outer ones, and to open much later in floral ontogenesis. This led to a review of all reports on species with four sepals and it was found that in all cases the outer and inner ones differ. Furthermore, all species having this character state have a compound inflorescence. This, together with observations on teratoid flowers of I. balsamina L., suggests that the outer sepals may in fact be bracts. It was then suggested that the missing sepals may instead be represented by the costa of the vexillum.

3. The fruit of a number of species was examined at maturity, and it was found that the fruit is of two types. In Type I, the dehiscence begins at the midpoint of one suture, and proceeds outward, eventually causing the fruit to double over. The placenta and much of the seed is trapped until the fruit abcisses several days later. This type of capsule easily could have given rise to the fruit of Hydrocera if certain published drawings are correct. In Type II capsules, all five valves split at the sutures beginning at the base and proceeding almost to the apex. Seed and capsule are thrust violently away from the parent plant. This is the type of fruit that has been thought to characterize Impatiens, but it may occur in only some relatively advanced phylogenetic lines. The fruit is very much in need of further study. There are a large number of species for which fruit characteristics have never been observed, and it would not be surprising to find additional fruit types.

4. The cytotaxonomy of the genus was reviewed, and it was found that different chromosome numbers do not uniquely characterize the sections.

Consequently, if chromosomes are to be a useful character, they must be individually identified. Idiograms were prepared of ten species for which a sufficient number of good metaphases was availabe. Chromosomes varied from metacentric to submetacentric, and satellites were present in a number of complements, but no interpretable pattern was observed. Obviously, it will be necessary to study many more species. On the other hand, comparison of idiograms of four closely related species in the I. walleriana aggregate from Africa, indicate that karyotypes per se may be difficult to interpret. Three of the species have satellite chromosomes, which based on length and arms ratios are not strictly homologous. Chromosome banding was then attempted in order to obtain additional markers for distinguishing individual chromosomes. Giemsa banding has so far been unsuccessful, but Hy-bands were observed in a number of species following a standard procedure for staining with basic fuchsin. It was then possible to identify the homeologous chromosomes in the prometaphases of three plants of I. leschenaultii Wall. ($2n = 6$) from the same population. The fact that the chromosomes are apparently not strictly homologous, that is, that they show minor variation suggests that rather than attempting detailed mapping of every band on each chromosome of the complement, marker chromosomes should be identified and their distribution in the genus analyzed. Chromosome 2 in I. leschenaultii is one such marker chromosome, and two other potential candidates were observed. All of these marker chromosomes were found only in some groups of species. This may prove to be a relatively quick means of gaining information on the cytoevolution of Impatiens.

Meiotic abnormalities were observed for the first time in non-cultivated species. The irregularities included: lagging chromosomes, bridges, secondary associations, micronuclei, additional cells at the quartet stage, and pollen grains varying in size. In the latter both large and small pollen grains stained with cotton blue, and preliminary germination tests were positive in both cases. Pollen dimorphism has not been reported in Impatiens. Techniques must be developed to remove the pollen exine so that most, not only a few chromosome counts, can be carried out to determine the distribution of chromosomes in the pollen grains of different sizes. Alternatively, DNA determinations using Feulgen cytophotometry may prove useful. The resulting data may facilitate our understanding of aneuploidy and dysploidy in Impatiens.

5. In his later years, Hooker stressed the endemism found in Impatiens, and the theme was carried on by subsequent writers. After a survey of the genus as a whole, it is evident that two different phenomena have been confused. The major phylogenetic lines are not restricted to one phytogeographic region, but are fairly wide ranging. Six of these groups are described and discussed as examples. On the other hand, the individual species in the tropics do tend to be localized and few occur in more than one phytogeographic region. In the tropics, Impatiens is an orophytic genus, and the mountain systems of the tropics are relatively isolated. The vegetation formation in which Impatiens occurs is a subtemperate type which cannot survive in the tropical lowlands. Hence montane habitats are analogous to islands in a phytogeographic sense. In contrast, in the temperate zone, the climate of lowlands is suitable to Impatiens, and there are no endemic

species at higher latitudes.

6. Seven genera have been recognized in the family Balsaminaceae. A review of these demonstrated that most were described by authors unfamiliar with the great variability which is found in the largest genus, Impatiens. It is curious that taxonomists have chosen to accord generic rank to such minor discontinuities as characterize Hydrocera and Petalonema while ignoring the distinction between the butterfly- and bee-pollinated species of Impatiens, which is probably the oldest dichotomy in the Balsaminaceae. It is clear that if one is to keep some of these obscure genera merely for the sake of tradition, then the genus Impatiens as now constituted would have to be broken up into several genera on the basis of major flower and fruit characters. This solution would be disastrous in terms of nomenclature, and cannot be advised. The alternative is to recognize only one genus, Impatiens, in the Balsaminaceae thus allowing a within-group reorganization which will conserve the nomenclature of the overwhelming number of taxa.

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