TAXONOMIC STUDIES IN THE TRIBE VICIEAE (LEGUMINOSAE)

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ABSTRACT

The aim of the thesis is to trace the historical progress of systematics in the Vicieae; to investigate the characters of its species; to criticise the present taxonomic structure, replacing it with a more natural classification, and one in which the neglected American representatives are taken fully into account; and finally, to interpret patterns of character-variation and geographical distribution in terms of the evolutionary development of the tribe.

The Vicieae, as defined by De Candolle (1825), comprised the genera Vicia, Lathyrus, Lens, Pisum and Cicer. Most modern authors accept this delimitation, some also recognising Vavilovia, which was segregated from Pisum by Fedorov (1939). Vicia and Lathyrus, which are much larger than the remaining genera, each contains about 140 species. Their infra-generic classifications have been extremely mutable, and the two are linked by a phenetically striking group of species which Linnaeus (1753) and others placed together in the genus Orobus (now a synonym of Lathyrus). The relationship of Lens to Vicia and/or Lathyrus, and the position of Cicer within the subfamily Papilionoideae, have long been subjects of controversy.

The Vicieae are popular for experimental work, due to the presence of several economically important species (e.g. Vicia faba, Lathyrus odoratus, Pisum sativum, Lens culinaris and Cicer arietinum); their literature, in consequence, is voluminous. I have collated this information (which includes many

cyto-genetic data), and made fresh observations on the macro- and micro-morphology of vegetative and reproductive parts and on the anatomy of the tribe. Some serological experiments were also carried out, using antisera to Lens culinaris and Cicer arietinum. New and significant details of vascular anatomy and chemistry have been discovered, as well as interesting correlations between variation in different morphological and other characters. The thesis contains 100 figures, including 43 distribution maps, and 36 tables.

On the basis of these studies, the following taxonomic decisions have been made. The Vicieae, as a natural assemblage, should exclude Cicer; this now becomes the tribe Cicereae. A new monotypic genus, Anatropostylia, is recognised, based on the species A. (Vicia) koeieana. The traditional mutual delimitation of Vicia and Lathyrus is confirmed, and it is argued that the 'oroboid' species in each are similar as a result of parallel evolution. Lens is demonstrated to be a valid, distinct and probably ancient group, not closely related to the 'ervoid' members of Vicia. The generic status of Vavilovia is accepted. Vicia is classified into two subgenera: Vicilla, with sixteen sections, and Vicia, with five. Lathyrus is represented by thirteen sections, while the subgenera proposed by Bässler (1966) and Czefranova (1971) are abandoned.

The evolution of the Vicieae is discussed in the last chapter. It is proposed that the ancestral stock of the tribe arose in the cool-temperate flora of high northern latitudes at the beginning of the Tertiary. During the latter half of

this period, members of the Vicieae are thought to have migrated south under the influence of deteriorating climatic conditions, and, being present in the zone of Alpine orogenesis and major Tethyan changes, sustained a phase of enhanced evolution. Thus the contemporary centre of diversity of the tribe is in the Mediterranean - S.W. Asian area; the majority of Eurasian species are Mediterranean and Irano-Turanian elements, while a smaller proportion, composed mainly of less advanced species, is Euro-Siberian. A similar development probably occurred in the New World: American and Eurasian parts of Vicia and Lathyrus have been isolated since the Eocene epoch, and their S. American representatives, which are more specialised than those of N. America, are believed to have evolved autochthonously since the Pliocene.

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Chapter 1

INTRODUCTION

The tribe Vicieae is one of the most advanced groups of the Leguminosae, Subfamily Papilionoideae. It comprises some 350 species of annual and perennial herbs which are native to temperate regions of Eurasia and America. The Vicieae include several economically important species, notably Vicia faba (broad or horse bean), Lathyrus odoratus (sweet pea), Pisum sativum (garden pea), Lens culinaris (lentil) and Cicer arietinum (chickpea). Their presence has served to focus attention upon the tribe, and its members have consequently been favourite material for many kinds of pioneering experimental work, such as investigations into cytogenetics and plant chemistry. The literature pertaining to the Vicieae is voluminous. However, despite its comparative popularity, the tribe is far from having a stable, satisfactory classification, and its delimitation and internal structure have been subjects of controversy since the beginning of systematics.

The aims and format of this thesis are as follows:

1. To set out the taxonomic problems of the Vicieae. In Chapter 2, I trace the historical development of classification in the tribe, emphasising the areas of taxonomic difficulty.

2. To collate existing information about the characteristics of the Vicieae, and to amplify this with fresh observations. Chapters 3 and 4 are devoted to a detailed examination of the vegetative and reproductive structures of the plants. I found variation of taxonomic significance inmany different morphological characters, especially in leaf indumentum and stomatal distribution, the type of leaflet vernation, the form of petals

and styles, and in the seeds. While most of these attributes had been studied by previous workers, their results were often of limited range and were sometimes unreliable. Chapters 5 and 6 contain discussions of the vascular anatomy and chemistry of the tribe; in each I report some new and interesting data based on my own studies. The cytogenetics of the Vicieae are reviewed in Chapter 7.

3. To propose a more natural classification of the Vicieae. The primary objective and the justification of this work is the production of a sound, useful classification. Ideally, it should be based on evidence drawn from the maximum number of different sources, because a natural, phenetic system of this kind is most able to absorb new species and new discoveries of character-variation (i.e. it has predictive value). The circumscription of the tribe is discussed in Chapters 8 and 9; the delimitation and interrelations of its genera are dealt with in Chapter 10; and the infra-generic classifications of Vicia and Lathyrus are covered in Chapters 11 and 12, respectively. In this part of the thesis I frequently refer back to the data given in earlier sections, and the numbers in the top right-hand corner of each page are intended as an aid to this process of cross-reference.

4. To speculate on the progress of evolution in the Vicieae. Chapter 13 gives a brief account of the geological and climatic history of areas now inhabited by the Vicieae, from late Mesozoic times up to the present. This résumé provides a framework and perspective for the final discussion. The geographical

distributions of the revised taxa of the Vicieae are mapped in Chapter 14. In Chapter 15, I attempt to estimate the relative evolutionary advancement of the sections of Vicia and Lathyrus, and of all the genera of the Vicieae, on the basis of trends which can be recognised in a number of variable characters. The resulting pattern of primitiveness and specialisation among the different groups is then related to their geographical distributions, this synthesis leading on to a concept of the course of evolution in the tribe.

It is fortunate that the Vicieae have recently been treated in a number of Floras and regional monographs (listed in part 14.1) which cover nearly all the areas where the tribe is represented. This means that, while spending relatively little time on specific revision, I was able to carry out wide surveys of the variation in many morphological characters as well as making anatomical and serological investigations. For all these studies I used herbarium material, chiefly that of the Royal Botanic Garden, Edinburgh, but also from the collections at Kew and the British Museum (Natural History). This was supplemented by about 70 species of living plants (named in Appendix 1), grown at Edinburgh. In addition, in May to June, 1970, I spent three weeks in the south of Spain, gathering plants and seeds of species of the Vicieae.

Chapter 2

A TAXONOMIC HISTORY OF THE VICIEAE

2.1. Introduction.

2.2. The tribe Vicieae.

2.3. *Vicia*.

2.3.1. Old World species.

2.3.2. New World species.

2.3.3. Summary.

2.4. *Lathyrus*.

2.4.1. Old World species.

2.4.2. New World species.

2.4.3. Conclusion.

2.5. *Lens*.

2.6. *Pisum* and *Vavilovia*.

2.7. *Cicer*.

2.1.

INTRODUCTION

The purpose of this chapter is not to provide a complete history of nomenclature in the Vicieae, but to describe the changes in opinion which have occurred in the past concerning its systematics, and the reasons, so far as I can judge, for each alteration; it is a preparation for the taxonomic discussions in Chapters 8 to 12. The limits of many taxa within the tribe have been extremely mutable, and so, for clarity, I have not always followed the rules about citation of the author of a taxon; sometimes a group is attributed to a later taxonomist when it is in his sense, and not that of the original authority, that one is regarding the group. However, when an author's name is put directly after the name of a group (as in Sect. Pedunculatae Rouy), this of course implies that he is the true authority.

Whenever a species is referred to, either in the text or in the tables, I have used the binomial which is nomenclaturally correct, having accepted the generic delimitation in the most recent Floras, even when it is not the same as that used by the taxonomist whose system is being considered. In Chapters 3 to 7 I have classified members of the Vicieae into the genera, subgenera and sections which are usually recognised in contemporary publications. Thus, for example, Anatropostylia koeieana is called Vicia koeieana until part 10.4. is reached, where the reasons for the creation of the new genus are fully discussed. These methods are adopted with the aim of giving a clear picture

of the species and their characters so that the taxonomic structure which is finally advocated can be seen in perspective.

2.2.

THE TRIBE VICIEAE (Adanson) DC.

The first post-Linnaean taxonomist to define the Vicieae was Adanson(1763); he called this group a 'section', and included in it the Tournefortian genera Aphaca, Cicer, Clymenum, Ervum, Lathyrus, Lens, Nissolia, Orobus, Pisum and Vicia. Bronn (1822) also used the name Vicieae; in his classification it was a subtribe of the 'Curvembryae Diadelphae' (not a tribe, cf. Gunn, 1969). De Candolle was the first to give the Vicieae tribal status; In his Mémoires sur Légumineuses (1825) he stated that the essential characters of the tribe are:

1. Cotyledons fleshy, not becoming leafy but remaining underground and within the testa during germination.
2. Primordial leaves alternate, never opposite.
3. Leaves paripinnate, the rachis prolonged into a tendril which is either short and setiform, or curled and branching.

Seringe (1825) qualified the third character, saying that the leaves of Cicer may be imparipinnate. He also added that the leaves of the Vicieae are epulvinate. The genera accepted by De Candolle as members of the tribe were: Cicer, Ervum, Faba, Lathyrus, Orobus, Pisum and Vicia.

The number of genera into which the species of the Vicieae are grouped has tended to decrease with time. Bentham & Hooker (1865) described six, viz. Cicer, Vicia, Lens, Lathyrus and

Table 1. Characters separating Abrus from the Vicieae.

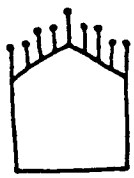
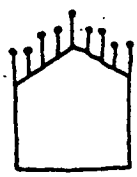
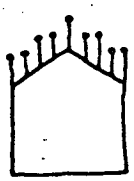
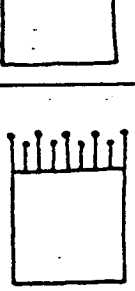
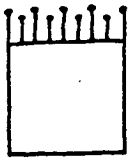
ABRUS	VICIEAE sensu DC.
Shrubs.	Herbs.
Stems twining.	Stems not twining.
Stems not containing cortical vascular bundles.	Stems containing cortical vascular bundles (except in Cicer).
Phyllotaxy polymerous.	Phyllotaxy dimerous.
Leaves not tendrillous.	Leaves often tendrillous.
Leaflets pulvinate.	Leaflets epulvinate.
Inflorescence terminal.	Inflorescence axillary.
Androecium with 9 stamens.	Androecium with 10 stamens.
Style glabrous.	Style pubescent (except in Cicer).
Seeds brightly coloured.	Seeds dull coloured.
Germination epigeal.	Germination hypogeal.
Haploid chromosome number: n = 11.	Haploid chromosome number: n = 5, 6, 7 & 8.

The separation of Abrus from the Vicieae has been advocated by Streicher (1902), Popov (1928), Senn (1938b) and Dormer (1946a). See also Fig. 42.

Pisum (comprising the Vicieae sensu DC.), and Abrus. The inclusion of Abrus was not entirely satisfactory to these authors, as can be seen from the note which follows the generic description: "Genus with woody stems, anomalous in the tribe in its type of inflorescence and in the absence of a vexillary stamen. It could be placed in the Phaseoleae or Dalbergieae instead of on the Vicieae." (free translation). Several later authors acceded to the judgment of Bentham & Hooker, e.g. Taubert (1894), Ascherson & Graebner (1909) and Gams (1924); this taxonomic problem was not tackled seriously by writers of temperate regional Floras, since Abrus is a tropical genus and its distribution was out of their range. Hutchinson (1964), in the most recent generic and tribal revision of the Leguminosae, placed Abrus in its own tribe, the Abreae, immediately before the Vicieae. The main characters separating this genus from the 'true' Vicieae are shown in Table 1. Nevertheless, the tradition of associating Abrus with the Vicieae is slow to die, and it is still sometimes cited as a member of the tribe (cf. Plitmann, 1967). In this thesis I have accepted Hutchinson's delimitation of the Vicieae as a working basis.

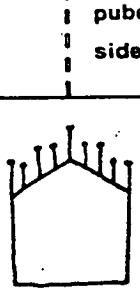
Apart from the controversy over Abrus, the boundaries of the Vicieae have remained constant since the early 19th century. Within the tribe, on the other hand, there has been continual change in the systematic arrangement and delimitation of genera and infrageneric taxa. Ascherson & Graebner (1909) commented that "the classification of this group is one of the more difficult tasks in the middle-European flora. Experience again confirms that the more natural a group is, the harder it is to

Table 2. Distribution of the main generic characters in the Vicieae.

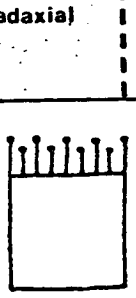
	STYLE	STAMINAL TUBE	LEAFLET VERNATION
CICER	terete; glabrous		
VICIA	dorsally or laterally compressed, or terete; pubescent all round or bearded on abaxial side		
LENS	dorsally compressed; pubescent on adaxial side		
LATHYRUS	dorsally compressed; pubescent on adaxial side		
PISUM	dorsally compressed, with retroflexed margins; pubescent on adaxial side		

♀ KEY

Staminal tube:



ends obliquely;



ends squarely.

Vernation:



conduplicate;



supervolute.

separate the genera." (freely translated). They added that perhaps the only decisive characters here are the nature of the style, the shape of the end of the staminal tube, and the leaflet-vernation. Table 2 shows the variation in these characters throughout the tribe, and the distribution of character-states. Vavilovia is not mentioned in the table as it is a relatively recent segregant from Pisum. In its floral characters it agrees completely with Pisum, but the leaflet-vernation is unknown. Rouy (1899) divided the genera between two subtribes on the basis of the different types of androecium: the Cicerineae, comprising Cicer, Vicia and Lens, in which the staminal tube ends obliquely, and the Lathyreae (Lathyrus and Pisum) in which it ends squarely.

Alefeld (1859, 1860 & 1861), whose treatment of the Vicieae has received repeated criticism from later authors, promoted the tribe to the rank of subfamily and made within it three tribes. These were the Ciceridae (containing Cicer), the Viciidae (equivalent to Vicia) and the Orobidae (with Lens, Pisum and Lathyrus). The Viciidae contained two subtribes, with 7 and 8 genera respectively *, while the Orobidae was divided into three subtribes **. Although his work has created annoyance among

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* Subtribus Viciosae, containing Hypechusa, Wiggersia, Vicia, Atossa, Cujunia, Faba and Tuamina; Subtribus Ervosae, containing Abacosa, Cracca, Ervum, Endiusa, Swantia, Parallosa, Sellunia and Ervilia.

** Subtribus Pisosae, containing Pisum; Subtribus Orobosae, containing Clymenum, Graphiosa, Lens, Aphaca, Orobus and Nissolia; Subtribus Lathyrosae, containing Lastila, Navidura, Cicercula and Lathyrus.

Table 3. Linnean species in the Vicieae.

LINNAEUS' 1753 BINOMIAL	LATER TRANSFERS OR SYNONYMS
Pisum	
P. sativum	
P. arvense	P. sativum var. arvense (L.) Poiret
P. maritimum	Lathyrus japonicus Willd.
P. ochrus	Lathyrus ochrus (L.) DC.
Orobus	
O. lathyroides	Vicia oroboides Wulfen
O. hirsutus	Lathyrus laxiflorus (Desf.) O. Kuntze
O. luteus	Lathyrus gmelinii (Fisch.) Fritsch
O. vernus	Lathyrus vernus (L.) Bernh.
O. tuberosus	Lathyrus linifolius (Reichard) Bässler
O. angustifolius	?
O. niger	Lathyrus niger (L.) Bernh.
O. pyrenaicus	Lathyrus linifolius (Reichard) Bässler
Lathyrus	
L. aphaca	
L. nissolia	
L. amphicarpos	
L. cicera	
L. sativus	
L. inconspicuus	
L. setifolius	

Table 3, continued.

L. angulatus	
L. bithynicus	Vicia bithynica (L.) L.
L. articulatus	L. clymenum L.
L. odoratus	
L. hirsutus	
L. tingitanus	
Lathyrus	
L. clymenum	
L. tuberosus	
L. pratensis	
L. latifolius	
L. heterophyllus	
L. palustris	
L. pisiformis	
Vicia	
V. pisiformis	
V. dumetorum	
V. sylvatica	
V. cassubica	
V. cracca	
V. onobrychioides	
V. nissoliana	V. cassubica L
V. biennis	
V. benghalensis	

Table 3, continued.

V. sativa
V. lathyroides
V. lutea
V. hybrida
V. peregrina
V. sepium
V. narbonensis
V. faba

Cicer

C. arietinum

Ervum

E. lens	Lens culinaris Medik.
E. tetraspermum	Vicia tetrasperma (L.) Schreber
E. hirsutum	Vicia hirsuta (L.) S.F. Gray
E. monanthos	Vicia articulata Hornem.
E. ervilia	Vicia ervilia (L.) Willd.

successive generations of taxonomists, by swelling the lists of synonymy, Alefeld provided a rather new approach to the problem. He emphasised the separateness of Cicer and highlighted some new and interesting characters, e.g. the presence of stipular nectaries in Subtribus Viciosae, and the unusual position of the lens in seeds of Hypechusa.

During the history of the classification of the tribe, the areas of most change and taxonomic doubt have been the relationship of Lens to Vicia and Lathyrus, and the internal structure of Lathyrus (whether or not it should be divided into two genera, Orobus and Lathyrus). In addition, the detailed infrageneric structure of the Vicieae has been sporadically revised, either in regional Floras or in publications on individual genera. It must be emphasised, however, that the Vicieae have never been treated monographically, and the species of Lathyrus and Vicia in America have not been brought into the sectional grouping which was created for their Old World relatives. The remainder of this chapter deals with the history of classification at and below generic level.

2.3.
VICIA L.
2.3.1.
OLD WORLD SPECIES

It is estimated that the genus Vicia contains about 130 species, distributed throughout the north temperate regions and in S. America (Fig. 55). Linnaeus listed 17 species within

Vicia, including one pair of synonyms, and six more were later transferred from the neighbouring genera Orobus, Lathyrus and Ervum (Table 3). Two of the earliest treatments of what is today considered to comprise the genus Vicia were those of Godron (1849) and Visiani (1852). Their classifications are set out diagrammatically in Table 4 (most, but not all, of the species are given), and the characters they used to define the taxa are shown in the following keys, translated from their works. Lens is included too, and its treatment will be discussed in part 2.5.

Keys to the genera and sections in Table 4.

Godron (1849).

1. Calyx oblique (rarely regular), with teeth shorter than the corolla (equal in Ervilia)
   2. Style dorsally compressed, heavily bearded below the stigma on the outer (abaxial) side, more rarely pubescent all round at the apex; legume sessile or stipitate, oblong, many-seeded, not moniliform, obliquely truncate at the apex from the lower suture, prolonged into a beak; flowers solitary or paired in the leaf-axils, or in racemes borne on short peduncles; seeds spherical, more rarely reniform, hilum linear or oval — Vicia
   2. Style laterally compressed, pubescent all round at
      3. Flowers axillary, solitary or twinned, not borne on a peduncle — Section 1
      3. Flowers in more-or-less pedunculate racemes — Section 2

the apex, not bearded; legume stipitate, oblong, not moniliform, obliquely truncate at the apex, beaked; flowers always in racemes borne on axillary peduncles; seeds spherical, hilum linear — Cracca

4. Legume many-seeded; flowers large, coloured — Sect. Eucracca

4. Legume with 2-4 seeds; flowers small, pale — Sect. Ervoides

2. Style slightly dorsally compressed, pubescent all round at the apex, not bearded; pod stipitate, linear, 3-4-seeded, not moniliform, rounded at the apex, not beaked; inflorescence axillary, pedunculate, few- to 1-flowered; seeds spherical, hilum linear or oval — Ervum

2. Style subulate, pubescent at the apex all round, not bearded; ovary folded, wavy; pod stipitate, moniliform, both sutures tapering at the apex into a short beak; inflorescence axillary, pedunculate, few-flowered; seeds spherical, hilum oval — Ervilia

1. Calyx regular, with the five equal teeth exceeding the corolla — Lens

Visiani (1852).

1. Style filiform, terete; legume linear or oblong — Vicia

2. Flowers subsessile in the leaf-axils, solitary or in racemes — Sect. Euvicia

2. Flowers borne on long axillary peduncles, solitary or in racemes — Sect. Cracca

1. Style compressed or dilated at the apex; legume linear, oblong or rhomboidal — Lathyrus

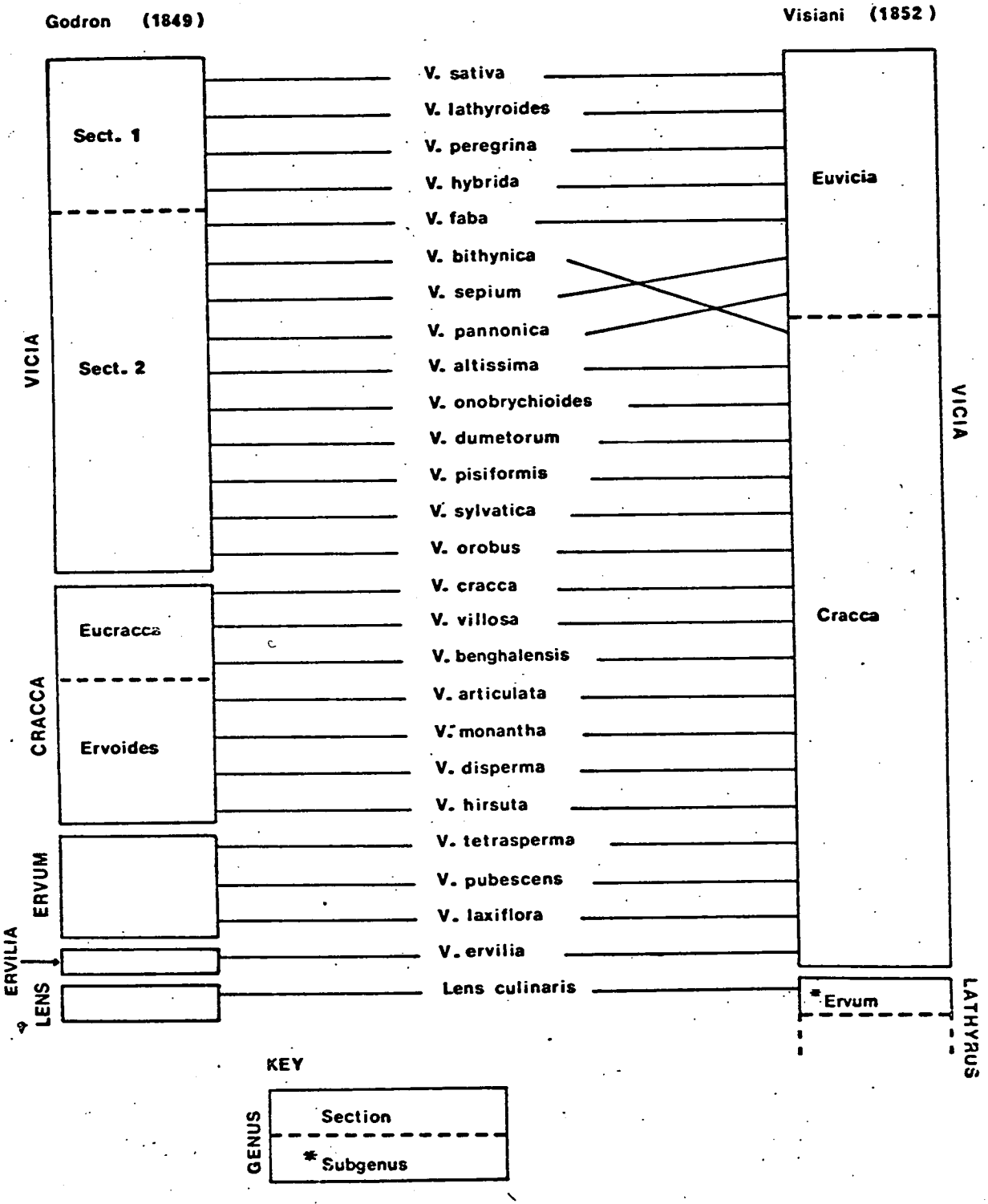
3. Corolla subequal with the calyx; legume rhomboidal; leaves with tendrils — Subgen. Lens

3. Corolla longer than the calyx; legume linear or oblong; leaves with or without tendrils — Subgen. Lathyrus

The first post-Linnean taxonomist to use the name 'Cracca' for part of the Vicieae was Medikus (1787); in his sense it denoted a genus, comprising V. benghalensis and V. cassubica, distinguished from Vicia by one character: the presence of nine united, and one free, stamens. In fact, all members of the tribe are diadelphous! However, the existence of the Linnean genus Cracca (syn. Tephrosia, in the Galegeae) invalidated the name, and Godron is also incorrect in his use of it. S.F. Gray (1821), who is often quoted as the authority for Sect. Cracca, used the name for an infrageneric taxon of unspecified rank - Vicia a) Cracca. The correct authority for Sect. Cracca is Visiani (1852).

A comparison of the systems of Godron and Visiani shows that there is very little agreement between them; this is because each used a small number of heavily weighted characters which were derived from different parts of the plant. Godron relied primarily on the detailed shape of the style and the

Table 4. Part of Vicia, and Lens: comparing the systems of Godron and Visiani.



distribution of hairs upon it, and found sufficient differences here to enable him to define four genera with their help. Visiani, although making use of stylar characters within the tribe, dismissed all the variation in this structure in Vicia as "style filiform, terete". The same greater attention to detail on the part of Godron explains why the boundary between Vicia Sects. 1 and 2 in his scheme does not coincide with that between Sects. Euvicia and Cracca in Visiani's, although they were using the same pair of character-states as a basis for this division: Godron only admitted to Sect. 1 species which are completely without peduncles; Visiani made a looser distinction between pedunculate and sessile inflorescences, and included V. sepium and V. pannonica in Sect. Euvicia. In Table 4 the species of Godron's genus Vicia are arranged, not in the most convenient way, but exactly as in Flore de France, because the author subdivides the sections, as follows:

Section 1

1. Legume not stipitate; calyx regular — V. sativa, V. lathyroides
1. Legume stipitate; calyx irregular — V. peregrina, V. hybrida

Section 2

1. Legume not stipitate — V. faba, V. bithynica
1. Legume stipitate
   2. Style thick, bearded below the stigma — V. sepium, V. pannonica, V. altissima, V. onobrychioides, V. dumetorum

2. Style thin, hairy all round — *V. pisiformis*, *V. sylvatica*, *V. orobus*
and not bearded

These two systems are described in detail because it seems that each formed an important foundation for the classifications of later taxonomists; one can trace a predominant influence of either Godron or Visiani in all succeeding treatments of *Vicia*, although with time the two structures have tended to approach one another.

Alefeld (1859, 1860 & 1861) based his classification on that of Visiani; he introduced several new characters which have been used by many authors, but his system itself found little favour, due to his unorthodox concept of taxonomic categories. The genus *Vicia* itself was raised to tribal status, under the name Viciidae, and contained Subtribes Viciosae (Sect. *Euvicia* of Visiani) and *Ervosae* (Sect. *Cracca* Vis.). The Viciosae comprised seven genera, including *Hypechusa* whose members were distinguished by having the lens of the seed opposite the hilum, no spongy parenchyma within their pods, and yellow or white flowers. Boissier (1872) also followed Visiani, dividing *Vicia* into Sects. *Euvicia* and *Cracca*; the latter he divided into perennial and annual species. Boissier made *Lens* a separate genus, under the name *Ervum*. Taubert (1894) followed the same pattern but introduced a few modifications from Godron's scheme: he made *Ervilia* and *Ervum* sections of *Vicia* (including *V. hirsuta* in Sect. *Ervum*), and restored the generic name *Lens* (see Table 5).

Rouy (1899), in contrast, turned again to the classification

of Godron, although he united Cracca, Ervum and Ervilia into one genus with Vicia. Godron's genus Vicia with Sects. 1 and 2 became Subgen. Euvicia, containing Sects. Subsessiles and Pedunculatae. (The four species V. pisiformis, V. sylvatica, V. orobus and V. cassubica were, however, segregated as the subgenus Vicilla (Schur)Rouy, on the basis of their styles being pubescent all round at the apex.) Similarly, Sects. Eucracca and Ervoides of Godron became Subgen. Pseudervoidea and Ervoidea.

The classification of Ascherson & Graebner (1909) was a synthesis and modification of several previous systems. These authors had a confusing concept of the taxonomic hierarchy, and although it is not quite clear from the text of their Synopsis der Mitteleuropäischen Flora, the index shows that taxa at sectional rank were sometimes grouped into higher taxa also called sections. I have followed the synopsis of their classification by Janchen (1957), and accept the groups Vicilla, Atossa and Hypechusa as correctly published sections. The higher taxa into which these are assembled are referred to as 'sections'. According to Ascherson & Graebner, Vicia comprised four 'sections': Euvicia, Faba, Cracca and Ervum. Euvicia had the same delimitation as Visiani's section of that name, and contained two sections, Atossa and Hypechusa. These groups were distinguished on the relative length of hilum in each: in the first it encircled more than half the circumference of the seed, in the second, less than half. Following Alefeld, these authors also made use of the lens-position character: in Sect. Atossa the lens was near the hilum, in Sect. Hypechusa it was

on the opposite side of the seed. However, variations in hilum length and lens position are not absolutely correlated, so that Sect. Hypechusa in fact contained several species (e.g. V. lathyroides and V. peregrina) with the lens near the hilum. Like Alefeld and Boissier, Ascherson & Graebner confused the lens with the radicle (see part 4.5.5). V. faba was segregated into a monotypic 'section' on the basis of two characters: the hilum being at the end of the oblong seed, and the legume containing spongy parenchyma between the seeds. 'Section' Cracca contained two sections, Vicilla and Eucracca, distinguished by the following characters;

1. Leaflets linear to lanceolate, sometimes the lower ones shorter; style mostly distinctly laterally compressed Sect. Eucracca

1. Leaflets ovate to linear-ovate; style thin Sect. Vicilla.

Sect. Vicilla (Schur) Aschers. & Graebner was basically the same as Rouy's Subgen. Vicilla, but it contained additional species which Rouy had placed in Subgen. Euvicia Sect. Pedunculatae (V. dumetorum and V. altissima) besides an entirely new species (V. unijuga). Sect. Eucracca was as in Godron's classification, but contained also V. argentea, V. onobrychioides and V. biennis. The remaining 'section', Ervum, contained all species with few-flowered racemes and small, pale flowers (Table 5).

Gams (1924) divided Vicia into three subgenera: Euvicia (equivalent to Sect. Euvicia of Visiani), Ervum (comprising the species in Godron's genera Ervum and Ervilia, and Cracca Sect. Ervoides; synonymous with Ascherson & Graebner's 'Sect.' Ervum)

and Cracca. The account of Vicia by Fedtschenko in Flora USSR (1948) followed the main lines of Visiani's classification, although with rather curious judgment about taxonomic status. The genus contained three subgenera; two (Ervilia and Faba) were monotypic, while the third, Craccoidea, contained the remaining species! Subgen. Craccoidea comprised four sections: Euvicia, Ervum (like the genus in Godron's scheme), Lenticula (V. hirsuta and V. articulata) and Cracca; the latter was a large and heterogeneous group with 19 series.

The treatments of Ball (1968) and of Davis & Plitmann (1970) both parallel that of Gams, although Gams' subgenera become sections and Sect. Faba is reinstated. In both works Sect. Faba is expanded to contain V. bithynica and V. narbonensis as well as V. faba; these three species are characterised by leaves with few pairs of large leaflets. In the Flora of Turkey there are two additional monotypic sections: Sect. Anatropostylia Plitmann, based on V. koeieana, and Sect. Trigonellopsis Rech. fil., based on V. lunata. Both of these species are annual; V. koeieana is very distinctive, having finely laciniate stipules, bright yellow flowers and the style pubescent on its adaxial side; V. lunata has papery, crescentic, indehiscent legumes and lenticular seeds.

Finally Radzhi (1970), dealing with Caucasian species, also follows the system of Gams, maintaining his three subgenera and creating within them a detailed hierarchical structure; a synopsis of this is given on the following page.

Subgen. Cracca (S.F. Gray) Gams (This name is illegitimate and is also antedated by the subgenera of Rouy, 1899.)

1. Sect. Crocea Radzhi

Style filiform, evenly hairy below the stigma. Leaves mucronate. Corolla yellow. Keel large, equalling the standard. Plants perennial, of mesophytic forests. - Monotypic.

V. crocea.

2. Sect. Cassubicae Radzhi

Style dorsally compressed, regularly hairy all round. Keel large, 2 mm shorter than standard. Plants of wooded regions. (3 Subsections.)

V. cassubica, V. pisiformis, V. biennis.

3. Sect. Variegatae Radzhi

Perennial, rarely annual, plants, alpine, 25-45 cm high. Leaves tendrillous. Stipules usually simple, semi-sagittate. Flowers large (18-26 mm), in dense, many (8-13)-flowered racemes. Style dorsally compressed below the stigma, long-bearded on the outer side. Legume pubescent. (2 Subsections.)

V. variegata, V. argentea, V. serinica, V. canescens, V. holoasia.

4. Sect. Cracca Vis.

(4 Subsections.)

V. cracca, V. alpestris, V. ciceroidea, V. villosa, V. monantha.

Subgen. Ervum (L.) Gams

1. Sect. Ervum (L.) Taubert

(2 Subsections.)

V. tetrasperma, V. hirsuta.

Subgen. Vicia

1. Sect. Sepium Radzhi (Antedated by Sect. Atossa (Alefeld) Aschers. & Graebner.)

Plants perennial, of mesophytic, wooded regions. Stems usually straight. Racemes axillary, 4-6-flowered. Stipules small, 3-5 mm long. Legume glabrous. Hilum two-thirds seed circumference. (2 Subsections.)

V. sepium, V. truncatula.

2. Sect. Vicia

(4 Subsections.)

V. grandiflora, V. sativa, V. lathyroides, V. bithynica, V. cappadocica, V. peregrina, V. hybrida, V. lutea, V. hyrcanica.

3. Sect. Faba (Miller)Ledeb.

(2 Subsections.)

V. narbonensis, V. faba.

2.3.2.

NEW WORLD SPECIES

The vetches of the United States were treated by Hermann (1960). He listed 35 species of Vicia which occur in N. America; of these, only thirteen are native to the New World, the rest having been introduced from Europe (and, perhaps, China in the case of V. unijuga). No attempt was made to arrange the species systematically either within the area covered by the survey or

with respect to the Old World members of Vicia. Gunn (1968a) made a special study of the taxonomically most difficult species of Vicia in N. America, and was able to reduce 33 names to a single species, V. americana Willd. (Hermann had already recognised this as one complex species with five varieties.)

The S. American species of Vicia have never been dealt with as a whole. Members of the genus were described principally by Hooker & Arnott (1830 & 1833), Vogel (1839), Clos (1847) and Philippi (several publications from 1872). The Index Kewensis lists about 60 names, of which perhaps three-quarters are synonyms. The species native to the Pampas and Mesopotamian plains of Argentina have been described by Burkart (1966); he records ten species from this area, and comments on the great variability of these plants. Again, these members of Vicia are treated in isolation, without reference to the rest of the genus. It is evident that within Vicia one of the most necessary tasks for the taxonomist is to make a thorough survey of its New World members so that their relationships with the rest of the genus can be considered.

2.3.3.

SUMMARY

The genus Vicia, as accepted by recent authors, contains a few groups which have been recognised by most systematists and a large residue of species whose relationships are difficult to determine and whose taxonomic history is one of continual change. As Vicia has been dealt with only in regional Floras,

its taxonomic structure is not comprehensively based and the species from America and the Far East have received much less attention than the European and S.W. Asian ones. This does not invalidate the recognition of 'good' groups like Sect. Vicia, but it leaves open the possibility that the difficult species may make more sense when seen in a world context. In the following paragraphs, each part of Vicia is discussed briefly in order to highlight the problematic areas. These will be considered again in Chapters 10 and 11, where the taxonomy of the tribe and of Vicia itself is reviewed with the aid of characters drawn from all parts of the plant.

Sect. Vicia (including Sect. Faba (Miller) Ledeb.; sensu Davis & Plitmann, 1970).

This group is distinguished from the rest of the genus by a number of characters: style dorsally compressed, with a tuft of hairs on the outer side; peduncles absent or much shorter than the leaves; stipules with a nectariferous spot; legumes with spongy parenchyma between the seeds. The species within it possess a wealth of useful characters by which it can be subdivided. Those usually employed are: calyx regular or irregular; degree of development of 'woolly' parenchyma within the legume; presence or absence of peduncle and pedicel; length of hilum; position of the lens on the seed; shape of legume. V. faba is included in this group by some authors, while others place it in a separate section or even subgenus. This is done mainly for two reasons: the leaves are mucronate rather than

tendrillous and have few pairs of large leaflets; and the legumes contain a very well-developed spongy parenchyma. V. bithynica, which in the type of style and presence of stipular nectaries has strong affinities with members of Sect. Vicia, has had a remarkably unsettled history. This was due to two factors: the leaves have few (1-3) pairs of large leaflets, and the peduncles vary in length, even on a single specimen, from almost absent to equalling the leaf. The first of these led Linnaeus to place V. bithynica in Lathyrus (a decision which he changed in 1759 - see Table 3); the second caused Visiani to classify it in Sect. Cracca (Table 4). Most authors have agreed that V. bithynica belongs in Sect. Vicia, but Ball (1968) and Davis & Plitmann (1970) put it in Sect. Faba because of the type of leaf. V. oroboides, which Linnaeus placed in Orobus, is remarkable within Sect. Vicia in having etendrillous leaves with few pairs of large, papery leaflets. It is a perennial which strongly resembles, in its vegetative features, the 'oroboid' members of Lathyrus (e.g. L. gmelinii, L. vernus) and Vicia Sect. Cracca (V. crocea, V. venosa, etc.). In other respects, however, it is typical of Sect. Vicia: it has stipular nectaries, a subsessile inflorescence and a dorsally compressed, tufted style.

Sect. Cracca Vis. (sensu Radzhi; syn. Cracca Sect. Eucracca of Godron).

The species in this group (e.g. V. cracca, V. benghalensis, etc.) have dense inflorescences borne on long peduncles; their

styles are laterally compressed and evenly hairy all round. This assemblage of species has not been as universally recognised as the previous one; many authors, e.g. Ascherson & Graebner; Gams; Ball; Davis & Plitmann, include it within 'Sect. Cracca' of much broader definition. With the exception of some 'ervoid' species, all the rest of Vicia, discussed below, is currently considered by most taxonomists to form part of this large and heterogeneous section.

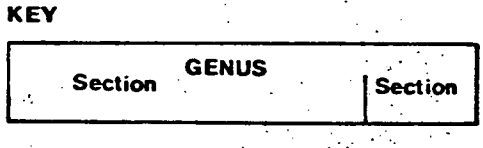
'Ervoid' species.

Table 5 sets out a synopsis of the various ways in which taxonomists have treated the 'ervoid' members of Vicia. In his Species Plantarum, Linnaeus grouped together all annual members of the Vicieae which possess small, pale flowers borne in few-flowered racemes into the genus Ervum. Since then it has been apparent to every taxonomist who classified the tribe that these characters do not define a natural group. Lens Miller (based on Ervum lens = Lens culinaris) was soon removed as a separate genus, and the rest of Ervum (including its lectotype E. tetraspermum) was eventually united with Vicia. Godron maintained the genus Ervum, but removed several of its original species to Cracca, besides using the monotypic genus Ervilia Link (containing Ervilia sativa = Vicia ervilia). Ervum now contained a small, well-defined group of species (V. tetrasperma etc.), characterised by dorsally compressed styles and linear legumes. The species which Godron removed to Cracca Sect. Ervoides had laterally compressed styles and stipitate, beaked fruits (see Table 4 and the accompanying key).

Explanation of Table 5.

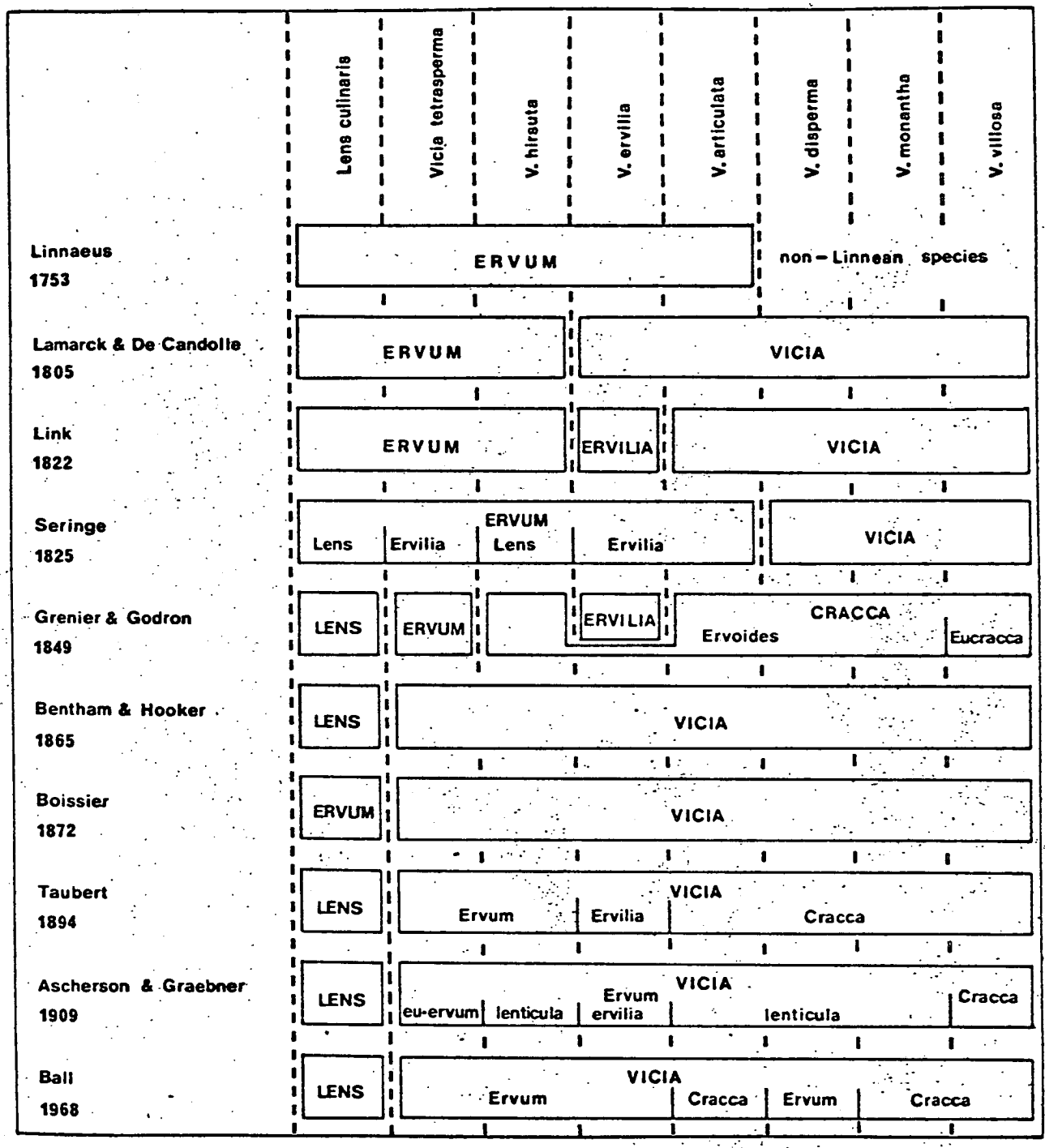
The eight species listed at the top of the table include the five original members of the genus Ervum L., taken from Table 3. V. disperma and V. monantha are given as just two of the many species which have sometimes been associated with the ervoid group by post-Linnean authors. V. villosa is not 'ervoid', but is included as a representative member of the adjacent part of Vicia, which is generally known as Vicia Sect. Cracca s.l. (see Table 4).

The classification system of each author is shown as follows. Each box represents a genus, whose name is given in capitals. Where the genus is divided into sections, the sectional names are written in lower case letters.



This applies to all authorities except Ascherson & Graebner, whose anomalous concept of taxonomic categories is mentioned on p. 41. In their classification, the seven ervoid species in Table 5 are all placed in 'Sect. Ervum', which is then subdivided into sections - Sects. Eu-ervum, Lenticula and Ervilia. I have accepted these three taxa as correctly published sections.

Table 5. Synopsis of the taxonomic history of 'ervoid' members of the Vicieae.



See explanation on opposite page.

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Except for Ascherson & Graebner, other authors grouped these species differently from Godron, some considering that V. hirsuta is close to V. tetrasperma and all disagreeing over the boundary between Sects. Ervum and Cracca. It is noticeable that in recent treatments taxonomists have virtually returned to Linnaeus' system; few give prominence to fine details of legume shape or stylar hair distribution, but rely mainly on habit as a guide to classification in this part of the genus. Even so, it is surprising that Radzhi (1971) has decided to reinstate Ervum as a genus in Linnaeus' sense, including in it both the ervoid members of Vicia and Lens itself.

The classification of the rest of the genus is difficult to describe under separate headings, and so will be treated merely in a series of paragraphs.

V. onobrychioides, V. altissima and V. dumetorum have the same type of style as members of Sect. Vicia, but none of the other characters which typify this group. They were placed by Rouy (1899) in Vicia Subgen. Euvicia Sect. Pedunculatae Rouy, together with V. pannonica and V. sepium; then Ascherson & Graebner (1909) moved them to 'Sect. Cracca' where they were divided between Sects: Eucracca and Vicilla on the shape of the leaf. Succeeding taxonomists have unanimously put them in the large, heterogeneous Sect. Cracca.

V. pisiformis, V. sylvatica, V. orobus and V. cassubica were grouped by Schur (1866) as the genus Vicilla, characterised

by the possession of dorsiventrally compressed styles evenly hairy all round at the apex. Ascherson & Graebner made Vicilla a section within 'Sect. Cracca', but changed its definition by the inclusion of V. dumetorum and V. altissima (see previous paragraph). More modern taxonomists have usually 'lumped' Vicilla together with the V. cracca and V. onobrychioides groups into Sect. Cracca, although Radzhi (1970) has in effect resurrected Vicilla as his Sect. Cassubicae.

The two morphologically distinctive annuals V. koeieana and V. lunata have recently each been placed in a new monotypic section: Sects. Anatropostylia and Trigonellopsis, respectively. These groups are discussed in detail in part 10.4 and Chapter 11.

Sect. Cracca s.l. also contains the following groups:
A. An assemblage of species (V. canescens, V. argentea etc.) with dorsally compressed styles which are glabrous adaxially but densely bearded on the abaxial side. They are alpine plants, often with villous, mucronate or even imparipinnate leaves. Radzhi (1970) places them in Subgen. Cracca Sect. Variegatae.
B. A large number of species with a predominantly E. Asian distribution, typically possessing leaves without tendrils and with few pairs of large leaflets, although some are tendrillous and have smaller, more numerous leaflets. Their styles are terete or dorsally compressed and evenly hairy all round, like the members of Vicilla Schur. Some of these species, e.g. V. crocea, V. venosa, V. kulingiana, strongly resemble in facies the members of Lathyrus Sect. Orobus native to the same area; this

apparent similarity poses one of the most interesting taxonomic problems of the Vicieae - is the likeness due to close phylogenetic relationship, or to convergent evolution? This question is discussed in part 10.2.

C. A number of isolated species, including

a) V. subvillosa - a perennial alpine species, distinguished by its imparipinnate leaves and remarkably large flowers.

b) V. biennis - an annual or biennial. The style is dorsally compressed and evenly hairy all round. Alefeld (1859) stated that this species is unique within the genus in having leaflets with supervolute vernation, and I have confirmed this observation. This important character has been overlooked by other authors.

c) V. cappadocica - an annual in which the leaves have few pairs of leaflets and the style is tufted abaxially. It has had several names and changes in taxonomic position: for example, Boissier (1872), who described the style wrongly, placed it in Sect. Cracca; Fedtschenko (1948) put it in Sect. Ervum; Radzhi (1970) in Sect. Vicia Subsect. Bithynicae; and its synonyms include Lathyrus trijugus Bornm. and L. paucijugus (Trautv.) Schischkin.

d) V. cassia and V. cretica, annuals which in most characters approach the V. cracca group, but whose styles are dorsally compressed and tufted abaxially.

2.4.

LATHYRUS L.

2.4.1.

OLD WORLD SPECIES

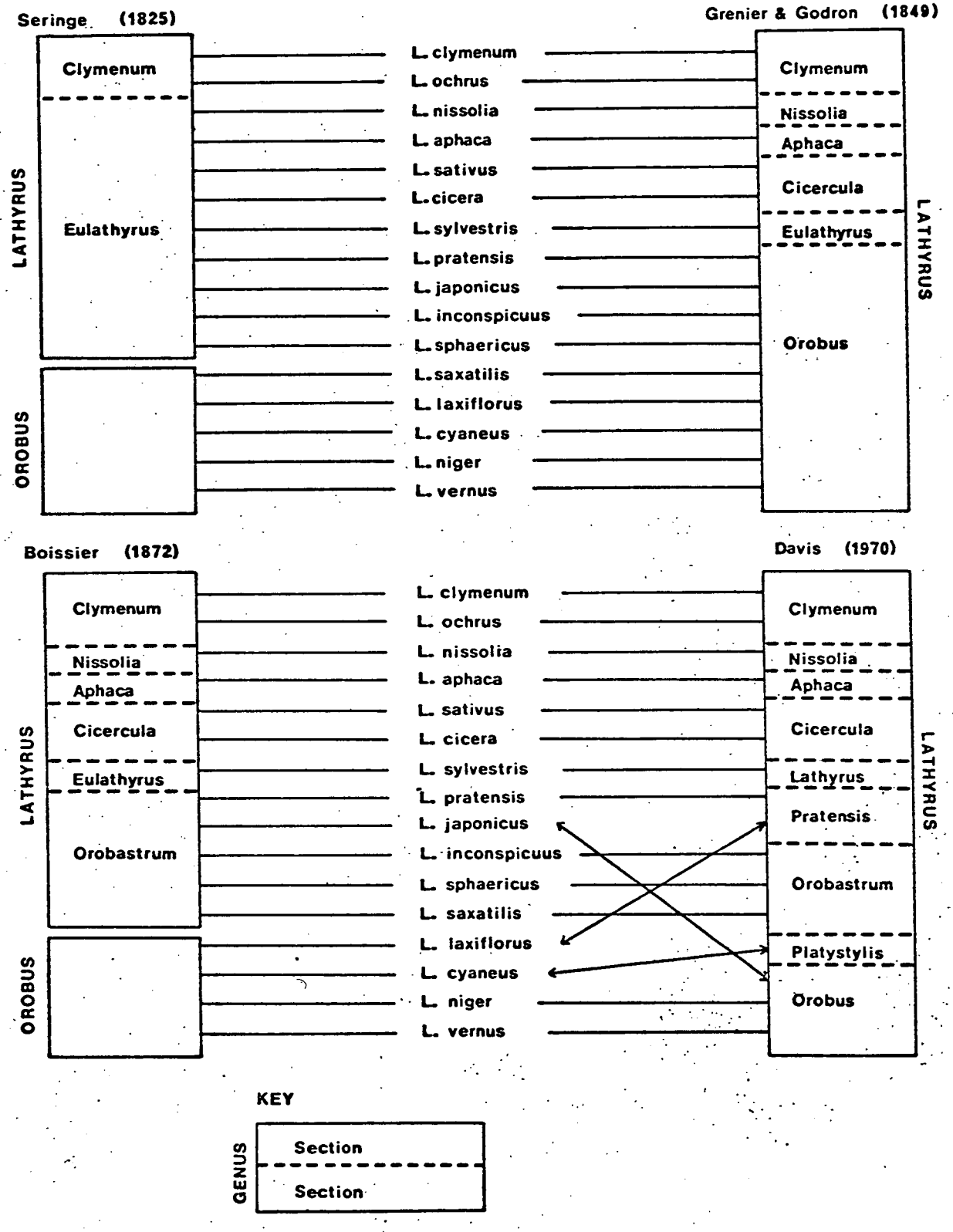
The genus Lathyrus is usually considered to be rather smaller than Vicia, but I estimate that the two genera are approximately equal in size, each having about 140 species; their distribution also covers much the same area (Fig. 55). The taxonomy of Lathyrus has evolved along somewhat simpler lines than that of Vicia; until very recently there has been little controversy over the grouping of species, and most changes have involved merely an increase in the number of sections. Four systems are summarised in Table 6: those of Seringe (1825), Godron (1849), Boissier (1872) and Davis (1970); the latter is based partly on the work of Bässler (1966).

Twenty-nine species which are today considered to belong to Lathyrus were classified by Linnaeus (1753) in three genera: Pisum, Orobus and Lathyrus (see Table 3). Pisum maritimum and P. ochrus were transferred to Lathyrus in 1802 and 1805, respectively, and since then the small genus Pisum has been recognised as a completely separate group. In contrast, Orobus (lectotype O. tuberosus, syn. Lathyrus linifolius) was maintained, with modifications, for a long time, and most of the difficulties in the systematics of this part of the Vicieae have been due to doubt about whether Orobus is a natural group. De Candolle (1805) distinguished between Orobus and Lathyrus as follows:

1. Style flattened, enlarged towards the apex, pubescent on the anterior side; petiole terminating im a tendril — Lathyrus

1. Style slender, pubescent at the apex; petiole terminating in a short, simple point — Orobus

Table 6. Lathyrus: comparing four classification systems.



Thus essentially, Orobus was characterised by the absence of tendrils; the type of style did not provide any guide in this matter, since (regarding the situation from a modern viewpoint) Orobus contained species which are nowadays classified in both Lathyrus and Vicia, which are themselves separated on stylar characters (see Table 2). Several authors followed this system, including S.F. Gray (1821), Link (1822) and Seringe (1825). The latter divided Lathyrus into two sections: Clymenum, containing all species in which the standard has two conical pouches at its base, and whose lowest leaves are phyllodic, and Eulathyrus, with the remaining species.

In 1828 Sweet described a new genus, Platystylis, characterised by the presence of a flattened, broadly spathulate style. The type of Platystylis was P. cyaneus (syn. Lathyrus cyaneus). This genus has not been maintained by any later taxonomist, and it is only very recently that the group delimited by its possession of the flattened style has been recognised as an entity distinct from the genus (or section) Orobus.

Sect. Eulathyrus was further divided by Reichenbach (1832), who separated two monotypic sections, Aphaca and Nissolia. Both of these had been described as genera by Miller (1754). Sect. Aphaca is characterised by its large, hastate stipules and the leaf which is reduced to a simple tendril in the mature plant; Sect. Nissolia is unique in having phyllodic leaves throughout the plant's life-cycle. Reichenbach included the tendrillous species L. japonicus and L. palustris in Orobus; he did not define this genus, and it would have been a difficult task,

since no distinguishing character was left to separate it from Lathyrus. In 1843 Döll produced a completely new answer to this dilemma by adopting a much narrower concept of Lathyrus. In his classification this genus comprised only species which possess a twisted style, and the remaining species were placed in Orobus.

Godron (1949) was the first author to combine both genera under Lathyrus (see Table 6). He stated that Lathyrus is characterised by a dorsally compressed style pubescent on the upper (inner, adaxial) face, and he thus effectively excluded the few 'oroboid' members of Vicia. Godron followed Döll in recognising the assemblage of species with twisted styles, placing them in two sections, Cicercula and Eulathyrus. In the former the style was stated to be canaliculate on the abaxial side; in the latter it was tubular and arcuate. Having accepted the small sections Clymenum, Nissolia and Aphaca, and having narrowly defined Sects. Eulathyrus and Cicercula, Godron put all the remaining species in Sect. Orobus. The system of Boissier (1872) was the same as that of the previous author, except that Orobus was reinstated as a distinct genus, characterised, in the traditional manner, by the absence of tendrils. The tendrillous species of Godron's Sect. Orobus were placed in a new section, Orobastrum (Table 6). Although Boissier used this structure, he was not satisfied with the delimitation of the groups; this can be seen from his comments before the description of Lathyrus in his Flora Orientalis (1872), and from some changes which were made in this publication compared with earlier works. Thus in 1845

Boissier had described two new species, Orobus nervosus and O. trachycarpus. Later, in 1872, these were moved to Lathyrus together with certain other etendrillous species which had been placed in Orobus by earlier taxonomist (L. inconspicuus, L. saxatilis and L. roseus). He did this without altering the written definition of Orobus, but allowed his judgment to over-rule the system, as he was unconvinced of its validity. L. roseus and L. boissieri (Orobus nervosus) were placed in Sect. Eulathyrus, on account of their twisted styles. Orobus, according to Boissier's delimitation, contained only perennial species.

The classification of Taubert (1894) was exactly as Boissier's, except that the genera Orobus and Lathyrus became two sections, Orobus and Archilathyrus, within Lathyrus. Ascherson & Graebner (1909) and Fedtschenko (1948) both adopted Taubert's system, but abandoned Sect. Archilathyrus and gave its subgroups the sectional status which they had in Boissier's scheme. Rouy (1899), on the other hand, closely followed the classification of Godron, as he had done in Vicia (i.e. he did not accept Sect. Orobastrum).

Up to this point, in the history of the classification of Lathyrus, it is apparent that the genus consisted of a number of small, well-defined sections and a residue of species which were either placed in a single 'dustbin' section, Orobus, or divided between Sects. Orobastrum and Orobus on the presence or absence of tendrils, sometimes combined with the annual/perennial

habit. The taxonomic value of tendrils was discussed at length by Fritsch (1900); the evidence he put forward is summarised in part 3.2. He concluded that it is inadmissable to define Orobus by the absence of tendrils or even to make sections based on this character. Fritsch was perhaps the first to speculate about the evolutionary relationships of groups within Lathyrus: he suggested that L. aphaca and L. laxiflorus (Orobus hirsutus) are both close to L. pratensis, as these three species are distinctive in possessing hastate stipules; that L. nissolia has affinity with L. inconspicuus; and that Sect. Orobus is the most primitive group within Lathyrus, standing nearest to Vicia.

Bässler, who recently (1966) published a detailed taxonomic study of part of Lathyrus, undoubtedly greatly improved its classification. It is, however, difficult to agree with the decision, implied by but not discussed in his work, to divide the genus into two subgenera, Lathyrus and Orobus. Subgen. Orobus was based on the taxon of this name in Hooker's Flora of British India (1879), although it was predated by Subgen. Orobus (L.) Petermann (1847). Lathyrus is poorly represented in India and Baker, who prepared the account of this genus, put only two species in Subgen Orobus: L. gmelinii (syn. Orobus luteus L.) and L. inconspicuus. Bässler chose the former as the lectotype of the subgenus. The species which Bässler included in Subgen. Orobus were all the perennial members of Sect. Orobus sensu Godron (Table 6). This group cannot be defined by any character and seems purely arbitrary, or at least based only on historical tradition.

Within Subgen. Orobus, Bässler surveyed the variation in characters taken from all parts of the plant, including some not previously used in this genus, e.g. epidermal structure; he used the data to produce a new sectional classification. Sect. Orobus sensu Bässler was described as follows: plants erect or ascending; stems wingless to broadly winged; leaves multijugate, leaflets often elliptical or ovate-oblong, rarely lanceolate or linear; stipules broadly semi-sagittate or rarely sagittate; peduncle many-flowered or rarely few-flowered; calyx teeth unequal; style not contorted and not dilated at the apex. It was a large group containing 10 series. Species with spathulate or dilated styles and with mucronate, etendrillous leaves possessing one to three pairs of leaflets were placed in Sect. Platystylis (Sweet) Bässler. In some of these species (e.g. L. spathulatus, L. filiformis and L. boissieri) the style is twisted. According to Čelakovsky (1888), this feature results from lack of space inside the keel for the developing style, and is only superficially equivalent to the contorted styles typical of Sects. Lathyrus and Cicercula. Bässler pointed out that since this feature also occurs in some species in which the style is not spathulate (e.g. L. sulphureus from N. America), Čelakovsky's explanation does not seem completely convincing. More recently, Bässler (1971) has changed the name of this group from Platystylis to the nomenclaturally correct Sect. Lathyrostylis (Griseb.) Bässler.

Bässler placed L. roseus in the monotypic Sect. Orobon Tamamsch.; he recognised that this species resembles members of

Sect. Lathyrus (e.g. L. rotundifolius, L. grandiflorus) in its possession of a twisted style, but considered that its terete stem and etendrillous leaves are sufficient justification for this separation. It is surprising, even so, that he put Sects. Orobon and Lathyrus in different subgenera. Species with sagittate stipules and subequal calyx segments were divided between two sections, Sect. Pratensis (with yellow flowers and tendrils) and Sect. Eurytrichon (with blue flowers and no tendrils). Finally, Sect. Neurolobus was created to contain the isolated perennial species L. neurolobus, which has a broadly winged stem, unijugate tendrillous leaves and a style neither contorted nor dilated at the apex. The annual species with non-contorted styles which were excluded from Subgen. Orobus formed, by implication, a smalland fairly well-defined Sect. Orobastrum.

Many of Bässler's innovations were accepted by Davis (1970), as shown in Table 6. The only important modifications involved the abandonment of the subgenera and the amalgamation of Sects. Pratensis and Eurytrichon; the two characters separating these groups (flower colour and presence or absence of tendrils) were found to break down. Thus etendrillous forms of L. pratensis are known to occur occasionally (Fritsch, 1900), and L. layardii, a species not cited by Bässler but having an obvious affinity with the L. pratensis group, has blue flowers and tendrillous leaves.

The most recent classification of Lathyrus to date is that of Czefranova (1971), who dealt with Eurasian species. Her concept of its infrageneric structure differs in several respects

from those just described, and in addition she did not accept Bässler's lectotype of Orobus, but rather the species chosen earlier by Green (1929), viz. L. montanus (Orobus tuberosus) - see also Gunn (1969). This fact alone is partly responsible for the nomenclatural discrepancy between her system and that of Bässler. Czefranova divided Lathyrus into six subgenera: Orobus, Lathyrus, Clymenum, Nissolia, Cicercula and Aphaca; this pattern exactly parallels Godron's sectional classification of Lathyrus, but on a different level of the hierarchy (see Table 6). Subgen. Orobus contained five sections, as follows: L. montanus, L. vernus and L. venetus were grouped together with the species of Bässler's Sect. Lathyrostylis into Sect. Orobus; the 'oroboid' species were placed in Sect. Lathyrobus (Tamamsch.) Czefr.; and the other three sections are Eurytrichon, Pratensis and Neurolobus. Subgen. Lathyrus contained three sections, Lathyrus, Orobon and Orobastrum, all sensu Davis (1970). The four remaining subgenera are equivalent to sections of the same names in the Flora of Turkey. See Addendum.

2.4.2.

NEW WORLD SPECIES

The N. American species of Lathyrus were revised in detail by Hitchcock (1952); thirty-nine species were listed, of which nine are introductions from Europe and two (L. palustris and L. japonicus) have holarctic distributions (L. japonicus is found also on the east coast of S. America). Unlike the Eurasian species, those in N. America are frequently capable of

hybridisation (fide Hitchcock) and their delimitation is consequently more problematical for the taxonomist. The species native to this area form a complex of rather narrow morphological variation; they are typically robust perennials with tendrillous, multijugate, pinnate-veined leaves and many-flowered racemes. Their styles are never expanded at the apex and are seldom twisted (the exception is L. sulphureus). Although they have never been included in a systematic survey of the genus, Bässler (1966) has suggested that these species have affinity with members of Sect. Orobus. Hitchcock himself did not attempt to make a hierarchical structure with the species of N. America, or to relate them to Old World members of Lathyrus.

The S. American species of Lathyrus are markedly different in morphology from those of N. America, having unijugate leaves with parallel venation and styles which are often spathulate. With the exception of L. pusillus agg., all are perennial. They were considered by Simola (1968a) to represent a highly advanced group within the genus, whereas those of the United States she thought comparatively primitive. As Bässler has commented, "the systematic structure of the S. American species and their relationship with Eurasian and N. American species is still unclear" (translated). Fortunately, the nomenclature of the species, which form a complex parallel to that in N. America, has been practically straightened out by Burkart; he published a key and descriptions for the Argentinian members of Lathyrus in 1935 and a list of the Chilean species in 1942. There are about 25 species, reduced from over 70 names.

2.4.3.

CONCLUSION

The genus Lathyrus has been popular among botanists as a subject for many kinds of investigation (morphological, anatomical, chemical and cytological), and some authors have suggested that their findings in these various fields are of taxonomic significance. For example, Tutin (1956) proposed that Orobus and Lathyrus might be defined, respectively, by the possession of reticulate-veined and parallel-veined leaflets. Again, Pecket (1959) considered that the distribution-pattern of leaf-extract flavonols and coumaric acids which he found within Lathyrus lent support to the scheme of Tutin (1952), where L. hirsutus, L. pratensis, L. palustris and L. japonicus were placed together. However, as has been shown, the type of evidence upon which Lathyrus has in practice been classified has remained almost unchanged since the beginning of systematics. It will be the aim of this thesis to co-ordinate all aspects of the plant, with the hope of achieving a more widely-based and therefore a more 'natural' taxonomy.

2.5.

LENS Miller

The genus Lens comprises about six species of annuals native to the Mediterranean area and S.W. Asia (Fig. 55). In habit these plants resemble members of Vicia, especially those of Sect. Ervum, having delicate leaves with few to several pairs of small leaflets and usually pale, inconspicuous flowers.

The main characters which distinguish Lens from the other genera are shown in Table 2, and the history of the group is summarised in Table 5. Only one species of Lens was known to Linnaeus, L. culinaris; he placed it in the genus Ervum as E. lens. Seringe (1825) divided Ervum into two sections, Sect. Lens with broadly oblong, 2-seeded pods, and Sect. Ervilia with oblong-linear, 4-6-seeded pods. By this method of classification all species of Lens were segregated together, but were placed with some other species which are nowadays regarded as members of Vicia (e.g. V. hirsuta, V. vicioides). Godron (1849) was the first modern taxonomist to recognise Lens as a genus. He distinguished it from Ervum by the calyx, which has five equal teeth exceeding the corolla; by the style, which is similar to that of Lathyrus; and by the lens-shaped seeds. Visiani (1852) put members of Lens into Subgen. Ervum of Lathyrus (see Table 4 and the corresponding key in part 2.3.1), but otherwise since then most taxonomists have followed the treatment of Godron. However, very recently Radzhi (1971) has resurrected the genus Ervum and has once again 'lumped' together the ervoid members of Vicia and the lentils.

The species of Lens are on the whole remarkably alike, forming an easily-recognised group. L. montbretii is the most aberrant member of the genus; it has fairly large and attractive whitish flowers, relatively short sepals (though they still exceed the length of the calyx tube) and densely sericeous legumes. Because of these characters, some taxonomists have placed this species in Vicia (as V. bombycina Stapf). Its tax-

onomic relationships are discussed more fully in part 10.3.

Since the decision to delimit Lens as a distinct group having generic status is supported by the concensus of taxonomic opinion, and as these species obviously have close affinity with other members of the Vicieae, they have presented few problems for taxonomists engaged in preparing regional Floras. On the other hand, to those concerned with the phylogenetic aspects of systematics, Lens is both interesting and puzzling. The traditionally-used characters point almost equally to affinity with both Vicia and Lathyrus, and yet this small, highly-evolved group, composed entirely of weedy annuals, might be supposed to be of recent origin. This problem is one of the main subjects of discussion in Chapter 10.

2.6.

PISUM L. and VAVILOVIA A. Fed.

Pisum has been universally recognised as a separate taxon within the Vicieae. A few members of Lathyrus with large ovate leaflets or with foliaceous stipules, e.g. L. ochrus, L. japonicus and L. nervosus (Pisum americanum Miller), were included in Pisum by several early taxonomists: Linnaeus (1753), De Candolle (1805) and Seringe (1825); but the conduplicate vernation of its leaflets and its distinctive style with retroflexed margins have generally served to define its limits with great constancy (Table 2).

Jaubert & Spach (1842) divided Pisum into two sections, based on the following characteristics:

1. Plants annual; petiole not canaliculate; leaves tendrillous; stipules large, foliaceous; keel cristate ..... Sect. Lophotropis

1. Plants perennial; petiole canaliculate on the upper side; leaves mucronate; stipules small; keel not cristate ..... Sect. Alophotropis

Sect. Alophotropis contained a single species, Pisum aucheri Jaub. & Spach (syn. Orobus formosus Stev., 1812-13). In 1939 Fedorov elevated this section to generic rank, calling it Vavilovia. V. formosa is a dwarf alpine perennial native to Asia Minor and Caucasia (Fig. 55). It inhabits mobile screes and is distinctive in having etendrillous leaves with a single pair of coriaceous, strongly-nerved leaflets. A new species has recently been discovered in Greece, and named Pisum graecum (Quézel & Contandriopoulos, 1965); it differs from V. formosa only in leaflet-shape (lanceolate-ovate rather than sub-orbicular), in its narrower stipules and in having a short, simple tendril. Unfortunately the vernation-type, which is an important generic character within the tribe, is unknown in both these species.

Pisum s.s. (Pisum Sect. Lophotropis) is a large complex of weedy annuals whose variation has been influenced by man's selection. In concordance with modern opinion, Davis (1970) reduces this to two species, P. sativum and P. fulvum; they are distinguished only on flower colour (which is, respectively, lilac-pink (rarely white) and orange), although P. fulvum usually has unijugate, toothed leaves while P. sativum often has

entire leaflets and up to 4 pairs per leaf. Pisum is Mediterranean in distribution (Fig. 55).

The relationship of Pisum and Vavilovia to the rest of the tribe is problematical, since these genera combine the generic characters of Vicia and Lathyrus. Their distinctive flowers point to a close affinity between Pisum and Vavilovia, but these genera are rather dissimilar in vegetative characters. They are discussed further in part 10.5.

2.7.
CICER L.

The genus Cicer comprises about 40 species. C. arietinum, the chickpea, is an important pulse crop widely cultivated in India, C. and S.W. Asia, the Mediterranean countries, Ethiopia, Mexico, Peru and Chile. The wild species of Cicer have a more limited and somewhat disjunct distribution within W. and C. Asia, the Mediterranean area and Ethiopia. Their greatest concentration lies in the Irano-Turanian region, from Anatolia to Iran, Afghanistan and the Pamirs. Cicer is very sparsely represented in the W. and S. Mediterranean; there is a single endemic species in Morocco (C. atlanticum), another in Ethiopia (C. cuneatum), and only three members in Greece (van der Maesen, 1972). The delimitation of this group from all other members of the Vicieae has never been questioned, but on the other hand, all taxonomists have agreed that, although anomalous in several respects, Cicer is properly placed within this tribe.

Since the majority of its species do not occur in Europe,

Cicer has received rather less attention than have the other members of the Vicieae, and in consequence its taxonomic history is comparatively uneventful. The first infrageneric classification of Cicer was that of Jaubert & Spach (1842); they made four sections: Arietaria, Vicioides, Spiroceras and Tragacanthoides. The first two contained herbaceous species and were, respectively, identified by the absence and presence of tendrils. Sects. Spiroceras and Tragacanthoides consisted of woody species; the leaves of the former possessed stiff, curled tendrils while those of the latter ended in a straight spine. Boissier (1872) followed the same system, but 'sank' the species of Sect. Spiroceras into a larger Sect. Vicioides, which was characterised by the presence of tendrils.

A monograph of Cicer by Popov appeared in 1928. In this work the genus was divided into two subgenera on floral characters, as follows:

1. Flowers small (5-10 mm long), rarely (in varieties of C. arietinum) up to 15 mm; calyx subregular or slightly gibbous, segments subequal, narrowly linear; plants annual or perennial Subgen. Pseudononis

1. Flowers medium (12-15 mm long) or large (17-27 mm); calyx very oblique, gibbous at the base; segments unequal; perennials Subgen. Viciastrum

Each subgenus was divided into two sections and then into series, using characters such as habit, presence or absence of tendrils, and shape of leaflets and stipules. Popov's system was followed by Linczevski (1948), except that the four sections Monocicer,

Chamaecicer, Polycicer and Acanthocicer were no longer grouped into subgenera. A new monograph of Cicer has very recently been published by van der Maesen (1972), which provides a useful modern revision of the species. The author has aimed at a working classification and is apparently not strongly concerned with the naturalness of the taxa; he accepts Popov's subgeneric and sectional framework, and most of the series of Linczevski.

It must be pointed out, in criticism, that the rules of nomenclature which apply to super-specific taxa have not been followed by these authors, and several names need revision. Sect. Monocicer M. Pop. (= Sect. Arietaria Jaub. & Spach, based on C. arietinum) should be called Cicer Sect. Cicer. Sect. Polycicer M. Pop. includes C. spiroceras, the only species of Sect. Spiroceras Jaub. & Spach, and also C. songaricum and C. jacquemontii, the two members of Sect. Vicioides Jaub. & Spach; I propose that Sect. Polycicer should be made a synonym of Sect. Vicioides. Sect. Acanthocicer M. Pop. is synonymous with Sect. Traganthoides Jaub. & Spach, whose type is C. traganthoides.

Many authors have commented on the isolated position of Cicer within the Vicieae and have speculated on its possible relationship with other parts of the Leguminosae. In his Mémoires sur Légumineuses, De Candolle (1825) pointed out the apparent affinity of Cicer and Ononis: "The aristate peduncle is not the only similarity between these two genera. The sharp teeth of the leaflets and stipules of Cicer, the form of its hairs, the arrangement of the flowers, the shape of calyx and corolla and the appearance of the fruit, all recall certain

species of Ononis, particularly those with pinnate leaves. The swollen cotyledons and mode of germination are the best characters to distinguish Cicer from Ononis." (translated). Ononis itself has had a very unstable taxonomic history. In the earliest classifications, e.g. Bronn (1822), it was associated with members of the Genisteae. In 1865, Bentham & Hooker decided that Ononis was more properly placed in the Trifolieae; the evidence on which they based this judgment was summarised briefly as follows: "A most natural genus, belonging somewhere between the Genisteae and Trifolieae. Having usually monadelphous stamens and dimorphic anthers it is like the Genisteae; in its leaflets, inflorescence and filament apices it resembles the Trifolieae." (translated). Širjaev, who monographed Ononis (1932) felt that it should be in a separate tribe; and this was effected by Hutchinson (1964) who created the tribe Ononideae, containing Ononis and Passaea, while the Trifolieae, in the sense of this author, contained six genera: Parochetus, Melilotus, Trigonella, Factorovskya, Medicago and Trifolium. Gams (1924) was of the opinion that Cicer has more affinity with Ononis than with the rest of the Vicieae; he asserted that Ononis has no true connections with either the Trifolieae or the Genisteae, but is an advanced genus, related to Cicer and, indirectly, to the Vicieae, having evolved from ancestors resembling the Dalbergieae. Despite these subversive remarks, Gams placed both Ononis and Cicer in their traditional tribes.

Popov (1928) was strongly impressed by the intermediate position of Cicer between the Vicieae and Ononis; he summarised

Table 7. Character-comparisons between Ononis, Cicer and Vicia. (after Popov, 1928)

ONONIS	CICER	VICIA
Indumentum glandular-villous.	Indumentum glandular-villous.	Indumentum not glandularvillous.
Leaves reduced towards top of stem.	Leaves becoming larger towards top of stem.	Leaves becoming larger towards top of stem.
Stipules adnate to petiole.	Stipules not adnate to petiole.	Stipule not adnate to petiole.
Leaf imparipinnate, usually ternate.	Leaf imparipinnate, usually multijugate, rarely ternate, or paripinnate, with tendril.	Leaf paripinnate, leaf mucronate or ending in a tendril, or rarely imparipinnate.
Calyx regular.	Calyx regular or gibbous.	Calyx regular or gibbous.
Standard wide, with very short claw.	Standard wide, with very short claw.	Standard narrow, with long claw.
Wing free.	Wing free.	Wing adnate to keel.
Style glabrous.	Style glabrous.	Style pubescent below stigma.
Pod inflated.	Pod inflated.	Pod compressed.
Seed ovoid, rough, with 'beak'.	Seed ovoid, rough, with 'beak'.	Seed spherical or bean-shaped, rarely flattened.
Germination epigeal.	Germination hypogeal.	Germination hypogeal.
Stamens monadelphous, rarely diadelphous.	Stamens diadelphous.	Stamens diadelphous.
Filaments dilated at the apex.	Filaments dilated at the apex.	Filaments not dilated at the apex.
Anthers alternately medifixed and basifixed, of two sizes.	Anthers alternately medifixed and basifixed, all the same size.	Anthers all medifixed, all the same size.

the situation in a table of characters which is reproduced in Table 7. These facts led him to propose an eccentric theory to explain the origin of Cicer. In the late Palaeocene (beginning of the Tertiary, see Table 29), according to Popov, Ononis appeared as a hybrid between members of the Genisteae and Trifolium. At this stage Ononis and Vicia were vicarious genera, separated by the Tethys sea and belonging, respectively, to the xerophytic Welwitschia flora of Africa and the mesophytic Ginkgo flora of Asia. At the end of the Tertiary period, geological and climatic changes, including the partial drying-up of Tethys, allowed the components of these floras to mix and hybridise. Crossing took place between Vicia and Ononis; the first generation hybrid, 'Onono-Vicia', underwent selfing and produced a number of segregants comprising the parental types Ononis and Vicia and intermediates, each of which formed a section of Cicer. Popov decided that, in spite of its equal affinity with Ononis, Cicer should be included in the Vicieae according to the traditional taxonomic practice.

In the light of modern evolutionary theory, this story cannot be accepted as a serious explanation of the origin of Cicer, or any other genus; if this kind of wide and free intergeneric mixing of genetic material were possible, these taxa would inevitably lose their distinctness and their status. Popov's theory also suggests that hybridisation at specific level must be common within these tribes. In the Vicieae, however, only a very few experimental crosses have been successful, and these involved closely related species (see part 7.5).

Several authors (e.g. Senn, 1938b; Simola, 1968a) have quoted Popov's conclusions about the origin and taxonomic relationships of the genus which he monographed, accepting his authority without questioning the reasoning behind these judgments. Having examined and rejected the theory which underlies his systematic treatment of Cicer, one is nevertheless left with the unsolved problem which Popov stated so clearly: what are the true relationships of Cicer? This is undoubtedly the most critical issue in the Vicieae, as presently defined.

Chapter 3

CHARACTERS OF THE VEGETATIVE PLANT

3.1. Ontogeny.

3.2. Tendrils.

3.3. Vernation of leaflets.

3.4. Leaf venation.

3.5. Number and shape of leaflets.

3.6. Stipules.

3.7. Indumentum.

3.8. Epidermal structure of leaves.

3.9. Phyllodes and winged stems.

3.10. Rootstocks.

3.1.

ONTOGENY

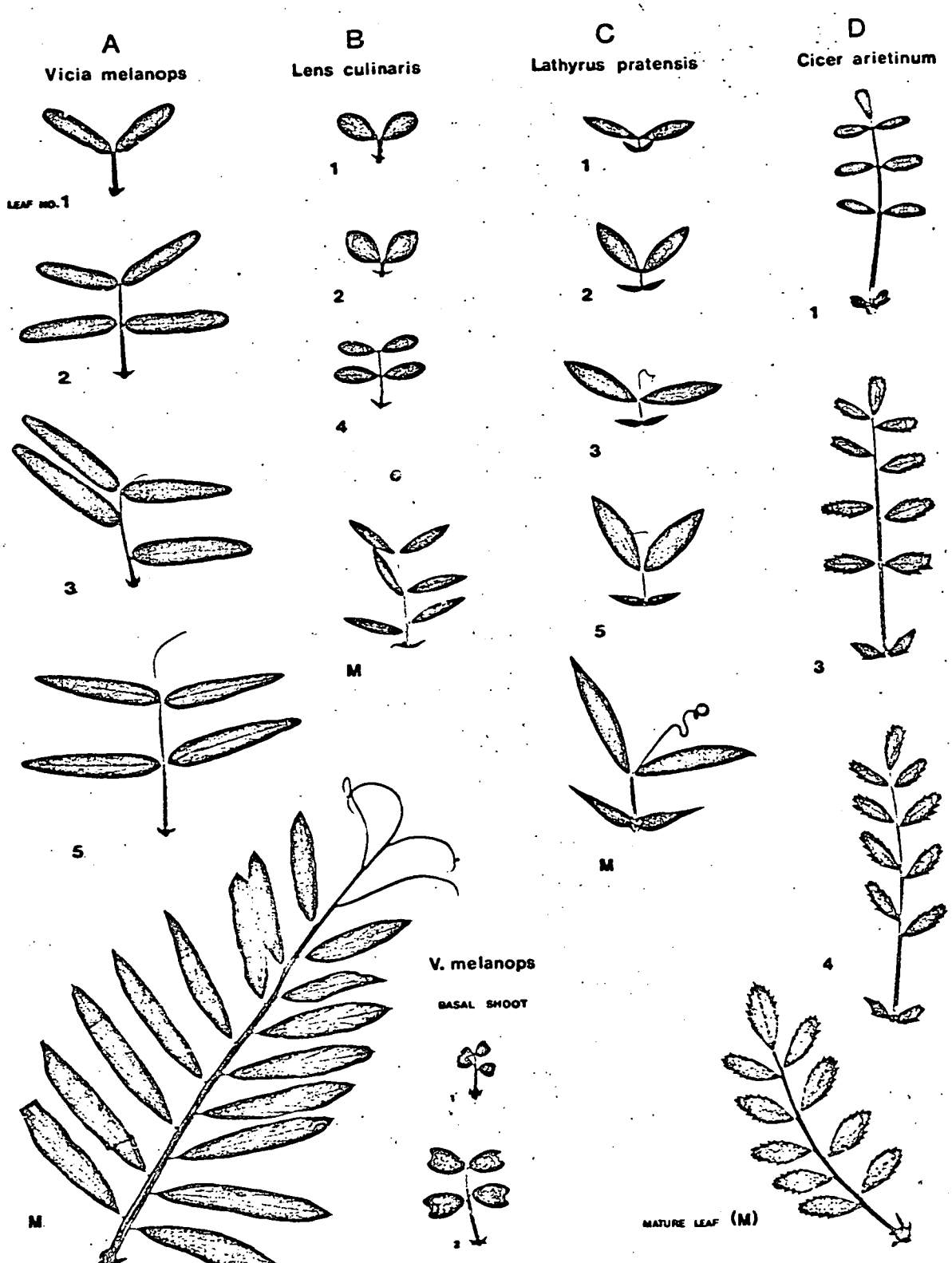
One of the most characteristic features of members of the Vicieae is their hypogeal germination. The distribution of the two types of germination throughout the rest of the Leguminosae has been described by Compton (1912) as follows. "Of the two most primitive tribes (of the Papilionoideae), the Sophoreae appear to contain a majority of hypogeal species, while the Podalyrieae are, so far as known, exclusively epigeal. ... The Genisteae, Galegeae, Loteae, Trifolieae and Dalbergieae are uniformly epigeal, and so are the Hedysareae, with the partial exception of Arachis hypogaea. The only other tribe of the Papilionoideae, viz. Phaseoleae, shows both types in abundance. Among the ... Mimosoideae and Caesalpinioideae the epigeal type prevails ..., while in the Bauhinieae several species seem to be intermediate in type. In several instances hypo- and epigeal germinations occur within the limits of a single genus, as in Pithecolobium, Caesalpinia, Sophora, Phaseolus, Erythrina, etc. It thus appears that the distinction between epi- and hypogeal germination is easily overstepped, and that the change has occurred repeatedly in the evolution of the Leguminosae. The question as to which type is to be regarded as the more primitive probably cannot receive the same answer in all cases." This survey shows that the Vicieae represent one of the few examples of the occurrence of hypogeal germination on a large scale, and the tribe is unusual in being so uniform in this character. For these reasons it has been heavily weighted as

a tribal character, especially in debates on the position of Cicer (De Candolle, 1825).

The ontogeny of a few species of Vicia and Lathyrus has been described by Lubbock (1892), while Csapody (1968) illustrates seedlings of species of these genera and of Cicer arietinum. I studied the seedling development in some 70 species of the Vicieae (these are listed in Appendix 1), and found the pattern of ontogeny very uniform within Vicia, Lathyrus Pisum and Lens; the only significant variation occurs within species of Lathyrus Sects. Nissolia and Clymenum, whose growth is described in part 3.9.

Vicia melanops provides an example of the main kind of ontogenetic pattern. The epicotyl emerges from the soil with its apex bent over in a hook, but soon it straightens out. The shoot bears trifid scale-leaves at the first two or three nodes, followed by leaves with leaflets. The first true leaf is usually unijugate and mucronate (Fig. 1:A, leaf 1); successive leaves have additional pairs of leaflets and a simple tendril appears in the third or fourth. After several more nodes the adult form of organ is attained (Fig. 1:A, leaf M). Having reached a few inches in height the primary shoot slows down in growth while more vigorous secondary branches arise from the lowest nodes. (This is apparently found in all members of the tribe except V. faba and species of Cicer.) In some annual species of Vicia these lateral shoots bear leaves with truncate leaflets; this is illustrated in V. melanops (Fig. 1:A, basal shoot) and was also seen in V. anatolica, V. articulata,

Fig. 1. The ontogeny of four members of the Vicieae, illustrated by series of seedling leaves and mature leaf.



V. sativa, etc. As the plant matures, leaves with cuspidate leaflets may again be produced (as in *V. melanops*), while in other species (e.g. *V. grandiflora*, *V. peregrina*) truncate leaflets are characteristic of the mature leaf.

These types of ontogenetic sequence were observed in cultivated specimens which exhibited their genetic potential under very favourable growing conditions. It was noticeable that the leaves of these plants were larger than in most herbarium material of the same species, and it seems probable that in the wild, environmental conditions are important in controlling both the shape and size of leaflets. Characters like these, which are suspected of being rather plastic, and which are certainly very variable within the species (cf. Plitmann, 1967), cannot be used as taxonomic criteria with any confidence.

A comparison of the silhouettes of seedling leaves of *V. melanops* with those of *Lens culinaris* and *Lathyrus pratensis* (Fig. 1:B & C) shows that there is a considerable difference in the amount of change involved in their ontogenies; this depends chiefly on the number of leaflets characteristic of the mature leaf.

A few species of *Vicia* (*V. freyniana*, *V. argentea*, *V. subvillosa*) have imparipinnate leaves. *V. semiglabra*, which was grown from seed, had imparipinnate leaves in the first year but in the following season produced tendrillous leaves. It was observed that the first true leaf varied in construction from one seedling to another: on most plants it was trifoliolate, on one it was unifoliolate and on another one it was

unijugate as in most Vicia seedlings. In every case the successive leaves were imparipinnate, but (especially in the youngest) the terminal leaflet was slightly asymmetrically placed. The rachis ended abruptly at its articulation with this leaflet; there was no trace of a mucro. The ontogeny of this species thus gives some indication that the imparipinnate state is here secondary, and derived from the paripinnate condition. It would be most interesting to see the seedling development of the other imparipinnate-leaved species.

In marked contrast to the other genera of the Vicieae, the first true leaf in Cicer is typically imparipinnate. This information was very kindly supplied by Dr. van der Maesen (in litt.), who observed seedlings of C. bijugum, C. chorassanicum, C. judaicum, C. pungens and C. songaricum. I have grown C. anatolicum, C. arietinum and C. pinnatifidum; the two latter are illustrated in Fig. 1:D and Fig. 25:3, respectively. My own observations, and those of Muller (1937) and van der Maesen (1972) show that Cicer also differs from the rest of the tribe in that although the basal nodes often give rise to lateral branches, the plumular shoot maintains a strong growth throughout the life of the plant (in annuals) or during the first season (in perennials).

The early ontogeny of members of the Vicieae provides two kinds of taxonomic information. Firstly, there is the mode of germination. This has been thought of great significance by all taxonomists dealing with the group, although the genetic and physiological bases of the difference between hypogeal and

epigeal germination are not yet understood. I am not in a position to judge whether or not this *a priori* reasoning is justified, but at least one should be aware of its doubtful foundations. Secondly, the difference in their early leaves between *Cicer* on one hand and *Vicia*, *Lathyrus*, *Pisum* and *Lens* on the other is important evidence for the separation of the former from the latter, which has so far not been recognised.

The variations observed in ontogeny between and within these groups also provide a basis for speculation about the phylogeny of the leaf of the Vicieae, which is discussed in the next section.

3.2.
TENDRILS

The predominance of tendrils within the tribe Vicieae is its most characteristic vegetative feature. These organs are almost absent from the rest of the Leguminosae, although in several groups (e.g. Abreae) the leaf-rachis ends in a bristle. In consequence, the possession of tendrils is a heavily weighted character when the tribal limits are being considered. Within the Vicieae, however, the absence of tendrils is of more interest than their presence, from both taxonomic and phylogenetic viewpoints. Their occurrence throughout the tribe, and the importance attached to this distribution pattern in the past, will be described first; then the origin and significance of tendrils will be discussed.

Tendrils are present in most species of *Vicia*, the main

exceptions being the 'oroboid' group (V. unijuga, V. crocea, V. oroboides, etc.), some scattered perennials (V. truncatula, V. sparsiflora, V. orobus, some plants of V. canescens and V. semiglabra, V. sicula, V. glareosa, V. montenegrina, V. freyniana, V. argentea and V. subvillosa, of which the last four are imparipinnate) and the annuals V. quadrijuga, V. faba and V. ervilia. All New World species of Vicia have tendrils. In most tendrillous perennials these organs are branched in mature leaves, the exceptions with simple tendrils being V. dadianorum (closely related to the imparipinnate V. freyniana and V. montenegrina, and to V. cassubica which has branched tendrils), V. rafigae, V. glauca and V. pyrenaica. Annual species also commonly have divided tendrils, at least on the upper leaves, but simple ones are characteristic of V. laxiflora, V. caesarea, V. mollis, V. anatolica and V. lathyroides.

In contrast to the situation in Vicia, the presence or absence of tendrils in Lathyrus has been thought of great taxonomic importance, especially by botanists of the last century. Boissier (1872) defined the genus Orobus solely on the grounds of being etendrillous, and his Sect. Orobastrum included all species of Lathyrus (except the small Sects. Clymenum, Aphaca and Nissolia) without twisted styles and with tendrils. Taubert (1894) included Orobus as a section within Lathyrus, and distinguished it from the rest of the genus (Sect. Archilathyrus) by the occurrence of tendrils in the latter. The use of this character was never wholly satisfactory, even to these early taxonomists, because while some fairly natural groups were recognised

other obviously related groups became separated. Boissier himself changed his mind about the position of two species, Orobus nervosus and O. trachycarpus, which he described in the Diagnoses Plantarum Orientalium Novarum (1845) but later transferred to Lathyrus in his Flora Orientalis (1872). In this work he also expressed doubt about the validity of Orobus as a genus, and mentioned several species which on the key character ought to be classified here, but which 'belong' to Lathyrus (L. saxatilis, L. erectus (= L. inconspicuus) and L. roseus).

The value of tendrils as a taxonomic character was discussed by Fritsch (1900). He pointed out that several instances are known where normally tendrillous species have varieties lacking these organs (e.g. L. japonicus, L. pratensis, L. inconspicuus and L. sphaericus) and conversely, tendrillous forms of usually etendrillous species have been reported (e.g. L. niger, L. laevigatus subsp. occidentalis). The main source of evidence in Fritsch's argument against the excessive weighting of tendrils was from cases of closely related species which had been widely separated in the past on the basis of this character. For example, the tendrillous L. davidii was originally placed with L. japonicus and L. pisiformis, although in all other respects it appears rather to be related to the L. gmelinii group. Similarly L. laxiflorus (Orobus hirsutus) is allied to L. pratensis, but having no tendrils was classified by Boissier, Taubert and others in a different genus or section. Fritsch concluded that it is not possible to distinguish natural sections within Lathyrus on the grounds of presence or absence of tendrils, much less the genus Orobus. In spite of this, Tutin

Table 8. Leaf-characters in Lathyrus.

Key :

Venation	:	PI	pinnate
		IN	intermediate
		PA	parallel
No. of (leaflet-pairs)	:	1	one pair
		2	two or more pairs
Tendrils	:	T	tendrils present
		0	tendrils absent

SECTION (Davis, 1970)	SPECIES	VENATION	NO. LEAFLET PAIRS	TENDRILS	STOMATAL INDEX RATIO
OROBUS	aureus	PI	2	0	0.0
	davidii	PI	2	T	0.0
	venetus	PI	2	0	0.0
	niger	PI	2	0	0.0
	japonicus	PI	2	T	0.6
	pisiformis	PI	2	T	0.0
	incurvus	PI	2	T	0.7
	palustris	IN	2	T	0.4
	linifolius	IN	2	0	0.7
N. American species	jepsonii	PI	2	T	0.8
	pauciflorus	PI	2	T	0.7
	polymorphus	PI	2	0	1.1
	venosus	PI	2	T	0.6
LATHYROSTYLIS	pannonicus	PA	2	0	1.7

Table 8, continued.

	boissieri	PA	2	0	1.0
	spathulatus	PA	2	0	1.6
	karsianus	PA	2	0	1.1
OROBASTRUM	saxatilis	PI	2	0	1.4
	angulatus	PA	1	T	1.1
	sphaericus	PA	1	T	1.5
	setifolius	PA	1	T	1.0
	inconspicuus	PA	1	0-T	1.2
NISSOLIA	nissolia	(PA)	0	0	(2.6)
LATHYRUS	sylvestris	PA	1	T	0.8
	latifolius	IN	1	T	0.9
	odoratus	PI	1	T	1.0
	rotundifolius	IN	1	T	0.2
	tuberosus	PI	1	T	0.7
	grandiflorus	PI	1	T	0.4
	cirrhosus	IN	2	T	0.8
	tingitanus	IN	1	T	0.7
OROBON	roseus	PI	1	0	0.0
CICERCULA	blepharicarpus	IN	1	T	0.9
	sativus	PA	1	T	0.8
	hirsutus	IN	1	T	0.8
PRATENSIS	pratensis	PA	1	T	0.6

Table 8, continued.

	laxiflorus	PA	1	O	0.4
APHACA	aphaca	PA	1 - O	T	(0.4)
CLYMENUM	clymenum	PI	2	T	0.9
	ochrus	PI	2	T	0.9
S. American species	pusillus	PA	1	T	1.4
	cabrerianus	PA	1	T	5.2
	subulatus	PA	1	O	1.8
	multiceps	PA	1	O	1.7
	hookeri	PA	1	T	1.5

Stomatal Index ratio is Stomatal Index of upper leaf epidermis divided by Stomatal Index of lower leaf epidermis.

N.B. In L. nissolia it is a phyllodic leaf, not leaflets, to which the scoring applies; in L. aphaca the Stomatal Index ratio refers to the large foliaceous stipules of the adult leaf.

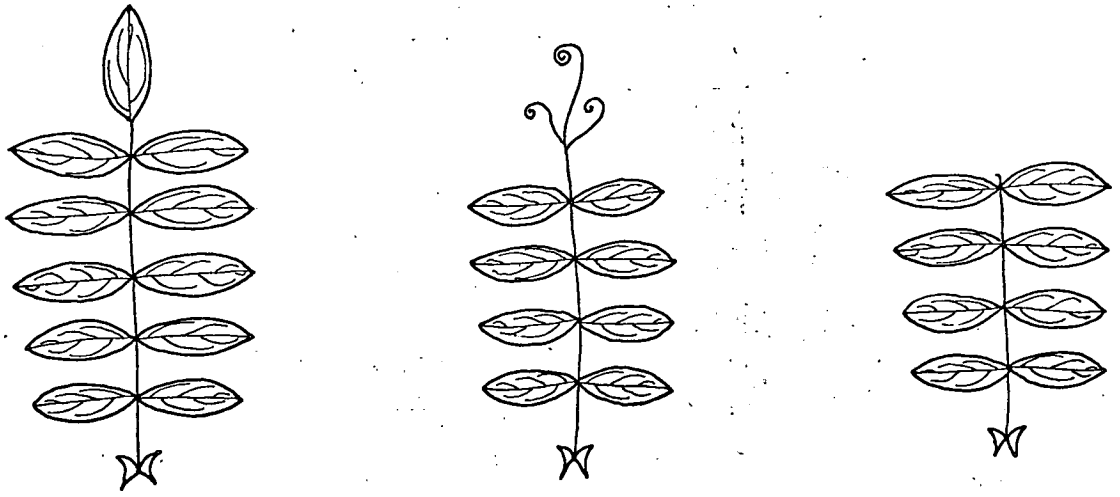
(1952) recently divided the British species of Lathyrus into two sections, Orobus and Eulathyrus, on this same character.

The occurrence of tendrils throughout Lathyrus is summarised in Table 8, where the species are arranged according to the classification of Davis (1970); this shows the degree of correlation which exists at present between the pattern of distribution of these organs and the sectional divisions of the genus. In the majority of tendrillous species of Lathyrus, these organs are branched. The main exceptions with simple tendrils are annuals : members of Sect. Orobastrum (L. vinealis, L. inconspicuus, L. tauricola and L. sphaericus), of Sect. Cicercula (L. amphicarpos, L. lycicus, L. lentiformis and sometimes L. blepharicarpus and L. cicera) and L. aphaca. The perennial L. neurolobus has simple tendrils on the upper leaves.

All members of Pisum and Lens possess tendrils, with the exception of Lens ervoides which is mucronate. Vavilovia formosa has mucronate leaves, while those of the recently described, closely related 'Pisum graecum' are said to be shortly tendrillous.

The use of presence and absence of tendrils as a taxonomic criterion depends very much on an understanding of the evolutionary trends which have produced or deleted them, and this in turn introduces the question: what is the structure of the primitive leaf of the Vicieae? Reinke (1897) considered that the ancestral form of leaf in Lathyrus was multijugate and imparipinnate, and that tendrils arose by a reduction of the terminal and lateral leaflets. The tendrils in some lines then

ecame functionless and further reduced, until an etendrillous eaf with a short mucro appeared, as in the following diagram.

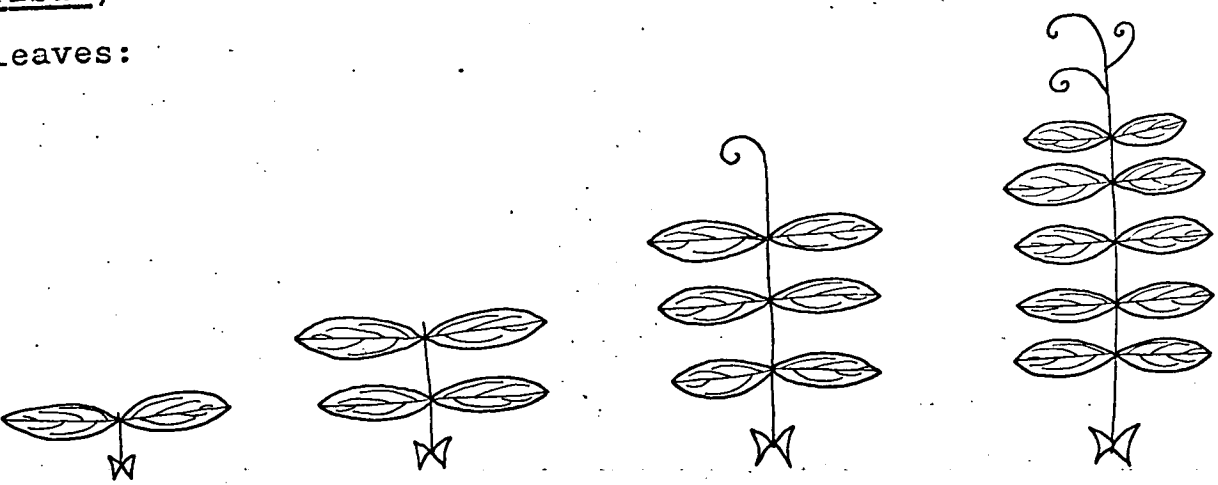


imparipinnate tendrillous paripinnate

EVOLUTIONARY TREND ⟶

This argument seems to me very reasonable. Since tendrils are physiologically specialised organs it is most improbable that they arose de novo from the rachis of a paripinnate leaf; it is much more likely that the tendril evolved from a terminal leaflet. Moreover, the homology of tendrils and leaflets is well established by the occasional mutants which have been found in Lathyrus odoratus (Punnett, 1923) and Pisum sativum (Yarnell, 1962). Sweet Pea plants homozygous for the incompletely recessive 'Acacia' gene have etendrillous, imparipinnate leaves, while the leaves of heterozygotes are intermediate in form between this type and the normal tendrilllous condition.

In the ontogenetic sequence of Vicia, Lathyrus, Lens and Pisum, mucronate seedling leaves precede tendrillous adult leaves:



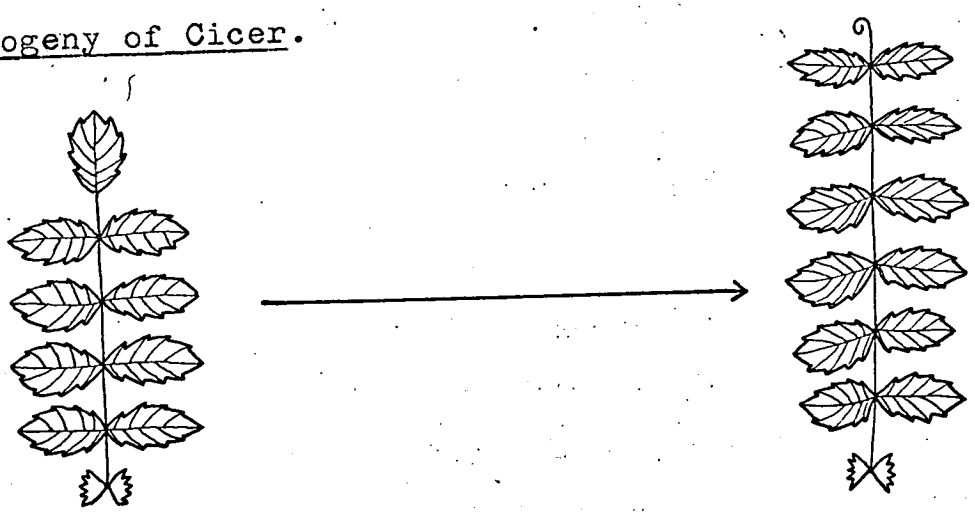
mucronate juvenile leaf → tendrillous adult leaf

This cannot be thought to represent the course of phylogeny; instead, the earliest seedling leaves are believed to be reduced, as indeed are the scale leaves which they follow (Corner, 1954). One would not expect to find mucronate, paripinnate seedling leaves followed in the mature plant by imparipinnate leaves; rather, the mucronate seedling leaves are seen as a legacy of the evolution of tendrils in the adult. I have assumed that the few species of Vicia whose leaves have a terminal leaflet are secondarily imparipinnate. If this is true, then the otherwise universal occurrence of paripinnate, mucronate seedling leaves in Vicia, Lathyrus, Lens and Pisum is evidence that the tendrillous condition is ancestral in these genera of the

icieae. The mucronate adult leaf was for a long time held to e of particular significance, especially in Lathyrus, so that ll species with this character were sometimes classified together. However, if this state is not primitive within the icieae, but has been achieved by reduction of tendrils, then t could have arisen at any time or in any group if tendrils were no longer necessary. This view is expressed by Simola (1968a) in a diagram showing possible trends in the evolution of leaves in Lathyrus. Since seedling leaves are always etendrillous, mucronate adult leaves could have developed by neoteny (or, more strictly, by paedomorphosis). These considerations lead to the conclusion that the absence of tendrils is no more important than any other character-state. Though it is a relatively advanced feature, it does not provide a measuring-stick by which to judge a whole genus, because the loss of tendrils has probably occurred more than once. See Addendum and Fig. 100.

Cicer presents a strong contrast to the other genera, for its seedlings have imparipinnate leaves. When the adult plant is tendrillous, the tendrils appear as a substitute for the terminal leaflet later on in the life-cycle, as shown in the diagram on the next page. (In several tendrillous species, e.g. C. anatolicum, C. baldschuanicum, C. graecum and C. songaricum, this transition is represented in intermediate leaves by the presance of leaflets whose midribs, and even sometimes the lateral veins, are produced into rudimentary tendrils.) If this genus is compared with the rest of the tribe, it seems as

Ontogeny of Cicer.



imparipinnate seedling leaf

tendrillous adult leaf

though the evolution of tendrils is at an earlier stage in Cicer: here the trend towards reduction of the terminal leaflet has not proceeded so far as to encompass the juvenile leaves, and the imparipinnate condition of the primitive leaf is thus still apparent in the seedling.

3.3.

VERNATION OF LEAFLETS

Within the Vicieae there are two types of vernation (ptyxis): Lathyrus has supervolute leaflets, while those of Vicia, Lens, Pisum and Cicer are conduplicate in bud (Table 2). Unfortunately I do not know the vernation-type in Vavilovia; I expect it to be conduplicate, but the character must be checked in living material. The difference in vernation within the tribe has been overlooked by most taxonomists, probably because the

character is seldom visible in the herbarium. On the other hand, it has the advantage of being apparent in living plants from the earliest stages of development to the end of the life-cycle. It has never been pointed out that this character provides an important confirmation of the division of 'oroboid' species into the two genera Vicia and Lathyrus (see Table 2).

The earliest mention of the character, as far as I can discover, is by Döll (1843). Later, Alefeld (1859) stated that the only species outside Lathyrus which has supervolute vernation is Vicia biennis. My own observations confirm this, and it is surprising that Hanelt & Mettin (1962), who made a special comparative study of V. biennis and V. neglecta, do not mention this important differential character. Gams (1924) says that V. oroboides and V. faba have rolled leaflets, but Hanelt & Mettin (1970a) deny this, and I find these species have the conduplicate vernation typical of Vicia.

As far as I can ascertain, conduplicate vernation is the predominant or exclusive type in the neighbouring tribes of the Papilionoideae, the Trifolieae and Genisteae. The occurrence of supervolute vernation in Lathyrus thus appears to be a specialised, recently-evolved feature; its presence in V. biennis is also particularly interesting, and must be taken into account in any discussion of the evolution of Vicia and Lathyrus.

The distribution of vernation types in the tribe provides some evidence for the relationship between Lathyrus and Pisum. These genera have several characters in common delimiting them from the rest of the tribe, and might be supposed to have a

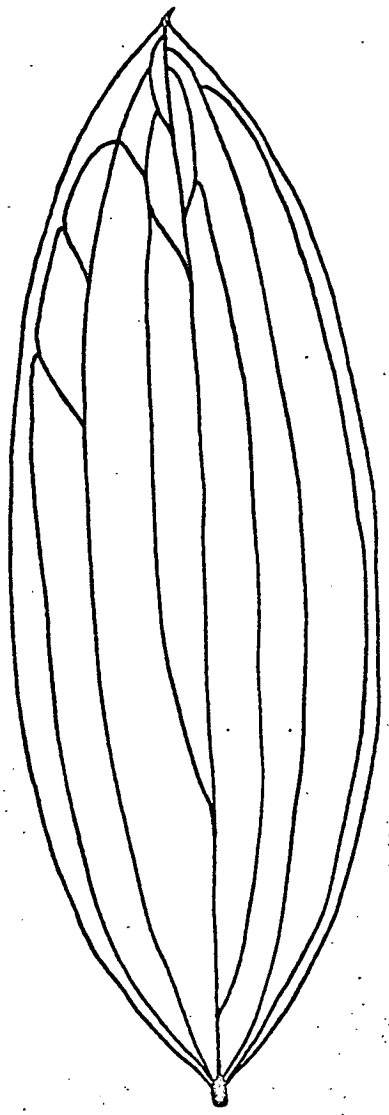
close affinity. However, the folded leaflets of Pisum suggest that the stock of this genus must have become separated from that of Lathyrus before the latter evolved its rolled leaflets; in this case, Pisum is not a recently segregated branch of Lathyrus.

3.4.
LEAF VENATION

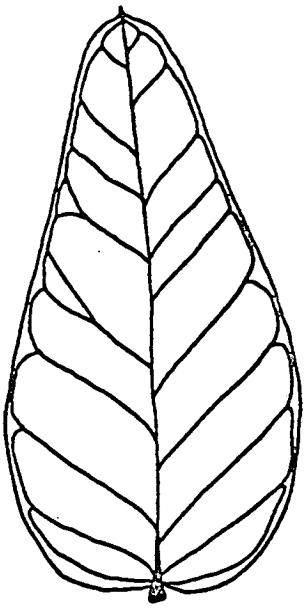
The terms used in the following paragraphs to describe different types of venation are taken from Stearn (1966). The genera Lathyrus, Vicia, Lens, Pisum and Vavilovia are characterised by brochidodromous venation: the lateral veins curve towards the leaflet-apex on approaching the margin, and fuse with the next vein, so that a series of loops is formed (Fig. 2:A & C). Most species have entire leaflets, and in the few exceptions (varieties of Vicia sativa, V. grandiflora, V. faba and Pisum sativum) the venation is still basically brochidodromous, each serration being supplied by a short trace which branches from the marginal loop.

In contrast, the leaflets of Cicer are serrate, and the main lateral veins run straight from the midrib to end blindly at the point of a tooth (Fig. 2:B). Their branches also lead to the margin, and there are no regular connections between the veins at the edge of the leaflet. This type of venation is termed craspedodromous. Brochidodromous venation is very common within the Leguminosae, but the craspedodromous type, which is usually associated with serrated leaflets, occurs only in the

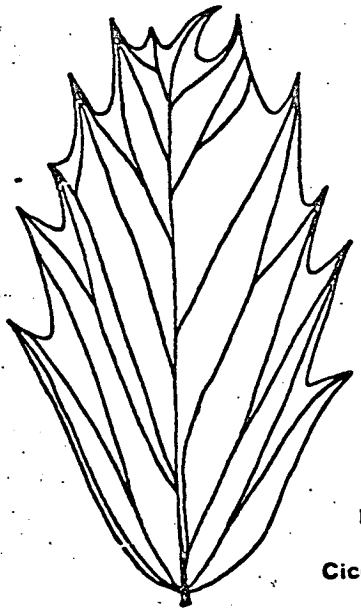
Fig. 2. Venation types in the Vicieae.



C.
Lathyrus pratensis
parallel;
brochidodromous



A. Vicia sepium
pinnate;
brochidodromous



B.
Cicer anatolicum
pinnate; craspedodromous

Trifolieae and in Ononis and Cicer. Its limited distribution makes this character worthy of considerable weighting.

The venation of Cicer and most of the rest of the Vicieae is pinnate, but in Lathyrus parallel venation occurs in several groups.(e.g. L. pratensis, Fig. 2:C). According to Corner (1954), this is due to a difference in the direction of growth of the leaflet; pinnate-veined leaves develop acropetaly, parallel-veined ones basipetaly. (I have not studied this myself). Until recently this character received little attention, and its variation has not influenced the formation of intrageneric groupings within Lathyrus. Tutin (1956) discussed this point briefly, probably considering only Western European species, and suggested that it is possible to distinguish the pinnate-veined members into a separate genus, Orobus. This proposal was criticised by Simola (1968a), who says that although leaf-venation deserves recognition as an important character, it cannot alone introduce systematic order into the group, any more than the floral characters (e.g. twisting of styles) which she considers to have been over-weighted in the past. It is one line of evidence among many. Simola and Bässler (1966) both find that pinnate-brochidodromous venation is the more primitive state within Lathyrus, because of its occurrence throughout the rest of the Vicieae and its correlation with other relatively primitive characters, e.g. multijugate leaves.

Table 8 shows the type of venation found in a representative selection of species; the Old World members are grouped into sections according to Davis (1970). Species of Sects.

Orobus, Clymenum and Gloeolathyrus, and those from N. America, have pinnate venation; Sects. Lathyrostylis, Orobastrum, Pratensis and the S. American species have parallel-veined leaflets. (L. saxatilis in Sect. Orobastrum is anomalous in being pinnately veined.) The venation of the leaflets on the first two leaves of L. aphaca is parallel; and it was observed, in all species raised from seed, that the leaf-venation does not change during ontogeny. The remaining two sections, Lathyrus and Cicercula, show variation in this character. Among the eleven species of Sect. Lathyrus which I studied, the distribution of venation types is as follows: 5 pinnate, 5 intermediate and one parallel. Of the fourteen species of Sect. Cicercula, none has pinnate venation, while six are intermediate- and eight parallel-veined. These results are interesting because the two sections are morphologically very close, being differentiated chiefly on the perennial/annual life-form. It seems, therefore, that the trend towards parallel venation is here correlated with the evolution of annual species; conversely, the situation provides additional evidence for the relative primitiveness of pinnate venation.

If one is correct in thinking that Sects. Lathyrus and Cicercula represent a line of development separate from the rest of the genus, then it seems that parallel venation has evolved more than once within Lathyrus. Two other groups of perennials, Sect. Lathyrostylis and the S. American species, are probably both examples of this; they are geographically isolated from each other, and each is a richly-developed complex characterised

by parallel-veined leaflets.

The adaptive significance of parallel-brochidodromous venation in Lathyrus is obscure. This character does not appear to be linked with a particular type of ecological situation, since it is found in relatively xeromorphic perennials (Sect. Lathyrostylis), mesophytic perennials (Sect. Pratensis), and in several diverse annual groups (Sects. Orobastrum, Cicercula and Aphaca).

The relationship between the venation and shape of leaflets in Lathyrus is discussed in the next section.

3.5.
NUMBER AND SHAPE OF LEAFLETS

As was mentioned in part 3.4, the majority of the Vicieae (besides Cicer) have entire leaflets. The few exceptions with serrated leaflets are all varieties of annual species associated with agriculture (e.g. Vicia sativa, Pisum sativum) and this character has no taxonomic significance.

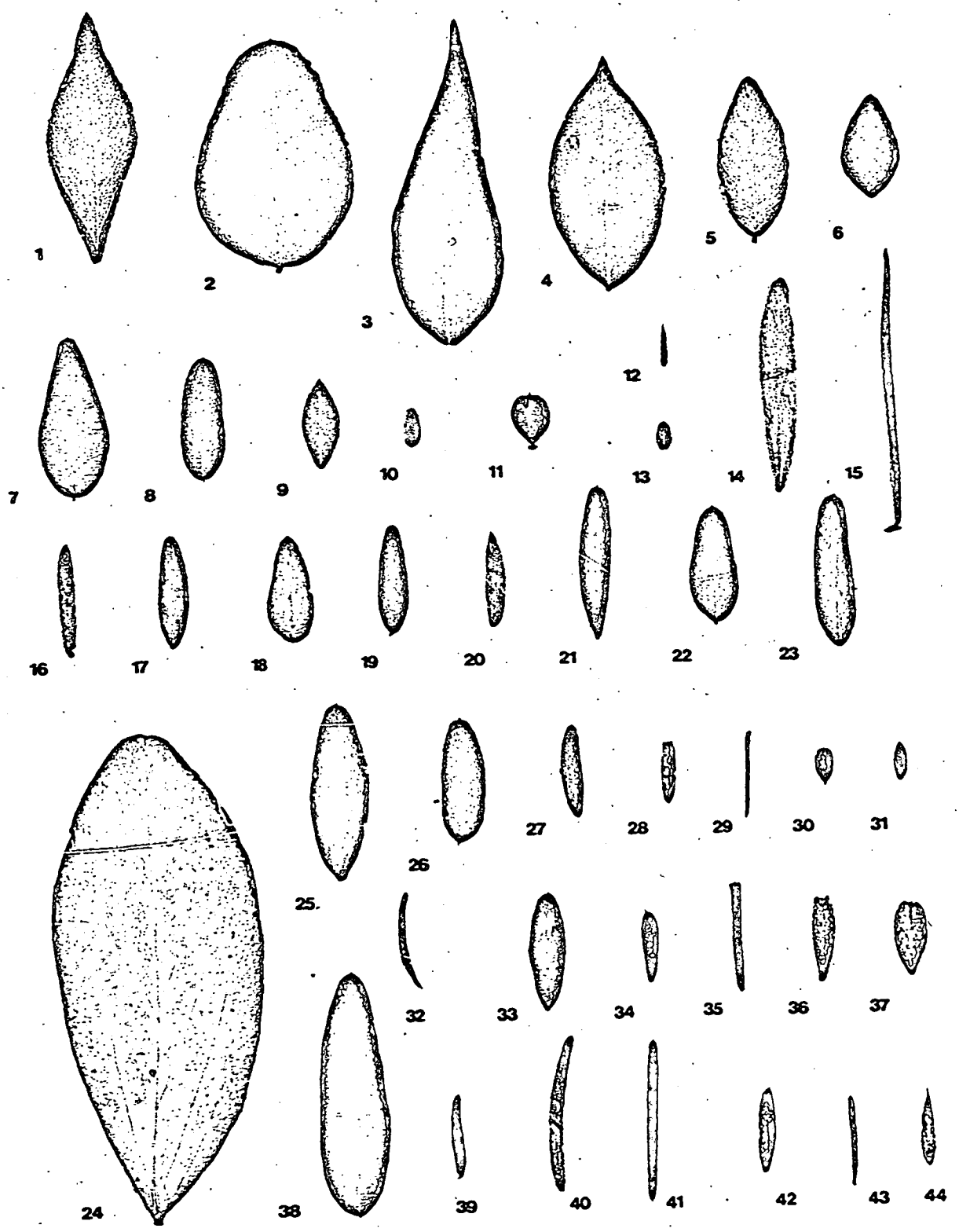
The range of variation in leaflet shape in Vicia is illustrated in Fig. 3. Most members of Vicia have leaflets which are linear, oblong or narrowly ovate and mucronate at the apex. V. koeieana (Fig. 3:44) is remarkable within the tribe in having long-aristate leaflets. A few species, e.g. V. articulata (:28), V. pyrenaica (:11), V. grandiflora (:37) and most of the V. sativa complex (:36) are characterised by their emarginate leaflets. Some other species produced leaflets of this relatively unusual shape at early stages of ontogeny but leaflets which

Key to Figure 3.

VICIA

1. V. unijuga
2. V. pisiformis
3. V. oroboides
4. V. crocea
5. V. pseudo-orobus
6. V. dumetorum
7. V. sepium
8. V. balansae
9. V. venulosa
10. V. alpestris
11. V. pyrenaica
12. V. subvillosa
13. V. rafigae
14. V. canescens
15. V. sicula
16. V. argentea
17. V. pinetorum
18. V. sylvatica
19. V. ochroleuca
20. V. cracca
21. V. onobrychioides
22. V. orobus
23. V. freyniana
24. V. faba
25. V. bithynica
26. V. villosa
27. V. benghalensis
28. V. articulata
29. V. filicaulis
30. V. lunata
31. V. pubescens
32. V. palæstina
33. V. melanops
34. V. pannonica
35. V. peregrina
36. V. sativa
37. V. grandiflora
38. V. nigricans
39. V. caroliniana
40. V. exigua
41. V. pulchella
42. V. bijuga
43. V. graminea
44. V. koeieana

Fig. 3. Vicia leaflets.

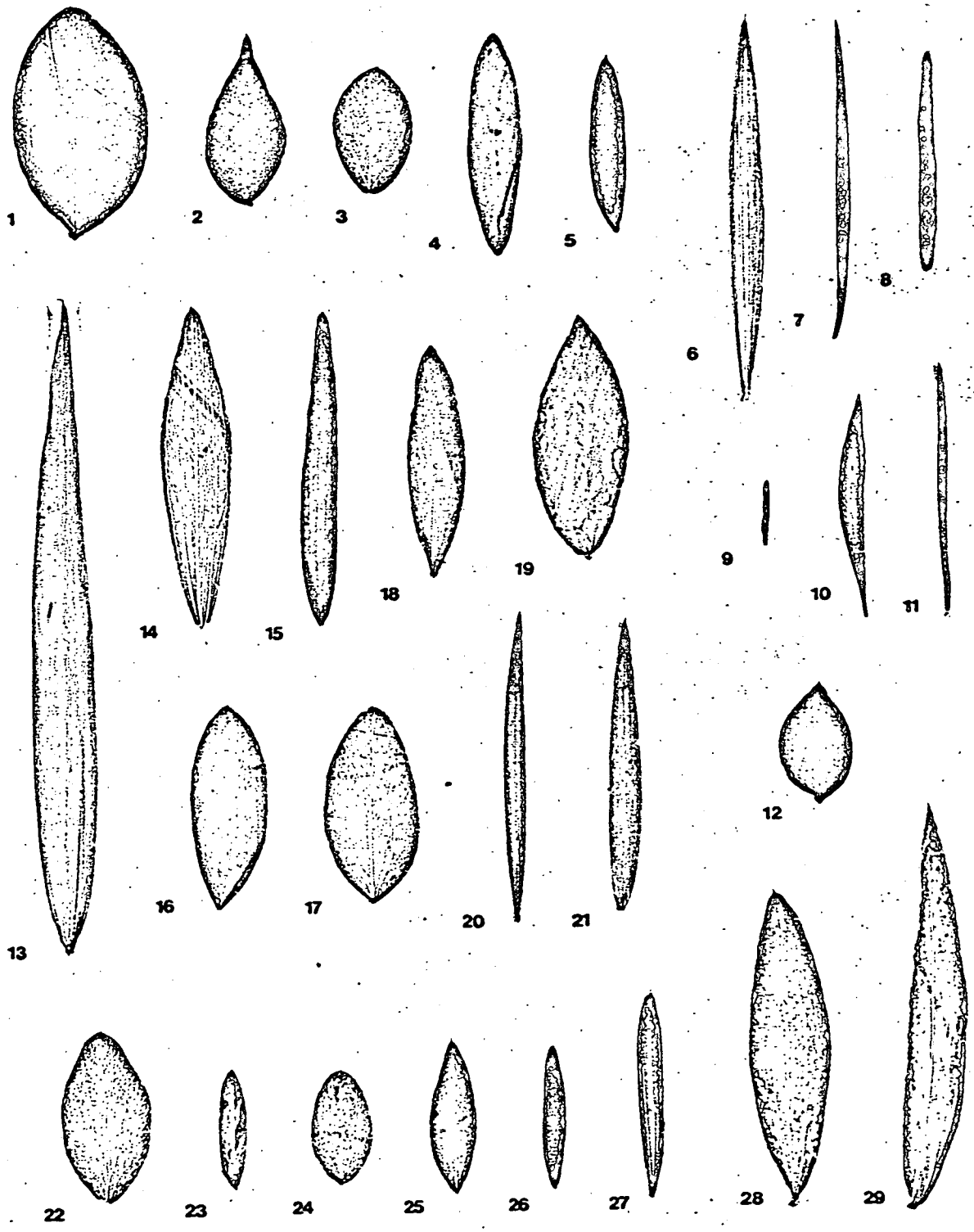


Key to Figure 4.

LATHYRUS

1. L. davidii
2. L. vernus
3. L. japonicus
4. L. palustris
5. L. linifolius
6. L. boissieri
7. L. pallescens
8. L. clymenum
9. L. saxatilis
10. L. inconspicuus
11. L. setifolius
12. L. laxiflorus
13. L. sylvestris
14. L. latifolius
15. L. tingitanus
16. L. tuberosus
17. L. grandiflorus
18. L. hirsutus
19. L. chloranthus
20. L. cicera
21. L. annuus
22. L. sulphureus
23. L. polymorphus
24. L. polyphyllus
25. L. vestitus
26. L. pusillus
27. L. multiceps
28. L. pubescens
29. L. hookeri

Fig. 4. Lathyrus leaflets.



are acute at the apex in the mature plant. An example of this phenomenon is shown by V. melanops, described in part 3.1 (Fig. 1:A). Most species with emarginate leaves belong to Sect. Vicia.

Lathyrus leaflets are shown in Fig. 4. In this genus, parallel-veined leaflets tend to be proportionally narrower than pinnate-veined ones, but there are exceptions; for example, L. laxiflorus (Fig. 4:12) has parallel-veined, broad leaflets while L. clymenum (:8) has pinnate-veined, narrow ones. Bässler (1966) implies that parallel venation in Lathyrus was induced by an evolutionary trend towards narrower leaflets. This may be so, but the two attributes are obviously not linked by necessity, since Vicia has many members with extremely tenuous leaflets (e.g. V. filicaulis, Fig. 3:29), yet all have pinnate-veined leaflets.

Generally speaking, the size of leaflets in the tribe is inversely related to the number of pairs per leaf. Thus in Vicia the majority of species have multijugate leaves with leaflets less than 2 cm long, while in the groups with few leaflet-pairs the leaflets are significantly larger. Examples of the latter are the 'oroboid' types, e.g. V. unijuga (Fig. 3:1) and V. oroboides (:3), and members of Sect. Faba - V. faba (:24) and V. bithynica (:25). Exceptions to this rule are provided by the small annual species of Sect. Ervum, e.g. V. pubescens (:31); some S. American species, e.g. V. bijuga (:42) and V. graminea (:43); and the xeromorphic V. filicaulis (:29). The North and South American V. nigricans (:38) is unusual in

having many pairs of large leaflets.

Whereas in Vicia leaflet number is a character of only sporadic systematic value, in Lathyrus it achieves special taxonomic significance as there is a marked trend towards reduction of leaflets within this genus. Leaves with several pairs are found in species of N. America and in Sects. Clymenum, Gloeolathyrus and Orobus. The latter contains the 'oroboid' group of species with broad, characteristically tapered leaflets (e.g. L. vernus, Fig. 4:2) which in facies so closely resemble some members of Vicia. In Lathyrus the 'oroboid' group has relatively many leaflets; in Vicia, relatively few. The occurrence of multijugate leaves in Sect. Orobus is one of the reasons why this group is considered the most primitive within Lathyrus (cf. Simola, 1968a). The sections Lathyrus, Cicercula, Pratensis, Orobastrum and most of the S. American species are characterised by unijugate leaves. It seems probable that reduction in leaflet number has occurred independently in different lines, as there are occasional species whose leaflets have more than two leaflets in several of these groups. Examples are L. cirrhosus (Sect. Lathyrus), L. saxatilis and L. vinealis (Sect. Orobastrum) and the S. American L. macropus. The leaves of Sect. Lathyrostylis have one, two, or rarely up to six, leaflet-pairs; in some species, e.g. L. variabilis, L. tukhtensis, L. boissieri, etc., there are four leaflets borne on an extremely short rachis, so that the leaf is subdigitate. The number of leaflet pairs per leaf in a selection of species of Lathyrus is scored in Table 8, which also shows that the trend towards

fewer leaflets is correlated with the development of parallel venation.

The leaves of Lens are very similar to those of Vicia Sect. Ervum in both leaflet shape and number. Pisum has relatively broad leaflets, and from one to four pairs per leaf. The members of Vavilovia have unijugate leaves: the leaflets are characteristically coriaceous and prominently veined, and sub-orbicular to broadly and acutely ovate.

Most species of Cicer have multijugate leaves, but C. incisum has from three to seven leaflets, while C. chorassanicum is uniformly trifoliolate. Several members of the genus (e.g. C. pungens, C. tragacanthoides) are markedly xeromorphic and their leaflets reflect this in their coriaceous texture and in the development of the serrations into short spines.

Since the juvenile leaves of the Vicieae (except members of Cicer) typically have few pairs of leaflets, the trend towards reduction in leaflet number in several groups may be seen as a neotenic process, like that involving loss of tendrils (cf. part 3.2).

A few members of the Vicieae are remarkable in that their leaves become black on drying. These include Vicia nigricans, Lathyrus niger, L. linifolius and L. hookeri, but the character is also seen in a variable and less extreme form in other species of these genera. The reason for the blackening phenomenon is not known.

3.6.

STIPULES

The use of stipular characters in the taxonomy of the Vicieae is very uneven: in some groups they have no value, in others they have a limited use as 'key' features of isolated species, while in a few cases they provide important evidence for relationship. The two outstanding examples of this latter category are described first.

In Vicia, all members of Sects. Vicia and Faba possess a more-or-less conspicuous nectariferous spot on the abaxial face of each stipule. The character was used by Alefeld (1861) as the basis for dividing his tribe Viciidae (equivalent to Vicia) into subtribes Viciosae (with nectaries) and Ervosae (without). Illustrations of the appearance and anatomy of the stipular nectary in V. sepium are given by Gams (1924). A transverse section of the stipule shows that the surface of the nectary is sunk below the level of the epidermis, and the floor of this shallow pit is densely covered with a mixture of glandular and simple hairs of the kind found generally throughout Vicia (types A and C in Fig. 5; see part 3.7). According to the figure in Guinea (1953), V. ervilia also has stipular nectaries, and the illustration is reproduced by Hermann (1960). Gunn (1969) actually states that this character is present. I have not found nectaries in V. ervilia or in any other species outside Sect. Vicia and Faba, but confirm that they occur in every member of these groups. The role of the extrafloral nectaries is discussed in parts 4.1 and 4.3.

Most species of the Vicieae have semisagittate stipules, and the infrequent occurrence of sagittate or hastate stipules in Lathyrus is taxonomically interesting. They are found in L. japonicus and L. pisiformis (probably closely related species, in Sect. Orobus), in most S. American members of the genus, and in Sects. Pratensis and Aphaca. Having studied the seedlings of L. japonicus, L. pratensis and L. aphaca, I found that semisagittate stipules were produced at the earliest nodes in all three species, and the mature hastate form appeared at about the third or fourth leaf. (The ontogenetic sequence in L. aphaca is shown in Fig. 9:A.) Sect. Aphaca is very remarkable in that its mature leaves have no leaflets, their function being 'delegated' to much-enlarged stipules. This peculiarity serves to make the group taxonomically isolated, but the shape of the stipules may indicate a relationship with Sect. Pratensis. The vascular anatomy of species with sagittate stipules is described in part 5.4.1, and is compared with that of the more usual semi-sagittate arrangement.

Stipules provide 'spot' characters in several members of Vicia. In V. crocea and V. articulata they are strikingly dimorphic; in V. koeieana they are finely laciniate; in members of the V. sativa complex and in V. sylvatica they are characteristically dentate. The stipules of V. pisiformis are small and semi-sagittate, like those of the majority of this genus, but in adult leaves the proximal pair of leaflets is borne so close to the axil that they imitate the large foliaceous stipules of Pisum (see part 5.4.1). This specific character appears in the

second seedling leaf of V. pisiformis; the first leaf has a normal petiole.

The stipules in Cicer are serrated like the leaflets and in xeromorphic species share their tendancy towards spininess. The most extreme examples of this are found in C. macracanthum and C. pungens, where the stipules are modified into hard, sharp spines without any trace of lamina.

In all genera of the Vicieae the stipules are free; in members of the Trifolieae and Ononidae they are fused to the petiole for some distance (see part 5.4.2 and Fig. 33).

3.7.

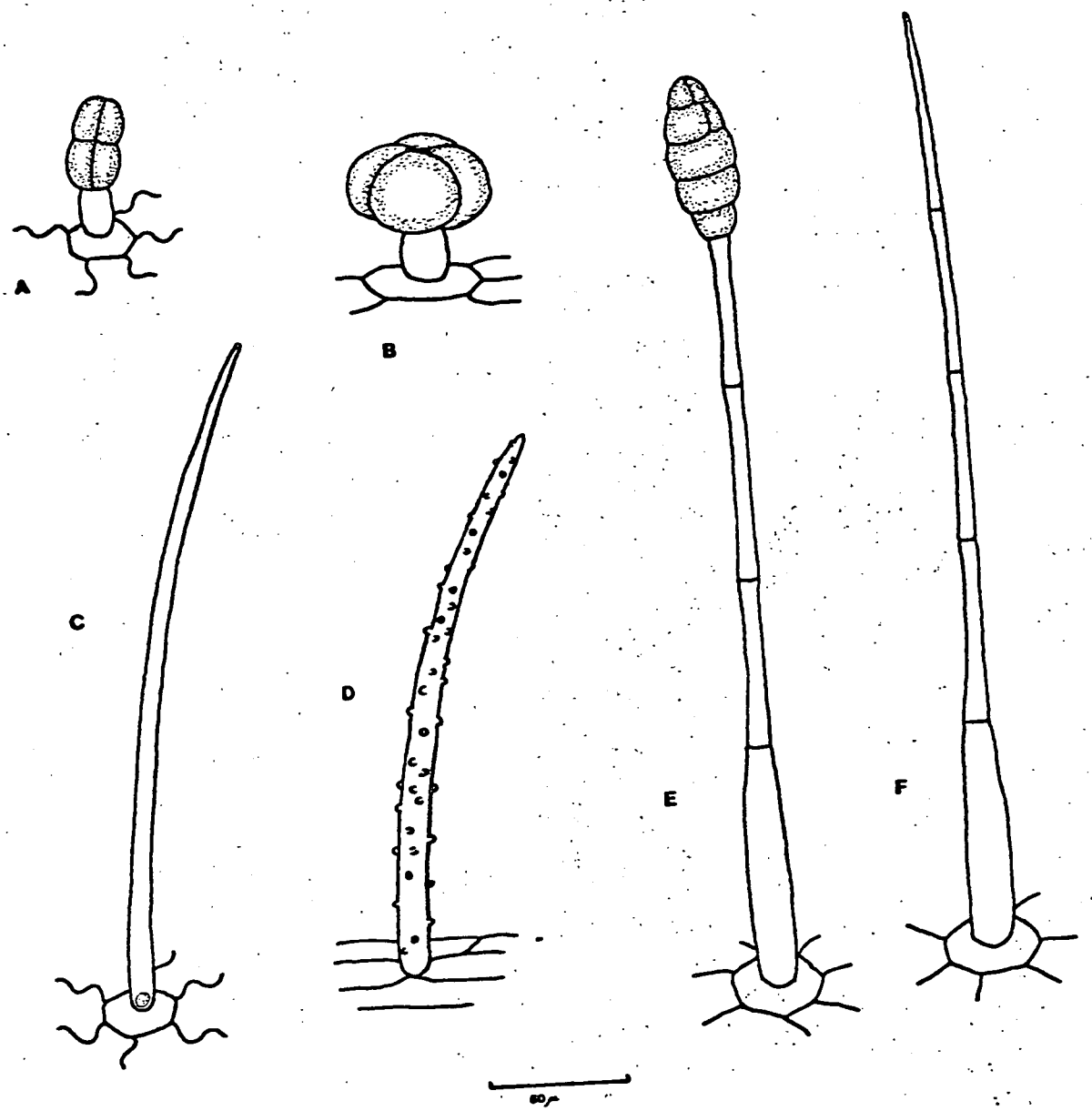
INDUMENTUM

Most members of Vicia, Lathyrus, Pisum, Lens and Vavilovia have sparsely hairy leaves, the hairs usually being most abundant on the lower epidermis and along the midvein of the leaflets. The indumentum in these genera is of three types, comprising unicellular hairs (Fig. 5:C) and short-stalked glands (Fig. 5:A & B). The simple hair varies considerably in length but is otherwise very uniform, having a thin wall which is always smooth. It arises from an isodiametric, straight-walled cell which projects slightly above the general level of the epidermis. At the base of the hair is often found a granular cytoplasmic body which can falsely give the impression of a separate cell. Pisum and Lathyrus tend to have nearly glabrous leaves; in Vicia and Lens they are more densely hairy. Occasional species (e.g. Lathyrus macropus, Vicia canescens, Lens montbretii)

have villous leaves. Vicia lutea, and a few species of Lathyrus (L. trachycarpus, L. chrysanthus, L. chloranthus, L. lycicus, L. hirsutus and L. odoratus) have legumes with tuberculate-based hairs. The hairs themselves are of the same type as that shown in Fig. 5:C, but the epidermal cell subtending each hair is produced into a prominent tubercle (see also part 4.4). The glandular hair illustrated in Fig. 5:A is as widely distributed as the simple hair, occurring sparsely on the leaves of most species. It is also found on the young legumes of a few species of Lathyrus (L. aureus, L. venetus, L. gorgoni, L. annuus, L. laxiflorus, L. czeczottianus). The cells of the head, which contain dense, brownish, granular cytoplasm, are usually eight, and there is always a single stalk cell. The glandular hair shown in Fig. 5:B was found in only two species, both in Lathyrus: on the young shoots of L. odoratus, and on the fruits of L. cassius. These species are placed in separate sections (Lathyrus and Cicercula, respectively) in the treatment of Davis (1970), and the distribution of this rare type of glandular hair may point to a need for revision of sectional limits in this area.

The remaining genus, Cicer, is very distinct within the tribe in possessing glands with multicellular stalks (Fig. 5:E). The exact form and dimensions of these hairs vary considerably, due both to specific differences and to their stage of growth. It was observed that they grow acropetaly, commencing as a simple filament; the distal cell then starts to divide both transversely and longitudinally, until the mature head is formed.

Fig. 5. Types of hair found in the Vicieae and Trifolieae.



A. Short-stalked glandular hair

B. Short-stalked gland (of very limited distribution)

C. Smooth-walled simple hair

D. Papillate simple hair

E. Long-stalked glandular hair

F. Multicellular hair

The hair arises from a large, convex cell which protrudes above the neighbouring cells of the epidermis, and the cuticle is wrinkled up around it.

While this type of hair is confined to Cicer within the Vicieae, it is found also in Ononis and some species of Medicago; according to Širjaev (1928) it occurs in Trigonella Sect. Lunatae. This distribution pattern (Table 9) is one of the strongest lines of evidence from vegetative characters suggesting that Cicer is related to the Ononidae and Trifolieae. It is interesting that this unusual hair is associated with the equally rare craspedodromous type of venation (see part 3.4).

Unfortunately, however, the taxonomic evidence provided by indumentum is not straightforward. Besides the long-stalked glands, Cicer also possesses simple, smooth-walled hairs like those of the rest of the Vicieae (sometimes these have very thick walls, e.g. in C. incisum). Members of the Trifolieae also have simple hairs, but these always have papillate walls (Fig. 5:D), and the basal cell does not project above the surrounding epidermis as in the Vicieae. The boundary between the Vicieae and Trifolieae is made more tenuous by the fact that in Ononis there are no simple hairs; instead, it has multicellular hairs (Fig. 5:F) which are obviously related to the long-stalked glands. Multicellular hairs are not found in Cicer, but occur in some species of Medicago. The short-stalked gland (Fig. 5:A) occurs throughout the Vicieae, Trifolieae and Ononidae, and is therefore of no systematic value within them.

Table 9. Distribution of indumentum types in the Vicieae and Trifolieae.

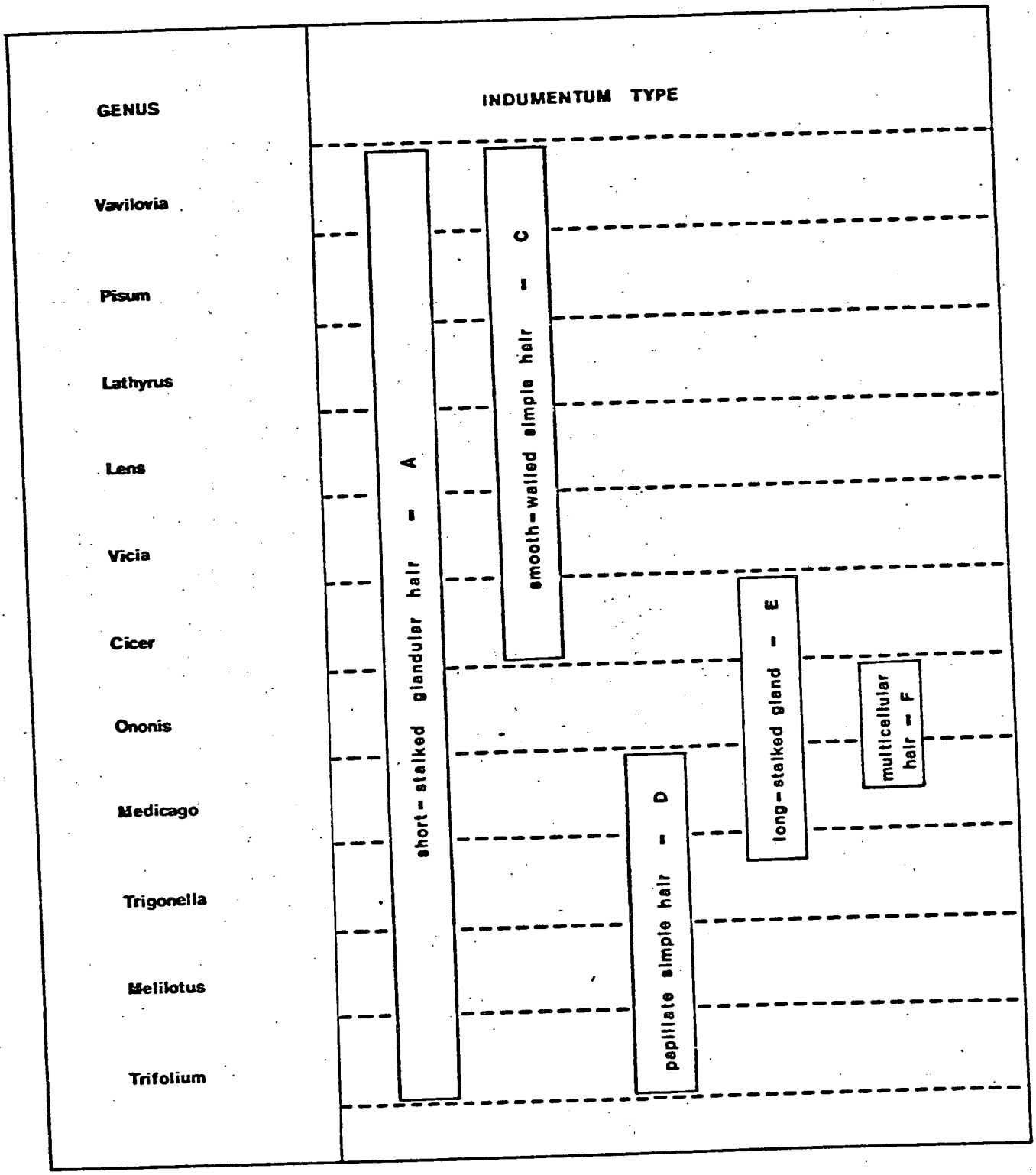


Table 9 shows that the distribution patterns of these indumentum types provide confusing data for taxonomy: on one hand, Cicer is linked with Ononis and the Trifolieae by the long-stalked glands; on the other, the micro-character involving variation in the wall-structure of the simple hair (smooth or papillate) supports the present systematic arrangement. The absence of simple hairs in Ononis and the limited distribution of the multicellular hairs both serve to obscure the significance of the other data.

3.8.

EPIDERMAL STRUCTURE OF LEAVES

The first investigation into the epidermal structure of the Vicieae was reported in 1902 by Streicher, who described the shape of the epidermal cells and the distribution of stomata, hairs, sclerenchyma and cell inclusions in several species of each genus. His work led him to conclude that these characters have little importance in the taxonomy of the group, and they have since been largely ignored, except in Lathyrus. In 1938 Senn published a paper which discussed some of the data useful in the classification of this genus, and included mention of the shape of epidermal cells and the distribution of stomata. His work was not critical, however; he merely stated that epidermal structure usually supports the classification of Aschersón and Graebner (1909) which he used as a framework.

The first to make a serious attempt to relate variation in the epidermal structure of Lathyrus to its taxonomy was Bässler

Table 10. Epidermal types found in Lathyrus by Bässler (1966).

SECTION (Davis, 1970)	SPECIES	EPIDERMAL TYPE (see page 116)	MEMBERS OF SUBGEN. OROBUS sensu BÄSSLER
OROBUS	L. davidii	1	*
	L. aureus	1	*
	L. humilis	1	*
	L. vernus	1	*
	L. niger	1	*
	L. linifolius	1	*
	L. pisiformis	1	*
	L. japonicus	2	*
	L. palustris subsp. palustris	1	*
	L. palustris subsp. nudicaulis	2	*
	L. incurvus	2	*
North American species	L. ochroleucus	1	
	L. vestitus	1	
	L. parvifolius	1	
	L. venosus	1	
	L. polyphyllus	1	
	L. nevadensis	1	
	L. jepsonii	1	
	L. sulphureus	1	
PLATYSTYLIS (Syn. LATHYROSYLIS)	L. pannonicus	3	*
	L. filiformis	3	*
	etc. (18 species)	3	*
LATHYRUS	L. latifolius	3	
OROBON	L. roseus	1	*

Table 10 continued.

CICERCULA	L. cassius	3	
	L. cicera	3	
	L. marmoratus	3	
	L. stenophyllus	3	
	L. quadrimarginatus	3	
	L. blepharicarpus	3	
	L. gorgoni	3	
CLYMENUM	L. clymenum	3	
PRATENSIS	L. laxiflorus	1	*
	L. czeczottianus	2	*
	L. hallersteinii	2	*
	L. pratensis	2	*
OROBASTRUM	L. setifolius	3	
	L. sphaericus	3	
	L. angulatus	3	
South American species	L. crassipes	3	
	L. berterianus	3	
	L. subulatus	3	

(1966). Having carried out a detailed survey of the degree of waviness of epidermal cell walls and the distribution of stomata on either side of the leaf, he found he could distinguish the three following leaf-types:

1. Leaves hypostomatic; epidermal cells isodiametric, with wavy walls.
2. Leaves amphistomatic; epidermal cells isodiametric or slightly elongated, with wavy or straight walls.
3. Leaves amphistomatic; cells of upper epidermis slightly elongated, with wavy walls; cells of lower epidermis more elongated, with straight walls.

Bässler investigated some 115 species of Lathyrus, taken from all sections, but as he was concerned particularly with 'Subgenus Orobus', his citation of the distribution of these three types within the genus is rather uneven. Table 10 summarises his results, using the classification of Davis (1970) for the sake of uniformity. Bässler found the epidermal structure useful in delimiting some species groups (e.g. Sect. Lathyrostylis) within the subgenus, but it gave no support for the division of Lathyrus into subgenera.

Simola (1968a) also paid considerable attention to these characters in her paper on the leaves of Lathyrus; she justified their reliability partly by the agreement between her results and those of previous workers, and partly by reference to the findings of Salisbury (1928) in his study on stomatal frequencies in British woodland plants. Salisbury showed, by a long and detailed series of experiments, that "the increased

stomatal frequencies in plants grown on dry soil as compared to those grown on wet soil, and of small leaves as compared to large leaves, are ... due chiefly to differences in the spacing of stomata and not to differences in the proportion of stomata developed. This appears to be true also for the variations in frequency in different parts of the same leaf. ... The frequency on the two surfaces of the leaf tends to augment or diminish in a parallel manner.". Having found that the proportion of stomata to other epidermal cells remains approximately constant, Salisbury devised a formula to express this relationship:

$$\text{Stomatal Index} = \frac{\text{number of stomata per unit area}}{\text{total no. of epidermal cells in same area}} \times 100$$

Simola used this expression to describe the relative distribution of stomata on both surfaces of the leaf in species from America and the Old World. Her results are interesting, but she does not draw many taxonomic conclusions from them, being concerned with more theoretical considerations of the evolution of the leaves of Lathyrus.

My own investigations repeat much of what has already been done in Lathyrus but are new for the other genera. The structure of the epidermis was determined from fully-grown leaflets, one specimen from each species being examined. Some material was fresh, while leaves from herbarium specimens were prepared by soaking in 5% KOH at room temperature for one to three days. Using a fine pair of forceps, pieces of epidermis

were stripped off the leaflet and mounted in glycerine jelly. The appearance of most epidermides was recorded by drawing them, using a camera lucida; a selection of these is reproduced in Figs. 6, 7 and 8. The epidermal cells were counted in five fields of view, totalling an area of 0.23 mm^2. Although this is less than one-third the area used by Simola in her calculations, I obtained results very similar to hers (in Lathyrus) and therefore have assumed that the method is sufficiently accurate, especially as only approximate results are necessary. From these scores the Stomatal Index for the upper and lower epidermis of leaves of each species was calculated, and then the latter divided into the former to express in a single number the relative distribution of stomata on each side; a result near zero indicates a strongly hypostomatic leaf, while a high result is given by an epistomatic leaf. The Stomatal Index Ratios for species of Vicia, Lens, Pisum, Vavilovia and Cicer are shown in Table 11 and those for Lathyrus in Table 8.

The stomata of all members of the Vicieae are anomocytic, as previous workers have noted. In L. magellanicus the arrangement of epidermal cells round the stomata is so regular that a diacytic appearance results (Fig. 6:8), but this is not absolutely constant and there are no true subsidiary cells.

My observations on the epidermal structure in Lathyrus confirm those of Bässler and Simola, but as will be shown I have found a more significant pattern of variation than either of these authors, by combining their approaches to the subject. Within Lathyrus, as Bässler pointed out, members of Sect.

Key to Figures 6, 7 and 8.

Fig. 6. Illustrations of the leaf epidermis in Lathyrus.

Species :
1. L. aureus
2. L. ochrus
3. L. pratensis
4. L. aphaca (epidermis of stipule)
5. L. pannonicus
6. L. inconspicuus
7. L. saxatilis
8. L. magellanicus

Fig. 7. Illustrations of the leaf epidermis in Vicia.

Species :
1. V. unijuga
2. V. orobus
3. V. oroboides
4. V. truncatula
5. V. villosa
6. V. filicaulis
7. V. pulchella
8. V. nigricans

Fig. 8. Illustrations of the leaf epidermis in some members of the Vicieae and Trifolieae.

Species :
1. Pisum sativum
2. Vavilovia formosa
3. Lens culinaris
4. Cicer macracanthum
5. C. montbretii
6. Medicago scutellata
7. Trifolium pratense
8. Melilotus alba

Key: U = Upper epidermis

L = Lower epidermis

Fig. 6.

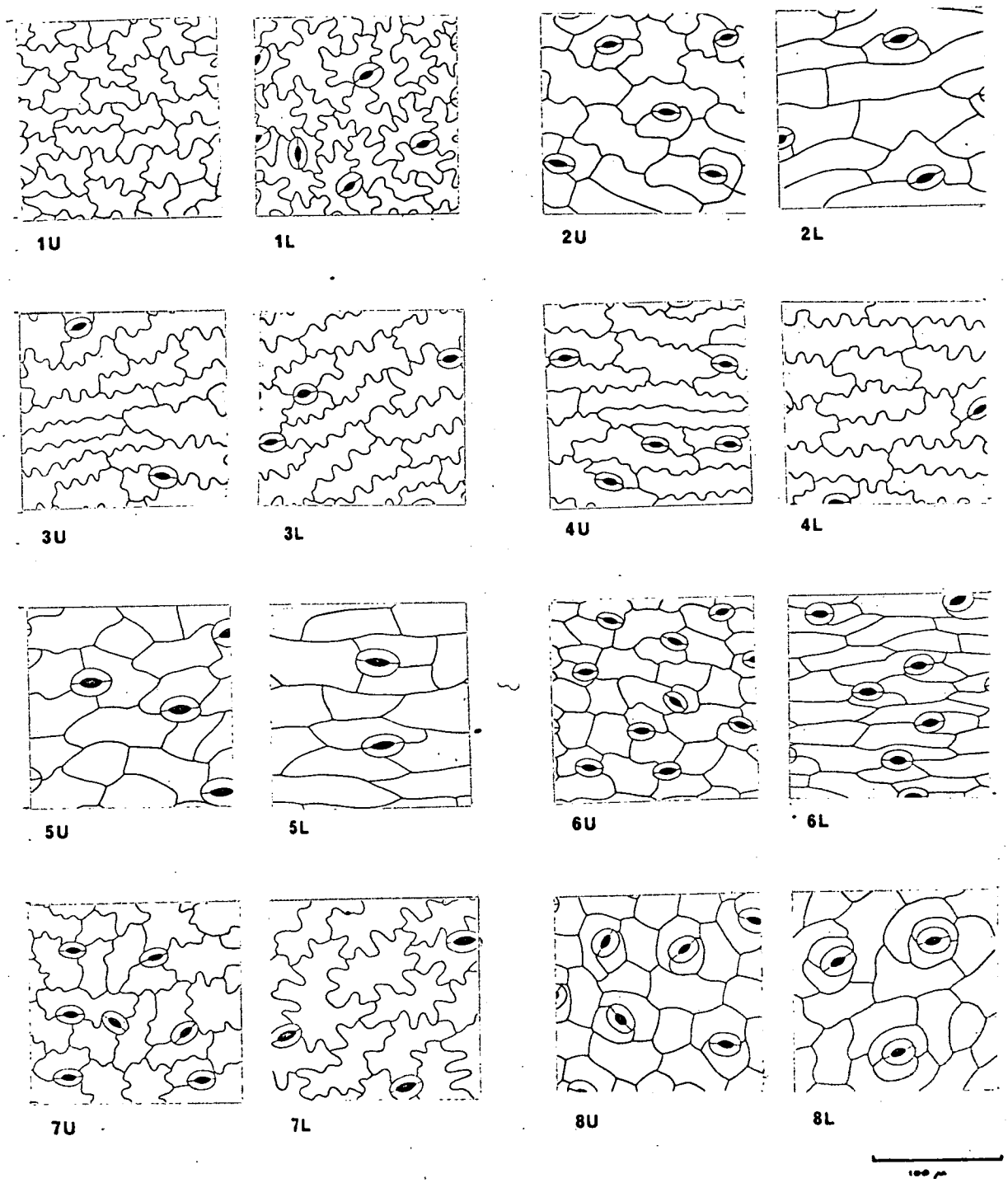


Fig. 7.

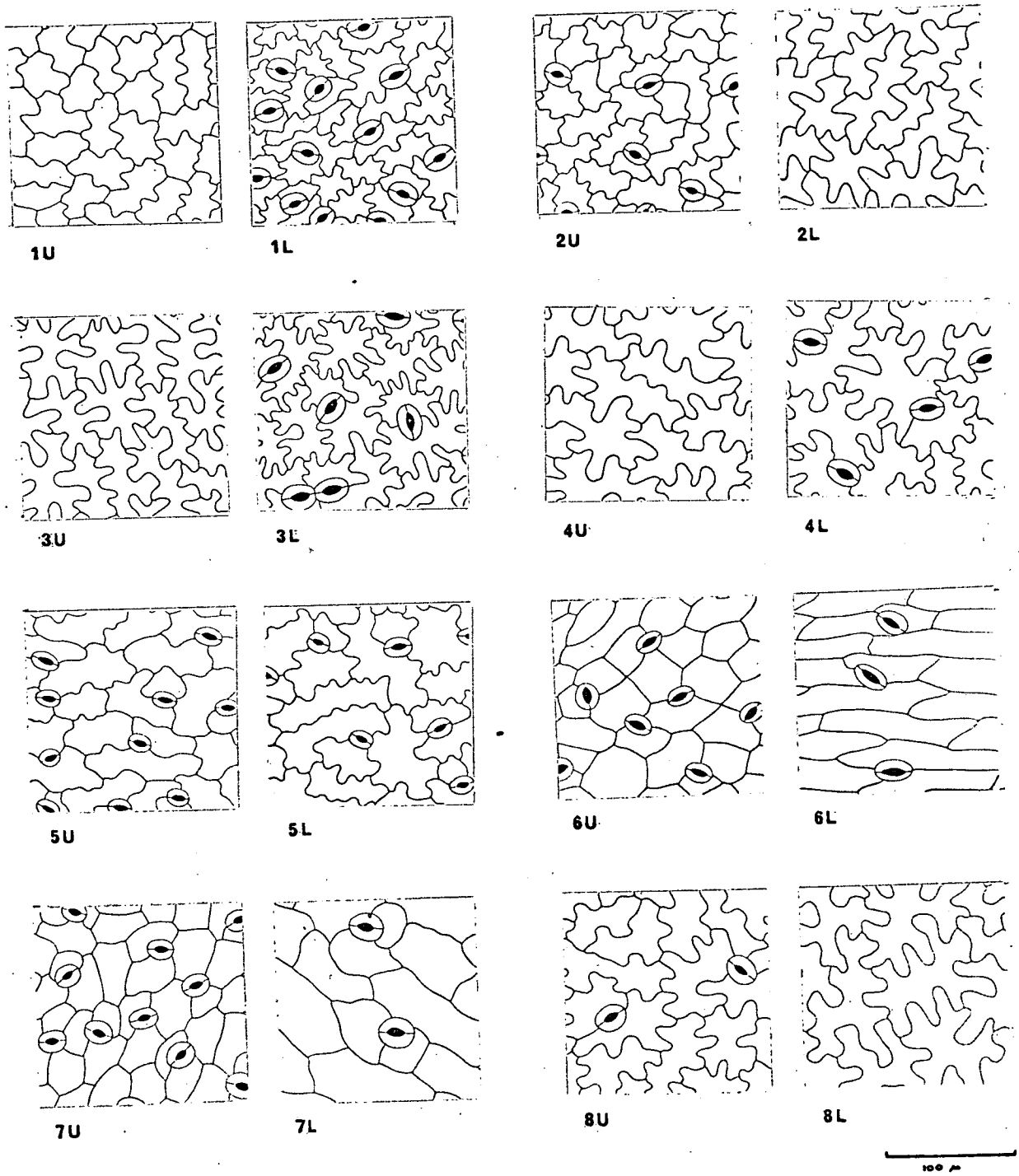
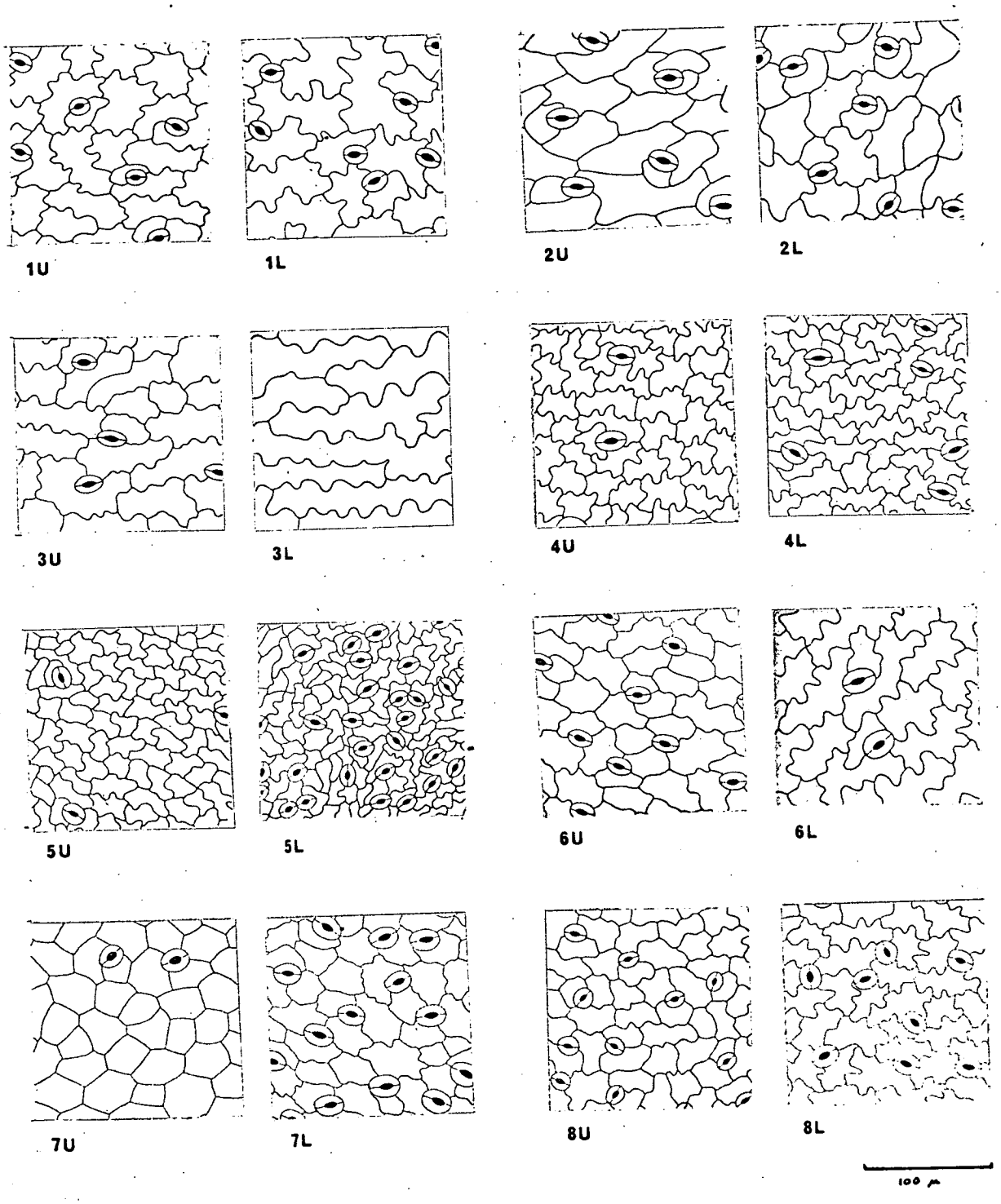


Fig. 8.



Orobus have strongly hypostomatic leaves with isodiametric, wavy-walled epidermal cells (e.g. L. aureus, Fig. 6:1); L. roseus (Sect. Orobon) also possesses this type of leaf. The remaining species, which Bässler attempted to divide on the basis of quantitative differences in cell-shape, are amphistomatic. The use of the Stomatal Index Ratio emphasises the boundary between the two types of amphistomatic leaf with proportionally more stomata on the lower or upper surface (here referred to as hypo-amphistomatic and epi-amphistomatic, respectively), and Table 8 shows that only members of Sects. Lathyrostylis, Orobastrum (sensu Bässler) and Nissolia, and species from S. America, belong to the latter category. This discovery is particularly interesting, though its significance is obscure, as it provides additional evidence in favour of Bässler's narrower concept of the Old World groups. Simola did not examine enough species to reveal this pattern, and she used a broader sectional framework. Most of these epi-amphistomatic species of Lathyrus have nearly straight-walled epidermal cells, as shown in L. pannonicus (Fig. 6:5), L. inconspicuus (Fig. 6:6) and L. magellanicus (Fig. 6:8); those of the lower epidermis are elongated, while those of the upper surface are more nearly isodiametric. L. saxatilis is exceptional in having wavy-walled, isodiametric epidermal cells on both sides of the leaf (Fig. 6:7). L. nissolia is quite strongly epistomatic, and has elongated, fairly wavy-walled cells; as the leaf in this case is phyllodic, and not strictly homologous with the leaflets which are the basis of investigation in other species, one does not know how much significance

ought to be attached to these findings; but they give some indication of similarity between L. nissolia and Sect. Orobastrum. Table 8 shows that there is a general correlation between parallel venation and the epistomatic condition. The hypo-amphistomatic species, comprising most of Sects. Lathyrus, Cicercula, Pratensis and Clymenum, as well as species from N. America, usually have slightly elongated, wavy-walled epidermal cells. Fig. 6:2 & 3 illustrates the epidermis of L. ochrus and L. pratensis, respectively.

The range of variation in stomatal distribution in Vicia is wider than in Lathyrus, as Table 11 shows; this variation is not random, but neither does it support the main taxonomic divisions of the genus. This is particularly evident in Sect. Cracca, which includes examples of strongly epistomatic andhypostomatic-leaved species as well as amphistomatic ones. In general, the extremes of stomatal distribution occur in perennial species. All annuals (except V. pubescens) are amphistomatic; thosе of Sects. Cracca and Ervum have proportionally more stomata on the upper leaf-surface, while those of Sect. Vicia range from weakly hypo- to epi-amphistomatic. Members of Sect. Faba are hypo-amphistomatic. These patterns of variation may provide new evidence for the relationship of Sect. Ervum to Sect. Cracca, and of Sect. Faba to Sect. Vicia. All perennials of Sect. Vicia (e.g. V. oroboides, Fig. 7:3, and V. truncatula, Fig. 7:4) are hypostomatic, strongly so except in V. pyrenaica. Inepidermal structure these species correspond with the broad-leafleted, etendrillous members of Sect. Cracca (e.g. V. unijuga,

Fig. 7:1) and with those of the 'oroboid' group in Lathyrus (e.g. L. aureus, Fig. 6:1). The majority of perennials of Sect. Cracca, which have narrowly linear leaflets, are epi-amphistomatic. This section also includes a small complex of species whose leaves have many pairs of leaflets and reduced tendrils and are strongly epistomatic (e.g. V. orobus, Fig. 7:2). Members of this group are morphologically very similar to V. balansae and V. truncatula in Sect. Vicia; it is interesting to find their superficial likeness belied by this cryptic vegetative character. The extinct species V. dennesiana, from the Azores, has strongly epistomatic leaves. The American species of Vicia, both annual and perennial, are weakly to strongly epistomatic; see, for example, V. pulchella (Fig. 7:7) and V. nigricans (Fig. 7:8).

Members of Lens, e.g. L. culinaris (Fig. 8:3), are epistomatic, providing another vegetative similarity between this genus and Vicia Sect. Ervum. Pisum and Vavilovia are both hypo-amphistomatic, like most members of Lathyrus; the epidermis of P. sativum is shown in Fig. 8:1, and that of V. formosa in Fig. 8:2. The epidermal cells in Vicia, Pisum, Vavilovia and Lens are rather uniform in shape, being generally wavy-walled and isodiametric to slightly elongated. A few species (e.g. V. filicaulis, Fig. 7:6 and V. pulchella, Fig. 7:7) are exceptional in having straight-walled cells. As in Lathyrus, the cells of the lower epidermis tend to be larger than those of the upper leaf-surface.

The epidermal cells of Cicer were found to be rather smaller

than those of the other genera. The upper epidermis in C. chorassanicum, and both surfaces of the leaf in C. incisum, have straight-walled cells; the epidermis of the remaining species which I examined had wavy-walled cells. Table 11 shows that the leaves of Cicer range from hypostomatic (e.g. in C. montbretii, Fig. 8:5) to amphistomatic (e.g. C. macracanthum, Fig. 8:4). Fig. 8:6, 7 & 8 illustrates the epidermis of three species of the Trifolieae (Medicago scutellata, Trifolium pratense and Melilotus alba); their Stomatal Index Ratios are given in Table 11. These very limited examples suggest that the cell shape and stomatal distribution of members of the Trifolieae are possibly similar to those of the Vicieae.

It is evident from the foregoing account that the distribution of stomata on the two surfaces of the leaf varies widely within the Vicieae, and that the pattern of variation sometimes supports and sometimes conflicts with the existing classification. The close agreement between the results of Bässler (1966), Simola (1968a) and myself, where these are duplicated, suggests that individual species are characterised by more-or-less constant Stomatal Index Ratios. In order to judge the value of this character in taxonomy it is important to understand something of the evolutionary trends which have caused its variation, and the physiological significance of these differences.

The increasing popularity of cuticular studies in plant taxonomy is discussed by Stace (1965). With regard to stomatal distribution, he asserts that since Salisbury (1928) demonstrated that the proportion of stomata to other epidermal cells

Table 11. Stomatal Index ratios in Vicia, Lens, Pisum, Vavilovia, Cicer and several members of the Trifolieae.

VICIA

Sect. Cracca: perennials	
V. unijuga	0.0
V. venosa	0.0
V. pisiformis	0.0.
V. kulingiana	0.0
V. dumetorum	0.0
V. pseudo-orobus	0.0
V. crocea	0.2
V. dichroantha	0.4
V. amurensis	0.6
V. amoena	0.8
V. venulosa	0.9
V. alpestris	0.8
V. canescens	1.0
V. subvillosa	1.0
V. rafigae	1.2
V. sicula	1,2
V. glareosa	1.2
V. altissima	1.3
V. pinetorum	1.7
V. glauca	1.8
V. sylvatica	1.9
V. ochroleuca	2.7
V. cracca	3.3
V. sparsiflora	3.5
V. multicaulis	3.8
V. semiglabra	3.9
V. onobrychioides	3.9
V. orobus	∞
V. freyniana	∞
V. dadianorum	∞
V. megalotropis	∞
V. dennesiana	∞
Sect. Cracca: annuals	
V. cassia	1.1
V. villosa	1.1
V. benghalensis	1.3
V. biennis	1.3
V. filicaulis	1.3
V. monantha	1.5
V. articulata	1.5
V. palaestina	1.6

Table 11, continued

Sect. Ervum	
V. caesarea	1.0
V. quadrijuga	1.0
V. vicioides	1.1
V. ervilia	1.3
V. disperma	1.5
V. tetrasperma	2.2
V. leucantha	2.8
V. hirsuta	3.8
V. pubescens	
Sect. Anatropostylia	
V. koeieana	1.1
Sect. Vicia: perennials	
V. oroboides	0.0
V. balansae	0.0
V. sepium	0.0
V. truncatula	0.5
V. pyrenaica	0.9
Sect. Vicia: annuals	
V. sativa	0.4
V. grandiflora	0.5
V. cuspidata	0.7
V. galeata	0.7
V. melanops	0.9
V. noeana	0.9
V. pannonica	0.9
V. peregrina	1.0
V. michauxii	1.0
V. assyriaca	1.0
V. hyrcanica	1.0
V. hybrida	1.3
V. anatolica	1.3
V. lutea	1.6
Sect. Faba	
V. narbonensis	0.7
V. faba	0.8
V. bithynica	0.9
N. American species	
V. americana	1.3
V. exigua	1.3
V. ludoviciana	1.5
V. humilis	1.6
V. pulchella	1.6
V. acutifolia	1.7
V. caroliniana	2.1
V. leucophaea	2.5
V. hugeri	6.9
V. mexicana	

Table 11, continued

S. American species	
V. nana	1.1
V. graminea	1.3
V. bijuga	1.4
V. nigricans	∞
LENS	
L. culinaris	7.1
L. nigricans	1.9
PISUM	
P. sativum	0.7
VAVILOVIA	
V. formosa	0.6
CICER	
C. montbretii	0.1
C. macracanthum	0.6
C. anatolicum	0.8
C. chorassanicum	0.8
C. incisum	1.0
C. arietinum	1.3

TRIFOLIEAE	
Ononis rotundifolia	0.5
Medicago scutellata	1.5
Melilotus alba	0.8
Trifolium pratense	0.2

Stomatal Index ratio is Stomatal Index of upper leaf epidermis divided by Stomatal Index of lower leaf epidermis.
Each Ratio was determined by examining one leaflet of the species concerned.

remains constant despite the apparent modifying effects of the environment, this character has been recognised as one of considerable systematic value, especially in palaeobotany. Stace suggests that ecological factors are important in determining the type of stomatal distribution of a species, and cites examples of hydrophytes in which the stomata are vestigial or confined to the upper epidermis. In his study, Salisbury found that "whereas trees rarely have stomata on the upper epidermis, they are frequent in the upper epidermis of the herbaceous woodland flora.". It appears, however, that very few workers have attempted to use stomatal distribution as a taxonomic character on a wide scale, and little is known about the causes of its variation.

In the Vicieae the evidence for a relationship between this character and ecology is inconclusive and confusing, as will be shown. Broadly speaking, the amphistomatic-leaved species (including the majority of the tribe) live in open habitats. Many of the annuals are weeds; some perennials are found in hedgerows and moist fields (e.g. L. sylvestris, L. pratensis, V. cracca), while others colonise screes and rocky pastures (e.g. V. pyrenaica, Vicia rafigae, V. alpestris, Vavilovia formosa, Cicer incisum). On the other hand, the greater frequency of epi-amphistomatic types in Vicia and Lens as compared with Pisum and Lathyrus cannot be explained by reference to ecology, nor can the apparent correlation in Lathyrus of this character with parallel venation.

Throughout the tribe are a number of woodland species with

broad leaflets and without tendrils, which are uniformly hypostomatic. These include the 'oroboid' members of Vicia Sects. Cracca and Vicia, and Lathyrus Sect. Orobus, and also L. roseus. Within Cicer an analogous example is found in C. montbretii, whose leaves possess a terminal leaflet (not a tendril or spine, as in many species) and whose leaflets are relatively broad. The association of these three characters in plants with similar types of habitat, especially as they belong to several distinct taxonomic groups, seems to link the facies with the ecology, and suggests that the hypostomatic condition is in some way particularly adapted to this type of environment. This correlation is broken, however, by the occurrence of the V. orobus group in Sect. Cracca; these species are also woodland plants, but have strongly epistomatic leaves.

It is difficult to draw any generalised conclusions about the relationship of ecology to stomatal distribution on the basis of these findings, although they do suggest that such a connection exists, as has been assumed in the past. If this is the case, it is a complex situation which requires much more detailed investigation.

Bässler (1966) considers that the hypostomatic condition is primitive within Lathyrus, while Simola (1968a) favours the amphistomatic type, on the grounds that it is the most common within the tribe. Since the factors which influence the evolution of stomatal distribution are unknown, and as it is equally uncertain whether every change from one type to another can take

place, or with what facility, any judgement of what is primitive or advanced must be made *a priori* and is therefore of little value. On the other hand, the variation in this character in the Vicieae suggests that definite trends have been followed, and that the elucidation of this problem by studies in other taxa would be a worth-while and interesting subject.

The taxonomic value of the degree of undulation of epidermal cell walls has been fully considered in *Lathyrus* by Bässler and Simola. They agree that the wavy-walled condition is more primitive than the straight-walled, which in that genus occurs in Sects. *Lathyrostylis* and *Orobastrum*, the S. American species and some members of Sect. *Cicercula*. Straight-walled epidermal cells are rare outside *Lathyrus*; I found them in *Vicia filicaulis*, *V. graminea* and *V. pulchella*, all relatively advanced species.

3.9.
PHYLLODES AND WINGED STEMS

One of the more remarkable traits found in *Lathyrus* is the development of wings on the stem and petiole. The anatomical basis for this character is discussed in part 5.3.1, where it is pointed out that all members of the Vicieae (except *Cicer*) have angled stems with cortical vascular bundles in the internodes. The delegation of photosynthetic capacity from the leaf-blade to other parts of the plant is generally accepted to be an advanced attribute within the genus (cf. Bässler,

1966), and therefore it is useful as evidence when the structure and evolution of the group is being considered; on the other hand, since the character is a matter of degree rather than a simple presence or absence, it is sometimes difficult to assess the taxonomic significance of wings on the stem.

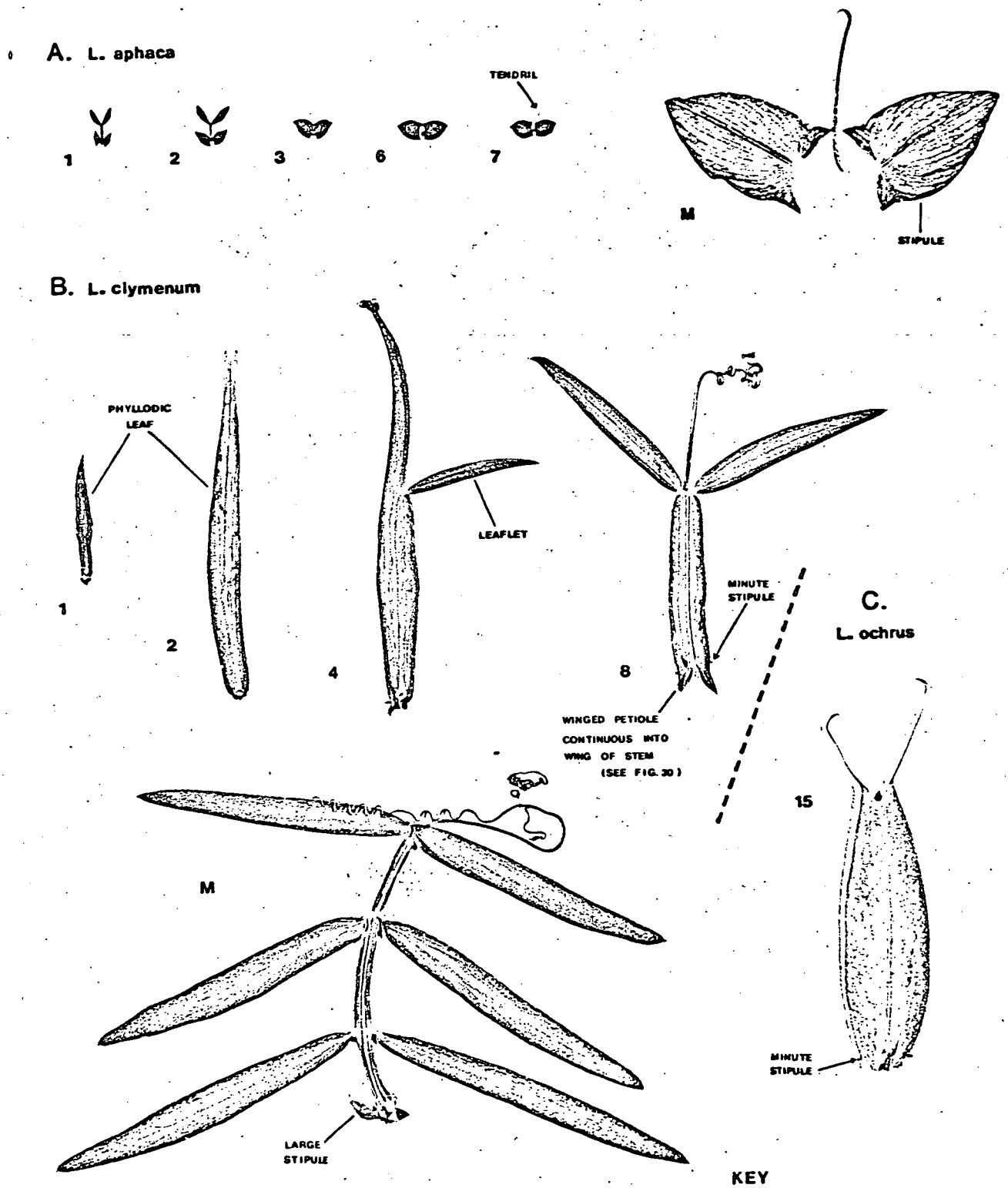
More-or-less strongly winged stems and petioles are found in species of Sects. Lathyrus, Cicercula, and Clymenum, in some members of Sect. Orobus (L. linifolius and L. palustris), and in a few representatives from N. and S. America. Sects. Lathyrostylis, Pratensis, Aphaca, Orobastrum, Gloeolathyrus and Nissolia characteristically have unwinged stems. An example of the use of this character is presented by L. roseus; this species was traditionally a member of Sect. Lathyrus, but was transferred in 1962 to a section of its own, Orobon Tamamsch. It is distinctive in several ways, and was particularly anomalous in its original group in having terete stems; despite this morphological difference, this species possesses the typical cortical vascular bundles in the stem internodes.

The most extreme examples of the development of phyllodes occur in Sects. Clymenum, Gloeolathyrus and Nissolia, and in all these groups the ontogeny of the species is strikingly different from that of the rest of the tribe. Sect. Clymenum comprises two species, L. clymenum (including L. articulatus) and L. ochrus; the ontogeny of L. clymenum is illustrated in Fig. 9:B. The seedling at first produces two or three scale leaves, followed by a series of true leaves. Initially these organs consist of a grass-like phyllodic blade; after a few nodes,

the phyllodes are terminated by a simple tendril and leaflets are produced, either at the apex or lower down (see leaves 4 and 8). The stem of L. clymenum is broadly winged, the wings of each internode continuing up unbroken into the phyllode at the next node; minute stipules are borne on the margins of these wings as they pass out from the node (Fig. 9:B, leaf 8). The stem apex is enclosed by a number of young phyllodes, the older blades curled round the younger. The mature form of leaf is attained after an unusually long series of intermediate stages. It is no longer phyllodic, but has a moderately-winged petiole and rachis and several pairs of leaflets. The development of L. gloeospermus (Sect. Gloeolathyrus) resembles that of L. clymenum. The pattern in L. ochrus is also similar, but leaves with leaflets are produced only at the end of the plant's life-cycle. During most of its growth this species bears simple, phyllodic leaves, often curiously divided at the apex and with unbranched tendrils from each point (Fig. 9:C).

In its ontogeny, L. nissolia is very similar to species of Sects. Clymenum and Gloeolathyrus, but unlike them it undergoes no change in leaf-construction during growth; no tendrils or leaflets are produced. Moreover, the venation of its phyllodes is parallel-brochidodromous, while that of the other groups is pinnate. Due to its anomalous vegetative characters, this species has always been given an isolated taxonomic position within the genus. On the other hand, the fact that Sects. Clymenum and Gloeolathyrus share the same distinctive ontogenetic pattern strongly suggests that they are closely related.

Fig. 9. Ontogenetic leaf-series in Lathyrus aphaca & L. clymenum and an intermediate leaf of L. ochrus.



3.10.

ROOTSTOCKS

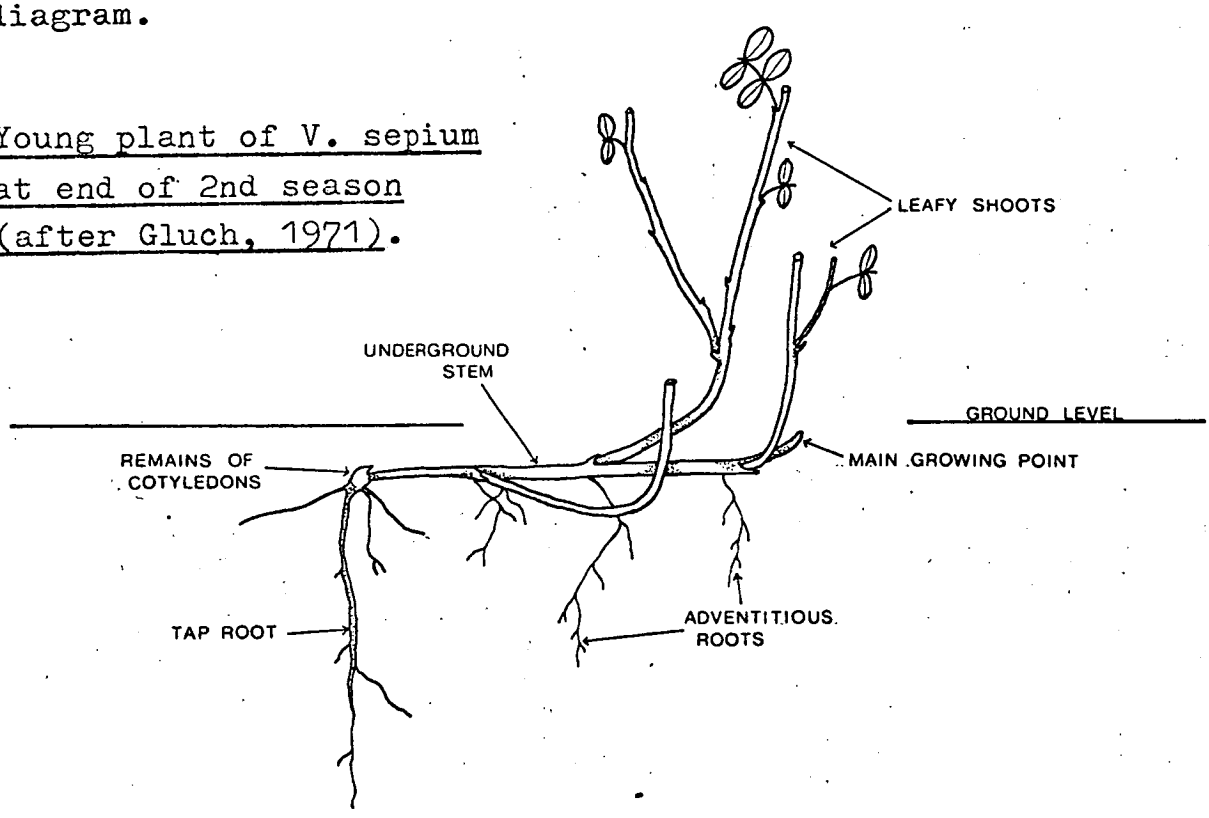
All perennial species of the Vicieae are chamaephytes or hemicryptophytes, i.e. the aerial parts of the plant die back each year and the new growing points are at or just below ground level. The pattern of growth of the subterranean parts is comparatively uniform in Vicia, but more diverse in Lathyrus, where the scattered occurrence of tubers throughout the genus is of taxonomic interest. Floras often give only a brief and sketchy description of the rootstocks of different species; this is a neglected area of morphology, due mainly to inadequate collecting techniques. More information is needed before a complete picture of variation in the tribe with respect to this subject can be assembled. However, Gluch (1971) has recently made a detailed study of a number of species, and the following review is based largely on his paper.

As was stated in part 3.1, in the seedlings of the Vicieae (excluding Cicer) the plumule stops growing after a few nodes and is soon overtopped by more vigorous lateral shoots. At the end of the first season, in perennial species, all the green parts die leaving the primary tap-root surmounted by a short cotyledonary region. The next year's growth is renewed by buds in the axils of the cotyledons or the first plumular scale-leaf. In some members of the Vicieae these buds develop into long, horizontal, branching, subterranean caudiculi which in turn produce phototropic shoots; in others the rootstock remains short, and is a vertical or oblique rhizome giving rise to both

leafy stems and adventitious roots which surround the tap-root. All the rootstock modifications in the Vicieae can be related to these two basic growth-patterns.

Vicia sepium is an example of a species which spreads vegetatively by thin underground stems, as in the following diagram.

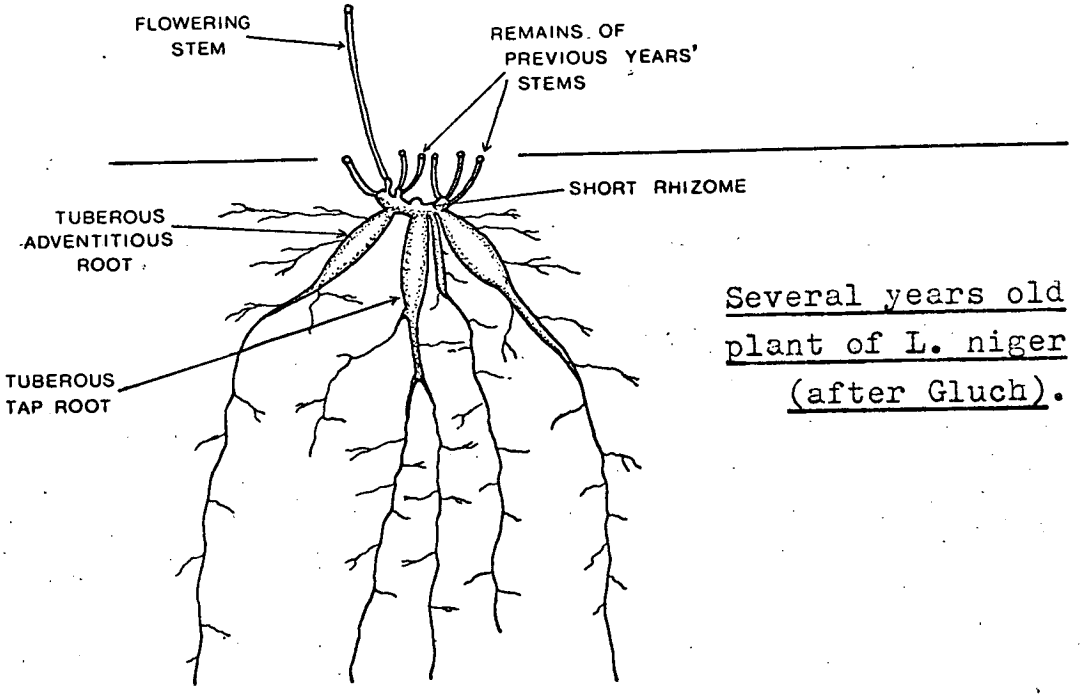
Young plant of V. sepium at end of 2nd season (after Gluch, 1971).



This type of rootstock is very common in Vicia; it is found, for example, in V. cracca, V. cassubica, V. pisiformis, V. dumetorum and V. sylvatica (Gluch, 1971), in V. venulosa and V. pseudo-orobus (Fedtschenko, 1948) and in V. freyniana, V. alpestris, V. semiglabra and V. glareosa (Davis & Plitmann, 1970). It also occurs in Lathyrus pratensis, L. japonicus and L. palustris (Gluch) and in L. cyaneus and L. variabilis (Davis, 1970). L. tuberosus also spreads by means of subterranean caudiculi, but here the adventitious roots are thickened,

forming fusiform or subglobose tubers (Fedtschenko, 1948).

L. vernus, L. karsianus and L. nivalis have short, woody rhizomes (Davis, 1970). L. niger, too, has a short rootstock, but both the primary root and the adventitious roots are modified into spindle-shaped tubers, as the diagram shows.



Several years old plant of L. niger (after Gluch).

This type of storage organ also occurs in L. pannonicus (Gluch) and L. digitatus (Ball, 1968). In L. sylvestris there is a thick, fleshy and very long tap-root, and the plant produces widely spreading underground shoots each year; however, according to Gluch (1971), these do not function as a means of vegetative propagation. In L. linifolius (= L. montanus), which has a short rhizome, it is the cotyledonary region of the seedling, and the rhizome itself, which become swollen and tuberous. Fedtschenko (1948) reported that L. laxiflorus has a thin, creeping rootstock, whereas Davis (1970) described a tuberous

specimen of the same species; further study is needed in this case to clarify the development of its underground parts.

Vavilovia formosa has prostrate caudiculi which help to spread the plant throughout the screes in which it lives. Mr S.D. Albury reported finding a pea-sized tuber at the end of one of these underground stems; but Mr J.M. Watson, who has a plant in cultivation at present, has suggested to me in litt. that this tuber was in reality the persistent hypogeal seed. Tubers are not mentioned by Bobrov (1948) in his description of V. formosa, and further investigation is needed on this subject. It would be most interesting if Vavilovia proved to be tuberous, since this would provide some evidence of a link with Lathyrus.

Tubers are unknown in Cicer, but the rootstock and roots are often thick and woody (van der Maesen, 1972).

Chapter 4

CHARACTERS OF FLOWERS, FRUIT AND SEEDS

4.1. The inflorescence.

4.2. The flower.

4.2.1. General remarks.

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4.1.

THE INFLORESCENCE

The inflorescence in the Vicieae is basically racemose. In most species a simple scape arises from the axil of an undifferentiated leaf and bears several to many flowers which are spirally arranged but secund. A few perennial species of Vicia are distinguished by the possession of compound racemes (i.e. panicles) in which reduced, bractiform leaves subtend each branch of the inflorescence. This character is found in some E. Asian 'oroboid' members, e.g. V. kulingiana, V. pseudo-orobus, V. unijuga, V. venosa and V. nipponica.

Bracteoles occur sporadically throughout the Vicieae, but being small and often deciduous can easily be overlooked, especially if only herbarium material is available. These structures are frequently present in perennial species of Lathyrus; in Vicia they are rare and found only in the paniculate species mentioned above and a few other E. Asian members of Sect. Cracca, e.g. V. dichroantha, V. amoena and V. amurensis. Bracteoles are absent from Pisum, Vavilovia and Lens. They occur in all members of Cicer, though they are often minute (van der Maesen, 1972); in xeromorphic species the bracteole is sometimes represented by a spine, as shown in C. pungens (Fig. 22:21).

In Vicia most perennials have dense, many-flowered racemes; exceptions include V. pyrenaica, V. subvillosa and the American V. bijuga and V. americana. Annuals usually have inflorescences with one to five flowers (except for some members of Sect. Cracca, e.g. V. villosa and V. benghalensis).

In Lathyrus the inflorescence is most usually few-flowered. Only a few members of Sect. Orobus (e.g. L. aureus, L. vernus) have dense racemes, and this character, being associated with a bushy habit and broad, etendrillous leaves, contributes towards the 'oroboid' facies which occurs in both Lathyrus and Vicia. The remaining members of Sect. Orobus and the species of N. America have several flowers per raceme (i.e. about 5 to 10), and this is typical also of Sect. Lathyrostylis and S. American species. Members of other sections usually have few- to one-flowered racemes. Thus in Lathyrus, as in Vicia, the evolution of annual groups has been accompanied by a decrease in flower number. Species of Lens, Pisum, Vavilovia and Cicer all have racemes bearing one to four flowers.

Peduncle length is a significant and useful character within Vicia: in members of Sects. Cracca and Ervum the scape is equal to or longer than the leaf, while in Sects. Vicia and Faba the peduncles are very short or absent. All members of the latter two groups possess stipular nectaries (cf. part 3.6), and it seems likely that these traits are linked functionally. It may be that insects which are attracted to the stipules, being automatically brought close to the flowers, may then effect pollination (Plitmann, 1967); on the other hand, Proctor & Yeo (1973) consider the stipular nectaries to be decoys which distract undesirable visitors from the flowers. I have seen ants on the stipules of V. sativa, and they are shown by Gams (1924) on V. sepium. Knuth (1908) says that these ants protect the plants against caterpillars. The role of the extra-

floral nectaries is mentioned again in part 4.3. V. bithynica (Sect. Faba) is anomalous in having peduncles and petioles of very variable length; sometimes the flower is sessile, while in other specimens (or at other nodes of the same plant) it is borne on a stem as long as the leaf. There does not seem to be any pattern underlying this variation. Most perennials of Sect. Vicia (V. oroboides, V. truncatula, V. sepium) have very short, close-flowered peduncles, as do the annuals V. pannonica and V. melanops. V. pyrenaica and other species with regular calyces (V. sativa s.l., V. cuspidata, V. lathyroides and V. grandiflora) have one or two sessile flowers per node. This is also the case with the large group, characterised by unequal calyx segments, which includes V. lutea and V. anatolica. In V. michauxii, V. peregrina and V. aintabensis the solitary flower is borne on a relatively long pedicel, but the peduncle is absent. The only other examples of sessile flowers in the Vicieae are V. linearifolia and V. bijuga from S. America (which, apart from the distribution of hairs on the style, do not have the other characters of Sect. Vicia), Lathyrus sphaericus, L. inconspicuus and L. gloeospermus.

In species with many-flowered racemes the scape appears to end in a flower-bud (although, of course, a raceme is indeterminate) and its apex is concealed within the inflorescence. Where there are only one or two flowers, however, the articulation between the peduncle and pedicel is better defined and provides variation which is of some use in taxonomy. In many cases the scape is prolonged past the last (or only) flower

to form an arista. This is seen in Cicer, where it frequently is represented by a sharp spine, and also in Pisum, Vavilovia and Lens. In Vicia only a few annual species show this feature, including V. filiformis and V. articulata (Sect. Cracca) and several members of Sect. Ervum: V. caesarea, V. ervilia, V. disperma, V. tetrasperma, V. hirsuta and V. pubescens. In most Lathyrus species with few-flowered racemes the pedicel is articulated smoothly with the peduncle. A few species have a small projection at this point, suggesting that the axil is continuing past the flower (e.g. L. nissolia, L. aphaca, L. annuus and L. gorgoni), while in others the scape actually ends in a long sterile process (e.g. in L. sphaericus and L. chloranthus; in the latter the length of the process is rather variable). Illustrations of these types are shown in Fig. 23.

Throughout the Vicieae there appears to be a trend towards greater simplicity in the inflorescence: from panicles to racemes, from bracteolate to ebracteolate pedicels, from many to few flowers, from long to short peduncles. The trend is 'read' in this direction because complex inflorescences tend to occur in species which are thought to be primitive in other characters, while simple inflorescences are found in advanced species.

4.2.
THE FLOWER
4.2.1.
GENERAL REMARKS

In this section each part of the flower is treated separately in order that its morphological variation may be followed throughout the tribe. However, because this approach has the disadvantage of obscuring the functional unity of the flower of each species, one whole flower is described first in these introductory paragraphs. Lathyrus aureus has been chosen as a convenient example to illustrate the general floral plan of the Vicieae. The flowers of several other widely separated species are also shown, entire and dissected, in Figs. 11 to 18; these diagrams are intended to convey the idea of the flower as a unit, as it would be too lengthy to describe each as such in the text.

The flower of Lathyrus aureus and its parts are illustrated in Fig. 10. The calyx is gamosepalous, with unequal free lobes of which the uppermost are the shortest. The petals are intricately shaped, and fit together in a precise manner by which the flower forms a unit with a mechanism well adapted to pollination by bees. This is discussed in part 4.3.

The lower edges of the two keel petals are fused from their apex to half-way along the claw. The anthers are clustered round the end of the style, and are held closely in this position within the apex of the carina. The upper edges of the keel petals are free, and on each side there is a long groove. The alae correspond in shape with the carina; each wing has a thumb-like process (x in Fig. 10:Db) whose papillate lower surface is firmly united with the keel at x', while the upper

part of the wing forms a shelf (y) which rests on the upper part of the carinal groove at y'. The standard turns back sharply from the wings, while its lower part grasps the claws of the keel and wings firmly in place round the staminal tube.

The androecium is basically diadelphous; the filament of the uppermost (vexillary) stamen is lightly adnate to the staminal tube formed by the other nine. At the base, however, it is free and raised up, leaving an opening on each side. Nectar, produced abundantly at the base of the ovary, exudes from these pores. All filaments become free from the staminal tube at the same level (the tube ends squarely). The stamens are alternately long and short, the shortest being the vexillary stamen and the longest the abaxial one. The anthers are introrse, of uniform size and all versatile.

The ovary is linear and compressed laterally, densely covered with glandular hairs of the type shown in Fig. 5:A. The style is strongly dorsally compressed and has a brush of hairs near the apex on the inner (adaxial) side. The stigma is terminal.

The flower is slightly protandrous; pollen escapes from the bursting anthers into the pouched apex of the keel, and collects in a mass round the stigma. The hairs on the adaxial side of the style also help to brush the pollen up into this position, where it is ready to be transferred to a bee or other insect visiting the flower for nectar.

Key to Figure 10.

A. Flower of *Lathyrus aureus*.

B. Calyx.

C. Standard:

prominently folded.

D. Wing petal:

a) from outside;

b) from inside.

E. Keel:

process x of wing is fused to shelf x' of keel;

process y of wing rests upon groove y' of keel.

F. Androecium (from outside):

staminal tube is truncate;

filaments not dilated at apex;

vexillary stamen lightly adnate to staminal tube;

nectar is accessible only through pores (p) at the base.

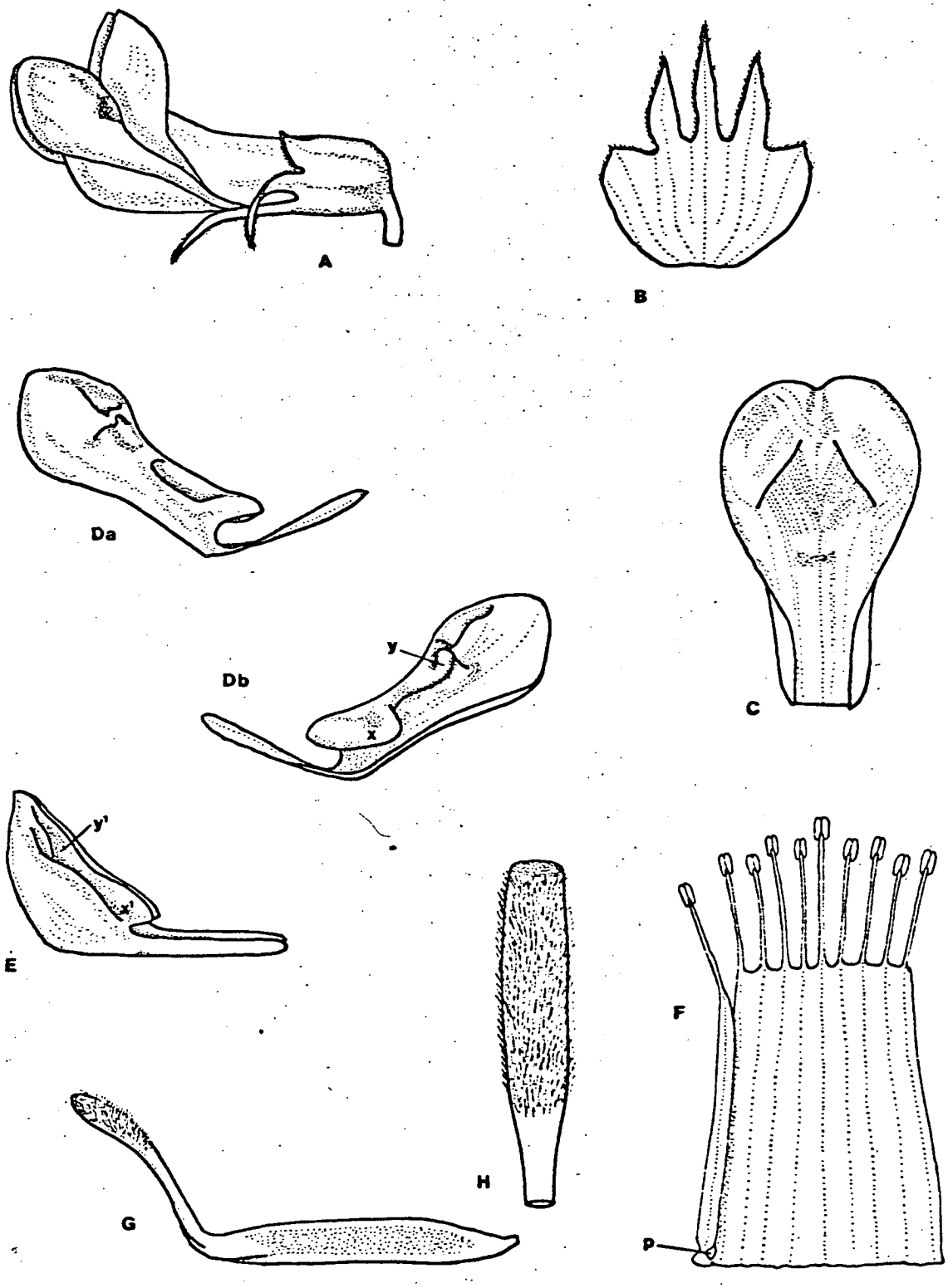
G. Gynoecium.

H. Terminal portion of style, seen from adaxial side;

style is strongly flattened and hairy only on the inner surface.

Scale: A - E x 3; F, G x 4; H x 10.

Fig. 10. The flower of Lathyrus aureus.



Key to Figure 11.

A. Flower of Lathyrus tuberosus.

B. Calyx.

C. Standard:

banner very wide, with two faint bosses.

D. Wing:

a) from outside;

b) from inside.

E. Keel:

a) and b) are two side views of the same carina, to show distortion caused by twisted style;

process x of wing is fused with shelf x' of keel.

F. Gynoecium :

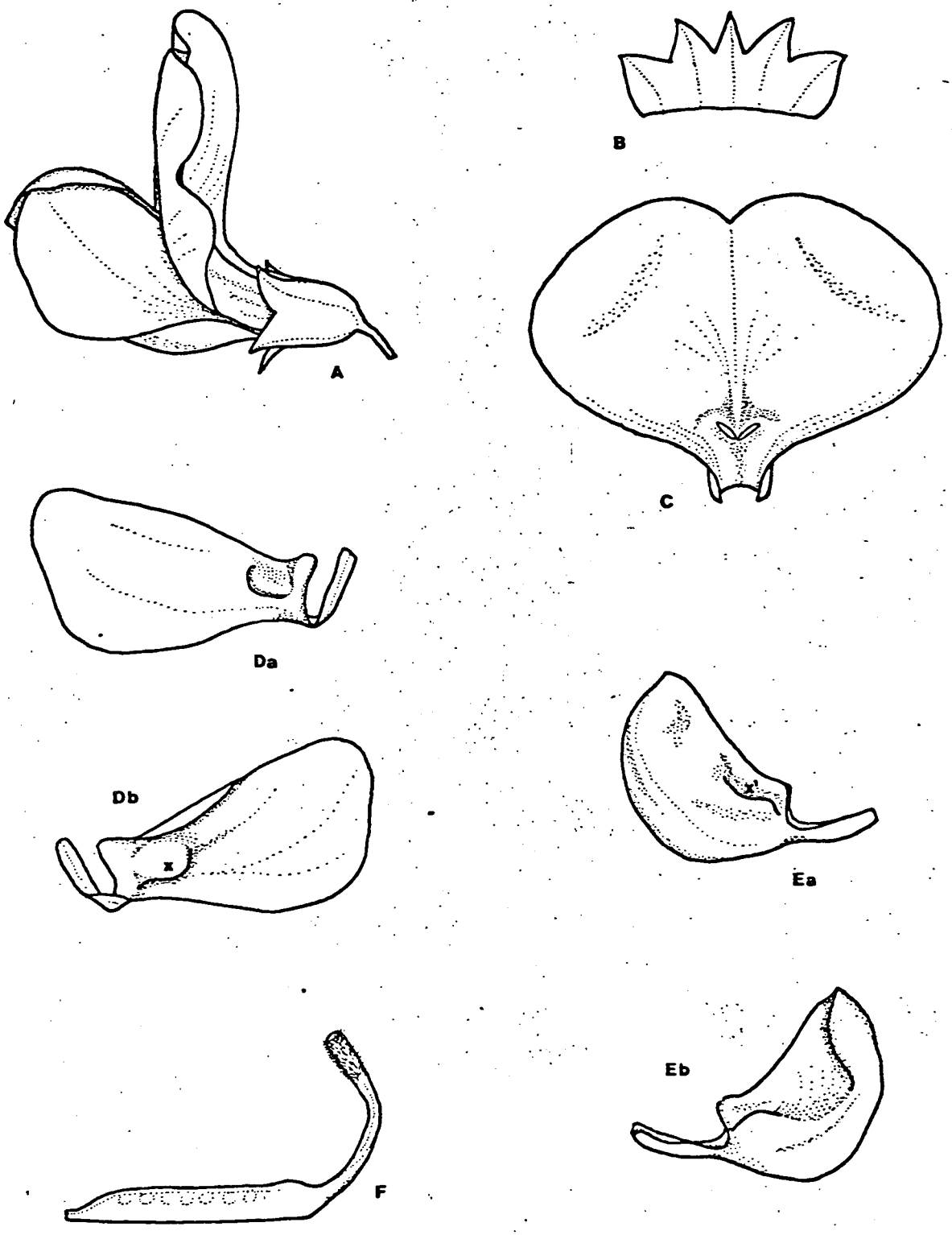
style is flattened dorsally and is hairy only on adaxial side;

style is twisted through 90°, always in the same sense (anticlockwise, when flower is viewed from above).

The Androecium is as in Lathyrus aureus (Fig. 10).

Scale: A - E x 4; F x 5.

Fig. 11. The flower of Lathyrus tuberosus.



Key to Figure 12.

A. Flower of Vicia sylvatica.

B. Calyx.

C. Standard: no distinct folds.

D. Wing: a) from outside; b) same petal, from inside.

E. Keel: process x of wing is fused to shelf x' of keel.

F. Gynoecium.

G. part of F, enlarged, showing dorsiventrally flattened style equally hairy all round.

The Androecium is as in Vicia cracca (Fig. 13).

Scale: A x 3; B - E x 4; F x 5; G x 15.

Key to Figure 13.

A. Flower of Vicia cracca: calyx gibbous.

B. Calyx.

C. Standard: with pronounced folds.

D. Wing: a) from outside; b) same petal, from inside.

E. Keel: process x of wing is fused to shelf x' of keel.

F. Androecium: staminal tube ends obliquely;
filaments not dilated at apex.

G. Gynoecium: flattened laterally;
evenly hairy all round, somewhat tufted abaxially below stigma.

Scale: A - E x 5; F x 7; G x 10.

Fig. 12. The flower of Vicia sylvatica.

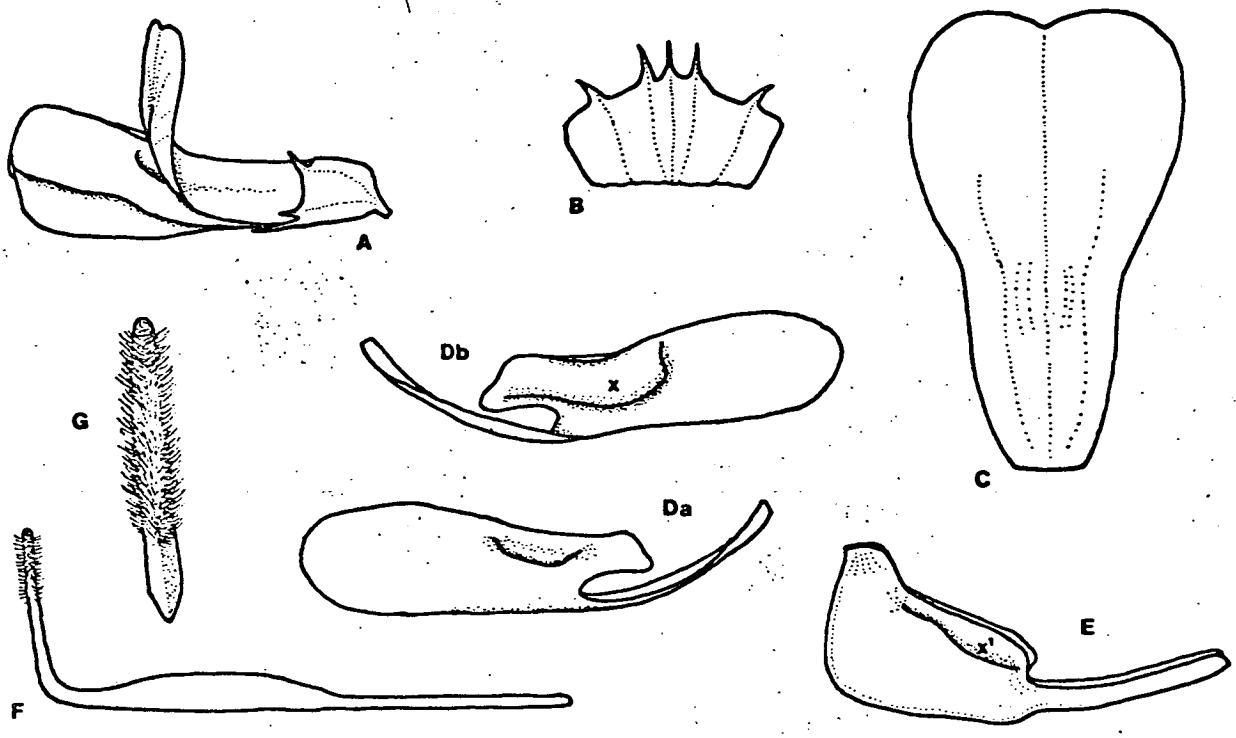
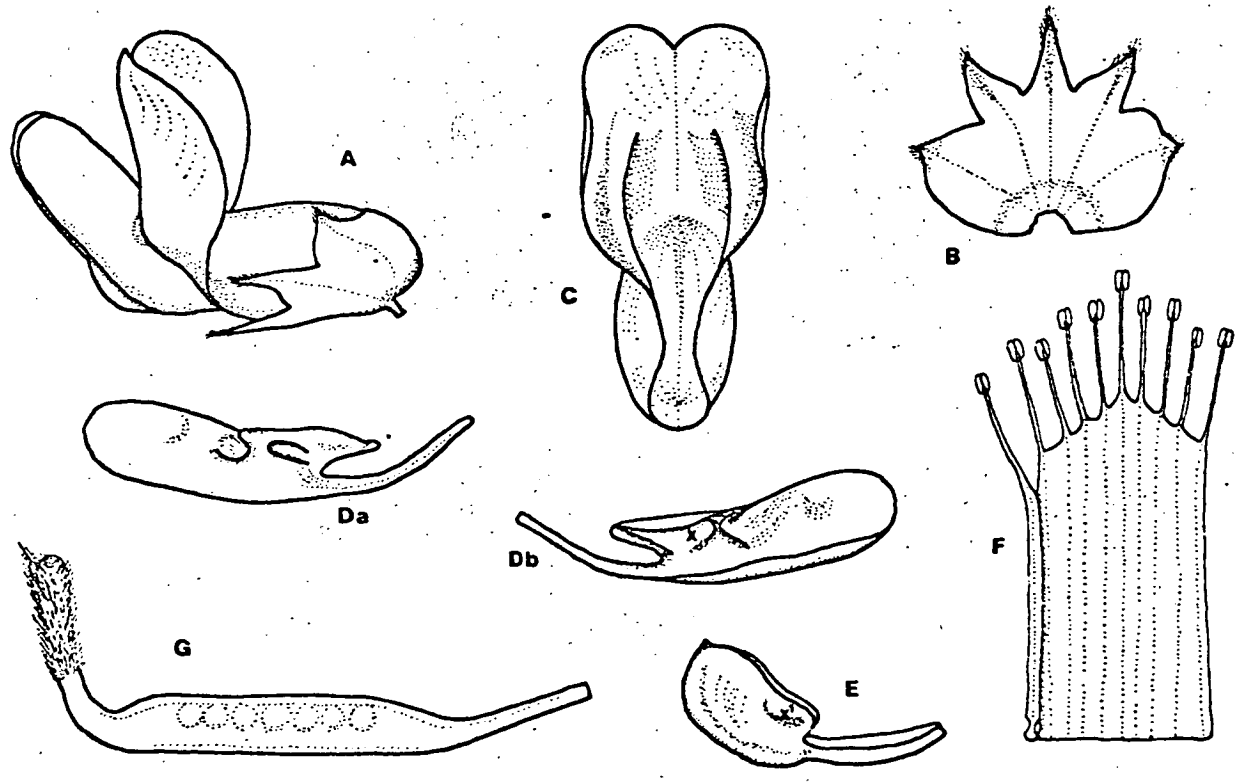


Fig. 13. The flower of Vicia cracca.



Key to Figure 14.

A. Flower of Vicia sepium.

B. Calyx.

C. Standard: folds weakly defined.

D. Wing: a) from outside; b) from inside.

E. Keel: process x of wing is fused to shelf x' of keel.

F. Gynoecium.

G. Part of F, enlarged, showing tuft of hairs at apex of dorsally compressed style.

The Androecium is as in Vicia koeieana (Fig. 15).

Scale: A x 3; B - E x 4: F x 6: G x 40.

Key to Figure 15.

A. Flower of Vicia koeieana.

B. Calyx: the 5 segments are equal and as long as the tube.

C. Standard: banner very wide, claw very narrow, two small but prominent bosses.

D. Wing: a) from outside; b) from inside.

E. Keel: process x of wing is fused with shelf x' of keel.

F. Androecium: staminal tube ends obliquely.

G. Gynoecium.

H. Part of G, enlarged and viewed from adaxial side, showing dorsally compressed style hairy on the inner surface alone.

Scale: A - E x 4; F x 8; G x 5; H x 10.

Fig. 14. The flower of Vicia sepium.

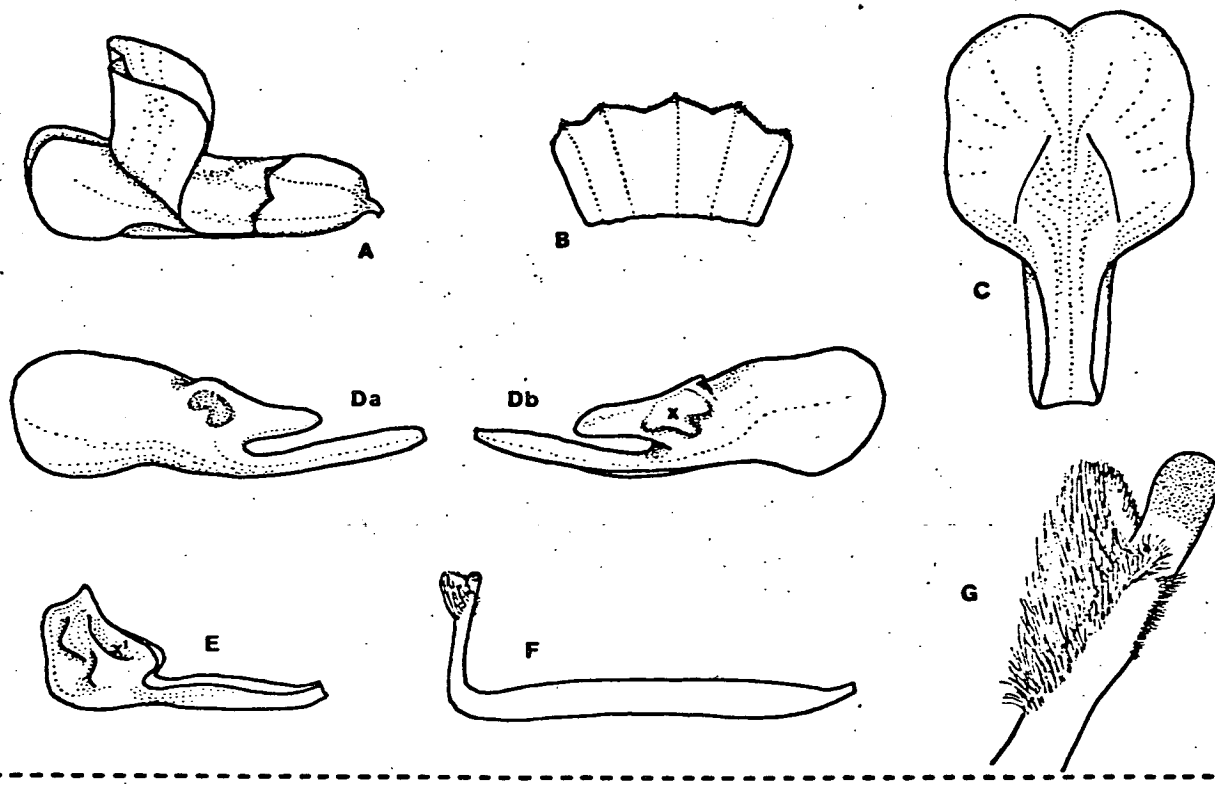
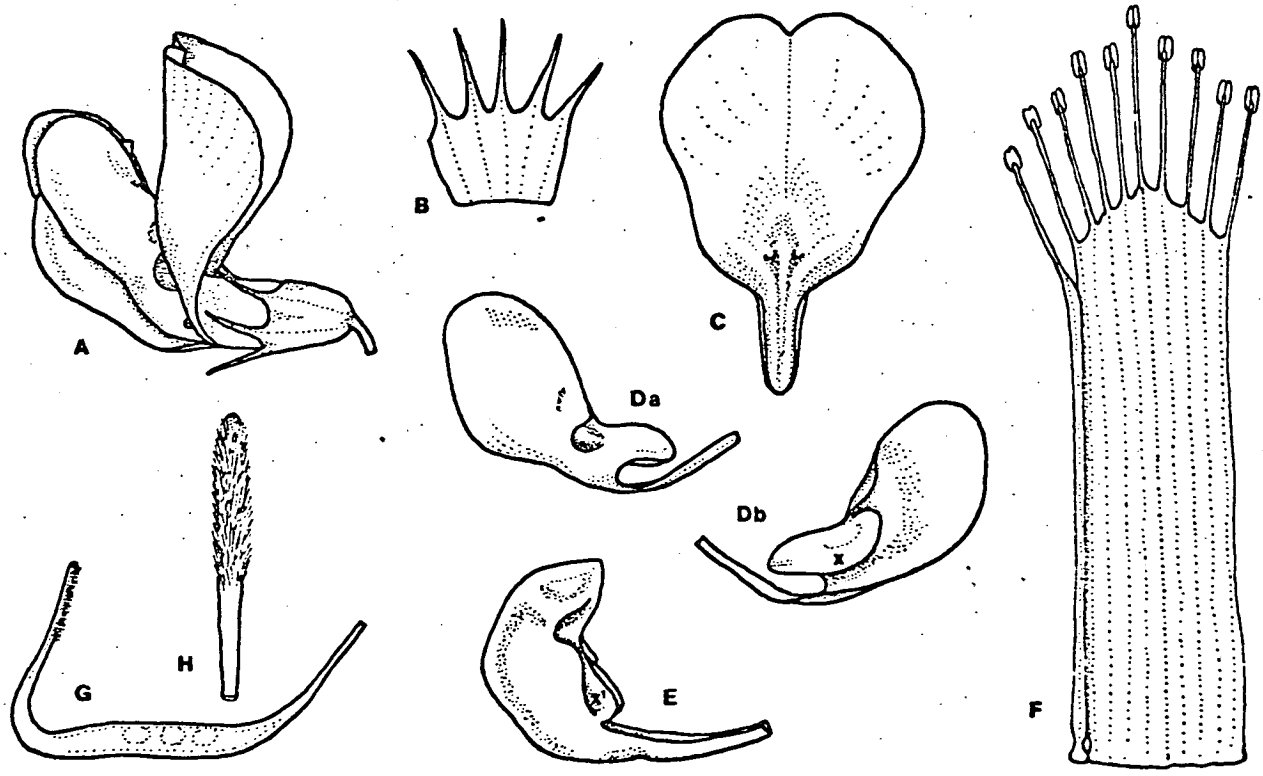


Fig. 15. The flower of Vicia koeieana.



Key to Figure 16.

A. Flower of *Lens culinaris*.

B. Calyx.

C. Standard:

with two bosses.

D. Wing:

a) from outside;

b) from inside.

E. Keel:

process x of wing is fused with shelf x' of keel.

F. Androecium:

staminal tube ends obliquely.

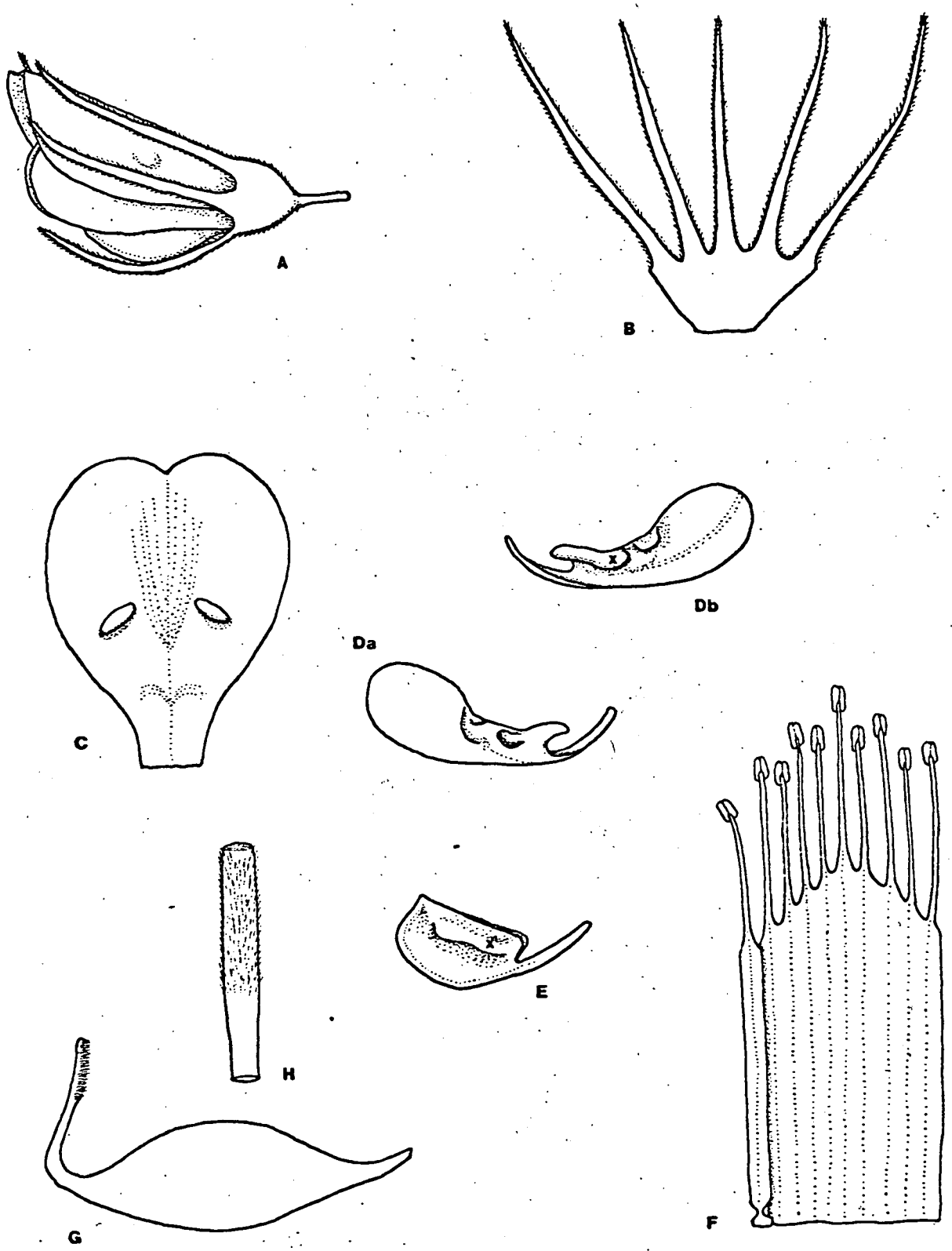
G. Gynoecium:

the style is dorsally compressed, and hairy only on adaxial side.

H. Enlargement of style with adaxial side facing.

Scale: A - E x 10; F x 20; G x 15; H x 40.

Fig. 16. The flower of Lens culinaris.



Key to Figure 17.

A. Flower of Pisum sativum.

B. Calyx.

C. Standard:

sharply folded;

boss in centre of petal between claw and banner.

D. Wing:

a) from outside;

b) same petal, from inside.

E. Keel:

process x of wing is fused to shelf x' of keel.

F. Androecium:

staminal tube ends squarely;

filaments of alternate stamens slightly dilated at apex;

vexillary stamen lightly adnate to staminal tube.

G. Gynoecium:

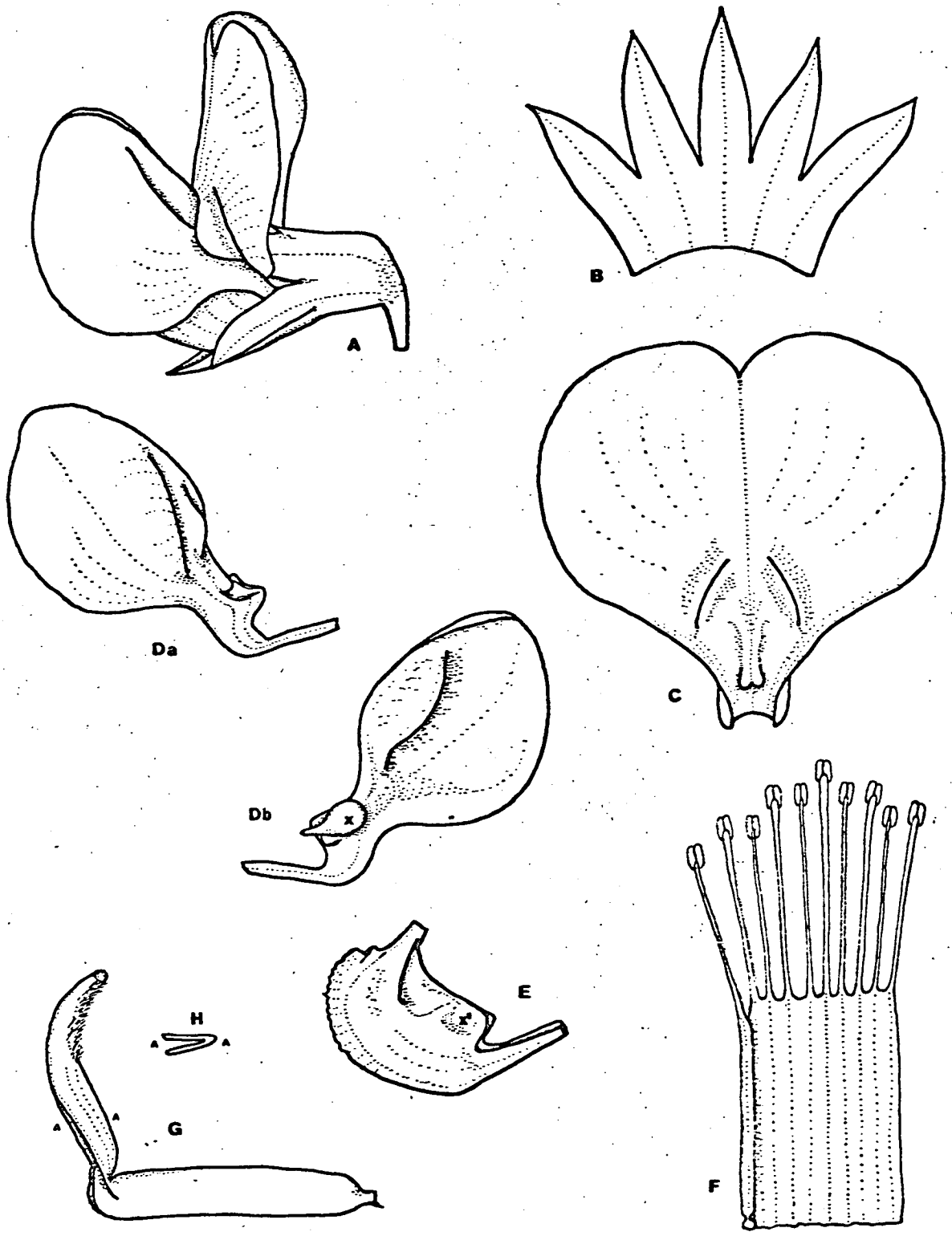
sides of style folded back and joined below stigma;

style hairy only on adaxial face.

H. Transverse section through style at A - A.

Scale: A - E x 3; F - H x 5.

Fig. 17. The flower of Pisum sativum.



Key to Figure 18.

A. Flower of *Cicer arietinum*.

B. Calyx (see illustration of glandular hair, Fig. 5:E).

C. Standard:

no distinct folds.

D. Wing:

a) from outside;

b) same petal, from inside.

E. Keel:

process x of wing rests upon shelf x' of keel, but these surfaces are free.

F. Androecium:

staminal tube ends obliquely;

filaments dilated at apex;

anthers alternately basi- and medifixed;

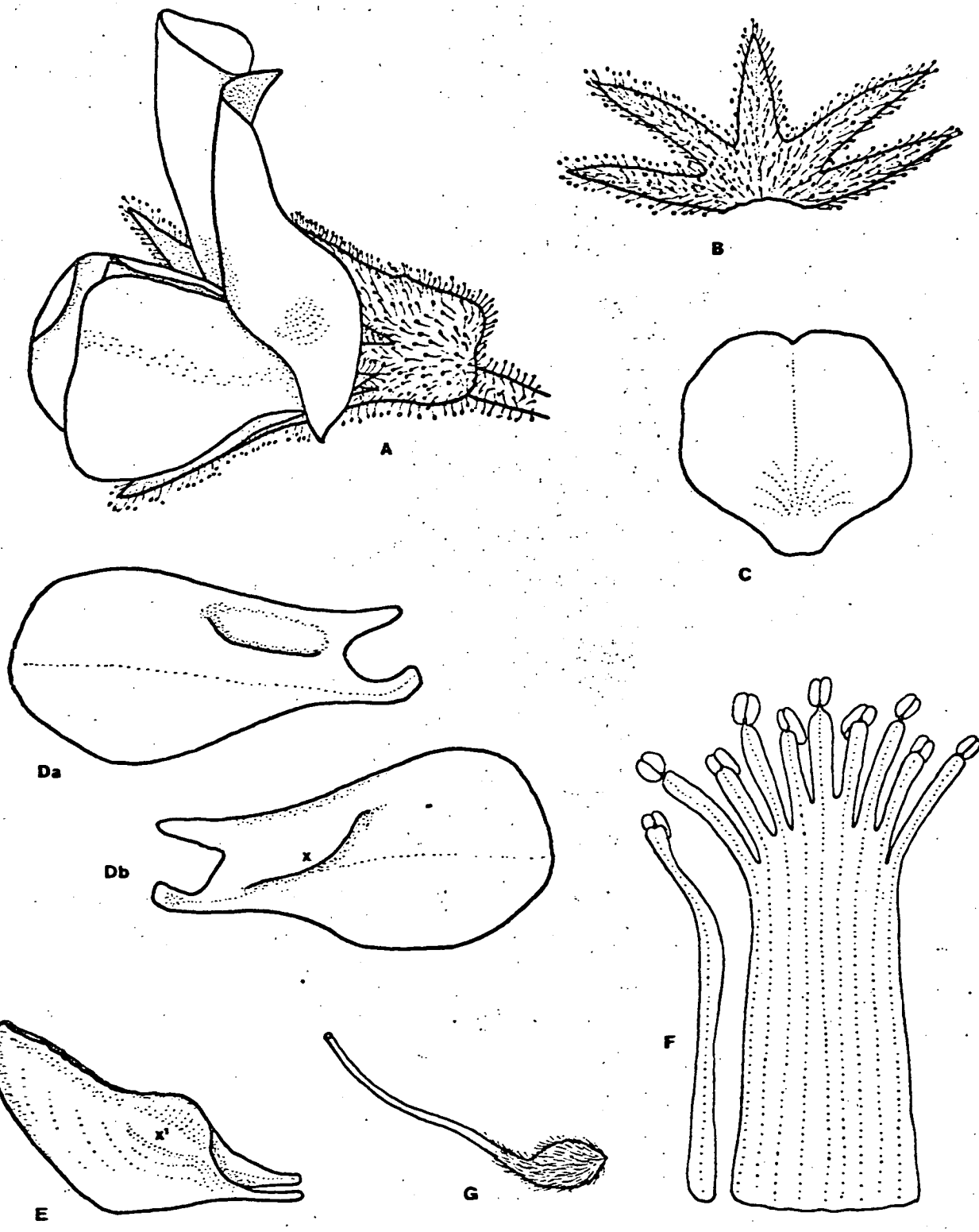
vexillary stamen is free.

G. Gynoecium:

style is glabrous.

Scale: A, D, E, G x 8; B, C x 4; F x 10.

Fig. 18. The flower of Cicer arietinum.



4.2.2.

CALYX

In Vicia the free lobes of the calyx are shorter than, or equal to, the tube; they are almost always unequal in length, the abaxial one being the longest (as in V. cracca, Fig. 13). The few exceptions with a regular calyx include the V. sativa group in Sect. Vicia (V. sativa s.l., V. grandiflora, V. pyrenaica, V. cuspidata and V. lathyroides); V. subvillosa, V. articulata and V. cappadocica in Sect. Cracca; some members of Sect. Ervum (e.g. V. vicioides, V. hirsuta, V. leucantha, V. pubescens, V. ervilia); and the anomalous V. koeieana (Fig. 15). V. caesarea is unusual in having the upper calyx lobes longer than the lowest one. The irregular calyx, while typical of most members of Vicia, is particularly pronounced in some species of Sect. Cracca (e.g. V. cracca, V. villosa, V. benghalensis, etc.). Here the calyx is moderately to strongly gibbous at the base, on the adaxial side (Fig. 13).

Most members of Lathyrus have more-or-less regular calyces, as shown in L. tuberosus, Fig. 11. Flowers with unequal calyx lobes are typical of Sect. Orobus (e.g. L. aureus, Fig. 10) and of all N. American species. They are also found in some members of Sect. Lathyrostylis, e.g. L. pannonicus, L. digitatus and L. satdaghensis, and some representatives from S. America (L. magellanicus).

The genus Lens is characterised by flowers in which the free parts of the sepals are several times longer than the calyx tube (Fig. 16). The calyx is subregular, with the

uppermost lobes slightly longer than the lowest, as in Vicia caesarea. In L. montbretii the calyx lobes are only twice as long as the tube.

The calyx in flowers of Pisum resembles those of Sects. Cicercula or Clymenum in Lathyrus, being glabrous with equal, rather broad teeth (Fig. 17). That of Vavilovia formosa is similar.

Variation in the form of the calyx in Cicer was used by Popov (1928) to divide the genus into two subgenera: members of Subgen. Pseudononis are characterised by having subregular or slightly gibbous calyces, with narrowly linear, subequal segments, while in Subgen. Viciastrum the calyx is very oblique and gibbous, with unequal segments. C. arietinum (Fig. 18) is an example of the first type;. C. pungens (Fig. 22:21) shows the second.

4.2.3.
COROLLA
4.2.3.1.
MORPHOLOGY

Except for isolated 'spot' characters, e.g. the presence of pubescent standards in some members of Vicia Sect. Vicia, taxonomists have paid comparatively little attention to the petals of the Vicieae. Having made a wide and detailed survey of the flowers of the tribe, I found considerable variation in the corolla, some certainly of systematic significance. The description and comparison of petal shapes is a difficult task,

since the variation in every trait is more-or-less continuous. The ideal method of presentation would be to illustrate every flower, but as this is impossible I have attempted to summarise my findings with a combination of tables and diagrams of examples chosen to span the range of variation.

Vicia. The shape of the standard in Vicia varies appreciably, and three main forms can be distinguished (the terms used for the different shapes are taken from Davis, Fl. Turkey 3:51, 1970):

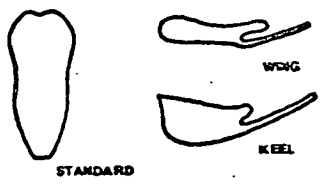
A. Oblong: the banner and claw are approximately equal in width and are not (or scarcely) separated by a 'waist' (Fig. 19:1, 2 & 12).

B. Platynychioid or pandurate: the banner and claw are equal in width but are separated by a pronounced 'waist'; the standard is usually deeply cleft at the apex (Fig. 19:4, 5 & 6).

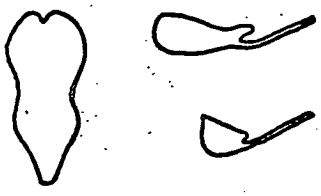
C. Stenonychioid or obovate: the banner is wider than the claw (Fig. 19:3, 7, 13, etc.).

These three types are not always well-defined, but their distribution is of taxonomic interest. In one area this character appears to be particularly significant: there is a strong correlation between the pandurate vexillum (type B) and the laterally compressed style (see Table 12). As far as I know, this has not been noted previously. The occurrence of species with these two characters in both Sect. Cracca and Sect. Ervum (sensu Ball, 1968) is evidence of the heterogeneity of these

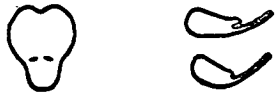
Fig. 19. Petal shapes in Vicia.



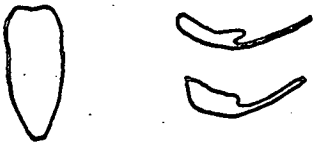
1. V. crocea



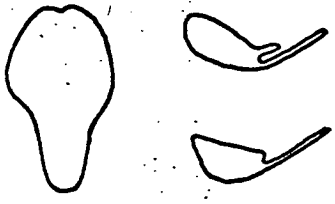
6. V. canescens



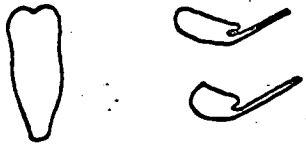
11. V. koeieana



2. V. freyniana



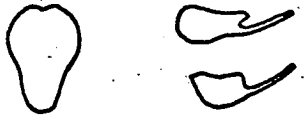
7. V. subvillosa



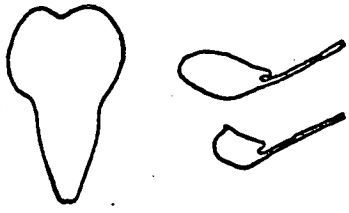
12. V. truncatula



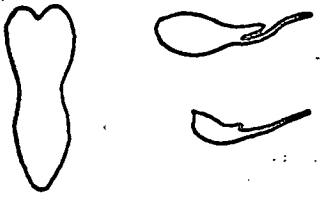
3. V. onobrychioides



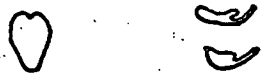
8. V. cypria



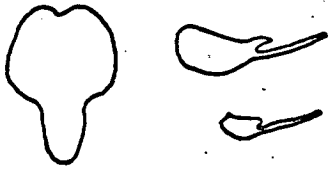
13. V. galeata



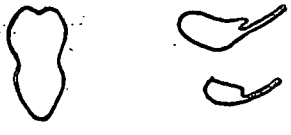
4. V. alpestris



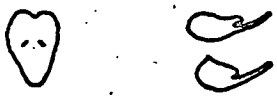
9. V. ervilia



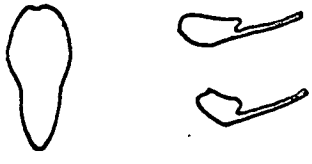
14. V. sativa



5. V. ciceroidea



10. V. caesarea



15. V. narbonensis

Scale: x 1

Table 12. Distribution of vexillum and style types in Vicia.

Key : ○ style terete;
◁ style laterally compressed;
▫ style dorsally compressed, evenly hairy all round;
▪ style dorsally compressed, tufted abaxially.

	Standard type A 	Standard type B 	Standard type C 
Sect. Cracca s.l.	○ crocea ▫ kulingiana ▫ pseudo-orobus ▫ dichroantha ▫ amurensis ▫ amoena ▫ pisiformis ▫ sylvatica ▪ dumetorum ▫ cassubica ▫ freyniana ▫ orobus ▫ dadianorum ▫ multicaulis ▫ articulata ◁ dennesiana	▪ variegata ▪ canescens ▪ megalotropis ▪ argentea ◁ cracca ◁ pinetorum ◁ ochroleuca ◁ sibthorpii ◁ sicula ◁ alpestris ◁ ciceroidea ◁ rafigae ◁ multijuga ◁ benghalensis ◁ villosa ◁ scandens	* subvillosa ▫ biennis ▪ altissima ▪ onobrychioides ▫ cypria ▫ lunata

Table 12, continued.

	A	B	C
Sect. Cracca s.l.		◁ cirrhosa ◁ chaetocalyx ◁ glauca ◁ filicaulis ◁ palaestina ◁ monantha ▫ cassia ▫ cretica ▫ cappadocica	
Sect. Ervum s.l.	○ pubescens	◁ leucantha ◁ disperma ◁ durandii ○ vicioides	▫ tetrasperma ▫ laxiflora ▫ ervilia ** koeieana ▫ caesarea ○ hirsuta
N. American species	▫ americana ▫ nigricans	◁ caroliniana ◁ pulchella ◁ acutifolia ◁ exigua ◁ ludoviciana	○ leucophaea

Table 12, continued.

	A	B	C
S. American species	▫ andicola		▫ graminea ▫ nana ▫ bijuga ▫ linearifolia
Sect. Vicia	▫ oroboides ▫ balansae ▫ truncatula ▫ sepium ▫ pannonica ▫ melanops ▫ anatolica		▫ galeata ▫ hyrcanica ▫ lutea ▫ noeana ▫ hybrida ▫ assyriaca ▫ sericocarpa ▫ sativa ▫ grandiflora ▫ lathyroides ▫ cuspidata ▫ peregrina ▫ michauxii
Sect. Faba			▫ bithynica ▫ narbonensis ▫ faba

* V. subvillosa has a dorsally compressed style pubescent on adaxial and abaxial faces (Fig. 21:6).

** V. koeieana has a dorsally compressed style pubescent on adaxial face only (Fig. 15:G, H).

groups. The pandurate vexillum is found in three other species-groups, as Table 12 shows. Among Old World members of Vicia, these are the species which Radzhi (1970) places in Subgen. Cracca Sect. Variegatae (including V. canescens, Fig. 19:6), and the annuals V. cappadocica, V. cretica and V. cassia. All members of both these groups have a dorsally flattened style, but the distribution of hairs on the style is different in each group (see part 4.2.5). The third group comprises most N. American species of Vicia, and here the style is laterally compressed as in Sect. Cracca. This finding is of great importance in elucidating the relationships between Eurasian and American species.

The oblong standard seems to occur predominantly in perennial species (including those in facies most resembling Lathyrus Sect. Orobus). Species with vexilla of type C tend to be those with few-flowered racemes, where the individual flower, rather than the inflorescence, is the attractive unit.

In most members of Vicia the standard is marked by two strong fold lines where it recurves from the wings (see Figs. 13, 14 & 15). V. sylvatica (Fig. 12) is unusual in that this petal turns back quite smoothly. V. koeieana and V. caesarea are unusual in possessing a pair of small shallow pouches on the vexillum at this point (Fig. 19:10 & 11; Fig. 15). V. hybrida, V. pannonica and V. anatolica are distinctive within the tribe in having the standard pubescent on the adaxial surface. The indumentum consists of

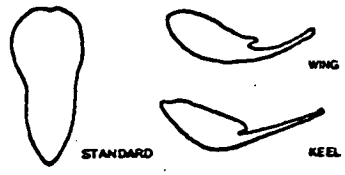
short unicellular hairs (Fig. 5:C).

Most members of Vicia have wing petals similar in shape to those of V. cracca (Fig. 13); there is a lower process (x) fused lightly with the keel at x' and an upper process which rests on the keel and is formed by a pleat or 'kink' in the upper edge of the ala. All species possess the lower process, but in a few the 'kink' is absent. In this category are found V. sylvatica (Fig. 12), V. koeieana (Fig. 15), V. ervilia, V. articulata, V. tetrasperma, V. cuspidata, V. caesarea and V. bithynica. These species obviously do not form a homogeneous taxonomic assemblage, and it seems that this trait may have arisen several times by a simplification of the wing shape. In some of the small-flowered annuals (e.g. V. tetrasperma) the simpler type of wing may be correlated with autogamy, since the flower is here no longer required to function as a mechanism in insect pollination.

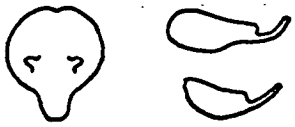
The shape of the keel varies in relationship with the wings. I have not observed any strikingly characteristic type except in Sects. Vicia and Faba, where the apical part, containing the style and anthers, is considerably pouched and the fused edge curves round above the style (see V. sepium, Fig. 14).

Lathyrus. The flowers of L. aureus (Fig. 10), L. laevigatus (Fig. 20:1) and other broad-leafleted, etendrillous members of Sect. Orobus have almost linear standards (i.e. of type A). However, as Fig. 20 shows, in most species of Lathyrus the vexillum is stenonychioid, with a relatively wide banner and narrow claw

Fig. 20. Petal shapes in Lathyrus.



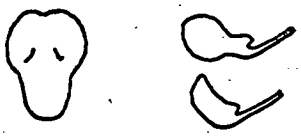
1. L. laevigatus



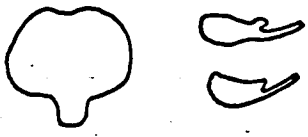
6. L. ochrus



11. L. angulatus



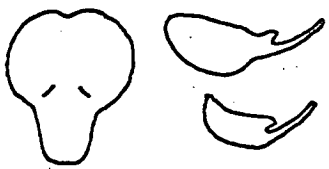
2. L. montanus



7. L. sylvestris



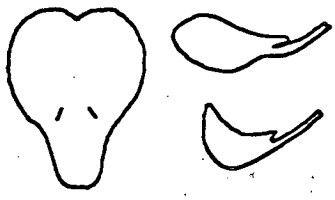
12. L. nissolia



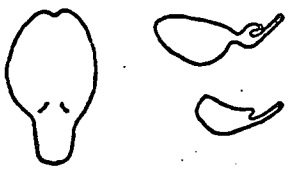
3. L. boissieri



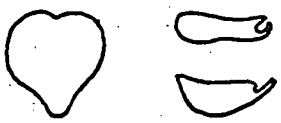
8. L. roseus



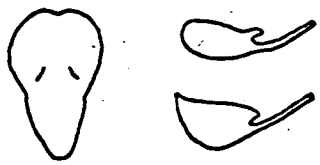
13. L. brachycalyx



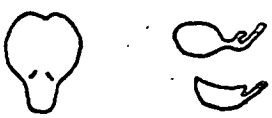
4. L. layardii



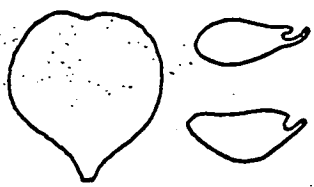
9. L. annuus



14. L. leucanthus



5. L. aphaca



10. L. chloranthus



15. L. magellanicus

Scale: x 1

(type C). As in Vicia, this type is characteristic of species with few-flowered racemes. In all groups except Sects. Lathyrus and Cicercula the vexillum possesses two more-or-less prominent pouches or bosses at the fold which carries the banner away from the wings. These processes rest against the alae and help to support the standard. L. clymenum and L. ochrus are characterised by a remarkably strong development of these pouches (Fig. 20:6). L. gloeospermus (Sect. Gloeolathyrus), which in several other characters shows affinity with Sect. Clymenum, has reduced, cleistogamous flowers with undeveloped petals. Sects. Lathyrus and Cicercula have flowers in which the tube is relatively short and the standard wide (Fig. 11; Fig. 20:7, 9 & 10), and this modification of the general floral dimensions also involves the wings, which are short-clawed. L. roseus, in Sect. Orobon, also has flowers of this type (Fig. 20:8). The N. American L. sulphureus is most distinctive in having a vexillum with the banner narrower than the claw.

The wings of most species resemble those of L. aureus (Fig. 10) in having a lower and an upper process but no pleat in the upper edge of the alae. A few species of Sect. Orobus (e.g. L. venetus, L. vernus) do, however, have this feature, which is more typical of Vicia. The wings of species of Sects. Lathyrus, Cicercula and Clymenum are simpler in construction; only the lower process is present (see L. tuberosus, Fig. 11). I find that members of Sect. Pratensis are unusual in having alae with a 'waist' between the limb and the middle area which is united with the keel (Fig. 20:4). The same form of wing is

found also in L. aphaca (Fig. 20:5), but in no other section; this distribution suggests a relationship between these two groups, although the former is perennial and the latter annual. These species are illustrated in more detail in Ross-Craig (1954).

Lens. Most members of the genus Lens have small, pale flowers similar in general facies to those of some species of Vicia Sect. Ervum. However, a close inspection of the flower of, for example, L. culinaris (Fig. 16) shows that its corolla has more features in common with those of Lathyrus than of Vicia. The standard is obovate and possesses two pouches at the fold; the wings have an upper and a lower process but no 'kink' in the upper edge. The same characters were found also in L. orientalis and L. nigricans, but in L. montbretii, a distinctive species with flowers somewhat larger than those of the rest of the genus, the upper edge of the wing was found to be pleated.

Pisum. The flower of P. sativum (Fig. 17) superficially resembles those of members of Lathyrus Sect. Lathyrus; the tube is short and the vexillum broad and conspicuous. However, this impression is belied by the complexity of the corolla. The vexillum is pouched at the fold and also has a small boss in the mid-line of the claw which rests on top of the staminal tube proximal to the wings. The wings have a prominent lower process (x) which involves the pleating of the upper edge, and a pronounced fold in the limb. The lower process projects backwards sharply. The keel in this genus is cristate along

the outer and lower fused edge.

Vavilovia. The flower of Vavilovia is very similar to that of Pisum, the chief differences being that there is no boss on the mid-line of the vexillum, and the carina is not cristate.

Cicer. The corolla of species of Cicer differs very markedly from those of the other genera described above, and it is surprising that this has had so little influence on the taxonomic position of the group. Fig. 18 (C. arietinum) shows that the shape of the petals is relatively simple. The vexillum is obovate, with no strongly-marked fold lines. Each wing has a shallow hollow (x) corresponding with the lower process (x) in Lathyrus aureus (Fig. 10), but although this rests in the shelf (x') of the keel, these two petals are not united at this point by interlocking papillae, as in the rest of the Vicieae. The two keel petals are fused, as in other members of the tribe.

The flowers of Vicia, Lathyrus, Lens, Pisum and Vavilovia are unusual within the Leguminosae in having petals of such complexity; this feature, though seldom mentioned, is one of the distinguishing characters of this undoubtedly natural (monophyletic) group of genera. In contrast, the simpler corolla found in Cicer is typical of many other tribes, e.g. the Trifolieae, Loteae and Genisteae.

4.2.3.2.

FLOWER COLOUR

Almost every colour is represented in flowers of the Vicieae. The two large genera each shows a wide range, but there is some tendancy for certain colours to be confined to or commoner in one or the other genus: thus bluish corollas predominate in Vicia, orange, yellow and pink in Lathyrus.

The majority of species of Vicia Sect. Cracca have bluish- or reddish-purple flowers (the wings and keel are often paler than the standard). Exceptions are V. crocea, with dull orange-yellow flowers, and V. ochroleuca in which they are a paler yellow. V. sicula and V. benghalensis have very dark crimson flowers. Sect. Ervum comprises mainly species with small, pale lilac flowers. V. caesarea, V. lunata and V. cypria have bicoloured, yellow and blue corollas. V. koeieana (Sect. Anatropostylia) is very unusual within the genus in having bright lemon-yellow flowers. The variation within Sect. Vicia is somewhat wider than in the other sections. Species of the V. sativa group (which have subregular calyces) have purplish corollas, except for V. grandiflora in which they are pale yellow. The perennials V. oroboides, V. truncatula and V. balansae have pale yellow or buff-coloured flowers. Among the V. lutea group (species which have the lens of the seed opposite the hilum, see part 4.5.5), yellow corollas again predominate; but the colour tends to be lurid or dirty-yellow, never bright as in V. koeieana. V. melanops, for example, has distinctive greenish flowers with a large black spot on each wing petal.

Within Lathyrus, flower colour is no guide in identifying species-groups, but is very useful in distinguishing between

related species. Each section comprises a range of different colours, the most variable in this respect being Sects. Lathyrostylis, Lathyrus and Cicercula. The flowers of Sect. Lathyrostylis range from pale sulphur (L. pallescens) to magenta (L. tukhtensis). The flowers of Sect. Cicercula may be yellow (L. chrysanthus), bluish (L. hirsutus), pink (L. cassius), orange (L. pseudo-cicera) or brick-red (L. cicera). This unusual colour occurs sporadically in the rest of Lathyrus: in L. sphaericus and L. setifolius (Sect. Orobastrum), and in L. nissolia. L. aphaca and L. pratensis have yellow flowers; L. laxiflorus (Sect. Pratensis) is purple-flowered. In Sect. Clymenum, one species (L. clymenum) has purplish or pink flowers while in the other (L. ochrus) they are pale yellow.

The flowers of Pisum are lilac and purple (P. sativum) or orange-buff (P. fulvum); those of Vavilovia formosa are carmine. The flower colour in Pisum graecum is unknown. Species of Lens have mainly mauve or lavender flowers; in L. montbretii they are whitish. Cicer arietinum has white, blue or pinkish flowers. In other members of the genus pink, purple and white prevail, but C. oxyodon has yellowish corollas.

4.2.4.

ANDROECIUM

In Vicia, Lathyrus, Lens, Pisum and Vavilovia the androecium is diadelphous, but the filament of the vexillary stamen rests upon and closes the staminal tube by being lightly fused with it in the same way in which the wings are fused to the

keel (see Figs. 10 & 13). This contrasts with the situation in Cicer, where the vexillary stamen has a terete, rather than a flanged, filament, and is quite separate from the staminal tube (Fig. 18). Thus in Cicer the nectar produced at the base of the ovary is easily obtainable, while in the other genera it can only be reached through the two small pores left in the staminal tube.

In Vicia, Lathyrus and Lens the filaments are delicate structures which taper towards the anthers. The latter are introrse, equal in size and all medifixed. In Cicer the filaments are dilated below the anthers and the latter, though of uniform size, are alternately basifixed and versatile. These most significant characters were pointed out by Popov (1928) in his monograph of Cicer, but were overlooked by Hutchinson (1964). As a result, in Hutchinson's key to the genera of the Leguminosae, Cicer keys out as Ononis!

Characters of the androecium (filaments all or alternately dilated; anthers of two sizes; anthers alternately basifixed and medifixed; androecium monadelphous) were the chief factors which led early taxonomists, including De Candolle (1825), to place Ononis in the Genisteae. Later Bentham and Hooker (1865) and Boissier (1872) favoured the inclusion of this genus within the Trifolieae, due to the greater weight given to other characters. Most members of the Trifolieae have androecia similar to those of Vicia and Lathyrus, but in some species of Trifolium (T. pratense, T. ochroleucum) the filaments are dilated. Within the Vicieae, Pisum and Vavilovia

have alternate filaments dilated. Thus, within the Vicieae and Trifolieae, Cicer most resembles Ononis in androecial characters - except that the former is diadelphous and the latter monadelphous. However, the occurrence of dilated filaments within other genera in both tribes (Pisum and Trifolium) shows that these features are possessed to some degree by a wide taxonomic group and are not necessarily evidence of close relationship between Cicer and Ononis.

Lathyrus, Pisum and Vavilovia are characterised by androecia in which the staminal tube is truncate (Figs. 10 & 17). In contrast, those of Vicia, Lens and Cicer end obliquely (Figs. 13, 16 & 18). This character has been widely used in the taxonomy of the group (see Table 2 and part 2.2), and my investigations have shown it to be reliable in general; however, I agree with Burkart (1935) that some American members of Lathyrus - L. campestris and the closely related L. crassipes - have staminal tubes which end obliquely.

I have examined the pollen of a number of species of the Vicieae * and find it to be uniform within the group and similar to that of Medicago (Trifolieae), according to Lesins & Lesins (1963). The pollen of Ononis natrix and O. adenotricha is also

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* Vicia villosa, V. neglecta, V. filicaulis, V. pubescens, V. sativa, V. grandiflora, V. pannonica, V. faba, Lathyrus latifolius L. clymenum, L. blepharicarpus, L. nissolia, L. aphaca, Lens orientalis, Cicer arietinum, C. pungens, C. incisum.

of the same type. The grains are ellipsoidal and tricolporate, sometimes with a finely pitted extine; their size and relative dimensions vary slightly between species, but my limited survey did not reveal variation of taxonomic significance.

4.2.5.

GYNOECIUM

Characters derived from the gynoecium have traditionally held a prominent place in the taxonomy of the Vicieae. The genera themselves can be distinguished largely on the shape of the style and the distribution of indumentum on it (Table 2), and within Vicia and Lathyrus these details have provided guides for the formation of infrageneric groups. This is shown in the key to Godron's classification of Vicia in part 2.3.1, and in the history of the taxonomy of Lathyrus (part 2.4.1). During this century stylar characters within Vicia have been rather neglected, and sometimes loosely or wrongly described, but in the recent classification of Radzhi (1970) they again

receive special attention.

This part deals almost exclusively with variation in stylar characters, the ovary itself being considered in the section of the fruit (part 4.4). A binocular dissecting microscope was used for all my observations, which were made on both living and herbarium material.

Vicia. In most species of Vicia the style is compressed, either dorsally or laterally (see Table 12). It was most interesting to find that, with the single exception of the extinct V. dennesiana (from the Azores), all species with a laterally compressed style also have a platynychioid vexillum. These include many members of Sect. Cracca, some of Sect. Ervum (V. leucantha, V. disperma, V. durandii and V. vicioides), and most species of N. America. Apart from Godron (1849), who placed all species with laterally compressed styles together in the genus Cracca, most taxonomists have ignored this character. All members of Vicia have pubescent styles, although in the smallest-flowered annuals of Sect. Ervum (V. hirsuta, V. tetrasperma) they may superficially appear to be glabrous due to their size. The distribution of indumentum on the laterally compressed styles is usually even all round (see V. cracca, Fig. 13), and sometimes slightly tufted on the abaxial side just below the stigma. In V. ciceroidea, V. rafigae and V. multijuga the two flat sides of the style facing laterally are free from hairs (Fig. 21:5).

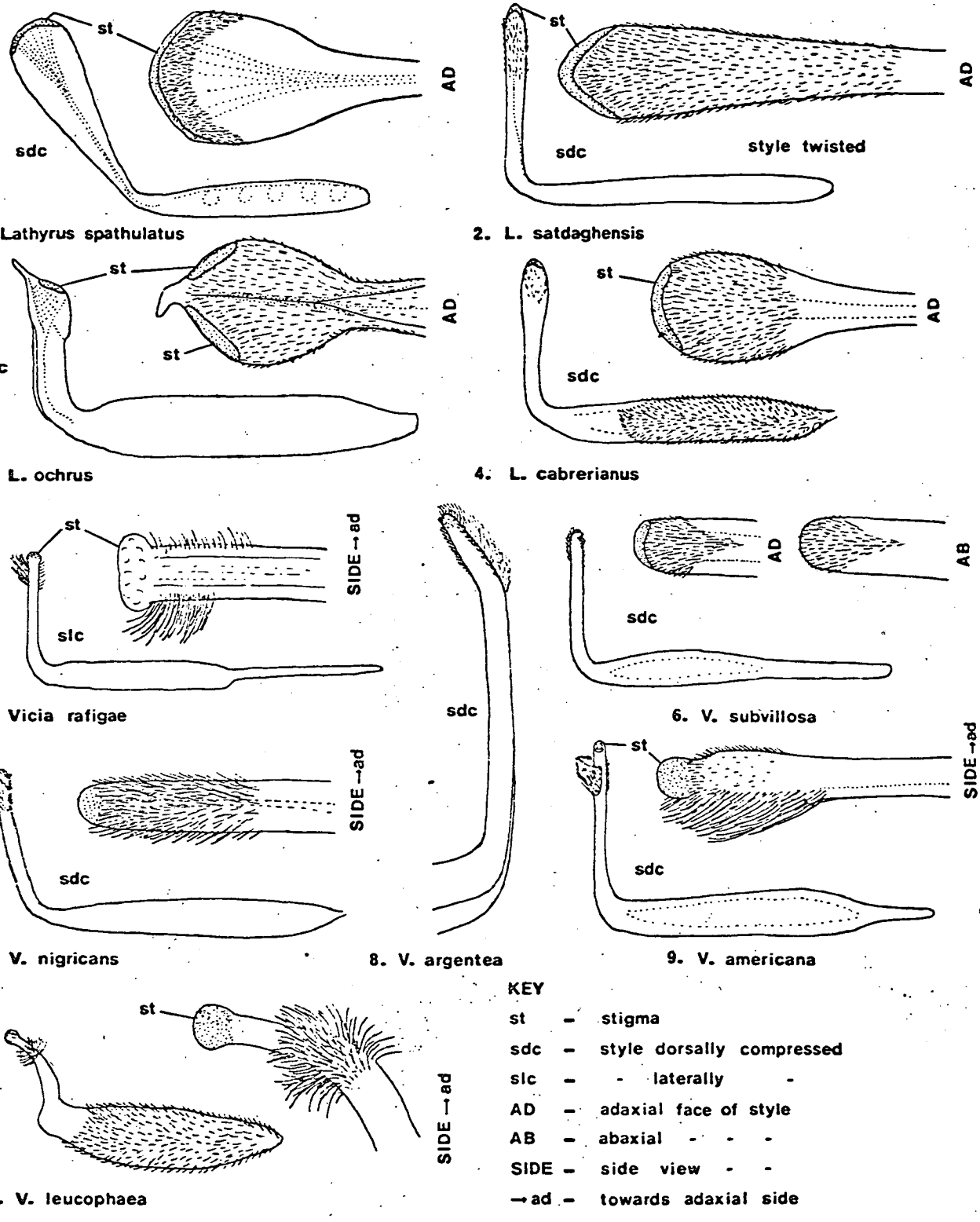
Among the dorsally compressed styles is found a much

wider range of indumentum-distribution types. A number of perennial species of Sect. Cracca have styles evenly hairy all round. These are the 'oroboid' group (V. venosa, V. pseudo-orobus, etc.; V. sylvatica (Fig. 12), though not strictly 'oroboid', is placed here too) and the non-oroboid species with strongly epistomatic leaves (V. cassubica, V. orobus, etc.). A few annuals and biennials of this section have a similar type, including V. biennis, V. cypria, V. lunata and V. articulata. The perennial American species V. nigricans also has a dorsally compressed style evenly hairy all round (Fig. 21:7).

All members of Sects. Vicia and Faba are characterised by styles which are tufted on the abaxial side (the adaxial side may have a few short hairs); an example, V. sepium, is shown in Fig. 14. This kind of style is found also in a few members of Sect. Cracca: the perennials V. altissima, V. onobrychioides and V. dumetorum, which have oblong to stenonychioid standards, and the annuals V. cappadocica, V. cretica and V. cassia, whose vexilla are platynychioid (Table 12). It occurs in the N. American V. americana (Fig. 21:9) and in all S. American species except V. nigricans.

V. argentea, V. canescens etc. (Subgen. Cracca Sect. Variegatae Radzhi) possess dorsally compressed styles with a dense tuft of hairs on the abaxial side; this is a different type from that found in Sect. Vicia (see Fig. 21:8). V. subvillosa has a unique type of style in which V-shaped areas on both the inner and outer surfaces just below the stigma

Fig. 21. Variations in stylar shape and indumentum in Vicia and Lathyrus.



bear hairs while the rest is glabrous (Fig. 21:6). V. leucophaea, a species of Central America, is similarly distinctive; the style is terete, and has a dense ring of hairs encircling it at a considerable distance from the stigma (Fig. 21:10).

V. koeieana (Fig. 15), which Plitmann (1970) has placed in the monotypic Sect. Anatropostylis, is anomalous within Vicia in having a dorsally compressed style which is pubescent on the adaxial face; this type is otherwise confined to, and characteristic of, Lathyrus and Lens. Because gynoecial characters are so important in the definition of the genera of the Vicieae, this species presents an interesting problem for the taxonomist. It is discussed in part 10:4.

Lathyrus. All members of Lathyrus have a dorsally compressed style which is pubescent on the (developmentally) adaxial side. Within this basic unity of structure, variations in stylar shape and indumentum-distribution provide important characters on which taxonomists dealing with the Old World members have relied heavily. These characters are considered separately below:

1. Styles twisted. The perennial Sect. Lathyrus and the annual Sect. Cicercula, defined by Godron in 1849, are based on the presence of a contorted style; in both it is turned through 90 to 180 degrees, always in the same direction (Fig. 11). In Sect. Lathyrus the lower part of the style is arcuate or cylindrical, in Cicercula flattened and channelled on the lower side. These two sections are characterised by several

other common features (e.g. a typical corolla shape - see part 4.2.3.1) and together form a natural group. L. roseus, which shares this same type of corolla, and also has an arcuate, twisted style, has been put in a separate section (Orobon) due to its ehendrillous leaves and unwinged stems.

The contorted style also occurs in other, more distantly related taxa. It is said to be present in some members of Sect. Lathyrostylis (e.g. L. spathulatus, L. filiformis, L. boissieri); this is perhaps a variable characteristic, as I have found straight styles in specimens of L. spathulatus. According to my investigations, the style of the recently described L. satdaghensis is twisted, though in the opposite direction to those of Sect. Lathyrus (Fig. 21:2). The N. American L. sulphureus sometimes has a twisted style. Burkart (1935), speaking of the relationship of S. American species to those of the Old World, says "I have not studied the differences based on the curvature of the style" (translated). This suggests that he found this character in some Argentinian species; my own survey, though comparatively limited, has not revealed its presence. According to Davies (1958), the style of L. setifolius (Sect. Orobastrum) is twisted; but having examined herbarium specimens, I do not agree.

2. Styles spathulate. Distinctly widened, spathulate styles are characteristic of most members of Sect. Lathyrostylis, a group united by several other characters (absence of tendrils, parallel leaflet-venation, perennial life-form, more-or-less erect habit). An example is illustrated in Fig. 21:1.

Čelakovsky (1888) was of the opinion that some of these species have twisted styles because there is no room for them, in the normal position, inside the carina. However, as pointed out in part 2.4.1, this hypothesis does not solve the problem in all cases; some members of the section, e.g. L. satdaghensis, Fig. 21:2, have quite narrow, twisted styles. Other members of the genus also possess spathulate styles, e.g. L. hirsutus, L. gorgoni, L. clymenum and many S. American species: L. cabrerianus, L. multiceps, etc.

3. Double stigma. The pistil in members of Sect. Clymenum is most distinctive, in that the style ends in a mucro of non-stigmatic tissue which divides the stigma into two (Fig. 21:3). It is most interesting that certain S. American species (L. pubescens, L. subulatus and L. tomentosus) also have this feature (Burkart, 1935, and my own observation). L. gloeospermus (Sect. Gloeolathyrus), whose vegetative characters are so similar to those of Sect. Clymenum, has cleistogamous flowers with a morphologically undeveloped style.

In the course of my studies on living material, I found several examples of specimens which did not conform with the species descriptions:

a) one specimen each of L. grandiflorus and L. cicera in which the style bore hairs on the abaxial, as well as the adaxial, face;

b) two specimens of L. tingitanus, in which the style was pubescent only on the abaxial face; and

c) material of L. gorgoni in which the style was not twisted.

Examples a) and b) are interesting, being occasional variant

forms which show how easily stylar differences may arise. In the case of c), having checked the character by dissecting herbarium material, I found the non-twisted style to be typical of L. gorgoni and the closely-related L. pseudo-cicera.

Lens. The style in all species of Lens is very uniform, being linear, dorsally compressed and pubescent on the inner face - as in most members of Lathyrus. This is illustrated in Fig. 16. L. montbretii, although in some ways anomalous within the genus, also has this type of style.

Pisum and Vavilovia. The type of style found in flowers of Pisum and Vavilovia is the most distinct feature which links these genera together. Like those of Lathyrus and Lens, it is dorsally compressed and pubescent on the inner face; but it is also folded backwards along the median line, the two edges meeting abaxially and fusing towards the apex (Fig. 17:G & H).

Cicer. The style in members of Cicer contrasts strongly with those of the other genera in being terete and glabrous. Moreover, whereas in the rest of the Vicieae it is held approximately at right angles to the ovary, in Cicer the style is curved gently away from the end of the fruit (Fig. 18:G). In all these characteristics, the gynoecium of Cicer resembles those typical of neighbouring tribes, e.g. the Trifolieae and Genisteae.

4.3.
POLLINATION

The pollination mechanism of Vicia and Lathyrus is described by Knuth (1908) and Proctor & Yeo (1973). The flower is protandrous, and the anthers dehisce while it is still in bud. At this stage the anthers are arranged closely and neatly in two rows round the style; after the pollen has been shed, they are retracted. The stylar hairs help to hold the pollen deposit. When a bee visits the flower for nectar, it lands upon the wings; and as these are firmly united with the keel, the insect's weight forces the keel down and the style, emerging from its apex, brushes against the underside of the bee. This action transfers pollen from the style to the insect, and also damages the stigma, bursting its papillae and rendering it receptive for pollination. If the bee has previously visited other flowers, it may leave foreign pollen behind on the stigma, and so effect cross-pollination.

Bumble-bees and honey bees are said to be the main pollinators in the Vicieae, and I have observed their visits. In the experimental plot at Edinburgh I found that a small species of bumble-bee (Bombus agrorum?) was very active in gathering nectar legitimately and hence bringing about pollination, while a larger species (B. terrestris?) regularly bit a hole in the calyx and corolla tube and stole nectar from the flowers. In Kent, I saw cultivated Lathyrus latifolius being visited by honey bees (Apis mellifera); they always approached each flower from its right-hand side (looking into the flower) and, because the hairy part of the style is turned to the left, they were able to suck nectar without becoming dusted with pollen or

touching the stigma. Knuth (1908) mentions that a similar behaviour-pattern was observed by Kirchner in L. sativus, which also has a twisted style.

According to Manley (1948), Apis mellifera gathers 'honey-dew' from the stipular nectaries of vetches, and this source can make a significant contribution towards the honey-yield of a hive, although it is considered to produce a poor quality honey.

Although Vicia, Lathyrus, Lens, Pisum and Vavilovia share a complicated floral structure which is well adapted for cross-pollination by bees, it seems that the breeding system in these genera is largely dependent on other factors (see part 7.4). Judging by the seed-set of isolated cultivated plants, it seems that perennial species are frequently self-incompatible, whereas annuals appear to be in general self-compatible. In species with large, attractive flowers or inflorescences out-breeding is probably predominant, but in members with small, inconspicuous flowers (e.g. those of Vicia Sect. Ervum and Lens), autogamy is common. Cleistogamous flowers are known in several species, for example Vicia sativa subsp. amphicarpa, Lathyrus nissolia and L. gloeospermus.

The flower of Cicer is simpler than that of the other genera (see part 4.2.3), the androecium being truly diadelphous and the wing petals not fused to the keel; despite its more primitive construction, it appears to be adapted for bee-pollination. C. arietinum is habitually autogamous (van der Maesen, 1972); I have no information about the pollination of

the other species.

4.4.

FRUIT

The Vicieae typically have legumes which dehisce upon maturity along both upper and lower sutures, the valves often twisting violently after separation so that the seeds are flung away from the plant. The number of seeds per pod varies from one or two (in annuals such as Lens species, Vicia hirsuta and Lathyrus lentiformis) to several in most species. This character is not of particular importance, being generally related to the size of the fruit, although where these are very small the seed number may be constant for a species (as in V. disperma and V. tetrasperma).

Vicia. Fruits of Vicia are illustrated in Fig. 22, and the numbers in parenthesis following the species cited below refer to these diagrams. Perennial members of Sect. Cracca typically have more-or-less stipitate pods, e.g. V. crocea (:7), V. cassubica (:8) and V. cracca (:9), and although variation in their morphology often provides information for identification at specific level, it is of little use on a broader scale. The annuals of this section sometimes have more distinctive fruit characters. For example, V. articulata has sub-moniliform legumes, and V. cappadocica has non-stipitate fruit with parallel sutures.

In the poorly-defined section Ervum (sensu Ball, 1968)

there is great variation in the shape and size of legumes, and four main types can be distinguished:

A. Fruits stipitate, over 2 cm long; sutures not parallel - e.g. V. disperma (:10), V. leucantha (:11), V. durandii (:12), V. vicioides (:13).

B. Fruits not stipitate, less than 2 cm long; sutures parallel - e.g. V. tetrasperma (:14), V. pubescens (:15), V. laxiflora.

C. Fruits not stipitate, less than 2 cm long; sutures not parallel - e.g. V. meyeri (:16), V. hirsuta (:17).

D. Fruits not stipitate, over 2 cm long, sub-torulose - e.g. V. ervilia (:18), V. caesarea (:19).

It is interesting to find that species with fruits of type A have flowers with pandurate standards and laterally compressed styles (Table 12), while the remaining members of Sect. Ervum do not possess these floral characters. These facts emphasise the heterogeneity of this section, and show the need for a redefinition of its limits.

The fruits of members of Sect. Vicia are never truly stipitate, though sometimes tapered towards the calyx, and are characterised by the presence of woolly endocarp partitions between the seeds. Most are generally rhomboidal, e.g. V. oroboides (:1), V. hyrcanica (:2), but linear legumes are found in the V. sativa group which includes V. grandiflora, V. pyrenaica, V. cuspidata, V. lathyroides and V. sativa (:3). V. lutea has pods which are densely covered with tuberculate hairs (cf. part 3.7). Members of Sect. Faba have fruits similar to those of Sect. Vicia; they are usually linear, e.g. V. narbonensis

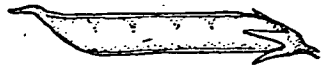
Fig. 22. Fruits of Vicia, Lens and Cicer.



1. Vicia oroboides



2. V. hyrcanica



3. V. sativa



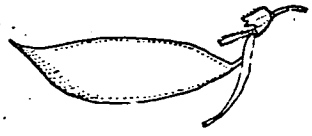
4. V. narbonensis



5. V. lunata



6. V. koeieana



7. V. crocea



8. V. cassubica



9. V. cracca



10. V. disperma



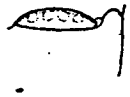
11. V. leucantha



12. V. durandii



13. V. vicioides



14. V. tetrasperma



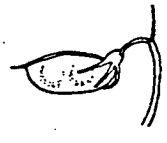
15. V. pubescens



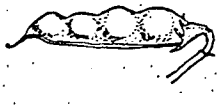
16. V. meyeri



17. V. hirsuta



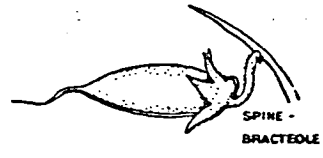
20. Lens culinaris



18. V. ervilia



19. V. caesarea



21. Cicer pungens

Scale: x 1

(:4), and have spongy endocarp tissue between the seeds.

The two isolated species V. lunata and V. koeieana, each of which has been placed in its own section, possess fruits of striking morphology. The pods of V. lunata (:5) are long-stipitate, strongly compressed and have papery, oblong-crescentic, reticulate-veined, indehiscent valves. The legumes of V. koeieana (:6) also have papery, strongly-veined valves, but they are oblong and sub-torulose. The upper suture is convex, so that the style appears to arise from the lower suture.

Amphicarpy is found in V. sativa subsp. amphicarpa. Apart from normal flowers borne in the leaf-axils, this plant also produces cleistogamous flowers on subterranean stems. The fruits which develop from the latter are not linear like the aerial legumes but ovoid, white and inflated.

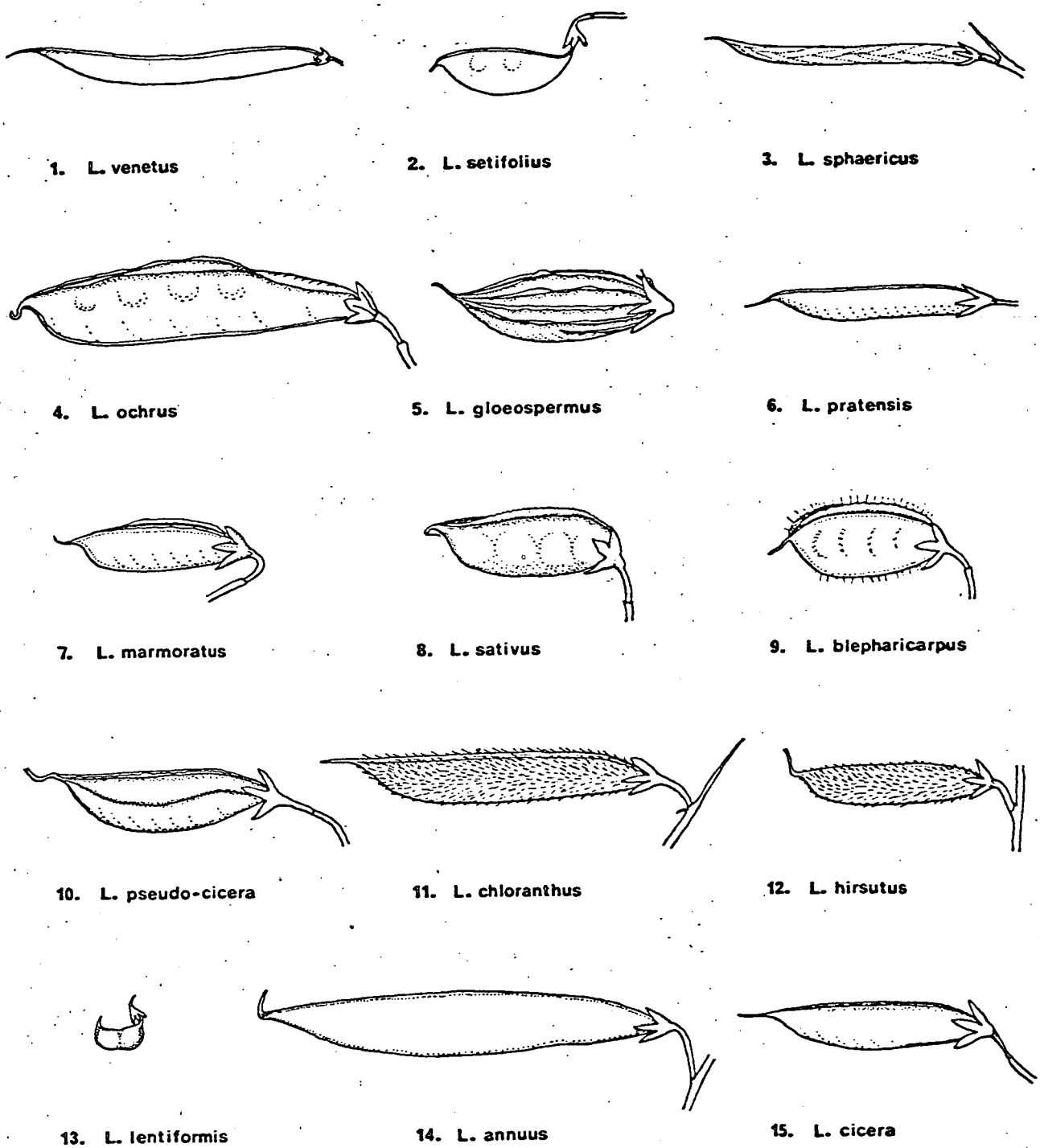
Lathyrus. Fruits of Lathyrus are illustrated in Fig. 23. In contrast to those of Vicia, they are typically linear and are seldom stipitate. The etendrillous members of Sect. Orobus, e.g. L. venetus (:1), can thus be distinguished from the 'oroboid' members of Vicia Sect. Cracca (e.g. V. crocea, Fig. 22:7) by the shape of their legumes. Fruit characters are not very useful for taxonomic purposes within the genus, except in Sects. Orobastrum, Clymenum and Cicercula. Most members of Sect. Orobastrum have long, linear pods. In some the valves are conspicuously veined, either reticulately as in L. vinealis, or in a 'herringbone' pattern as in L. sphaericus (:3). L. saxatilis has unusually short legumes, while those of L. setifolius (:2)

are strongly stipitate. The fruits of L. sphaericus and L. inconspicuus are distinguished by the presence of membranous septa between the seeds, though in L. sphaericus the character is not always present. L. nissolia has linear fruits with a 'herringbone' vein pattern very similar to that of L. sphaericus, and although they are usually non-septate I found a single specimen with partitions inside the pod; this is very suggestive of affinity between Sects. Nissolia and Orobastrum. It is interesting that some S. American members of Lathyrus, e.g. L. tomentosus, have fruits with woolly partitions between the seeds.

In Sect. Clymenum the legumes possess 'wings', which arise from the upper suture as shown in L. ochrus (:4); in L. gloeospermus (:5) (Sect. Gloeolathyrus) additional narrow wings, parallel to the sutures, are present on the valves themselves.

In the large section Cicercula variation in pod morphology is used as one of the main guides of classification. The legumes range in shape from relatively long and narrow, e.g. L. annuus (:14), to short and oblong or ovoid, e.g. L. cicera (:15), while in some this trend develops further with the production of wings, e.g. in L. sativus (:8), L. blepharicarpus (:9). The pods may be conspicuously veined, as in L. pseudocicera (:10), or, as described in part 3.7, they may be tuberculate-pilose, as in L. chrysanthus, L. chloranthus (:11) and L. hirsutus (:12). Finally, the recently-discovered species L. lentiformis (:13) has fruits unlike those of any other member of the genus: they are very small, stipitate and

Fig. 23. Fruits of Lathyrus.



1. L. venetus
2. L. setifolius
3. L. sphaericus
4. L. ochrus
5. L. gloeospermus
6. L. pratensis
7. L. marmoratus
8. L. sativus
9. L. blepharicarpus
10. L. pseudo-cicera
11. L. chloranthus
12. L. hirsutus
13. L. lentiformis
14. L. annuus
15. L. cicera

Scale : x 1

subtorulose.

Lens. The fruits of Lens are very uniform and characteristic of the genus: small, compressed and rhomboidal (e.g. L. culinaris, Fig. 22:20). They are not, or only very shortly, stipitate. The pods of L. montbretii are proportionally a little longer than those of the other species, and are densely sericeous with golden-brown hairs.

Pisum and Vavilovia. Members of Pisum and Vavilovia have pods similar to those of Lathyrus; they are linear and not stipitate.

Cicer. In all the genera mentioned above the fruit is typically compressed, subtorulose examples being found only in isolated and obviously advanced species (e.g. Vicia koeieana). In striking contrast, the legumes of Cicer are always inflated. Fig. 22:21 illustrates the fruit of C. pungens, which is typical of the genus, being rhomboidal, not stipitate and tapered towards the style. The fruits of Ononis resemble those of Cicer in being inflated. Those of the Trifolieae vary greatly, being an important basis for generic recognition, but none is like those of Cicer.

4.5.
SEEDS
4.5.1.
GENERAL REMARKS

The leguminous seed has been described in detail by Corner

(1951), and the following introduction is based largely on his paper. The ovule in most members of the Papilionoideae is campylotropous, and the seed is therefore asymmetrical about the transmedian longitudinal plane, the raphe being shorter than the antiraphe (see below). As the seed matures, the nucellus and inner integument are more-or-less obliterated, and the space becomes entirely occupied by the embryo and its surrounding endosperm. The radicle is usually long and curved, causing a ridge in the testa ending in a beak above the micropyle. The testa develops from the outer integument; its complex layered structure distinguishes the leguminous seed from those of all other families. The ovule is attached to the ovary wall by the funicle. This carries a single trace which enters the outer integument at the end of the hilum away from the micropyle and travels round the circumference of the seed to the chalaza (the point at which the vascular bundle enters the nucellus). The chalaza, which can be distinguished only as a slight thickening or spreading of the vascular bundle, separates the raphe from the antiraphe.

The most characteristic feature of the papilionaceous seed is its hilum, which is peculiar in possessing two recurrent vascular bundles which derive from the funicular trace (Fig. 24:B), and also a 'tracheid bar' directly beneath the median groove. Corner says that "there is much variation in the vascular supply of the papilionaceous (seed). The variation may be systematic with generic, if not tribal, value.". He finds that the vascular bundle usually ends at the chalaza, but

continues on into the antiraphe in some species. There are also examples where the pre- and post-chalazal traces, as well as the recurrent vascular bundles, give rise to extensively branched vascular systems spreading laterally in the testa.

Another feature of the seed is the lens, a small lump in the testa, darker in colour than the rest of the seed, positioned above the main vascular trace (Fig. 24:A). The function of the lens seems to be unknown. Corner states that it is "a local differentiation of the mesophyll, but without apparent significance" (the rather misleading term 'mesophyll' here means the middle layer of the testa), and Gunn (1968b) quotes Kopoosian who defines it as "all reinforcements of normal tissue of the seed, situated between the hilum and chalaza, on the trajectory of the principal vascular bundles; externally it is a lens-shaped structure near the hilum". According to Pitot (1935) the lens may be near the chalaza but is never directly above it.

4.5.2.

SEED SHAPE, SIZE AND MARKING

The seeds of the Vicieae, with the exception of Cicer, are compressed, spherical or oblong (though often slightly angled through contact with neighbouring seeds in the ovary), with only a slight ridge marking the position of the radicle. The latter is fairly long and curved and lies closely against the cotyledons (Fig. 24:1C & 2C). Seeds of Cicer, on the other hand, are grooved between the two cotyledons and the short

conical radicle causes a beak above the micropyle (Fig. 24:3A & 3C). Corner (1951) describes the radicle of Cicer as "short and straight", and he likens it to the median radicle of the mimosoid-caesalpinioid seed in contrast to the "long curved radicle typical of the bean seed". However, I disagree with this comparison and consider that the Cicer radicle is not truly of the mimosoid type, but is similar to that of the rest of the Vicieae, since its axis is turned at right angles to that of the cotyledons rather than being in line with them. The seeds of the Trifolieae are strongly beaked; the radicle is long and curved, and not adpressed to the cotyledons (Fig. 24:4C & 5C).

Seed shape is not of great systematic value within the Vicieae, except in one case: all members of Lens have strongly compressed, biconvex seeds. This is almost diagnostic for the genus, but a few species of Vicia also have lentil-like seeds, viz. V. caesarea, V. lunata and a variety of V. sativa which has been called 'V. leganyana' (see part 7.5.).

Seeds of the Vicieae range in length from 2 mm in some annuals of Vicia Sect. Ervum to 3 cm in V. faba, the cultivated broad bean; the average size is 4 to 5 mm. V. michauxii has unusually large seeds, about 8 mm long.

The colour of the testa varies from black through various shades of brown to yellow and is often beautifully mottled or speckled; this type of marking is certainly not a reliable character. Most seeds are smooth, but in a few cases the testa surface is uneven, providing a useful diagnostic character. In

Lathyrus Sect. Cicercula, for example, the species L. annuus, L. hierosolymitanus, L. cassius, L. hirsutus, L. chloranthus and L. lentiformis have rugose seeds. The seeds of L. nissolia are tuberculate, while those of L. angulatus and L. setifolius are papillose. Those of the closely related species Vicia cuspidata and V. lathyroides are ruminate-reticulate and tuberculate, respectively. V. koeieana, distinctive in many characters, is also unusual in having a finely verrucose testa. Finally, some varieties of Pisum sativum have papillose seeds.

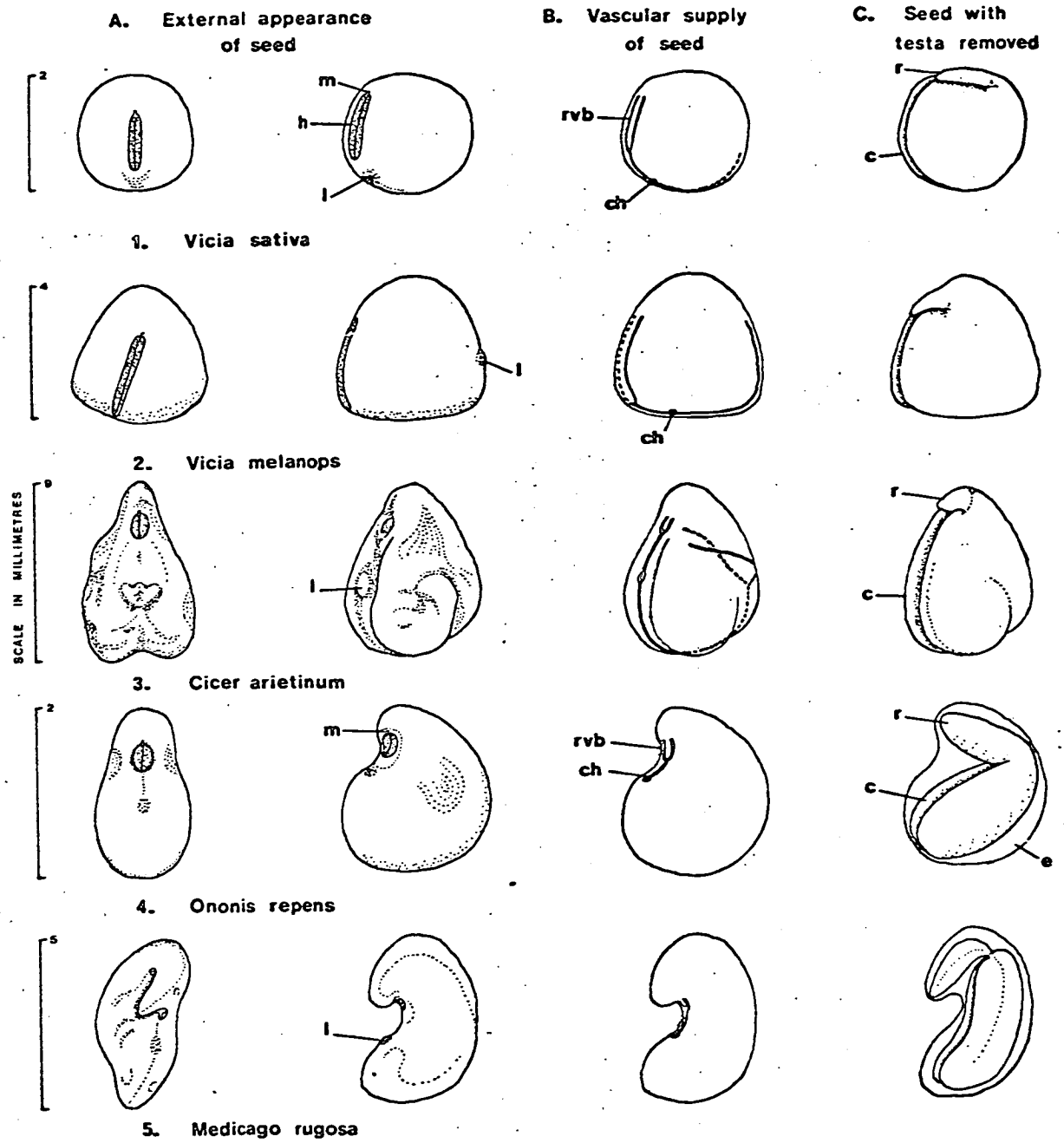
The seeds of Cicer present a contrast with those of other genera in having typically rough testas showing great variation in surface marking. For example, under low-power magnification the testa of C. pinnatifidum resembles pink rock-crystal, with sharp angles and facets, while the seeds of C. bijugum and C. echinospermum bear long curved spines.

4.5.3.

ENDOSPERM

Although members of the Vicieae have endosperm in the developing seed (as investigations of their embryology have shown, cf. Maheshwari, 1950), this tissue is broken down as they reach maturity and the cavity of the seed becomes entirely filled by the cotyledons and radicle (Fig. 24:1C, 2C & 3C). In contrast, the seeds of Ononis and the Trifolieae contain a large proportion of colourless endosperm which forms a tough hyaline sheath round the embryo (Fig. 24:4C & 5C). When the testa is cracked, the endosperm imbibes a large quantity of water, becoming

Fig. 24. Seeds of the Vicieae and Trifolieae.



KEY

h – hilum
m – micropyle
l – lens
rvb – recurrent vascular bundle
ch – chalaza
r – radicle
c – cotyledon
e – endosperm

swollen and mucilaginous; this property was very noticeable when I prepared seed extracts as antigens for serology (see part 6.4.2.2). The absence of endosperm in seeds of the Vicieae is related to their hypogeal method of germination, in which the cotyledons remain in the testa and are modified to act as food stores.

4.5.4.

VASCULAR SUPPLY

According to my investigations on the seeds of some 30 species of the Vicieae, in members of this tribe there is a long post-chalazal vascular bundle in the antiraphe. In Cicer the trace dichotomises at a point about opposite the chalaza (on the other side of the seed), and its branches run laterally in the testa, often dividing again (Fig. 24:3B). This pattern of seed vasculature was observed by Kühn (1928). In contrast, I find that in Vicia, Lathyrus, Lens, Pisum and Vavilovia there is always a simple, unbranched vascular bundle forming a hoop round the periphery of the seed (Fig. 24:1B & 2B). I do not agree with Kühn, who states that in Vicia faba this trace divides weakly at its extremity. In Ononis and members of the Trifolieae, the seeds have a very short vascular bundle which ends at the chalaza (Fig. 24:4B & 5B).

Despite the fact that a great deal of information on variation in seed vasculature has been available for many years, through the work of embryologists and morphologists, the characters provided have not been utilised to their full extent in

taxonomy. This is true in the Vicieae as in other groups, even though Corner pointed out in 1951 the systematic potential of these characters in the Leguminosae. The uniformity of the vascular pattem in Vicia, Lathyrus, Lens, Pisum and Vavilovia on one hand, and in the Trifolieae on the other, both confirms the reliability and stability of this data for taxonomic purposes, and emphasises the isolated position of Cicer.

4.5.5.

POSITION OF THE LENS

In most members of the Vicieae, and in Ononis and the Trifolieae, the lens is close to the hilum (Fig. 24:1A & 5A). The precise distance has been measured carefully in 100 species of Vicia by Gunn (1968b), and his results show that while this may be useful in specific identification, it is apparently not of broad systematic value.

In some species of Vicia Sect. Vicia * the lens is on the opposite side of the seed from the hilum (e.g. in V. melanops, Fig. 24:2A). This feature was first pointed out by Alefeld (1860), who placed all species possessing this trait in a separate genus, Hypechusa. Boissier (1872) subsequently used

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* V. anatolica, V. assyriaca, V. galeata, V. hybrida, V. hyrcanica, V. lutea, V. melanops, V. noeana, V. pannonica, V. sericocarpa.

lens-position as a primary diagnostic character within Vicia, as did Ascherson & Graebner (1909). All of these authors interpreted the lens and its varying position wrongly, confusing it with the tip of the radicle; thus Ascherson & Graebner describe the two main lens positions in Vicia as "radicle in front (on the side of the seed towards the distal end of the fruit), with its point towards the funicle" and " radicle behind, its point away from the funicle" (translated). Recent taxonomists dealing with Vicia, including Plitmann(1967) and Gunn (1968b), have mentioned the character but dismissed it as a feature of little significance. It is very interesting, therefore, to find that all species with this trait are also characterised by a modified type of nodal anatomy (partial replacement of the cortical bundles at the node - see part 5.3.2). The correlation of these two functionally unrelated characters is strong evidence of taxonomic affinity within the group which possesses them.

According to my investigations, in seeds with the lens opposite the hilum the chalaza is in its usual position near the hilum; this shows the independence of these two often closely situated points, and also qualifies Kopoosian's statement about their spatial relationship with the hilum (see part 4.5.1).

4.5.6.

HILUM LENGTH AND SHAPE

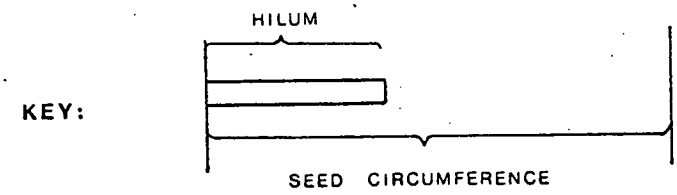
Hilum length has been extensively used as a character for

specific identification, especially in Vicia - see, for example, Swederski (1924), Žertova(1962), Utkin (1965), Leokene (1966) and Gunn (1968a & b) - but apparently no consideration has been given to the pattern of its variation throughout the tribe. Tables 13 and 14, which express the relative length of the hilum in representatives of the Vicieae, show that this variation does follow certain trends throughout the group. The most noticeable feature is that, in general, seeds of perennials have proportionally longer hila than those of annuals. This rule is broken in Cicer; all members of this genus, both annual and perennial, have very short, almost circular, hila. Seeds of Ononis, and of genera of the Trifolieae and Genisteae, resemble those of Cicer in having uniformly small hila.

This survey suggests that the Vicieae are unusual within the Papilionoideae in having seeds with long hila; and yet, within the tribe itself, it is the more primitive members of both Vicia and Lathyrus which possess this feature. It appears that the presence of short hila is a comparatively advanced trait in the Vicieae. This does not necessarily imply that the extremely long hila of Vicia sepium, V. grandiflora, etc. are of the most primitive type; during the evolution of the group there may have been divergent trends towards both increase and decrease in hilum length.

In his paper on the seeds of Vicia, Gunn (1968b) describes five hilum shapes; circumlinear, linear, oblong, wedge and oval. These character-states are quantitative rather than qualitative and are rather difficult to determine; their

Table 13. Relative hilum length in seeds of Vicia.



SECTION	SPECIES	ANNUAL (A) or PERENNIAL (P)	RELATIVE HILUM LENGTH
CRACCA	V. pisiformis	P	
	V. crocea	P	
	V. unijuga	P	
	V. dumetorum	P	
	V. sylvatica	P	
	V. amoena	P	
	V. amurensis	P	
	V. cassubica	P	
	V. orobus	P	
	V. semiglabra	P	
	V. cracca	P	
	V. biennis	A/biennial	
	V. neglecta	A	
	V. palæstina	A	
	V. articulata	A	
	V. filicaulis	A	
	V. monantha	A	
	V. villosa	A	
	V. benghalensis	A	

Table 13, continued.

ERVUM	V. hirsuta	A	
	V. disperma	A	
	V. pubescens	A	
	V. caesarea	A	
	V. ervilia	A	
ANATRO-POSTYLIA	V. koeieana	A	
VICIA	V. oroboides	P	
	V. balansae	P	
	V. sepium	P	
	V. pyrenaica	P	
	V. grandiflora	A	
	V. cuspidata	A	
	V. aintabensis	A	
	V. michauxii	A	
	V. peregrina	A	
	V. esdraelonensis	A	
	V. melanops	A	
	V. pannonica	A	
	V. lutea	A	
	V. hyrcanica	A	
	V. anatolica	A	
	V. hybrida	A	
	V. noeana	A	

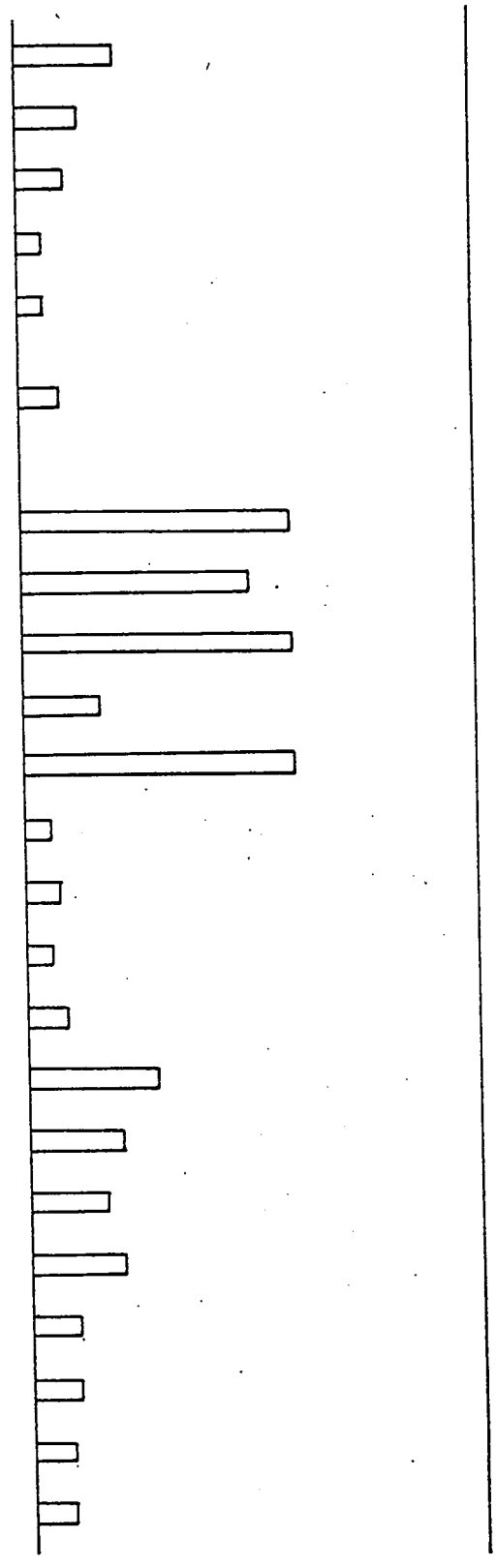
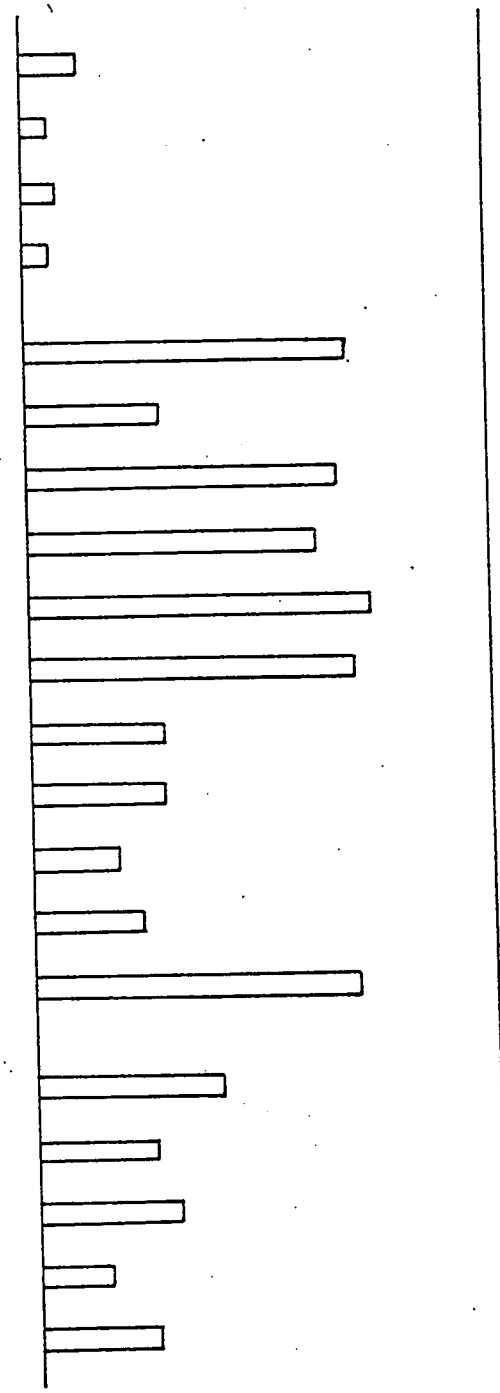


Table 13, continued.

FABA	V. faba	A
	V. narbonensis	A
	V. galilaea	A
	V. bithynica	A
North American species	V. acutifolia	P
	V. americana	P
	V. caroliniana	P
	V. floridana	P
	V. nigricans	P
	V. hugeri	P
	V. leucophaea	P
	V. pulchella	P
	V. exigua	A
	V. leavenworthii	A
	V. reverchonii	A
South American species	V. andicola	P
	V. setifolia	P
	V. linearifolia	A
	V. nana	A
	V. graminea	A



The number of seeds examined in each species varied from one to many; where many were available, it was found that the hilum length was almost constant within the species.

Table 14. Relative hilum length in seeds of Lathyrus, Lens, Pisum, Vavilovia and Cicer.

For KEY, see Table 13.

LATHYRUS

SECTION	SPECIES	ANNUAL (A) or PERENNIAL (P)	RELATIVE HILUM LENGTH
OROBUS	L. vernus	P	
	L. aureus	P	
	L. laevigatus	P	
	L. niger	P	
	L. incurvus	P	
	L. linifolius	P	
	L. pisiformis	P	
	L. japonicus	P	
LATHYRO-STYLIS	L. karsianus	P	
	L. digitatus	P	
	L. pallescens	P	
LATHY-RUS	L. rotundifolius	P	
	L. sylvestris	P	
	L. tuberosus	P	
	L. tingitanus	A	
OROBON	L. roseus	P	

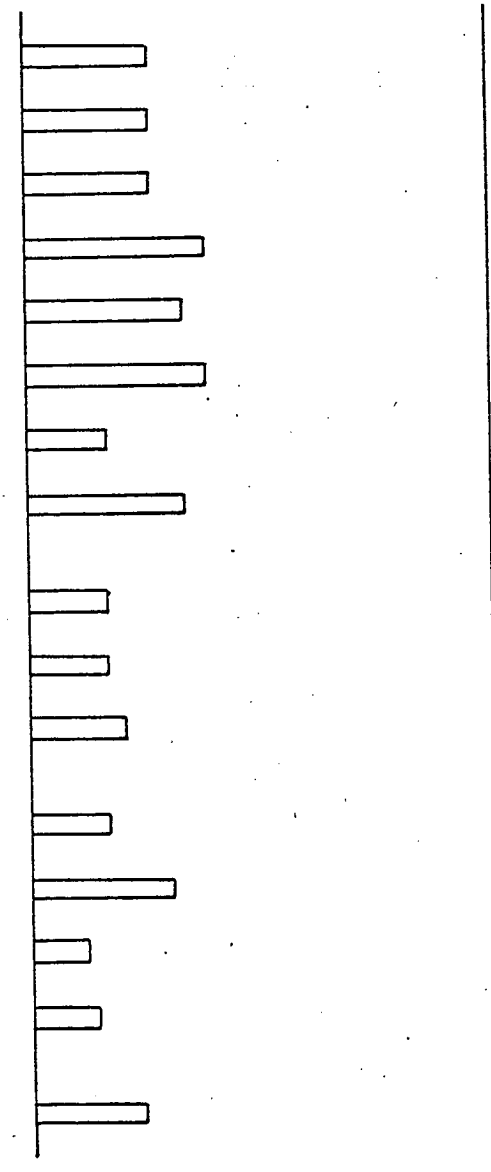


Table 14, continued.

CICER-CULA	L. hirsutus	A
	L. gorgoni	A
	L. marmoratus	A
	L. cicera	A
	L. cassius	A
	L. lentiformis	A
	L. chloranthus	A
	L. sativus	A
	L. annuus	A
	L. blepharicarpus	A
PRATEN-SIS	L. pratensis	P
APHACA	L. aphaca	A
CLYMEN-UM	L. clymenum	A
	L. ochrus	A
GLOEOLA-THYRUS	L. gloeospermus	A
OROB-ASTRUM	L. sphaericus	A
	L. inconspicuus	A
NISSOLIA	L. nissolia	A
North American species	L. ochroleucus	P
	L. polyphyllus	P
	L. vestitus	P

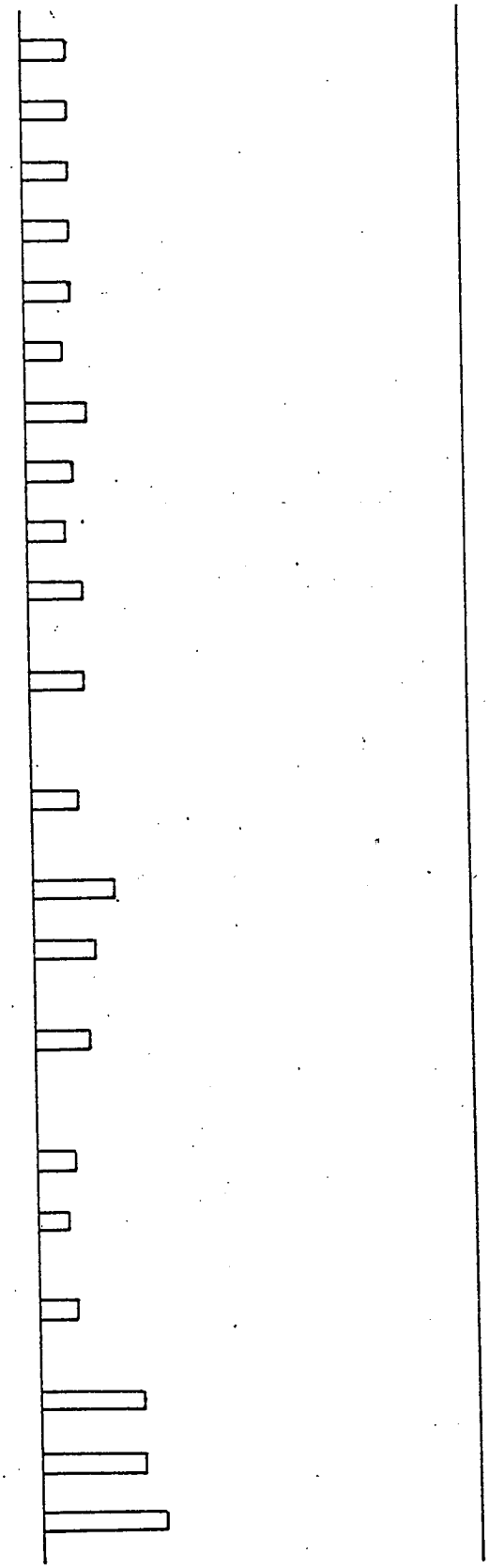
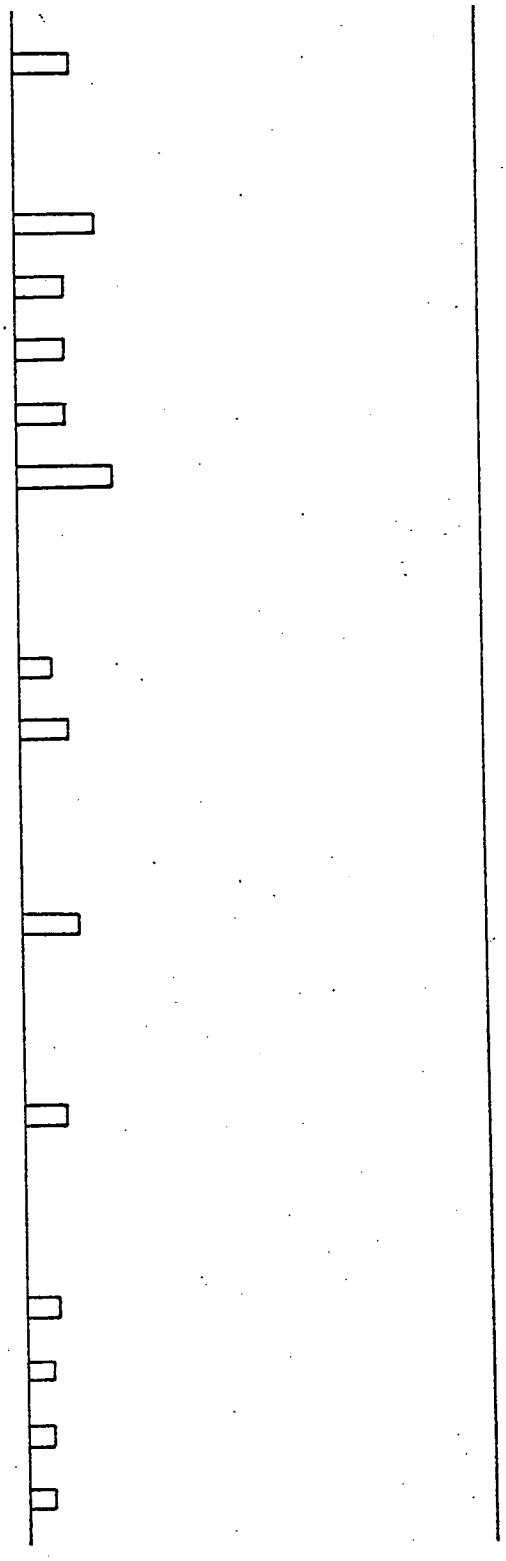


Table 14, continued.

North American species	L. zionis	P
South American species	L. cabrerianus	P
	L. linearifolius	P
	L. magellanicus	P
	L. multiceps	P
	L. pubescens	P
LENS		
	L. culinaris	A
	L. orientalis	A
PISUM		
	P. sativum	A
VAVILOVIA		
	V. formosa	P
CICER		
	C. anatolicum	P
	C. arietinum	A
	C. bijugum	P
	C. pinnatifidum	A



See comment at end of Table 13.

distribution suggests they do not have much systematic value on a broad scale, although, like hilum length, they are useful for discriminating between species.

Chapter 5

THE VASCULAR ANATOMY OF THE VICIEAE

5.1. Introduction.

5.2. Seedling anatomy.

5.2.1. Comparison of the Vicieae with other tribes.

5.2.2. The transition region.

5.2.3. The origin of the cortical vascular bundles.

5.2.4. Three cortical bundle replacement types.

5.3. Cortical bundles in the mature plant.

5.3.1. Species with winged stems.

5.3.2. Replacement of cortical bundles at nodes.

5.4. Vascular supply to leaves.

5.4.1. Species with cortical bundles.

5.4.2. Species without cortical bundles.

5.5. Primary cauline vascular systems.

5.1.

INTRODUCTION

As Dormer (1945) has pointed out, the vascular pattern of a species remains relatively stable and constant despite varying environmental conditions during ontogeny, and therefore differences in plant vasculature can provide interesting and valuable information for classification and even for phylogenetic interpretation. In practice, however, characters derived from anatomy are rather rarely used in taxonomy, due perhaps to the laboriousness of the work needed to obtain them. The situation in the Vicieae parallels that of other groups; as will be shown, although a considerable amount is known about the anatomy of its members, these facts have not been evoked by taxonomists and have therefore had no influence on its classification.

In this chapter I have brought together the results of investigations by several anatomists, most of whom confined their attention to a particular species or to one part of the plant, as well as adding to the information by my own studies. As plant vasculature involves complex three-dimensional systems of conductive tissues which cannot easily be described as a whole, the chapter is divided into four parts which deal with separate but interrelated aspects of the subject.

The first part is concerned with the anatomy of the seedling plant. As it was necessary to describe some of the morphological features of seedlings, these paragraphs are supplementary to the section on ontogeny at the beginning of Chapter 3

(part 3.1); they are also linked to some extent with the section on the seed (part 4.5). The data for the second and third parts (on the cortical bundles in the stem, and the vascular supply to leaves) were obtained by examining individual nodes of the stem; the behaviour of leaf-traces is quite easy to follow, and I have studied a reasonably large sample of species (Table 15). For the last part, which considers the primary vascular system of the stem as a whole, it was necessary to trace individual bundles through several internodes. This is much more difficult, and my conclusions in this part are based on a survey which is less comprehensive than one could wish (Table 16).

The technique used was as follows: fresh plants, or herbarium material which had been soaked for two to three days in 10% KOH, were sectioned by hand, stained in phloroglucinol and concentrated HCl, and mounted semi-permanently in glycerine jelly. The slides so prepared were then examined with a low-power binocular microscope, drawings being made of each section.*

Throughout the chapter, in all descriptions of the behaviour of the vascular bundles, I work from below upwards. In the seedling, the node at which the cotyledons are inserted is called node 0, that of the first leaf (usually a scale) node 1, etc; the first internode is between nodes 0 and 1.

5.2.

SEEDLING ANATOMY

5.2.1.

A GENERAL COMPARISON OF THE VICIEAE WITH OTHER TRIBES

*See Appendix 3.

Seedling anatomy in the Leguminosae has been investigated by relatively few workers, and by far the most extensive study in this field is that of Compton (1912). This author examined a fair sample of seedlings throughout the family, observed the distribution of various anatomical and morphological characters, and drew interesting conclusions from these data. Although members of the Vicieae comprised only a small part of his survey, Compton gave this tribe special attention in his discussion on account of its several peculiar features; his findings relevant to the taxonomy of the group are now summarised.

Compton found that the distribution of protoxylem in epigeal and hypogeal seedlings is significantly different, reflecting the fact that homologous parts of the seedling grow at different relative rates in these two types. He stated that "in the vast majority of epigeal seedlings it is found that the primary vascular system of cotyledons, hypocotyl and root is complete in itself", and ".. plumular traces are represented in the hypocotyl by secondary xylem only".

In most species having epigeal germination the radicle is tetrarch, but within the family is seen a tendency towards reduction in the number of protoxylems of the seedling axis, through triarchy, to the diarch condition. This trend is correlated with decreasing seedling size. In tetrarch seedlings, two of the hypocotyl protoxylems enter the cotyledons, providing one main trace to each, while the other two protoxylems both dichotomise, supplying the cotyledonary petioles with two lateral traces. In triarch seedlings (found in the Trifolieae,

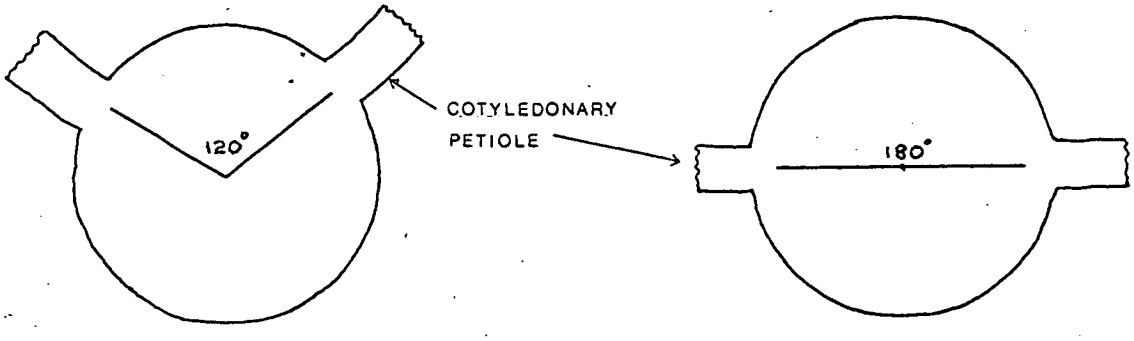
Galegeae, Hedysareae etc.), two of the hypocotyl protoxylems enter the cotyledons while the third either peters out or divides, each half entering one cotyledonary petiole. In the case of triarch seedlings, Compton found that the third (lateral) trace is directly beneath the first leaf of the epicotyl, and the primary xylem of the trace to this leaf is a continuation of metaxylem formed within the lateral trace of the radicle.

In contrast, hypogeal seedlings were found to have an open type of primary vascular system in which there is a direct connection between protoxylem elements in the root, hypocotyl and plumule.

As Compton emphasised, the Vicieae are characterised by a uniformly hypogeal type of germination, and apart from the tetrarch Vicia faba and Cicer arietinum, its members have triarch seedlings. He also described two new features which appeared to confirm the distinction between this tribe and its neighbours:

1. In the Vicieae, the cotyledons are inserted 120° apart on the seedling axis, while in the rest of the family they are opposite (see diagram below).

TRANSVERSE SECTION THROUGH SEEDLING AT COTYLEDONARY NODE



VICIEAE OTHER LEGUMINOSAE

2. In this tribe the first plumular leaf is inserted on the side of the seedling axis opposite to that on which it is borne in the other groups. In the Papilionoideae the embryo is typically bent in the seed (see Fig. 24); in the Vicieae the first leaf arises on the convex side, while in epigeal species it occurs on the concave side.

Compton considered that, on the grounds of these four characters, the Vicieae form a well-marked group within the family. However, his findings have not remained unchallenged.

Erith (1924) cast doubt upon the existence of a self-contained primary vascular system in seedlings of Trifolium repens. She found that here the lateral trace of the radicle continues up through the epicotyl to become the median leaf-trace of the first leaf, while the lateral traces to this leaf, as well as the median trace to the second leaf, can all be recognised in the top of the hypocotyl as procambial strands with one or two protoxylem vessels.

Muller (1937) pointed out that in the seedling of Cicer arietinum the cotyledons are opposed, rather than inserted at an angle of 120°. He also confirmed that the first leaf in this species occurs on the convex side of the seedling.

I have carried out a series of observations on the germinating seeds of Lens culinaris, Vicia sativa, Cicer pinnatifidum, Vicia faba and Trigonella foenum-graecum, in order to decide whether the position of the first leaf is indeed as constant as has been suggested by Compton and Muller. (Seeds of the

Key to Figure 25.

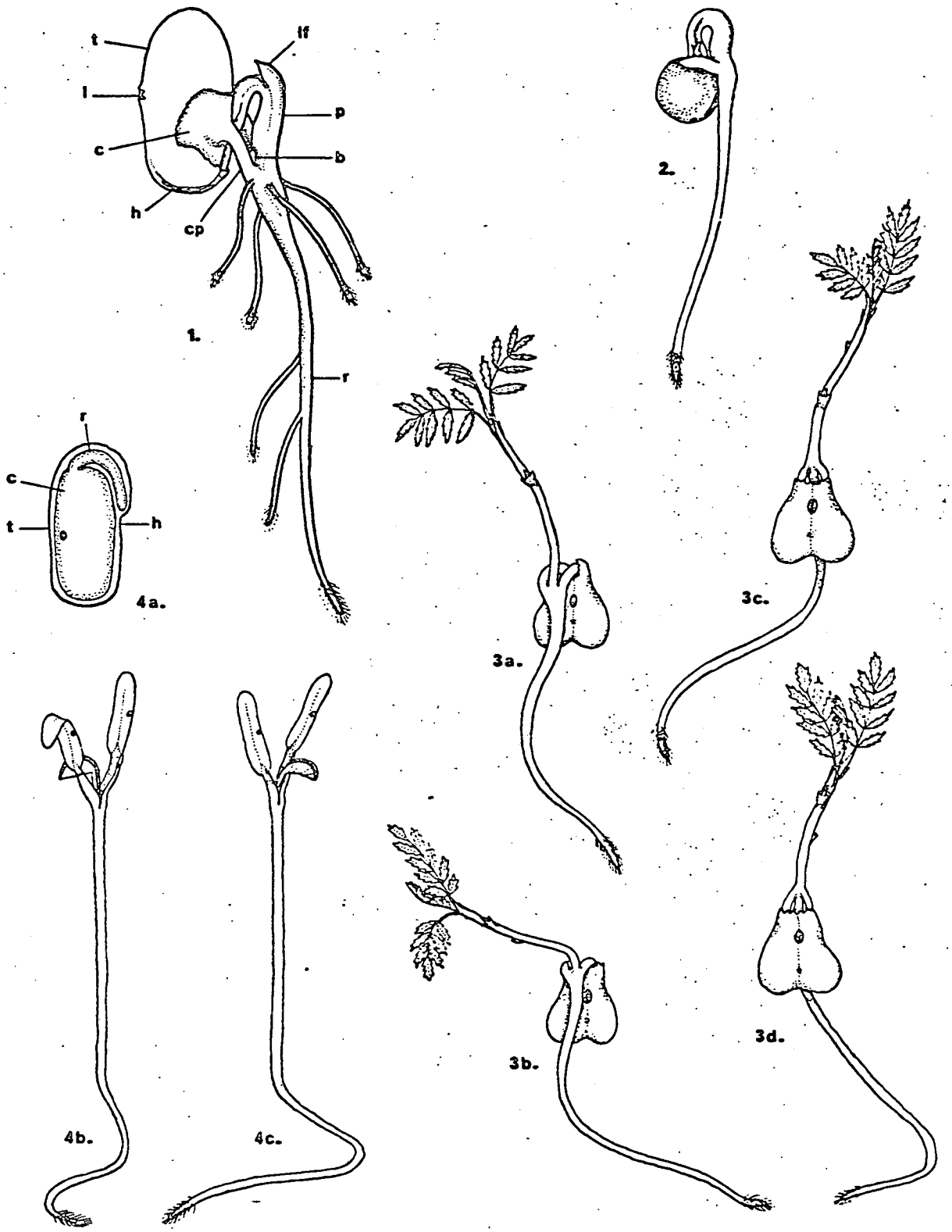
1. Vicia faba.
2. Lens culinaris.
3. Cicer pinnatifidum:
   a) radicle growing towards hilum, first leaf away from cotyledons;
   b) radicle growing towards hilum, first leaf towards cotyledons;
   c) radicle growing away from hilum, first leaf towards cotyledons;
   d) radicle growing away from hilum, first leaf away from cotyledons.

   (a) and c) are basically alike; so are b) and d).)
4. Trigonella foenum-graecum:
   a) Diagrammatic section through seed, with convex side of cotyledons marked with a spot; the cotyledons of the seedlings in b) and c) are marked correspondingly;
   b) first leaf towards 'concave' side of seedling;
   c) first leaf towards 'convex' side of seedling.

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t - testa
h - hilum
l - lens (described in part 4.5.5.)
c - cotyledon
cp - cotyledonary petiole
b - bud in axil of cp
r - radicle
p - plumule
lf - first leaf

Fig. 25. Seedlings of the Vicieae and Trifolieae.



first three species were obtained from Gatersleben Botanic Garden, those of V. faba were collected in Turkey, while those of Trigonella were bought as the spice fenugreek. The precise origin and variability of each sample were unknown.) The results are reported below and illustrated in Fig. 25.

Lens culinaris. Thirty-four seeds were germinated on wet tissue paper, and the first leaf was invariably found to be inserted on the convex side of the embryo (Fig. 25:2).

Vicia sativa. Each of the thirty seeds which germinated produced a seedling with the first leaf on the convex side of the embryo.

Cicer pinnatifidum. Eighteen seeds were germinated, and the results proved more complex than in the two previous species. In some of the seedlings the radicle grew down past the hilum, as expected (Fig. 25:3a & 3b) and the plumule emerged from between the cotyledons in the same manner as in Lens culinaris and Vicia sativa. In the other seedlings, the radicle turned back and grew away from the hilum, bringing the plumule out on the hilar face of the seed. It is important to recognise this difference, as it affects the relative positions of the first scale-leaf and the cotyledons. Some of the seedlings had the first leaf on the side of the plumule away from the cotyledons (3a & 3d) while in the rest it was borne on the same side as the cotyledons (3b & 3c). If these two variables (position of radicle and position of first leaf) are considered together with respect to the original arrangement of the embryo within

the seed, it becomes apparent that there are two types of seed in C. pinnatifidum: one has the first leaf on the convex side of the embryo, and germinates to give seedlings 3a and 3c; the other has the first leaf on the concave side of the embryo, and germinates to give seedlings 3b and 3d. The table below shows the proportion of each type of seedling in my sample of 18 seeds.

	RADICLE GROWS TOWARDS HILUM	RADICLE GROWS AWAY FROM HILUM
FIRST LEAF TOWARDS COTYLEDONS	Seedling 3b 4 seeds	Seedling 3c 3 seeds
FIRST LEAF AWAY FROM COTYLEDONS	Seedling 3a 8 seeds	Seedling 3d 3 seeds

Vicia faba. To determine whether it is possible to produce variations in the direction of radicle growth in Vicia, similar to those just described in Cicer, a large glass beaker was lined with blotting-paper and filled with sand; ten seeds of Vicia faba were placed firmly between the glass and paper. All were held in a vertical position, but in half the radicle pointed up, in the others it faced downwards. The seeds were allowed to germinate in darkness, so that effects of phototropism should not interfere with the experiment. It was found that in all ten seedlings the plumule emerged on the side away from the hilum (Fig.25:1), even though in the seeds which had been held with the radicle upwards this involved considerable distortion of the germinating seed.

It is concluded that the variable direction of growth of radicle and emergence of plumule in Cicer is a significant feature which distinguishes this genus from the rest of the Vicieae. (I observed this variation by chance in Cicer arietinum, as well as in the planned germination of C. pinnatifidum seeds.)

Trigonella foenum-graecum. In hypogeal seedlings the cotyledons are imprisoned laterally by the testa and this gives the seedling an asymmetry which reflects the organisation of the embryo before germination; but once the testa has been shed from the cotyledons of an epigeal seedling there is usually no way of telling its orientation. For this reason, the convex side of the cotyledons emerging from germination Trigonella seeds were marked with indian ink (Fig. 25:4a). A few days

after the testa had dropped off, the first leaf appeared between the cotyledons; it was found that of 17 seedlings, 11 had this leaf on the concave side while the rest bore it on the convex side (Fig. 25:4b and 4c, respectively).

From these simple experiments, the following points may be concluded:

1. Members of Lens and Vicia (and presumably also Lathyrus and Pisum) are characterised by a constant insertion of the first plumular leaf on the convex side of the seedling. This is correlated with the fact that the cotyledons are borne 120° apart on the seedling axis.
2. The genus Cicer differs from the rest of the Vicieae in that the position of the first scale-leaf is variable. This is correlated with the insertion of the cotyledons on opposite sides of the seedling axis.
3. Cicer is unusual in that the radicle of the germinating seed may grow either towards the hilum or away from it, and this also involves a difference in the way the plumule emerges from between the cotyledons. In this context it may be relevant to note that the seeds of Cicer are distinguished by their very short radicles (see part 4.5.2. and Fig. 24:3C); Corner (1951) has even described them as 'mimosoid' (i.e. with a straight radicle in line with the main axis of the cotyledons). Although this is not strictly true, it may be that since the radicle emerges almost vertically through the apex of the seed, its subsequent

growth is not constrained and directed by the testa to the same extent as in seeds with strongly curved radicles (see Fig. 24:1C & 4C).

4. I have examined the germination of seeds of only one species outside the Vicieae, viz. Trigonella foenum-graecum (in the Trifolieae). In this species the first leaf was found to be variable in position, not constantly on the concave side of the seedling, as stated by Compton. It would be interesting to extend these observations to further species. One would also like to know whether the position of the first leaf is genetically determined.

5.2.2.

THE TRANSITION REGION

Seedlings of the genera Vicia, Lathyrus, Lens and Pisum have received particular attention from anatomists (Compton, 1912; Gourley, 1931; Muller, 1937, etc.) because of the existence of an unusually prolonged transition region between root and stem which is located in the epicotyl up to the level of the third or fourth node. Within these lowest nodes of the stem the pith is usually obliterated, the centre of the stem containing a solid core of exarch xylem. The trace to the first leaf is the first to become distinct and endarch; that to the second leaf, on the opposite side of the stele, is next, becoming separate and endarch within the second internode. Between these poles are two lateral arcs of metaxylem, with exarch protoxylem located at each end of each arc. By the third node,

however, rearrangements have occurred within the stele so that these lateral bands have each divided into two distinct endarch bundles and the stem is medullated; it now has atypically cauline structure. In Cicer, in contrast, the transition region occurs within the hypocotyl and there is neither a solid core of xylem nor any exarch protoxylem in the epicotyl.

5.2.3.

THE ORIGIN OF THE CORTICAL VASCULAR BUNDLES

Vicia, Lathyrus, Lens, Pisum and Vavilovia are also distinctive in possessing cortical bundles in the stem. These have been studied by numerous botanists, for example van Tieghem (1884), Muller (1937) and Vescovi (1958). Muller described how, as the two cotyledonary traces pass out to the seed leaves, a small bundle is separated off from the edge of each cotyledonary leaf-gap on the side nearest to the third (plumular) trace. These two bundles remain in the cortex in the plant at right angles to the leaves and supply traces to the stipules and leaves at each node.

5.2.4.

THE THREE CORTICAL BUNDLE REPLACEMENT TYPES IN THE SEEDLING

At the first cauline node (where the first leaf is inserted), the plumular trace moves out and enters the scale-leaf as the main trace. Each of the cortical bundles divides in two; one half continues vertically in the stem, while the other moves horizontally round towards the scale. Thus the scale receives

* At the second node the cortical bundles again both divide, half of each moving round to enter the scale while the remaining strands continue vertically in the cortex; the latter are each soon augmented by a small bundle emitted from the main stele (Fig. 26:B).

two small lateral bundles as well as a main median one (Fig. 26:A). *

At the third node (by which time a true leaf with leaflets may have appeared) both cortical bundles move round in their entirety, supplying first the stipules and then entering the petiole. They are replaced by new bundles given off by the main stele (Fig. 26:C).

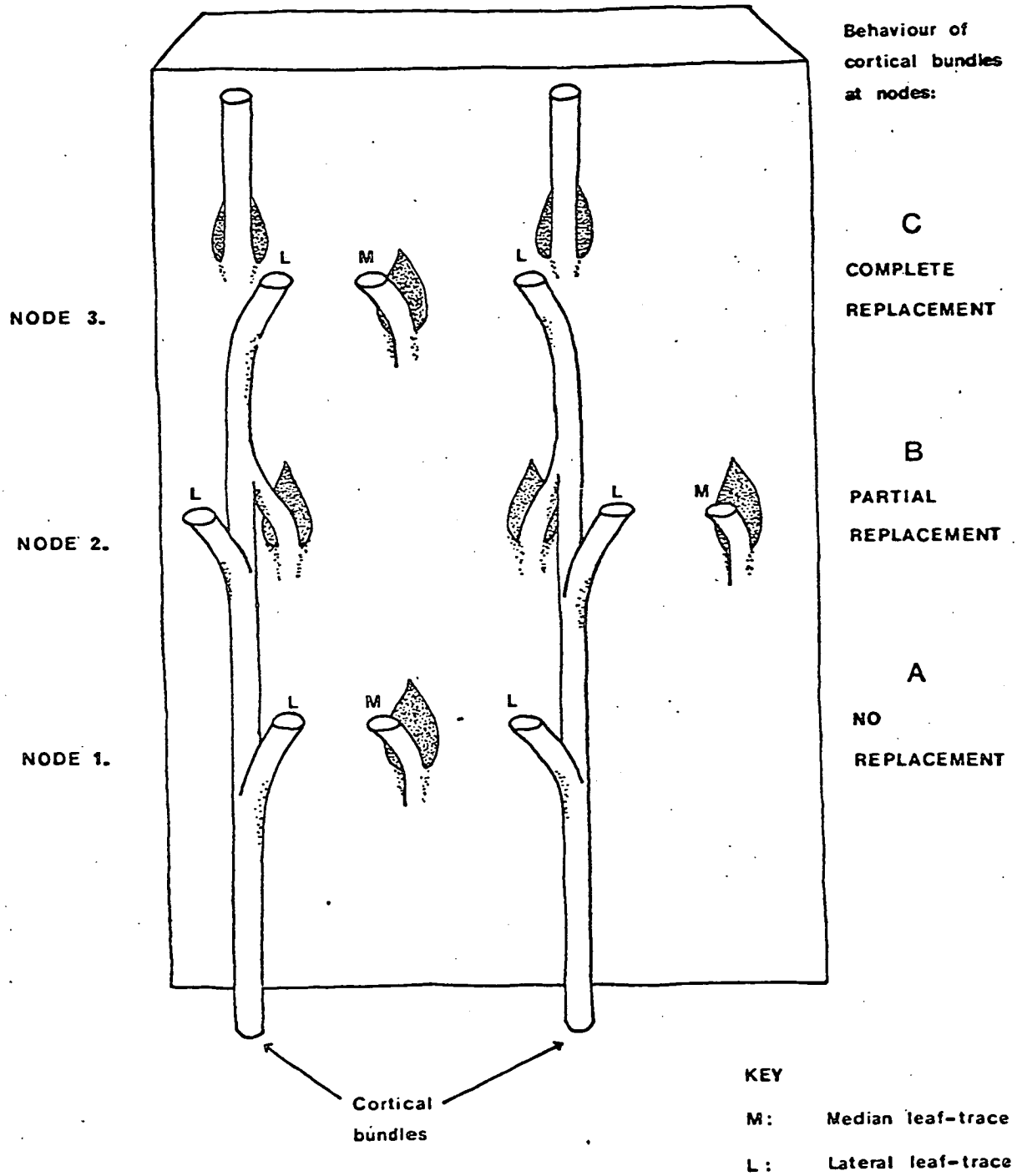
Muller named these three nodal types, respectively, 'no replacement', 'partial replacement' and 'complete replacement' (of the cortical bundles). By his own survey, and those of other anatomists who had studied the Vicieae, he concluded that although the exact pattern in individual plants or species might differ, the third type - 'complete replacement' - is typical of the mature plant in all species.

Muller noted that in the Vicieae (with the exception of Cicer) several features always occur together:

1. The first few nodes bear trifid scale-leaves, and the mature leaf-form is not attained until after many nodes.
2. The primary shoot stops growing while still quite short, and the main bulk of the plant develops from secondary stems arising from buds in the axils of the scale-leaves.
3. The stem, at these lowest levels, contains a central core of exarch xylem which is anomalous within the Leguminosae and among the Dicotyledons in general.
4. The stem contains cortical bundles which have a modified type of replacement-behaviour at the lowest nodes.

He postulated that points 3 and 4 are connected, in that

Fig. 26. Diagrammatic representation of the cauline vascular system of seedlings in members of the Vicieae with cortical bundles.



The main stele is shown solid and opened out flat; leaf-gaps are stippled.

the 'no replacement' type of node obviates the necessity of disturbing the central stele, which at this point (especially in the plane at right angles to the leaves) is more root-like than cauline. He agreed with Compton (1912) that the root-like structure of the young epicotyl is a functional adaptation enabling this region to bend, in relation to the climbing habit characteristic of the Vicieae. This hypothesis is supported by the fact that in Vicia faba (which is unusual in having a primary shoot of unlimited growth, leaves without tendrils and a stem which does not proliferate at the base) the transition region in the epicotyl is medullated.

In contrast to the other genera of the Vicieae, Cicer has no cortical bundles in the stem. This fact was thought by early taxonomists (Van Tieghem, 1884; Hérail, 1885) to be of such significance that they suggested Cicer should be excluded from the tribe; but although mentioned in more recent literature (e.g. Dormer, 1946a), it has not been taken into account by any of the taxonomists who have dealt with Cicer.

5.3.
THE CORTICAL BUNDLES IN THE MATURE PLANT

5.3.1.
SPECIES WITH WINGED STEMS

Members of the Vicieae typically have angular stems which are rhomboidal in section; the leaves are distichous and inserted alternately in the plane joining two of the angles. In Vicia, Lathyrus, Lens, Pisum and Vavilovia the other two angles

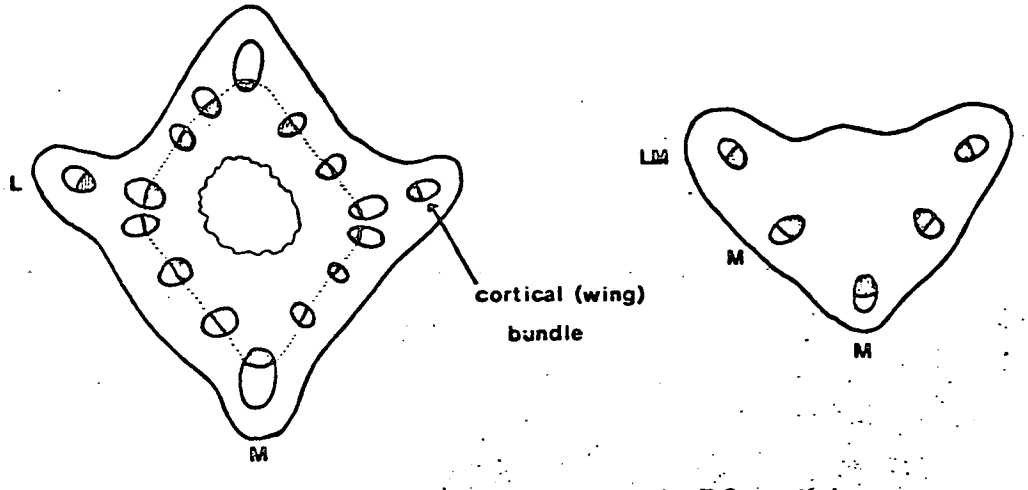
contain cortical bundles which are renewed at every node, run up through one internode and then become the lateral traces to the leaf inserted here. In Cicer, however, the 'wing' angles of the stem are not vasculated and the lateral leaf traces are given off from the central stele at the node of the leaf which they supply. These facts are illustrated in Figs. 27, 28 and 29, which show sections and three-dimensional reconstructions of the stems of Vicia faba and Cicer arietinum.

Many species of Lathyrus, particularly those in Sects. Lathyrus and Clymenum, and some representatives from S. America, have strongly developed, leafy wings which must contribute considerably to the photosynthetic area of the plant. The wings of the stem are continuous into the petiole of the leaf above, and in some species, e.g. L. ochrus (Fig. 9:C) and L. nissolia, the leaves themselves are almost or entirely phyllodic. L. clymenum, a typical example of a species with broadly winged stems, is illustrated in Fig. 30. The wings contain several bundles which coalesce at the top of the internode before taking part in the usual rearrangements associated with the change from stem to leaf (see part 5.3.2.).

L. roseus is morphologically unusual within the genus in having terete stems. However, in transverse section its stem shows the typical arrangement with a pair of cortical bundles separate from the main stele. This indicates that the absence of angles on the stem in this species should not be given undue taxonomic (or phylogenetic) weight.

Fig. 27. Diagram showing arrangement of vascular bundles in stem and peticle in members of the Vicieae.

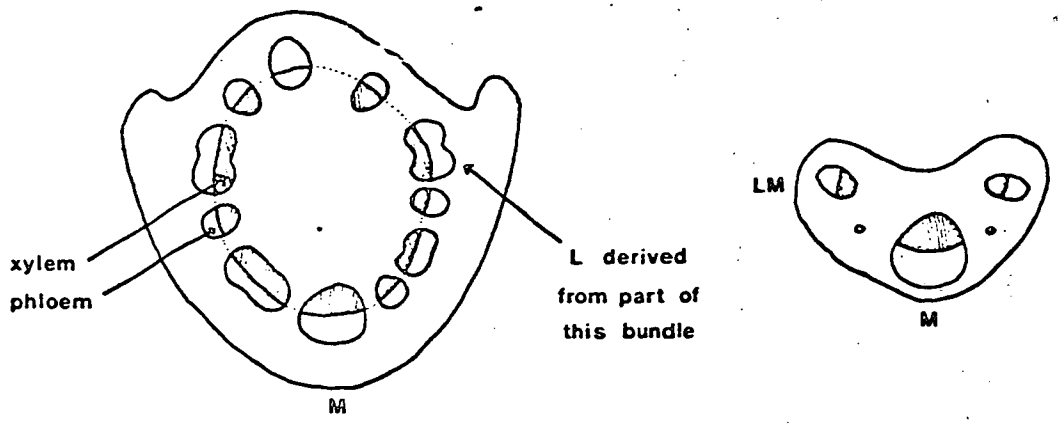
1. Vicia faba



a) T.S. stem internode

b) T.S. petiole

2. Cicer arietinum

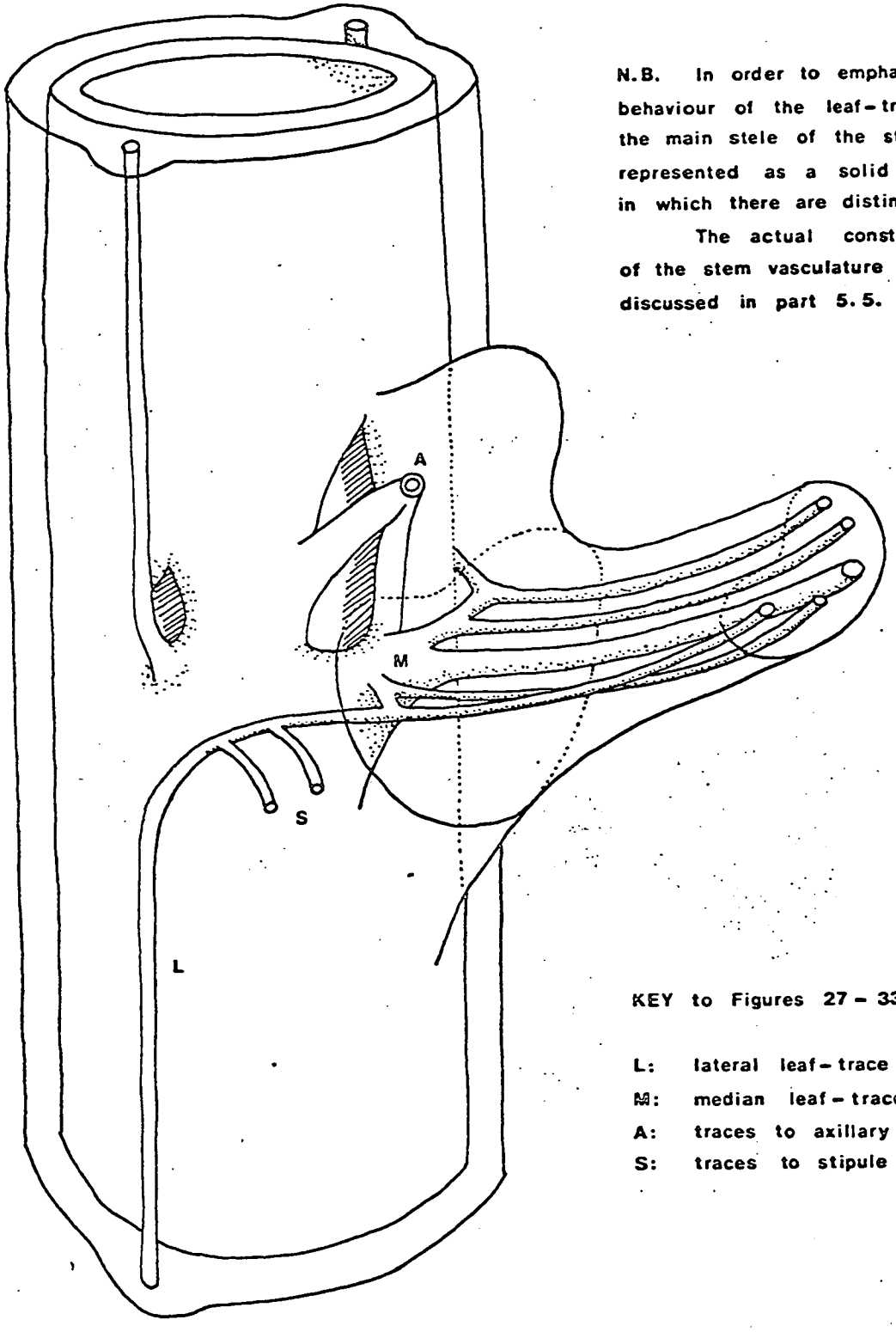


a) T.S. stem internode

b) T.S. petiole

For key, see Fig. 28.

Fig. 28. Three-dimensional reconstruction of the vascular anatomy of Vicia faba, showing supply to stipules and petiole.



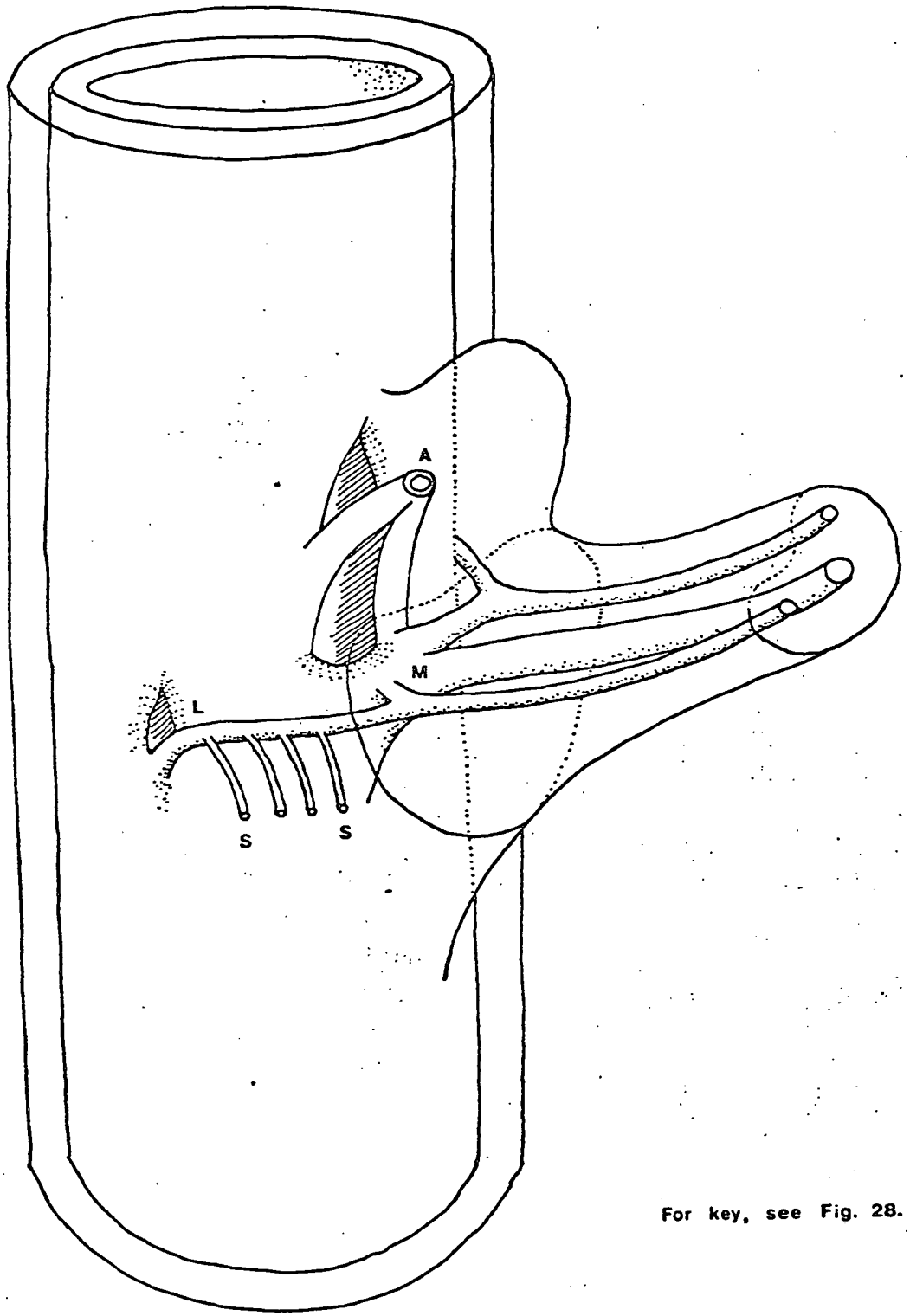
N.B. In order to emphasise the behaviour of the leaf-traces, the main stele of the stem is represented as a solid cylinder in which there are distinct gaps.

The actual construction of the stem vasculature is discussed in part 5.5.

KEY to Figures 27 - 33

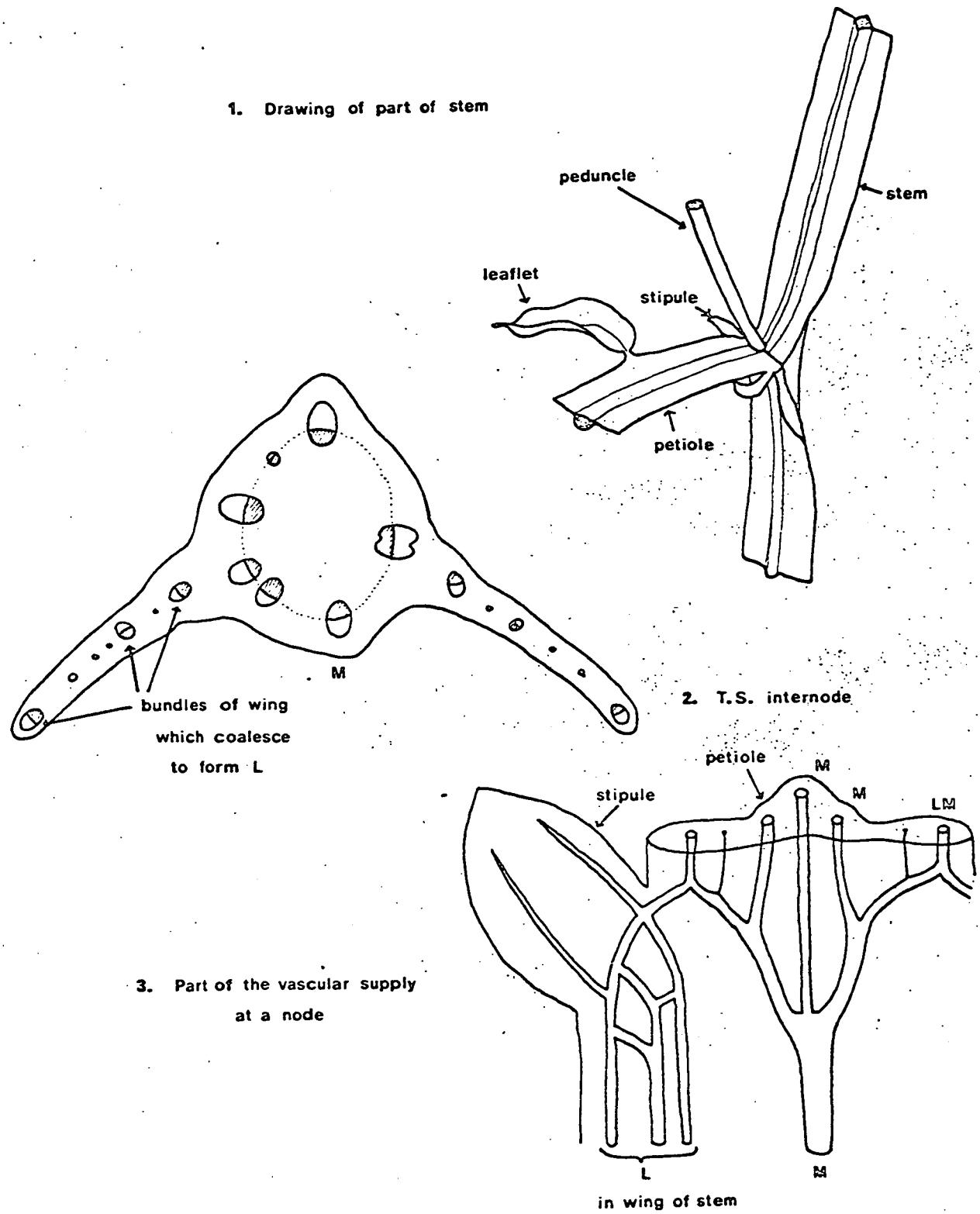
L: lateral leaf-trace
M: median leaf-trace
A: traces to axillary bud
S: traces to stipule

Fig. 29. The nodal anatomy of Cicer arietinum.



For key, see Fig. 28.

Fig. 30. Lathyrus clymenum: a species with broadly winged stems.



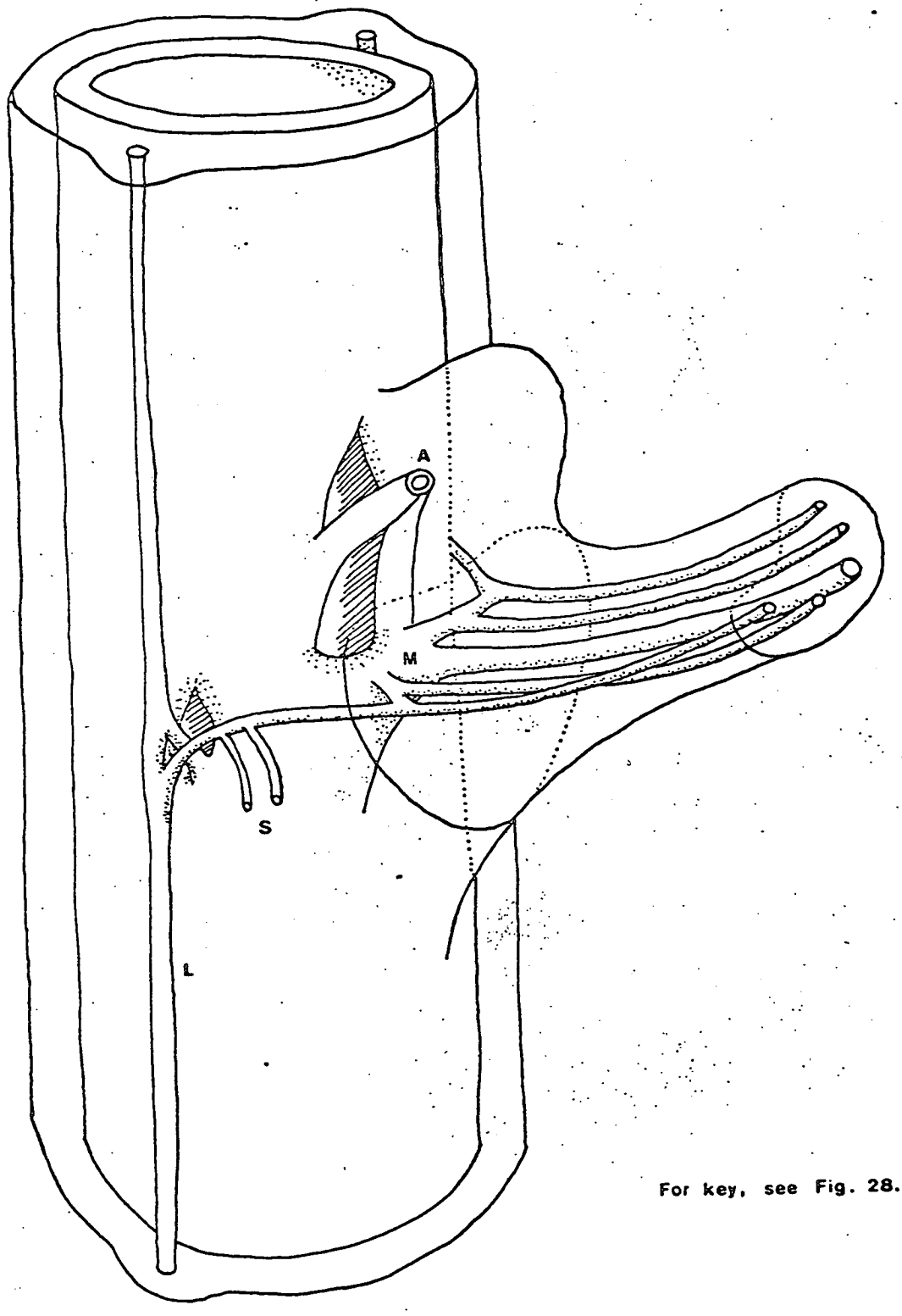
5.3.2.

THE REPLACEMENT OF CORTICAL BUNDLES AT NODES

As was mentioned in part 5.2.4., Muller (1937) concluded that the replacement behaviour of the cortical bundles is of the same type in the mature plant of all species of the Vicieae, viz. type C (Fig. 26). Van Tieghem (1884) stated that Vicia sepium and Lathyrus sylvestris are characterised by type B ('partial replacement'), and that Lathyrus odoratus and Vicia sativa have type A ('no replacement'); but Muller denied this and I confirm that these species have the usual 'complete replacement' type.

The species whose nodal anatomy I have investigated are listed in Table 15. Among them I found a group of members of Vicia Sect. Vicia which consistently have 'partial replacement' of cortical bundles. None of the species concerned had been studied before, which accounts for Muller's claim of uniformity of nodal type throughout the tribe (excluding Cicer). It is most interesting that this group, comprising V. lutea, V. pannonica etc., was once recognised as a separate genus - Hypechusa Alefeld - and is characterised by having seeds in which the lens is on the side opposite the hilum (see part 4.5.5. and Fig. 24:2). The 'partial replacement' type of node may be regarded as a neotenic character when it occurs in the mature plant, since it is represented at the youngest nodes of all species but superceded, in the great majority, by the 'complete replacement' type. A three-dimensional representation of the node of Vicia pannonica is shown in Fig. 31.

Fig. 31. The nodal anatomy of Vicia pannonica, showing partial replacement of cortical bundles.



For key, see Fig. 28.

Table 15. List of species in which nodal anatomy has been examined.

SPECIES WITH CORTICAL BUNDLES

'COMPLETE REPLACEMENT'

Vicia unijuga
V. amurensis
V. dumetorum
V. sylvatica
V. biennis
V. orobus
V. truncatula
V. cracca
V. neglecta
V. villosa
V. benghalensis
V. disperma
V. ervilia
V. sepium
V. grandiflora
V. sativa
V. cuspidata
V. peregrina
V. michauxii
V. aintabensis
V. bithynica
V. faba

Lens culinaris

Lathyrus japonicus
L. ochrus
L. clymenum
L. roseus
L. tingitanus
L. hirsutus
L. nissolia
L. sphaericus
L. pratensis
L. aphaca
L. pusillus
L. hookeri
L. americanus

Pisum sativum

Vavilovia formosa

'PARTIAL REPLACEMENT'

Vicia anatolica
V. assyriaca
V. galeata
V. hybrida
V. hyrcanica
V. lutea
V. melanops
V. noeana
V. pannonica
V. sericocarpa

SPECIES WITHOUT CORTICAL BUNDLES

Cicer arietinum
C. chorassanicum
C. oxyodon
C. pinnatifidum

Ononis pusilla
O. arvensis
O. repens
O. rotundifolia

5.4.
VASCULAR SUPPLY TO LEAVES

5.4.1.
SPECIES WITH CORTICAL BUNDLES

Usual pattern of vasculature. The fate of the three bundles supplying the leaf was described by Watari (1934) for several members of the Vicieae. According to this author, the two cortical bundles move round almost horizontally in the cortex at the top of the internode, each giving off one, two or more branches to the stipule before entering the leaf-base as a lateral leaf-trace. Meanwhile the median leaf-trace has divided into three, of which the middle branch becomes the lowest (abaxial) bundle of the petiole. Each lateral branch is met by a strand from the lateral leaf-trace; they fuse and continue in the petiole as a composite bundle. The petiole thus contains five main bundles arranged in an arc; the upper pair are derived entirely from the lateral leaf-traces, the lowermost one is from the median leaf-trace, and the pair between them is composite (Fig. 32:1). This type of nodal anatomy, with minor modifications, was recorded by Watari in the following species: Vicia unijuga, V. nipponica, V. sativa, V. hirsuta, V. tetrasperma, V. faba, Lathyrus vernus, L. japonicus, L. davidii and Pisum sativum.

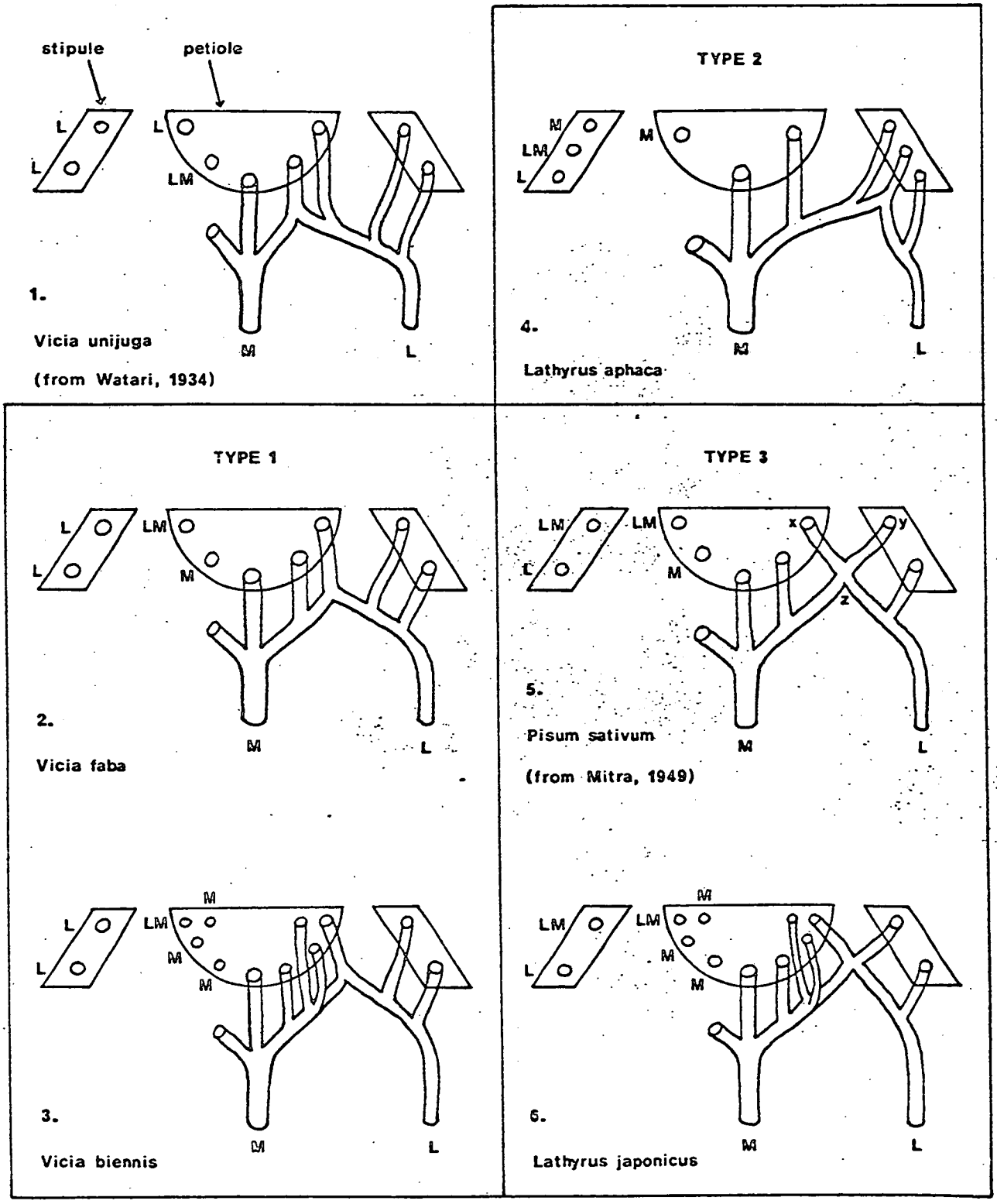
The results of my own investigations into some 40 species do not agree with Watari's interpretation of the nodal anatomy of the Vicieae. Rather, I found that the supply to the leaf in

most species takes place as follows. At the top of the internode the 'wing' bundles move round in the cortex, supplying the stipules and then entering the leaf-base. The median leaf-trace divides into three as it leaves the main stele and passes out to the leaf. Each lateral branch of this median trace then divides again, and the outermost bundle fuses with the incoming lateral leaf-trace. Thus of the five bundles in the petiole, the lower three are entirely median in derivation while the uppermost pair are composite. This is shown in Fig. 32:2 and in the three-dimensional diagram of Vicia faba (Fig. 28).

This description gives a generalised picture of the vascular anatomy of the node. In most species the arc of bundles in the petiole contains additional minor traces derived from the neighbouring major ones. A common pattern, found in species with stouter stems (e.g. V.biennis, V. dumetorum), is produced as follows: instead of fusing directly with the lateral leaf-trace, the branch of the median trace divides into three. The uppermost strand of this trio vasculates the upper (adaxial) side of the petiole, the lowermost remains in the main arc of petiole bundles and the middle one joins with the lateral leaf-trace to form the composite bundle (Fig. 32:3).

Pisum sativum. The nodal anatomy of Pisum sativum was investigated in detail by Mitra (1949), with the aim of elucidating the nature of its foliaceous stipules. His results confirm the basic pattern which I found in most members of the Vicieae, rather than that of Watari. However, according to Mitra, in

Fig. 32. Diagrams illustrating variations in the vascular supply to leaves in members of the Vicieae with cortical bundles.



this species the stipules as well as the petiole receive a composite bundle. In other words, the median leaf-trace contributes to the stipular supply. Fig. 32:5 shows the interpretation of this author. I think he is very probably correct, although it is extremely difficult to ascertain the composition of bundles 'x' and 'y' after the brief fusion which takes place between the median and lateral trace branches at 'z'.

Species with sagittate or hastate stipules. Vescovi (1958), who studied the nodal anatomy of Lathyrus aphaca, found that both the petioles in the true leaves of the seedling and the tendrils at later nodes are supplied entirely from the median trace, while the stipules receive the lateral leaf-traces plus some elements from the median one. My own investigations of matures nodes of this species confirm his observations (Fig. 32:4). Besides its anomalous ontogenetic behaviour, involving the reduction of the leaf to a simple tendril (illustrated by leaf-silhouettes in Fig. 9:A), L. aphaca is also unusual within the tribe in having hastate, rather than semi-sagittate, stipules. The only other species with this character are the members of Lathyrus Sect. Pratensis, L. japonicus, L. pisiformis and some species of Lathyrus from S. America.

I studied both L. pratensis and L. laxiflorus (Sect. Pratensis), and found that the nodal anatomy in these species is the same as in L. aphaca. In L. japonicus, the early nodes (i.e. those produced in the first season) bear semi-sagittate stipules, and the leaf-supply is of the normal type. At later

nodes, however, hastate stipules occur and the anatomy becomes rather more complicated; the behaviour of the traces is shown in Fig. 32:6. The petiole in section resembles that of Vicia biennis (Fig. 32:3), but the origin of the bundles on the petiole and stipules seems to be as in Pisum sativum (Fig. 32:5), although again it is difficult to be certain about the entry of median-trace elements into the stipules. Of the S. American members of Lathyrus with hastate stipules, I found that L. pusillus has the same type of nodal anatomy as L. aphaca, while L. americanus and L. hookeri resemble L. japonicus in this respect.

Summary. My investigations, and those of other authors, seem to show that there are three kinds of leaf-trace behaviour at the node, in members of the Vicieae with cortical bundles. These are:

1. The petiole is supplied by median and lateral traces, the stipules by lateral traces. This is by far the most common pattern; it is illustrated by V. faba and V. biennis, Fig. 32:2 & :3.
2. The petiole (or tendril) is supplied by the median trace, the stipules by median and lateral traces. Found in L. aphaca, L. pratensis, L. laxiflorus and L. pusillus, and illustrated in Fig. 32:4.
3. Both petiole and stipules are supplied by both median and lateral traces. Found in L. japonicus, L. hookeri, L. americanus and Pisum sativum; see Fig. 32:5 & :6.

It is most interesting to find that species in which the

median leaf-trace contributes to the stipular supply have strikingly large and usually sagittate or hastate stipules. On the evidence of morphological characters, these species are not all closely related; it seems reasonable, therefore, to postulate that variation in anatomy has occurred several times in the evolution of the group, and that the establishment of the new pattern has been accompanied in each case by an increase in the importance of the stipule as a photosynthetic organ. This hypothesis would account for the prominent foliaceous stipules of Pisum. The related genus Vavilovia, which has the normal kind of anatomy (type 1), has small, semisagittate stipules.

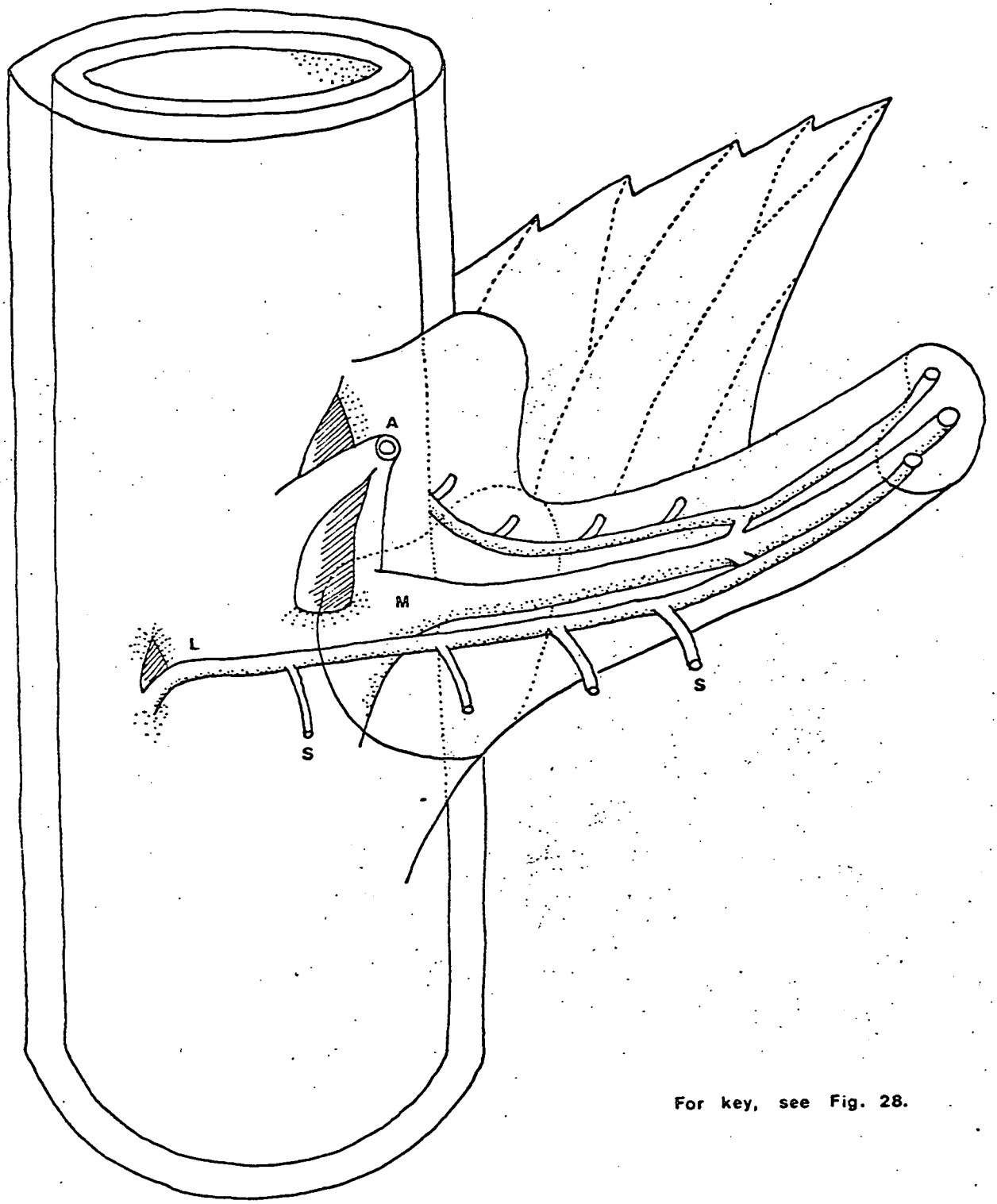
Nodal pattern type 2 is the most extreme variant, and one could say that from the vascular point of view, the stipules and leaf are here reversed in importance, compared with type 1. Viewed in this light, it is easy to envisage how Lathyrus aphaca may have arisen; the reduction of the leaf to a mere tendril, and the enlarging of the stipules, are simply the morphological expressions of its nodal anatomy which provides the stipules with a relatively strong conducting system to the detriment of the rest of the leaf. It is interesting that the same type of pattern occurs in Sect. Pratensis, whose members also have hastate stipules; it is possible that there is some taxonomic relationship between these two European groups.

5.4.2.

SPECIES WITHOUT CORTICAL BUNDLES

The behaviour of the leaf-traces in Cicer arietinum is

Fig. 33. The nodal anatomy of Ononis repens.



For key, see Fig. 28.

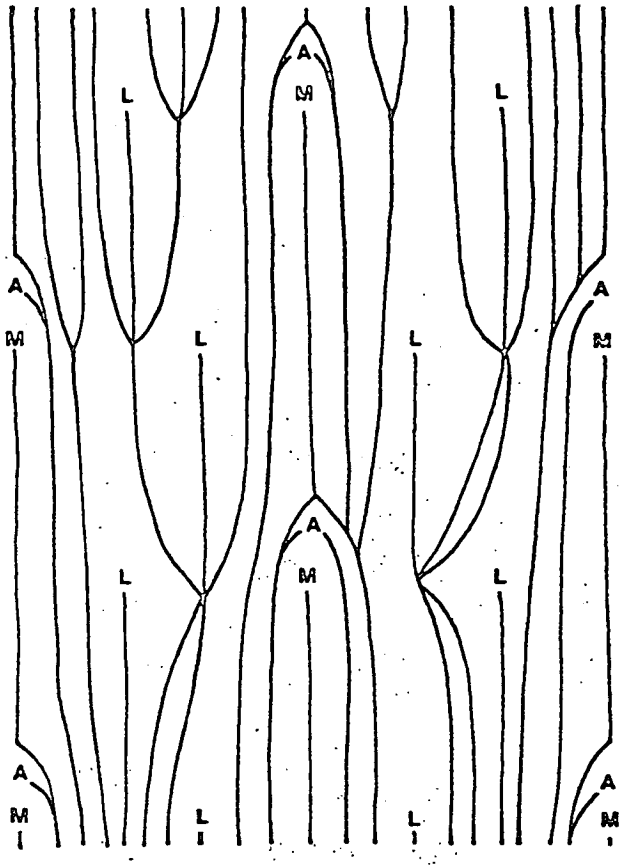
illustrated in Fig. 29. As the diagram shows, all three bundles leave the central stele at the same level. The median trace divides into three, of which the middle branch becomes the abaxial bundle of the petiole while the other two each fuse with a lateral trace to form a pair of composite bundles (see also Fig. 27:2b). Apart from the origin of the lateral traces, therefore, the nodal anatomy of Cicer is similar to that in most other members of the Vicieae.

In the neighbouring tribe Trifolieae, and in Ononis, the stipules are fused to the petiole for some distance. It was found that here the leaf traces behave as in Cicer (i.e. the free petiole contains three main bundles of composition LM : M : ML), but that their mutual rearrangement is delayed until the point at which the stipules leave the petiole (Fig. 33). Proximal to this point the lateral traces run parallel to the main trace, giving branches to the stipules. This pattern was described by Winter (1932) in Medicago sativa.

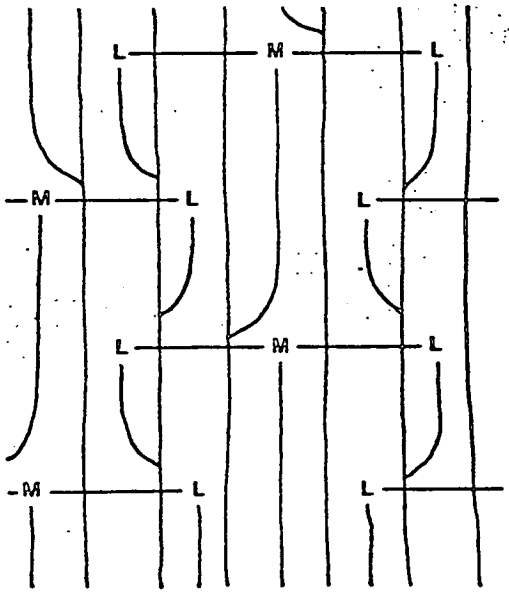
5.5.
PRIMARY CAULINE VASCULAR SYSTEMS

A survey of the patterns of vascular anatomy in the Leguminosae was made by Dormer (1946a) who showed that this rather neglected field of study provides useful taxonomic information. He also put forward some interesting suggestions concerning the evolution of systems of phyllotaxy and vasculature in relation to woody and herbaceous habits. Before discussing these ideas and my own investigations, a brief summary must be made of some

Fig. 34. Patterns of stem vasculature in the Vicieae.



1. Vicia villosa
diagram showing all bundles in the stem



2. Vicia hirsuta (simplified diagram)
insertions interlocked
no anastomoses between stem bundles

KEY
M: Median leaf-trace
L: Lateral leaf-trace
A: Traces to axillary bud

aspects of vascular anatomy.

The courses which the primary vascular bundles take through the stem form a pattern which may be represented exactly, as in Fig. 34:1, or more schematically, as in Fig. 34:2. These two diagrams show the stele cut down one side and opened out flat (in Fig. 34:1 the outermost bundles are represented twice); they belong to the same type of system. Four other types are illustrated in Fig. 35. The systems are analysed by examining serial transverse sections of stem, following individual traces through several nodes.

Most specimens which I examined were found to have considerable variation from node to node; for example, the median leaf-trace (M) sometimes had a dual origin while at other nodes it arose unilaterally. The peduncle and/or axillary bud traces (A), which are shown only in Fig. 34:1, also varied in direction of origin and in composition.

Since there is such plasticity, only the most constant and therefore most fundamental aspects of the systems can be compared. These may be considered to comprise three main characters: phyllotaxy, leaf insertion type, and presence or absence of anastomosing between stem bundles.

1. Phyllotaxy. There is considerable variation in phyllotaxy in the Leguminosae. All members of the Vicieae have alternate and distichous leaves; so too have the genera Trifolium, Medicago and parts of Ononis and Trigonella. In the rest of Ononis and Trigonella and in Melilotus the leaves are spirally arranged. The Genisteae are characterised by spiral phyllotaxy

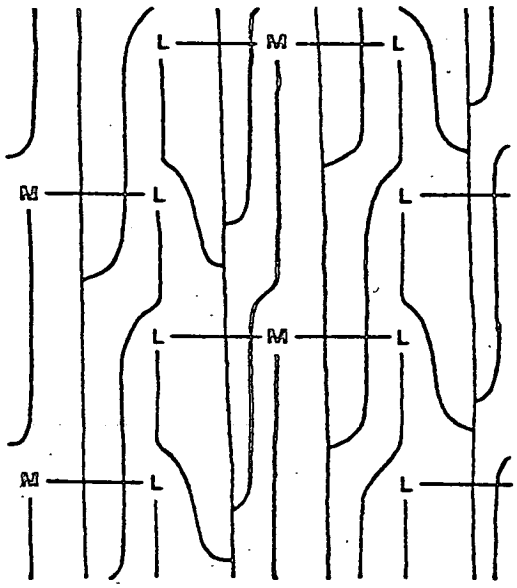
- (Gibbs, 1966).

2. Leaf insertion type. The leaves of the Leguminosae are characteristically supplied by three traces, as is usual in stipulate families (Bailey & Sinnott, 1914). There are three ways in which the traces to successive leaves may be arranged, relative to each other; this is illustrated most easily in stems with distichous phyllotaxy, as in Fig. 35. The lateral traces may be in contact, as in Ononis repens; separated by one or more stem bundles, as in Cicer arietinum; or interlocked, as in Trifolium repens. As will be described later, Dormer does not place much importance on this aspect of the vascular system; but he suggests that opposite and verticillate phyllotaxies may have developed within systems with the separated type of insertion (Dormer 1946b).

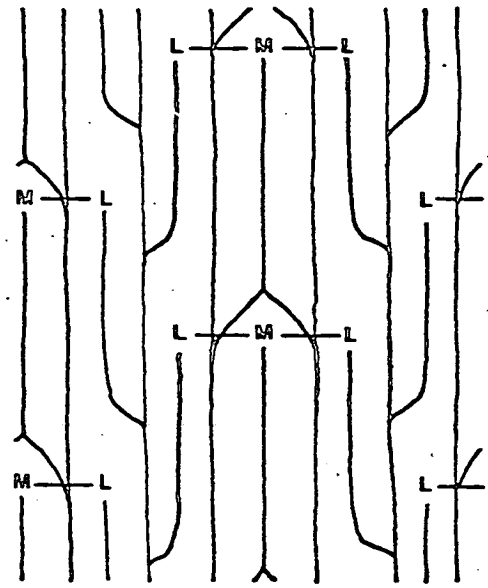
3. Anastomosing between stem bundles. The vascular system of a stem, as is emphasised by the simplified diagrams, consists of indefinitely prolonged stem bundles which supply traces to leaves and lateral branches. It has become customary to speak of the 'gap' left in the primary stele by a departing trace (e.g. Sinnott, 1914); but in perhaps the majority of Angiosperms the stem bundles do not fuse with one another in their courses, so that the gap is not closed. Fig. 35:1, 2 & 3 illustrates different kinds of system without anastomoses; Fig. 35:4 shows one in which these fusions are present. This character is discussed further below.

As a result of his investigations, Dormer (1945) concluded that the primitive system of primary vasculature in the Legum-

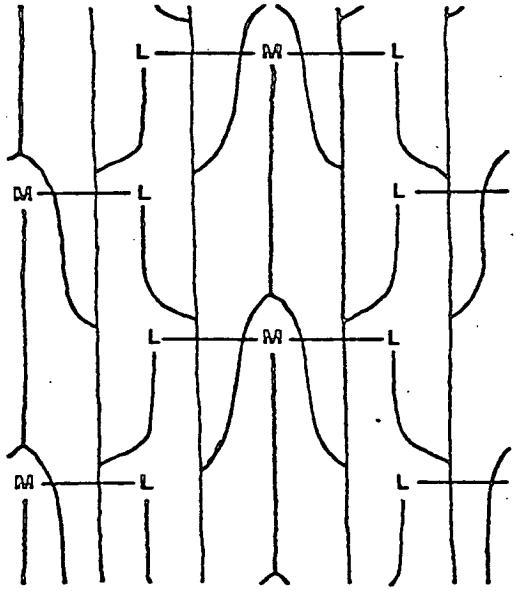
Fig. 35. Patterns of stem vasculature in Ononis, Cicer, Trifolium and Medicago.



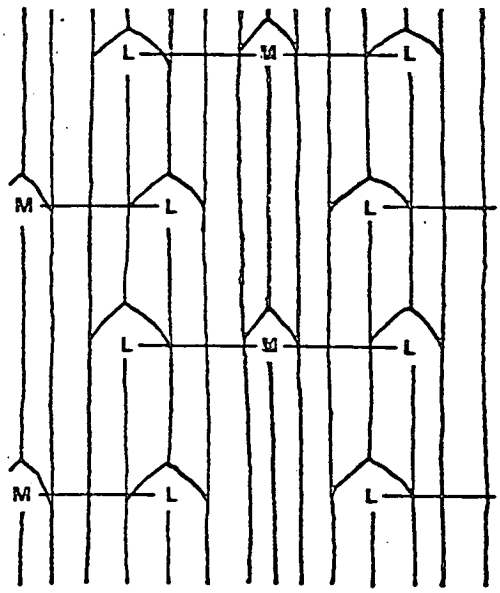
1. Ononis repens
insertions in contact
no anastomoses



2. Cicer arietinum
insertions separated
no anastomoses



3. Trifolium repens
insertions interlocked
no anastomoses



4. Medicago sativa
insertions interlocked
stem bundles anastomose

inosae, which he called the 'acacian' type, has the following characteristics:

1. spiral phyllotaxy;
2. absence of any anastomoses in the vascular system of the stem;
3. inclusion of a single stem bundle only between the median trace and each lateral;
4. the insertions of successive leaves are in contact.

Dormer considered the most significant character in the 'acacian' syndrome to be the lack of anastomoses between stem bundles. This type of anatomy was found by him only in woody plants and in annuals in which the primary bundles are connected early on by inter-fascicular conducting tissue, and he proposed that this is due to the inherent inefficiency of a stele divided into isolated parts. Truly herbaceous plants, those without secondary wood or in which this develops very late, he found to have primary systems which are 'closed' by anastomoses between adjacent stem bundles.

As far as the type of leaf-insertion is concerned, Dormer concluded that this may be taxonomically useful; but as it is not in general correlated with the presence or absence of anastomoses between the stem bundles, it is probably not of such fundamental phylogenetic importance.

In support of this theory, Dormer found that typically herbaceous groups like the Vicieae and Trifolieae had closed systems for the most part, while 'woody' exceptions, e.g. Ononis fruticosa, had the 'acacian' type of anatomy. He states

that the leaf-insertions of the Vicieae are in contact, while those of the Trifolieae are characteristically interlocked.

Having examined a number of species in the Vicieae and Trifolieae, I have come to rather different conclusions; and since Dormer has not supported his statements by either enumerating the species which he investigated or giving diagrams, it is impossible to know on what evidence he based them.

Table 16 shows the species which I have studied and their vascular characteristics. With the exception of Medicago sativa, the systems in every case are basically open, with occasional anastomoses in some species (e.g. Vicia villosa, Cicer anatolicum); Fig. 35 expresses some of the different kinds of anatomical pattern which were found.

Of the species with alternate, distichous phyllotaxy (i.e. the Vicieae and most of the Trifolieae), members of Cicer have insertions in contact or separated; members of Ononis have insertions in contact; and the remaining groups have interlocking insertions. In species with spiral phyllotaxy, the insertions of successive leaves are interlocked on one side and in contact or separated on the other side (except members of Ononis, which are 'acacian'). I agree with Erith (1924) in her description of the anatomy of Trifolium repens; with Dormer on Ononis; and with Winter (1932) and Dormer (1946b) on Medicago sativa.

Dormer used Medicago sativa as an example of a typical herb with its vascular system closed into a single unit by anastomoses between stem bundles, in contrast to the primitive

Table 16. List of specimens in which cauline vasculature has been examined, and their characteristics.

Species	Annual (A) or Perennial (P)	Amount of secondary xylem	Phyllotaxy	Leaf insertion type	Anastomosing between stem bundles
Vicia villosa	A	small	alternate	interlocking	occasional
V. hirsuta	A	small	alternate	interlocking	absent
Cicer arietinum	A	medium	alternate	separated	absent
C. anatolicum	P	large	alternate	separated	occasional
Ononis repens	P	large	alternate	in contact	absent
Medicago sativa	P	medium	alternate	interlocking	present
Trigonella lunata	A	small	alternate	interlocking	absent
T. coelesyriaca	A	small	spiral	variable	occasional
T. balansae	A	small	alternate	interlocking	absent
Trifolium repens	P	medium	alternate	interlocking	absent
Melilotus indica	A	small	spiral	variable	absent
M. italica	A	medium	spiral	variable	occasional
Genista tinctoria	P	large	spiral	in contact	absent?

'acacian' type. However, when Fig. 35:4 is examined, it is seen that the conductive tissues are still separated into four groups, just as much as in Ononis repens (Fig. 35:1).

It was found that in both Ononis and Cicer inter-fascicular xylem and phloem are produced early on, so that even at the youngest nodes it becomes difficult to trace the primary bundles. In the remaining genera, this is not so marked; the bundles of Vicia species, for example, are capped by thick crescents of schlerenchymatous tissue, but secondary wood is not formed until the stem is old. Cicer and Ononis are also different from the rest in having non-interlocked insertions.

These points may be summarised as follows:

1. The occurrence of anastomoses between stem bundles in the Vicieae and Trifolieae is much more limited than Dormer suggested.
2. Even when anastomoses occur, the system is not closed into a unit.
3. Woody members have insertions non-interlocked.
4. Herbaceous members have insertions interlocked.

These facts have led me to propose the following modification of Dormer's hypothesis, still based on the relationship between the open/closed system and the woody/herbaceous habit, but placing different emphasis on methods of closing the vascular system. A closed system of vascular anatomy is important for the most efficient functioning of the plant; there are three methods by which the primary bundles may be linked into a unit: secondary growth, anastomosing between bundles, and

interlocking of insertions. Dormer himself admits that where the insertions are interlocked the vascular system interconnects in the leaves, but he did not consider this as a factor tending towards closing the system into a unit. This situation, it is true, does not permit the conduction of water laterally from one stem-bundle to another; but it is doubtful whether this would occur even in systems with anastomosing bundles, since in most cases the bundles resulting from such anastomosing are themselves destined to become leaf-traces. The downward passage of nutrients from the leaves is affected equally by anastomoses and interlocking of insertions. Where insertions are interlocked, the supply to each leaf is drawn from such a large proportion of the circumference that damage to one side of the stem would be less harmful than in the 'acacian' system.

These considerations show that in the vasculature of herbaceous plants, the type of leaf-insertion is as important as fusion between stem-bundles.

Chapter 6

CHEMICAL TAXONOMY IN THE VICIEAE

6.1. Introduction.

6.2. Phenolic compounds.

6.3. Non-protein amino acids.

6.4. Proteins.

6.4.1. Summary of methods of analysis and comparison.

6.4.2. Serology.

6.4.2.1. General remarks.

6.4.2.2. Serological methods.

6.4.2.3. Results of experiments.

6.4.2.4. Summary.

6.1.

INTRODUCTION

Investigations into the biochemistry of plants have greatly increased during the last two decades, and as more species have been analysed, discontinuous distribution-patterns of substances have emerged to provide taxonomists with more characters on which to base their judgments.

The Vicieae is a popular tribe for experimental work, and its chemistry is better known than that of most taxa. Even so, as will be shown, the scope for further studies in this group is very wide. The application of biochemistry to taxonomy is still at an early stage, and because there is not enough co-operation between workers in these two fields of biology many of the results available in the literature cannot be used with confidence. For example, in some cases there is doubt about the identification of analysed material, and the number of species investigated is often too small to allow broad conclusions to be drawn. Moreover, experiments are frequently performed without any consideration of the taxonomic problems which involve the species under analysis, and their results summarised in such a way that the reader cannot extract any information besides that considered most significant by the author.

The most important chemical compounds which have been investigated from a taxonomic viewpoint in the Vicieae are phenolics, non-protein amino acids and proteins. This chapter begins with a survey of the work done in each field (with emphasis on taxonomically interesting features), and ends with the

description of my own experiments with serology.

6.2.

PHENOLIC COMPOUNDS

Under this heading is included a heterogeneous collection of chemical substances with different properties and functions in plants. The phenolics which have been studied in the Vicieae are mainly those involved in pigmentation, and the tribe is important in this context since much of the pioneering work on flower colouration was performed on material of the genus Lathyrus (Punnett, 1927).

The biochemical aspects of Punnett's work were developed by Scott-Moncrieff (1936) and Beale et al. (1939), and more recently by Pecket (1960). In red, purple and blue flowered species of Lathyrus the colour is due to the anthocyanidin delphinidin and its derivatives petunidin and malvidin, which exist in the form of glycosides. According to Harborne (1971), the glycosidic patterns of anthocyanins in the Vicieae are unusual within the Leguminosae. Instead of the common 3-glucoside or 3,5-diglucoside types, 3-rhamnosides and 3-rhamnoside-5-glucosides (Fig.36) were found in flowers of Cicer, Vicia, Lens, Pisum and Lathyrus. Relatively few taxa have been sampled in the family, and therefore it is not yet known whether the Vicieae can be separated from the other tribes by its anthocyanin chemistry; but the data so far available suggests that a thorough survey would be valuable and interesting.

The effects of anthocyanins in the flower are modified by

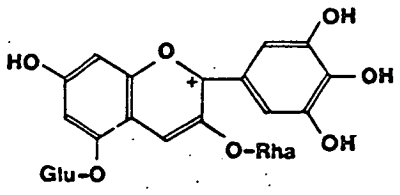
the presence of co-pigments, related compounds known as anthoxanthins. The co-pigments found in Lathyrus are the flavonols quercetin (Fig. 36) and kaempferol; although they are yellow when isolated, they have a marked blueing effect which is probably achieved by the formation of weak additive compounds with anthocyanins. A similar colour change is caused by higher pH values (most flowers have cell-sap of low pH); this also is genetically controlled.

The phenolic compounds mentioned above, which account for flower-colour in most species of Lathyrus, are water-soluble and occur in the cytoplasm of petal cells. However, a few species (L. aphaca, L. pratensis, L. annuus, L. ochrus etc.) owe their yellow flowers to the presence of the water-insoluble plastid pigments xanthophyll and carotene (Pecket, 1960). Plastid pigments are also said to be present in some mutants of L. odoratus (Thoday & Thoday, 1911). The occurrence of plastid pigments in L. pratensis and L. aphaca is perhaps significant, since these species have other similarities (e.g. hastate stipules and a characteristic shape of the wing-petal - see parts 3.6 and 4.2.3.1). However, the few yellow-flowered members of Lathyrus are scattered throughout the genus and are each closely related to blue-flowered species, suggesting that this character does not deserve to be heavily weighted.

It is interesting to note that in Vicia, where yellow flowers are again less frequent than blue, all members of Alefeld's segregant genus Hypechusa have yellow flowers, although one species (V. pannonica) has a purple-flowered form.

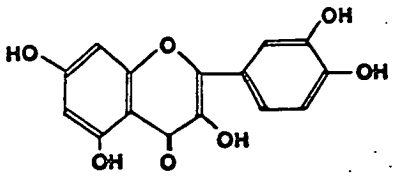
Fig. 36. Some chemical compounds of taxonomic interest found in the Vicieae.

ANTHOCYANIN



Delphinidin 3-rhamnoside-5-glucoside

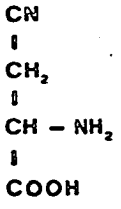
ANTHOXANTHIN



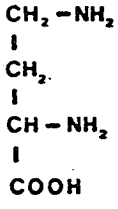
Quercetin

FREE

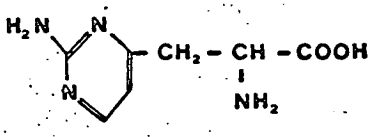
AMINO ACIDS



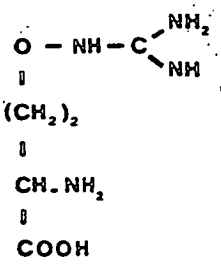
β-cyanoalanin



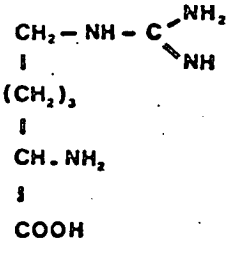
α,γ-diaminobutyric acid



Lathyrine



Canavanine



Homoarginine

The distribution of phenolic compounds in the leaves of Lathyrus has been studied by Pecket (1959) and Brunsberg (1965). Pecket analysed leaf-extracts of 28 species by paper chromatography and found two coumaric acids (caffeic and ferulic acids) together with quercetin and kaempferol, the flavonols which occur as co-pigments in the flowers. The pattern of their distributions confirmed the close morphological and cytological relationship of certain groups of species (L. cicera - L. sativus; L. hirsutus - L. odoratus; L. latifolius - L. sylvestris - L. heterophyllus; L. clymenum - L. articulatus - L. ochrus) whose cytology had been studied by other Manchester workers. From his results Pecket also concluded that he had provided evidence for the inclusion of L. hirsutus, L. pratensis, L. palustris and L. maritimus in Sect. Lathyrus sensu Tutin (1952).

However, in 1965 Brunsberg used the improved technique of thin-layer chromatography on about 50 species of Lathyrus, and found not only a much wider range of phenolics in the leaves but also modified distributions of Pecket's four substances which negate his argument concerning the species which should be placed in Sect. Lathyrus. From her own detailed experiments, Brunsberg concluded that in Lathyrus phenolic compounds have little value in defining subgroups, but can be used to distinguish between closely related species, e.g. L. binatus, L. hallersteinii and L. pratensis.

6.3.

NON-PROTEIN AMINO ACIDS

About 20 amino acids occur in all plants as protein subunits, but in addition there is a much larger number of free, non-protein amino acids (Fowden, 1962). Since these substances often have very limited distributions their occurrence can be of considerable taxonomic interest.

Little is known about the functions of non-protein amino acids in plants, as most of the investigations so far have aimed simply at identifying new substances. This is largely true of the Vicieae, where interest has focussed on the determination of amino acids found in seed extracts. However, recently Bell & Tirimanna (1965), Przybylska & Rymowicz (1965) and Simola (1968b) have analysed different parts of the plant and attempted to interpret their results in terms of possible functions of the various substances and their interrelations in metabolism. For example, Bell (1971) and others have suggested that the nitrogen-rich amino acids lathyrine, homoarginine and canavanine (Fig. 36), found in seeds of the Leguminosae, act as storage compounds which can be rapidly converted into more common metabolites upon germination. An understanding of the role of each amino acid is important for the taxonomist, because it enables him to judge more accurately the value of evidence from distribution-patterns.

The first investigations into the non-protein amino acids of the Vicieae were stimulated by attempts to discover the cause of lathyrism. This disease, which results from ingestion

of seeds of Lathyrus sativus and other species, was known in early times (Hippocrates cit. Selye, 1957) and is still widespread in India. Its symptoms include loss of muscular control, paralysis of the legs and even death. Selye found that there are two toxic syndromes associated with seed of Lathyrus; he named the classical disease of man 'neurolathyrism', while the effects produced on the skeletal systems of experimental animals he termed 'osteolathyrism'. Neurolathyrism is caused by several substances. The first to be isolated and identified was α, γ-diaminobutyric acid (Ressler et al., 1963), found in seed of L. latifolius; others are α-amino-β-oxalylaminopropionic acid, β-cyano-L-alanin and γ-glutamy-β-cyano-L-alanin. Osteolathyrism is caused by the peptide β-(γ-glutamyl)aminopropionitrile, isolated in 1954 by Dupuy & Lee and by McKay et al. from L. pusillus and L. odoratus, respectively.

As more species were investigated, new amino acids were discovered which had no poisonous properties; these included canavanine and lathyrine (tingitanine). The detection and identification of these compounds was made much easier by the introduction of paper chromatography (Consden, Gordon & Martin, 1944), and this method, coupled with electrophoresis, has been widely used in the analysis of seeds and other organs of the Vicieae. All the analyses described in the following account were made upon seeds.

The distribution of canavanine throughout the Leguminosae has been investigated by Tschiersch (1959 & 1961) and Birdsong et al. (1960). The latter found that this amino acid is

limited to the Papilionoideae, and within this subfamily is absent from the Sophoreae and Podalyrieae and occurs in only one species (of those studied) in the Genisteae, Boissiaea foliosa. It was found in all tested members of the Trifolieae (including species of Medicago, Melilotus, Ononis, Trifolium and Trigonella) and Loteae.

Within the Vicieae, canavanine has a limited distribution. The accounts by Birdsong et al., Przybylska & Hurich (1961), Przybylska & Nowacki (1961), Bell & Tirimanna (1965) and Tschiersch & Hanelt (1967) do not entirely agree, but it seems that the amino acid is absent from Pisum, Lathyrus, Lens and Cicer, and from all of Vicia except Sects. Ervum and Cracca. It is interesting that canavanine should be found in Vicia Sect. Ervum but not in Lens; its distribution pattern suggests that these two groups may not be as closely related as has often been thought.

Tschiersch & Hanelt found that species of Vicia without canavanine (members of Sects. Vicia and Faba) can be divided into two groups characterised by the possession of other amino acids. V. sativa s.l., V. grandiflora and V. sepium contain the lathyrogenic β-cyanoalanin and δ-glutamyl-β-cyanoalanin, while the rest do not contain any non-protein amino acid but rather a large quantity of arginine, which is present in smaller amounts throughout the other groups.

Within Lathyrus, lathyrine is found in L. tingitanus, L. aphaca, L. pratensis, L. japonicus and L. sphaericus (Przybylska & Rymowicz, 1965), species of N. and S. America (Simola,

1966) and many species of Sect. Orobus (Bell, 1964). The wide distribution of lathyrine throughout Lathyrus suggests that the ability to synthesise the amino acid is a primitive feature within the genus. Its absence from the rest of the tribe may show it to be a relatively advanced character within the Vicieae, especially as it has not been found outside the tribe. The absence of lathyrine from Pisum provides additional evidence for the opinion that the latter is not a recently-evolved branch of Lathyrus.

On the basis of his own analyses, Bell has divided Lathyrus into five groups of species characterised by the presence of different assemblages of non-protein amino acids in their seeds; but as Simola pointed out, there is doubt about the correct identification of his material.

According to Bell and Tirimanna (1965), there are no non-protein amino acids common to Lathyrus and Vicia; on the other hand, Simola (1968b) reports that β-cyanoalanin is found in seed of L. sylvestris.

It is evident that the distribution of these substances within the Vicieae is of great interest for the taxonomist, and a thorough and intensive survey on a wide scale would contribute valuable new characters for classification. In particular, one would like to know whether canavanine and lathyrine are truly mutually exclusive in Vicia and Lathyrus. The species which should be most closely screened for this feature are the 'oroboid' members of the tribe; in this area the genera Vicia and Lathyrus have traditionally been distinguished only on

three characters (form of androecium, stylar pubescence and leaf-vernation) and therefore any new evidence which supports or conflicts with the present classification would deserve special attention.

6.4.
PROTEINS
6.4.1.
SUMMARY OF METHODS OF ANALYSIS AND COMPARISON

A variety of approaches are used to analyse and compare proteins: amino acid sequence, amino acid composition, 'finger-print' pattern of peptides, catalytic activity, immunology, chromatography, electrophoresis and ultracentrifugation. Several of these have been used, alone or combined, on material from the tribe Vicieae.

Most of the investigations have used seeds as the source of protein; these are convenient, as they ensure that homologous parts of different species are being compared, are available in quantity and are rich in protein. In addition, it seems probable that storage protein (the category most abundant in seeds) is a particularly suitable material for comparisons of this type. Evidence from serology and electrophoresis suggests that in each species the number of different storage proteins is relatively small (Simola, 1969), and because of their specialised function they may be subject to a more rigorous selection during evolution than the structural proteins of the vegetative plant. If this hypothesis is correct, one would

expect storage proteins to be taxonomically more specific than structural ones. Some evidence in favour of this view, provided by serological techniques (Kloz & Klozova, 1960), is described in part 6.4.2.1.

In 1924, Osborne reported that the storage protein found in seeds of the Vicieae consists mainly of two components, which he separated by their different solubilities and called vicilin and legumin. Later, Danielsson (1949) found that the globulin of peas could be fractionated by ultracentrifugation into two components corresponding in solubility to those of Osborne. Investigating seeds of several other members of the Leguminosae, he obtained similar results which led him to believe that vicilin and legumin are widespread within the family. This conclusion has since been modified by techniques of finer resolution, especially those of serology (see part 6.4.2.1.).

Boulter and co-workers have carried out a variety of studies on legume seeds. They found (Boulter et al., 1967) that gel electrophoresis of globulins gave one or more band-patterns characteristic of tribes. The pattern in the Vicieae was quite uniform and consisted of one main band with a less distinct 'collar', together with occasional fainter bands. The Trifolieae was also uniform, having two bands. Unfortunately, they made no attempt to correlate these bands (representing globulin fractions) with vicilin and legumin, and also many of the results are summarised rather than stated in full. It would have been interesting, for example, to have seen the band-pattern of Cicer arietinum.

A similar method was used by Thurman et al. (1967) to compare the formic and glutamic dehydrogenases (FDH and GDH) within legume seeds. (These proteins belong to the albumin fraction.) Their presence in the gel after electrophoresis was detected by the enzymatic production of formazan from tetrazolium compounds. The same criticism about omission of the details of results applies also to this paper; but it is stated that all the Vicieae gave one FDH formazan band, while there were five GDH bands in all its genera except Cicer, which had two. The Rp value of FDH in Cicer was higher than those of the rest, approaching the Rp values of the Trifolieae. The number of FDH and GDH bands in the Trifolieae is not mentioned.

Jackson et al. (1967) investigated the globulin fraction of seeds of the Vicieae by 'fingerprinting' the peptides resulting from hydrolysis with trypsin. It was found, by comparing chromatograms, that the fingerprints of the five genera were very similar. Those of Lathyrus and Lens differed from Vicia each by three spots, while those of Pisum and Cicer differed from Vicia by seven and thirteen spots, respectively. Lathyrus and Vicia had 54 spots in common. One would very much like to know by how many spots the genera Lens, Lathyrus, Pisum and Cicer differed from each other, and the distribution of each spot between the genera. It would be most interesting to extend the range of the survey and compare globulins from neighbouring tribes, especially the Trifolieae.

Each of these experiments produced taxonomically interesting results, demonstrating the potential of proteins for

providing new characters. They also show very clearly that there must be closer co-operation between workers in different fields of botany, so that the specialised techniques of the biochemist may provide information in a form which the taxonomist can use fully and with confidence.

6.4.2.

SEROLOGY

The rest of this section is devoted to serology. Several abbreviations are sometimes used for convenience; thus antigen is shortened to a-g, while the antiserum produced after immunisation of an experimental animal with a-g A is designated a-s A. The reaction between a-s A and a-g A is 'homologous', while that between a-s A and a-g B is 'heterologous'.

6.4.2.1.

GENERAL REMARKS

The history of serological studies in the Leguminosae, and in the Vicieae in particular, is described by Kloz (1971). The following introduction deals in more detail with the most recent developments in this field which have a direct bearing on my own experiments.

In 1960, Kloz and Klozova reported their use of a quantitative immunological method to investigate the taxonomic specificity of proteins in different organs of several taxa of the Leguminosae, including Vicia faba. Some of their findings are summarised as follows:

1. Each of the organs which were investigated (the cotyledons, the subcotyledonous part of the seedling, and mature leaves) was found to contain proteins with characters specific to the taxon.

2. When heterologous reactions were carried out it was observed that there was a greater similarity in protein characters between closely related species than between members of different genera or families. However, the falling-off of serological correspondence was relatively more rapid with taxa which were close to the homologous one than with the more distant ones.

3. Protein characters of individual organs of the same taxon have relatively little in common, and in fact there is greater similarity between proteins of the same organ of related species than between different organs of one species. From this it was concluded that it is essential, when performing experiments of comparative serology, to use homologous organs from all the organisms being studied.

4. The reserve proteins of cotyledons produce weaker heterologous reactions between genera than do the constitutional proteins of leaves and the subcotyledonous parts of seedlings. The authors concluded that the storage proteins of seeds have evolved more recently than the structural proteins of the vegetative plant.

Seed reserve proteins have been most widely used to produce antisera and antigens in comparative immunology. They have the advantages of being relatively easily obtained in

quantity, and being both more stable and more active as immunogens than are the complexes of constitutional proteins. The relative stability of seed storage proteins may be the result of selection to enable the seed to remain dormant but viable for several years; it may also be due to the paucity of (damaging) enzymes in seed extracts, compared with extracts of leaves, etc. However, seeds often contain non-specific precipitins which give reactions even with normal sera, so it is essential to perform controls in each experiment to screen for this possibility.

The storage protein in seeds of Pisum sativum consists largely of the globulins legumin and vicilin, as mentioned in part 6.4.1. They have molecular weights of about 186,000 and 331,000, respectively (Danielsson, 1949). Although possessing different physical properties, these two proteins appear to be related, sharing several 'determinant groups' (regions of the molecule which are 'recognised' by antibody). This was demonstrated by Kloz & Turkova (1963), who purified legumin and vicilin, prepared antisera to each, and obtained cross-reactions between them. These authors also showed that legumin and vicilin are found in Pisum, Lathyrus, Lens, Vicia and Cicer; seeds of Medicago and Trifolium possess only vicilin; and neither protein occurs in Lupinus, Phaseolus or Glycine. Immunoelectrophoretic analysis showed that the legumin and vicilin components in seeds of Pisum sativum, Lens culinaris and members of Lathyrus are identical; species of Vicia have the identical vicilin but a slightly dissimilar legumin; and

Cicer arietinum has legumin identical but vicilin distinctly different. The vicilin represented in members of the Trifolieae is quite distinct from that of Pisum sativum.

A detailed serological investigation, using electrophoresis and absorption techniques, was made by Simola (1969) in the genus Lathyrus. The principle behind the use of 'absorption' is as follows. Since A a-s contains antibodies raised specifically against A a-g, the immunological reactivity of A a-s can be completely removed only by reaction with A a-g. The antiserum is here said to be absorbed by the antigen. A a-s absorbed with B a-g will give no reaction against B a-g, but will retain some antibodies to give a positive homologous reaction - unless, of course, A and B are identical (Moritz, 1966).

Simola prepared five antisera (to L. niger, L. sylvestris, L. ochrus, L. macrostachys and L. laetiflorus) and found that their homologous reaction patterns were very similar; that of L. ochrus had eight arcs, the rest had seven. Antigens to 27 species of Lathyrus were used to produce heterologous reactions against each of the five antisera, and it was found that while individual cross-reactions gave differing patterns, the crude mean value of reactions to all antisera gave a similar pattern for each antigen. Thus, for example, a-gs to species from S. America gave only two precipitation lines against L. laetiflorus a-s (a N. American species), but the proteins which failed to react could be detected with antiserum to the S. American

species L. macrostachys.

The correspondence of the precipitation lines of different species was established by absorption experiments. L. ochrus a-s was absorbed by L. macrostachys a-g, L. macrostachys a-s by L. ochrus a-g, and L. macrostachys a-s by L. niger a-g; these three absorbed antisera were then run against different antigens. In each case both homologous and heterologous reactions gave no precipitation arcs; absorption was complete. Simola concluded that all the Lathyrus antigens used were virtually identical, and that variation between one electrophoretic pattern and another was a quantitative, rather than a qualitative, phenomenon.

The results of these experiments using absorbed antisera are puzzling. Simola demonstrated in the first part of her paper that the various antigens were not identical, when run against un-absorbed antisera. The absorption experiments should therefore have produced a chequered pattern of positive and negative results, in which at least the three homologous reactions were positive. The only check which the experimenter has on the continued 'viability' of his antiserum is its ability to produce a positive homologous reaction. The negative results reported by Simola throw doubt on the whole experiment, and suggest that perhaps the method of preparation of absorbed antisera (which was not stated) was faulty.

When different genera of the Vicieae were compared, it was found that representatives of Vicia, Pisum and Lens gave serological reaction patterns against Lathyrus antiserum which

contained all the five precipitation lines commonly present in heterologous reactions within Lathyrus. The serological relationship of Cicer arietinum to Lathyrus was less distinct, the cross-reaction pattern containing only four lines.

Outside the Vicieae, antigen of Ononis arvensis gave a pattern with four arcs, while representatives from Lotus, Oxytropis, Abrus and Phaseolus gave only one; there was no reaction with Trifolium repens a-g.

By comparing the homologous reaction pattern of Lathyrus with that given by Kloz & Turkova (1963) for Pisum sativum, Simola identified two of the arcs as corresponding to legumin and vicilin, respectively. These lines were represented in the spectra of all members of the Vicieae and of Ononis arvensis; they were absent from the patterns of other species outside the tribe.

My own experiments with serology were made with the aim of providing additional taxonomic characters in two problematic areas of the Vicieae. I hoped the results would help to decide which are the closest relatives of Lens among the other genera of the tribe, and whether Cicer is more closely related to the Vicieae or the Trifolieae. I used antisera to two species, Lens culinaris and Cicer arietinum; from now on these antisera will usually be designated Lens a-s and Cicer a-s, respectively. The techniques used are described first, followed by the results and interpretation of the experiments.

6.4.2.2.

SEROLOGICAL METHODS

Production of antisera. The immunogens were prepared as follows. Seeds of the species concerned (Lens culinaris and Cicer arietinum) were ground to a fine flour and extracted overnight at 4°C in saline. The slurry was then centrifuged off, and the protein concentration in the supernatant solution determined by the Lowry method (Lowry et al., 1951). It was found to be approximately 1%, in 0.8% NaCl. This solution was stored at near freezing point, and used for the series of injections necessary to stimulate antibody production in the experimental animals.

In the first two injections, given a fortnight apart, the immunogen was mixed with an equal quantity of Freund's adjuvant. This is a mixture of lanolin derivatives, mineral oil and dead tubercle bacteria, which forms an emulsion with the aqueous immunogen solution. The adjuvant has several advantageous properties. The lanolin soaks up water from within the emulsion, this in effect concentrating the protein in each water droplet. When the immunogen/adjuvant emulsion is injected into the rabbit, the protein escapes slowly and continuously from the droplets into the tissues, and the tubercle bacteria cause a general stimulation of antibody production in the animal (Freund & Bonanto, 1946). The course of injections was as follows:

Day 1 1 ml immunogen/adjuvant emulsion in each thigh

(intramuscular)

Day 15 1 ml immunogen/adjuvant emulsion in <u>each</u> thigh (intramuscular)

21 1 ml neat immunogen solution in one thigh (intramuscular)

23 0.5 ml neat immunogen solution, marginal ear vein (intravenous)

25 0.5 ml neat immunogen solution, marginal ear vein (intravenous)

27 1 ml immunogen solution (intravenous)

29 " " " "

31 " " " "

33 " " " "

After three intravenous injections, the production of antibodies by the rabbit is checked by taking a 10 ml sample of blood from the marginal ear vein. The blood is allowed to clot at room temperature, the clot freed from the sides of the glass container, and the blood cooled in a refrigerator. The clot falls to the bottom of the tube and the serum can be decanted and tested. If the serum gives only a weak homologous reaction, the injections are continued; when a satisfactory level of antibodies has been achieved, the final bleed is performed.

The animal is given by injection a lethal dose of the anaesthetic Nembutol, together with the anti-clotting agent heparin (2.5 ml, containing 50% of each); the rabbit dies in three minutes. During this time, blood is taken from the right ventricle of the heart, using a 50 ml syringe which is filled

automatically by the pumping of the heart. The syringe is emptied gently (to avoid haemolysis) into one or two plastic bottles and allowed to clot as before. Sodium azide (1 p.p. 1000) is added to the serum as a sterilising agent.

Production of antigens. Whole seeds were ground to a fine flour using a pestle and mortar, and extracted for two days at room temperature. The extractant was 2% NaCl solution, ten parts of saline being added to one part flour. Sodium azide, made up to 1% in the extractant, was used as a sterilising agent. The protein solution was freed from debris by centrifugation, and stored at 4°C.

The protein concentration in the antigen solutions was not standardised, but was determined in a sample of extracts by the Lowry method. The results of these determinations were as follows:

ANTIGEN SOLUTION	% PROTEIN
Lens culinaris	0.82
Pisum sativum	1.52
Lathyrus ochrus	1.52
Vicia faba	1.33
V. unijuga	1.67
V. ervilia	0.71
Cicer arietinum	1.05
Medicago orbicularis	1.25

A list of the species from whose seeds antigens were prepared is given in Table 17. Each species was represented by a single

Table 17. List of species from which antigens were prepared.

1.	Lens culinaris	18.	V. palaestina
2.	Pisum sativum	19.	V. caesarea
3.	Lathyrus cicera	20.	V. koeieana
4.	L. ochrus	21.	Cicer arietinum
5.	L. vernus	22.	Ononis natrix
6.	Vicia sativa	23.	O. biflora
7.	V. melanops	24.	Medicago orbicularis
8.	V. faba	25.	M. lupulina
9.	V. unijuga	26.	Melilotus officinalis
10.	V. dumetorum	27.	Trifolium squamosum
11.	V. cracca	28.	Galega officinalis
12.	V. benghalensis	29.	Astragalus cicer
13.	V. articulata	30.	Lotus corniculatus
14.	V. disperma	31.	Coronilla scorpioides
15.	V. ervilia	32.	Laburnum alpinum
16.	V. pubescens	33.	Ulex europaeus
17.	V. hirsuta	34.	Sophora tetraptera

The numbers of the antigens correspond with those used in Tables 18 and 19 and in Figure 39.

seed sample.

Double-diffusion serology. Double-diffusion of antigens against antisera was carried out in a thin layer of agar on glass plates.

400 ml of agar medium was prepared as follows; 2.4 g ion-agar was melted in a water-bath with 200 ml water, and then 200 ml of Michaelis buffer added. The latter contained 7.184 g sodium barbitone in 51.6 ml N/10 hydrochloric acid, made up to 200 ml. The resulting medium was 6% agar at pH 8.6, with approximately 0.1% sodium azide as sterilising agent. It was poured into small screw-topped bottles (15 ml in each) and stored until needed, when the agar was re-melted by heating the bottles in a water-bath.

The glass plates, measuring about 8 x 10 cm, were washed and dried carefully, and placed on a flat surface protected from dust. Agar was then poured onto each to form a layer 2 to 3 mm thick, and left to cool. A pattern of trough and wells was cut out of each, using a cork-borer and scalpel, and the agar removed from the pattern by suction.

The wells were filled uniformly with antigen solutions, and about 0.25 ml antiserum pipetted into the trough. The plates were placed in a water-saturated atmosphere and incubated at room temperature until the precipitation spectra had developed fully. This took about three days.

The wells and trough were then cleaned out thoroughly with a soft paint-brush, and the plates left to wash in slowly

flowing tap water for another three days. After this, each was dried overnight, the agar being covered with a water-soaked filter-paper to ensure even evaporation. When completely dry, the paper was peeled off and traces of fluff removed by washing under a stream of water and rubbing the agar surface gently. The plates were stained for about 5 minutes in Ponceau S solution; then destained in running tap-water until only the precipitation lines retained the dye. Finally the plates were dried again, protected from dust.

Preparation of absorbed antisera. The amount of antigen necessary to absorb the antiserum was found by trial to be approximately 1 part antigen : 1 part antiserum. In order to avoid diluting the antiserum, the antigen solution was concentrated about ten times, using the method described by Kohn (1959). The antigen was placed in a cellophane bag immersed in a saturated solution of carbowax, which, having an extremely high molecular weight, caused an osmotic flow of water from the semipermeable bag. The concentration process took about four hours to complete. 0.1 ml was then pipetted up and added to 1.0 ml antiserum. Although the absorbed antiserum was cloudy, the antigen-antibody precipitate did not interfere with the operation of double-diffusion, and therefore it was not considered necessary to remove it by centrifugation.

6.4.2.3.

RESULTS OF EXPERIMENTS

Control. As a control, nearly all the antigens were run against normal serum (see Table 18). In one case a positive reaction was recorded; the antigen of Vicia pubescens produced a faint, diffused precipitate near to the antigen well. This feature (which does not show up well on the photograph, Fig. 39:18) occurred in all spectra of V. pubescens a-g; but fortunately, being distant from the specific antibody-antigen arcs, it did not interfere with the use of this antigen in the double-diffusion experiments. On the other hand, the presence of this non-specific precipitate was a confusing factor in the experiments which used absorbed antiserum, because here the positive results recorded all tended to be of faint and rather diffused arcs (see Fig. 39:12 to 17).

Experiments using Lens antiserum.

A. Homologous reaction. The homologous reaction pattern is illustrated several times in Fig. 39, and also diagrammatically, in Fig. 37. This shows that there are four main arcs - A, B, C and D - each of which appeared double on the best plates, although more frequently their composite nature was not visible. Arc A was very faint and occurred only in some plates. It was seen also in certain heterologous reactions (e.g. those of V. caesarea and V. koeieana, Fig. 39:9), but its sporadic appearance in the homologous spectra made it unreliable as positive or negative evidence of serological correspondence.

B. Range of reactivity. The reaction spectrum of every antigen was found to be highly reproducible, in the number, shape and

position of its lines. Table 18 expresses the range of species which gave a serological reaction to Lens a-s, and also, very roughly, the relative strength of each response (strong, weak or absent). All members of the Vicieae yielded antigens giving strong reactions against Lens a-s. Outside the tribe, a-gs of the Trifolieae, Galegeae, Loteae and Hedysareae gave strong to medium reactions. A weak response was recorded with Laburnum a-g; none with a-g of Ulex (both in the Genisteae). A weak reaction was given by Sophora.

It is evident that the storage proteins of legumes show some degree of serological correspondence over a wide taxonomic range. These results also confirm the conclusion reached by Kloz & Klozova (1960), mentioned in part 6.4.2.1, that while serological correspondence falls away rapidly in the immediate neighbourhood of the antiserum-taxon, at greater distances the relationship between serological and taxonomic affinity is not so marked and the falling-off of antigen-antibody response is slowed up. This phenomenon may possibly be a reflection of the pattern of evolution in seed storage proteins. It suggests that the members of the Leguminosae which have been used in serological experiments all share a similar 'background' fraction of seed proteins which has remained almost unchanged during the development of the family. In addition, their seeds contain more recently-evolved proteins which are common to only closely-related taxa.

C. Comparison of heterologous spectra. Lester (1966) and Fairbrothers (1966) have both discussed the methods of analys-

ing double-diffusion spectra and the principles underlying their interpretation. The number of arcs produced in each cross-reaction must be counted, and the quality of each arc described; and then the relationship between different patterns deciphered by noting identity, partial identity and non-identity of precipitation lines. Identity is confirmed when arcs from adjacent spectra meet and fuse completely (as in Fig. 39:10, between a-gs 21, 24 and 27); partial identity, when arcs meet and fuse, but a spur is produced from one of them across the other (as in Fig. 39:9, between a-gs 15 and 19); non-identity, when arcs from adjacent spectra cross (as in Fig. 39:3, between a-gs 7 and 1).

Within the Vicieae, I found that a-gs of Pisum sativum, Lathyrus species and some members of Vicia (V. unijuga, V. cracca, V. articulata and V. ervilia) produced spectra having almost complete identity with the homologous pattern (Fig. 39:1 & 2), suggesting that these species are closely related to Lens. Their reaction patterns differ from the homologous one in that lines B and C (and possibly A and D) are not separated, being represented either as a broad band or as a narrow, sharp line. Only in the spectrum of Lathyrus vernus are there two distinct arcs.

Members of Vicia Sect. Vicia (V. melanops and V. sativa) and V. faba produced spectra in which only arc B is represented (Fig. 39:3); they are therefore comparatively distantly related to Lens.

Since members of Vicia Sect. Ervum have frequently been

considered to be close relatives of Lens, antigens of several of them were prepared in this experiment. The spectrum of V. ervilia, as already mentioned, is quite similar to the homologous pattern. V. hirsuta (Fig. 39:8) has a rather individual pattern, shared only by V. palaestina: arc B is represented, and a line having partial identity with arc D; but C is absent. The strength of the spurs from the homologous pattern make it likely that V. hirsuta is not closely related to Lens. V. disperma a-g produces a spectrum containing two distinct arcs, one identical with B, the other having partial identity with C. There is also a faint precipitate nearer the trough which may have some correspondence with D. The pattern of V. pubescens consists of a broad band having the same composition as the spectrum of V. disperma. (The spectrum of V. pubescens (16) in Fig. 39:5 is interesting: arc C is nearer the antigen well than arc B.) These two species show considerable serological resemblance with Lens, but not as much as Lathyrus or Pisum.

Finally, Fig. 39:9 shows the spectra of the anomalous species V. caesarea and V. koeieana, each of which has some morphological traits in common with Lens. Their spectra, however, show only partial identity with the homologous pattern, and the spurs across each from V. ervilia are evidence that the latter is more nearly related to Lens than are either V. caesarea or V. koeieana.

Cicer arietinum a-g gave only one line against Lens a-s, partially identical with arc B.

As other workers have found, members of the Trifolieae had a closer serological correspondence with the Vicieae than other tribes. Medicago orbicularis and Trifolium squamosum a-gs produced spectra identical with that of Cicer arietinum (Fig. 39:10); Ononis natrix and Melilotus officinalis had weaker reactions, each consisting of a blurred line only partially identical with the arc of Cicer.

It is interesting to compare my results in this area with those of previous authors. Kloz and Turkova (1963) found that Cicer seed contained both vicilin and legumin, while seed of the Trifolieae had only vicilin. On the other hand, Simola (1969) found neither protein in Trifolium repens, but both in Ononis arvensis! With these data in mind, several conclusions can be drawn in interpreting the spectra obtained in the present experiments.

1. The single arc produced by Cicer a-g represents the occurrence in the seed of both vicilin and legumin.
2. Since this arc is identical (if only partially) with line B in the homologous pattern, B must represent both legumin and vicilin in Lens antigen. This line is known to be composite, and it is present in all heterologous reactions of the Vicieae, whereas A, C and D are sometimes absent.
3. Since no spurs are produced when the heterologous reaction-patterns of Cicer arietinum, Medicago orbicularis and Trifolium squamosum are arranged side by side, the two latter must also contain both vicilin and legumin in their seeds.

It is evident that there is disagreement about the occurrence of different storage proteins in the Trifolieae, which so far have been sampled very sparsely; only a more thorough analysis, centred on this tribe, will elucidate the situation.

The heterologous reaction produced by Astragalus cicer a-g contained one arc; this was strong and sharp and partially identical with that of Cicer. The spectrum of Galega officinalis a-g against Lens a-s had two less distinct lines, of which the one nearest the antigen well had partial identity with the arc of Astragalus. This indicates that the Galegeae have fairly strong serological correspondence with the Vicieae. Fainter lines were recorded for Lotus corniculatus and Coronilla scorpioides. Laburnum alpinum a-g produced an indistinct, broad band of precipitate, while Ulex europaeus gave no reaction against Lens a-s. A very weak band was observed when Sophora tetraptera a-g was used.

D. Absorption experiments. The antigens used to absorb Lens a-s, and the reactions involving absorbed antisera, are shown in Table 18. These antisera are expressed in general as A a-s - B a-g. Of the five absorbed antisera, the most limited range of reactivity was shown by Lens a-s - Pisum sativum a-g; a positive reaction was recorded only against Lens a-g. This result supports the conclusion, drawn from observation of the simple heterologous reaction of Pisum a-g against Lens a-s, that the antibody-stimulating storage proteins of these species are almost identical, and it shows that of all the species from which antigens were prepared, Pisum sativum is serologically

closest to Lens.

Lens a-s - Lathyrus ochrus a-g gave reactions with a-gs of Lens, Pisum and Vicia, but not with those of Lathyrus vernus or Cicer. When seed extracts of members of Vicia were used as absorbants, the resulting antisera reacted positively with Pisum and Lathyrus and most of Vicia. The three species chosen for this purpose were members of Sect. Ervum (V. disperma, V. ervilia and V. hirsuta). Lens a-s - V. disperma a-g produced arcs with antigens of all members of Vicia except V. disperma, V. hirsuta and V. palaestina; Lens a-s - V. ervilia a-g gave a similar pattern (see Table 18). It is interesting that Lens a-s - V. disperma a-g against V. ervilia a-g, and Lens a-s - V. ervilia a-g against V. disperma a-g, were both positive; this shows that these antigens have a similar degree of correspondence to Lens a-g; their mutual relationship is not very close, and neither can be said to be nearer to Lens than the other.

It was seen from the simple double-diffusion spectrum of V. hirsuta a-g against Lens a-g that this species is serologically remote from Lens within the Vicieae. This is confirmed by the negative results obtained with all the absorbed antisera mentioned above against V. hirsuta a-g, and by the strong positive results produced by all antigens against Lens a-g - V. hirsuta a-g. Even Cicer a-g, which gave no reaction with other absorbed antisera, here produced a faint response. V. palaestina gave no reaction, confirming the close relationship between it and V. hirsuta which was suggested by the similarity

of their simple heterologous spectra against Lens a-s.

It was surprising, and interesting, to find a positive reaction between a-g of Medicago orbicularis and Lens a-s absorbed with V. ervilia a-g and with V. hirsuta a-g. This, and the other experiments involving a-gs prepared from species of Vicia Sect. Ervum, all point to the conclusion: Sect. Ervum is not closely related to Lens, as far as serological characters are concerned.

In the last set of reactions, using Lens a-s - Cicer arietinum a-g, no line was recorded against Medicago a-g, but a positive reaction occurred with Ononis natrix and Galega officinalis a-gs. These few results suggest that certain taxa outside the Vicieae (Ononis, Galega) are equally or even more closely related to Lens than is Cicer. The remoteness of serological correspondence between this genus and other members of the Vicieae is emphasised by the strong reaction recorded with all antigens in the tribe against Lens a-s - Cicer a-g.

Experiments using Cicer antiserum.

A. Homologous reaction. The homologous reaction of Cicer consists of three main lines (seen most clearly in Fig. 39:21), but it is evident from the several examples illustrated in the photographs that these are composite, and in fact the spectrum seems more complex than that of Lens.

B. Range of reactivity. The range of species having serological affinity with Cicer is less than that found for Lens (see Table 19). No reaction was recorded against antigens of

Lotus, Coronilla, Laburnum, Ulex or Sophora; positive results were obtained only against antigens of members of the Galegeae, Trifolieae and Vicieae.

C. Interpretation of heterologous reactions. The heterologous reactions of other members of the Vicieae against Cicer a-s were found to be rather uniform, consisting mainly of a single line and forming few spurs between themselves. Where they were placed adjacent to the homologous pattern, the latter produced several spurs, confirming the relatively slight serological correspondence between Cicer and the other genera which was shown by the previous experiments.

Antigens of the Trifolieae also produced spectra containing a single line, and this arc had identity with those in patterns of the Vicieae. The two antigens of Cnonis species gave spectra which were similar to the rest, but weaker.

These results, which show the serological correspondence between Cicer and all its supposed nearest relatives, suggest that the genus is comparatively isolated. Although the homologous spectrum is rich in arcs, showing a wide range of different proteins within the seed, only one or two are represented in other genera, and these are common to such a wide range of taxa as to have little taxonomic value.

D. Absorption experiments. Cicer a-s was absorbed with two antigens, those of Lens culinaris and Medicago orbicularis. Cicer a-s - Lens a-g gave negative results against all members of the Vicieae except Cicer a-g and V. ervilia (providing more evidence that the latter is not very closely related to Lens).

Table 18. Results of experiments using Lens antiserum.

ANTIGEN		ANTISERUM							
				ABSORBED ANTISERA					
(The species are numbered as in Table 17.)		Normal serum	Lens a-s	Lens a-s + 2	Lens a-s + 4	Lens a-s + 14	Lens a-s + 15	Lens a-s + 17	Lens a-s + 21
1	Lens culinaris	-	▣	▣	▣	▣	▣	▣	▣
2	Pisum sativum	-	▣	-	▣	▣	▣	▣	▣
4	Lathyrus ochrus	-	▣	-	-	▣	▣	▣	▣
5	L. vernus	-	▣	-	-	▣	-	▣	▣
8	Vicia faba	-	▣	-	▣	▣	▣	▣	▣
9	V. unijuga	-	▣	-	▣	▣	▣	▣	▣
11	V. cracca	-	▣	-	▣	▣	▣	▣	▣
14	V. disperma	-	▣	-	▣	-	▣	▣	▣
15	V. ervilia	-	▣	-	▣	▣	-	▣	▣
16	V. pubescens	▣	▣	-	▣	▣	▣	▣	▣
17	V. hirsuta	-	▣	-	-	-	-	-	▣
18	V. palaestina	-	▣	-	-	-	-	-	▣
21	Cicer arietinum	-	▣	-	-	-	-	▣	-
24	Medicago orbicularis	-	▣	-	-	-	▣	▣	-
22	Ononis natrix	-	▣						▣
26	Melilotus officinalis	-	▣						-
27	Trifolium squamosum		▣						-
28	Galega officinalis	-	▣						▣
29	Astragalus cicer		▣						-
30	Lotus corniculatus	-	▣						
31	Coronilla scorpioides	-	▣						-
32	Laburnum alpinum	-	▣						
33	Ulex europaeus	-	-						
34	Sophora tetraptera	-	▣						

For key to symbols, see Table 19.

Table 19. Results of experiments using Cicer antiserum.

ANTIGEN		ANTISERUM			
(The species are numbered as in Table 17.)		Normal serum	Cicer a-a	Cicer a-a absorbed antisera – 1	Cicer a-a absorbed antisera – 24
1	Lens culinaris	–	▣	–	–
2	Pisum sativum	–	▣	–	–
3	Lathyrus cicera	–	▣	–	–
4	L. ochrus	–	▣	–	–
6	Vicia sativa	–	▣	–	–
9	V. unijuga	–	▣	–	–
12	V. benghalensis	–	▣	–	–
15	V. ervilia	–	▣	□	–
21	Cicer arietinum	–	▣	□	□
22	Ononis natrix	–	□	□	–
23	O. biflora		□	□	–
24	Medicago orbicularis	–	□	□	–
25	M. lupulina	–	□	□	–
26	Melilotus officinalis	–	▣	□	–
28	Galega officinalis	–	▣	□	–
30	Lotus corniculatus	–	–		
31	Coronilla scorpioides	–	–		
32	Laburnum alpinum	–	–		
33	Ulex europaeus	–	–		
34	Sophora tetraptera	–	–		

KEY TO SYMBOLS:

▣ strong reaction between antiserum and antigen
□ weak - - - - -
– no - - - - -
where no symbol occurs the reaction is unknown

Fig. 37. Homologous reaction double-diffusion spectrum of Lens culinaris.

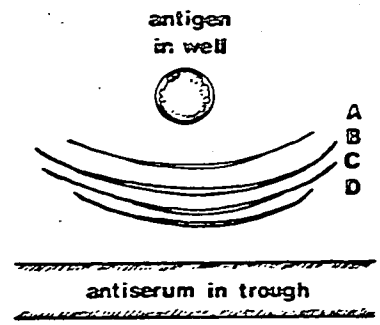


Fig. 38. Phylogenetic tree based on serological characters.

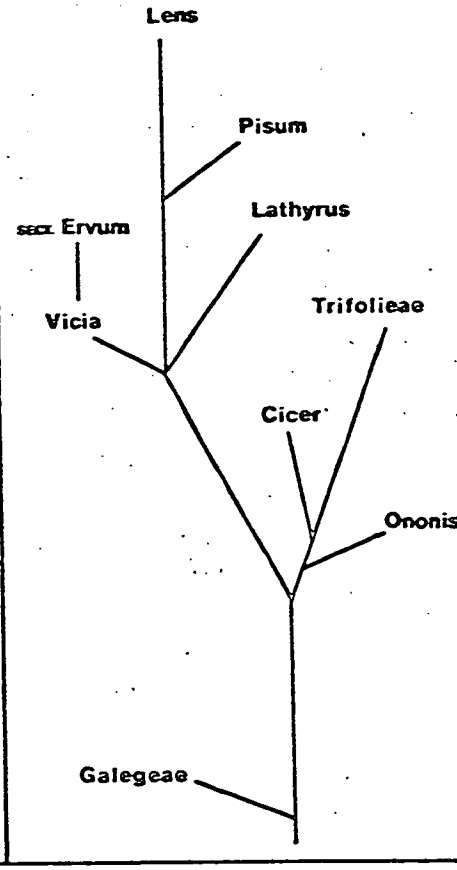
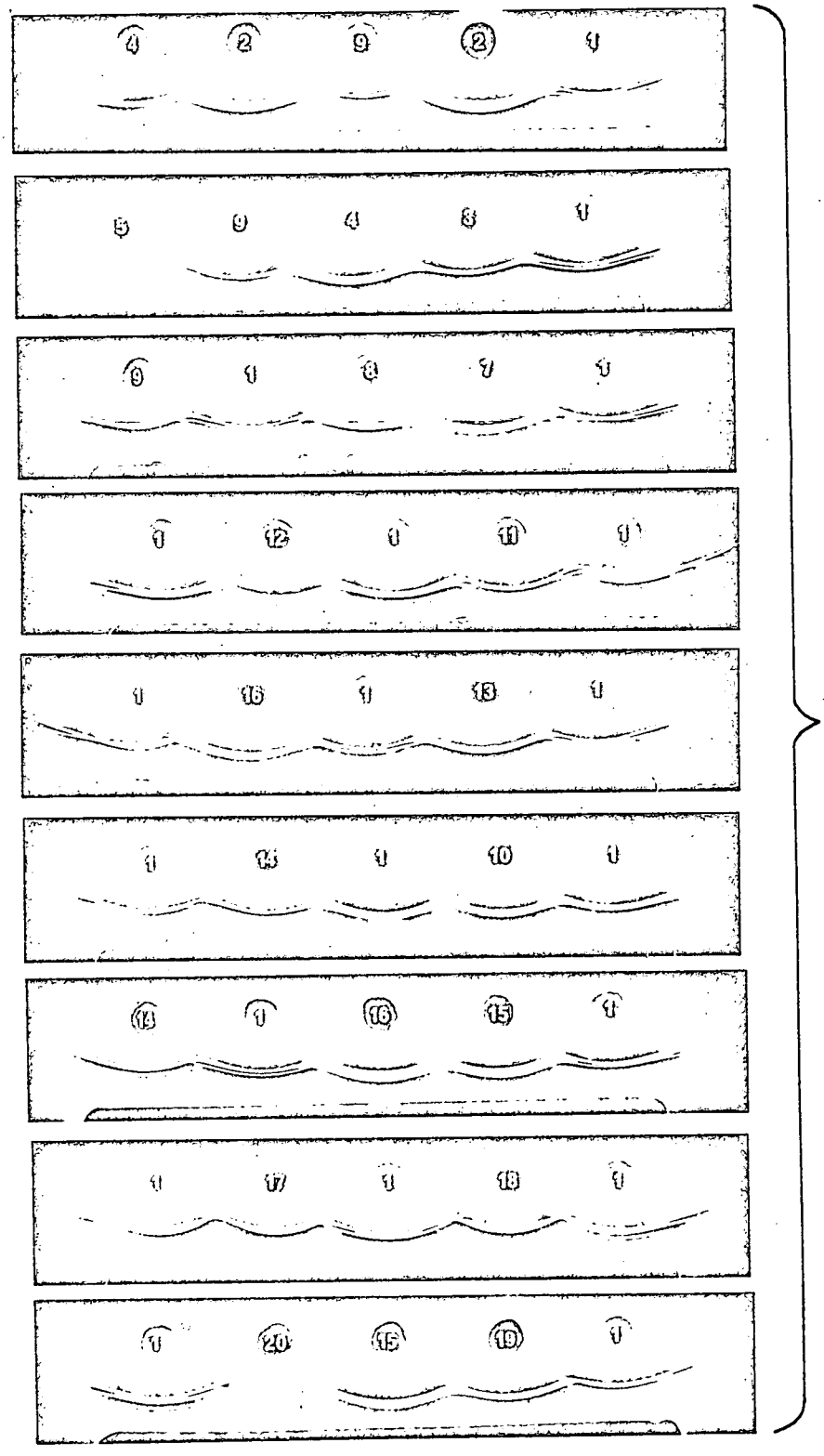


Fig. 39. Double-diffusion spectra.



For numbering of antigens, see Table 17.

Fig. 39, contd

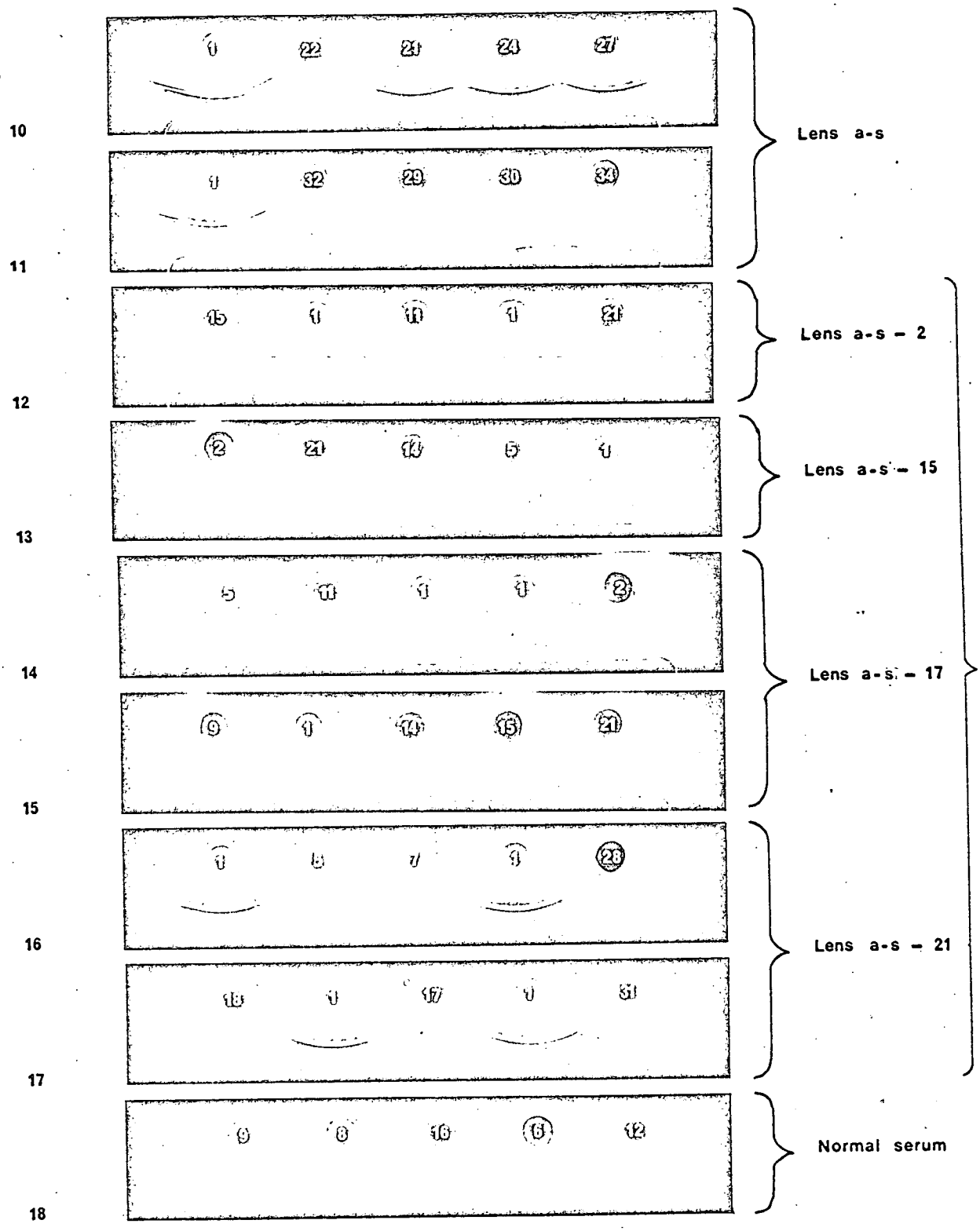
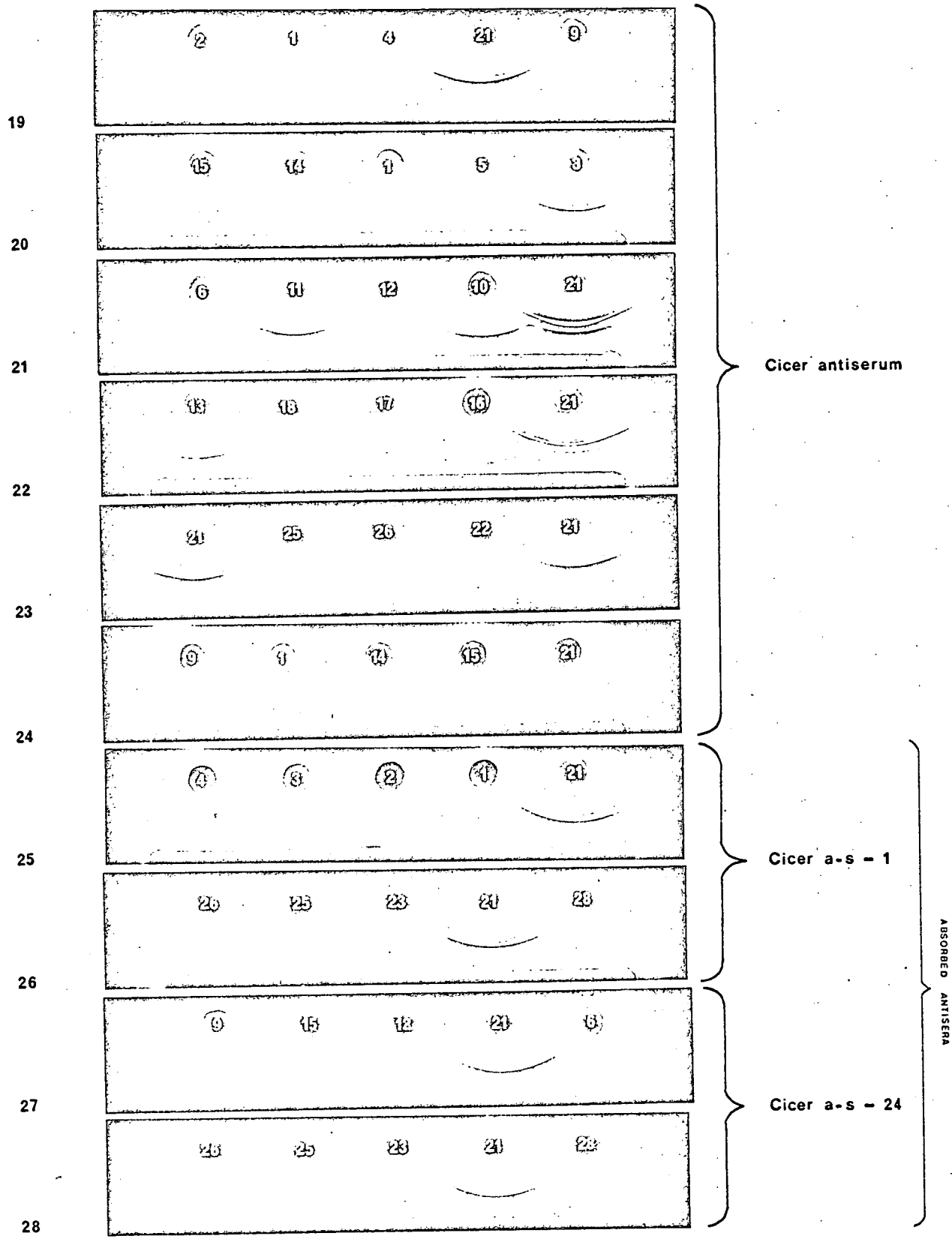

10
11
12
13
14
15
16
17
18
Lens a-s
Lens a-s – 2
Lens a-s – 15
Lens a-s – 17
Lens a-s – 21
Normal serum
ABSORBED ANTISERA

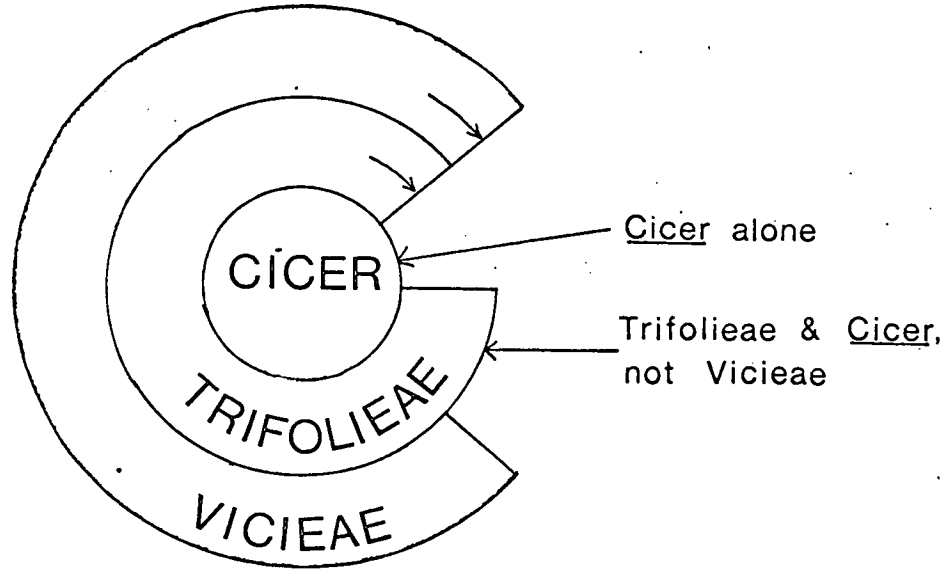
Fig. 39, contd


19
20
21
22
23
24
25
26
27
28
Cicer antiserum
Cicer a-s - 1
Cicer a-s - 24
ABSORBED ANTISERA

Very faint arcs were seen when this serum was run against a-gs of the Trifolieae; they can scarcely be discerned in the photograph, Fig. 39:26, but were clearly present on the plates. Cicer a-s - Medicago orbicularis a-g gave negative results for all antigens except in the homologous reaction.

These interesting results suggest that Cicer contains some seed storage proteins which are present in the Trifolieae but absent from most other members of the Vicieae. Conversely, since Cicer a-s absorbed with Medicago a-g gave a negative result with a-gs of Vicia, Lathyrus, Pisum and Lens, all the serological characters shared by these genera with Cicer are also possessed by Medicago. This is expressed in the following diagram.

Shared Protein Characters



These data, taken alone, lead to the following conclusion. The Vicieae and Trifolieae have a common ancestor; during the evolution of these tribes and their genera, the ancestral stock of

'Vicia-Lathyrus-Pisum-Lens' diverged from the ancestral stock of 'Cicer-Trifolieae' before the genus Cicer itself diverged from the Trifolieae. In other words, serological evidence suggests that Cicer is phylogenetically closer to the Trifolieae than the Vicieae.

6.4.2.4.

SUMMARY

The results of these experiments are summarised in the phylogenetic tree (Fig. 38). It must be emphasised that this scheme is based entirely on evidence from serology (itself concerned only with seed-proteins); it is not expected that the characters derived from other sources will necessarily confirm it, nor is it implied that serological characters deserve special weighting.

The three most important conclusions to be drawn from the experiments are:

1. The genus Lens does not show a particularly strong affinity with members of Vicia Sect. Ervum.
2. Lens has a closer serological relationship with Pisum than with the other genera of the Vicieae.
3. Cicer is serologically distinct from all other genera but shows a closer affinity with Medicago (Trifolieae) than with other members of the Vicieae.

The significance of these findings, in relations to all other characters, will be discussed in Chapters 8, 9 and 10.

With regard to points 1 and 2 above, it is interesting to

recall that Kloz & Turkova (1963) found that species of Vicia have a slightly different legumin in their seeds from members of Lens, Pisum and Lathyrus, in which this protein is identical (see part 6.4.2.1). It is probable that the results of the analyses made by Jackson et al. (1967) would have thrown further light on this comparison of seed proteins in the Vicieae, had they been more fully described (part 6.4.1). With regard to point 3, it was surprising that a-gs of Ononis gave only a weak reaction against Cicer a-s (and, indeed, against Lens a-s), since Simola (1969) found that the spectra of Ononis and members of the Vicieae against Lathyrus a-g were quite similar (part 6.4.2.1). Since only a few seeds were available to produce the Ononis antigens, they were possibly rather weak, and the experiments should be repeated in the future.

These experiments represent only a small part of the investigations which are possible using Lens and Cicer antisera, and an even smaller part of a full serological analysis of the Vicieae. The conclusions which were reached should be confirmed by a fuller programme of experiments, using electrophoresis to permit a more detailed comparison of spectra. A wider range of samples of all the taxa studied would be a desideratum. It is certain that such an undertaking would be a worthwhile and rewarding project.

Chapter 7

CYTOGENETIC CHARACTERS OF THE VICIEAE

7.1. Introduction.

7.2. The karyotype.

7.3. Chromosome number relationships in the Papilionoideae.

7.4. Breeding systems.

7.5. Hybridisation.

7.1.

INTRODUCTION

No taxonomic study can be thought firmly based unless it takes into account the cytogenetic aspects of its subjects. Two kinds of important information are included here: firstly, the karyotype provides new morphological characters, and secondly, evidence of relationships may be gained through experimental cross-breeding of taxa. Unfortunately lack of time did not allow me to make my own studies in this field, and this chapter is therefore based entirely on the work of others, whose results are collated and summarised for use in taxonomy. The tribe Vicieae is popular for cytogenetic investigations, because its members have relatively large chromosomes and their haploid numbers are low. It has also been the focus of attention because several species are economically valuable. The following account is divided into four parts, dealing with the karyotype, with chromosome number relationships in the Papilionoideae, with breeding systems in the Vicieae and with hybridisation in the tribe.

7.2.

THE KARYOTYPE

Vicia. Investigations into the karyology of Vicia were pioneered by Sveshnikova (1927), who, having examined some thirty species, showed that the genus can be divided into two groups on the basis of chromosome morphology. Members of Sects. Cracca and

Key to Fig. 40.

Sect. Cracca

1. Vicia dumetorum
2. V. sylvatica
3. V. cassubica
4. V. villosa

Sect Ervum

5. V. tetrasperma
6. V. hirsuta

Sect. Vicia

7. V. oroboides
8. V. sativa
9. V. pannonica
10. V. anatolica

Sect. Faba

11. V. narbonensis
12. V. faba

Sources of Karyotype data:

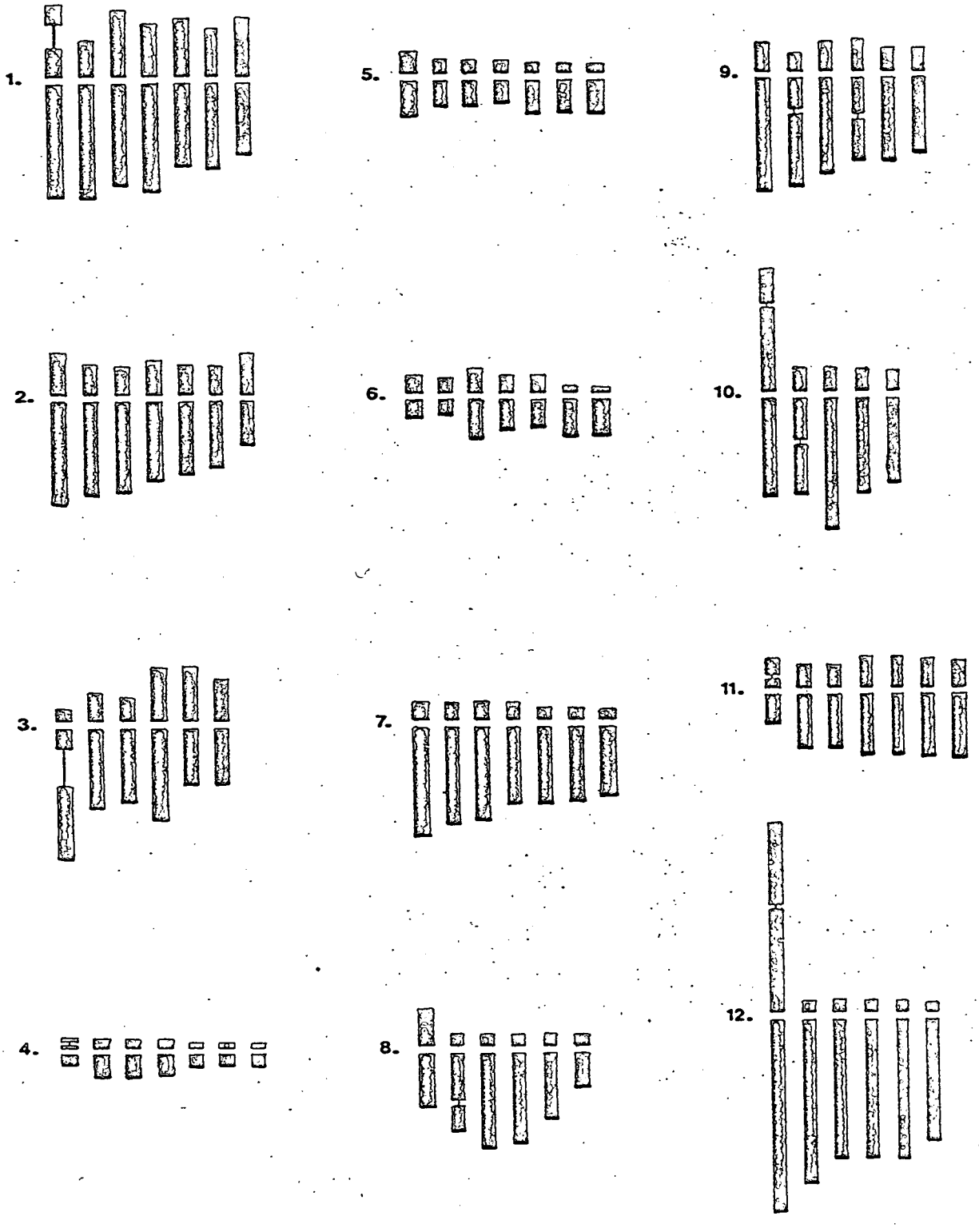
1 - 3, 8, 9. Hanelt & Mettin (1970b)

7. Hanelt & Mettin (1970a)

4 - 6, 10-12. Chooi (1971a)

Scale: length of chromosomes - x 3,000;
width of chromosomes - not to scale.

Fig. 40. Karyotypes in Vicia.



Ervum have relatively symmetrical chromosomes with median to submedian centromeres, while those of Sects. Vicia and Faba possess complements of mainly asymmetrical, acrocentric chromosomes. Although this distinction is not perfectly clear-cut, Sveshnikova's conclusions have been confirmed by many subsequent studies; idiograms of some representative species, taken from various sources, are illustrated in Fig. 40. This correlation between variation in karyotype morphology and the traditional infrageneric grouping of Vicia is a most significant discovery. It shows the success of classical taxonomy, based on morphological characters alone, in producing a classification with predictive value. Since karyotype variation follows the sectional limits so closely, these additional data cannot have much influence on broad taxonomic judgment, but the information is particularly useful in the case of certain anomalous species. For example, V. oroboides is an isolated species which presents special difficulties for the taxonomist. In general facies it is reminiscent of the 'oroboid' members of Vicia Sect. Cracca and Lathyrus Sect. Orobus (see part 2.3.3.), but it possesses the 'key' characters of Sect. Vicia (very short peduncles, stipular nectaries, the style dorsally compressed and bearded on its abaxial side). Recent classifications include V. oroboides in Sect. Vicia (e.g. Ball, 1968). Hanelt & Mettin (1970a) made a special study of this species, and found that its karyotype comprises only acrocentric chromosomes (Fig. 40:7). Their results show that V. oroboides is karyologically unlike members of either Lathyrus or Vicia Sect. Cracca, and confirm the position of this species within Sect.

Vicia. It would be very interesting to know the karyotypes of V. bithynica and V. cappadocica; both of these species have an unsettled taxonomic history (part 2.3.3), and additional data of this kind would probably prove valuable towards achieving a more certain view of their relationships.

The karyotypes of many species of Vicia have been investigated, and it appears that most haploid complements contain one chromosome with a secondary constriction. However, several species have none of this chromosome-type, while others have two per haploid complement.

Only two American species of Vicia have had their karyotypes worked out in detail, V. graminea (Mettin & Hanelt, 1968) and V. americana (Gunn, 1968a). Their chromosomes were found to be mainly symmetrical, like those of members of Sect. Cracca.

The most common base number in Vicia is seven, as reported by Sveshnikova (1927). However, throughout the genus there are many examples of species with x=6 and a few with x=5, and polyploidy is found in a few members. Table 20 summarises the distribution of known chromosome numbers. Several general observations can be made from this table. Firstly, the chromosome base numbers 6 and 5 occur equally in Sects. Cracca and Vicia, and in both perennial and annual species. Secondly, all members of Sect. Ervum have the high number x=7. Thirdly, polyploidy is apparently confined to Sect. Cracca, and is known only in perennials. The base number of these polyploids may be six or seven. Mettin (1958) and Hanelt & Mettin (1964, 1966) carried out a detailed cytotaxonomical study of the V. sativa

complex, and concluded that V. sativa s.l. contains six micro-species which comprise a descending dysploid series (2n=14 ⟶ 2n=12 ⟶ 2n=10). These taxa are listed in Table 20. These authors (Mettin & Hanelt, 1968; Hanelt & Mettin, 1970b) also describe the scattered occurrence in Sect. Cracca of perennials with low chromosome numbers (V. semiglabra, V. canescens subsp. variegata: 2n=10; V. pisiformis, V. cassubica, etc.: 2n=12); they consider them to be examples with relatively advanced karyotypes. Činčura (1970) takes the opposite viewpoint in the case of certain annual members of Sect. Vicia. Having studied V. hybrida (n=6), V. melanops (n=5) and V. anatolica (n=5), he concluded that there has been an increase in base number within this group from five to six; V. hybrida was thought to have evolved from an ancestor whose karyotype contained n=5 chromosomes. On the other hand, Chooi (1971a) considers it is more likely that this group of species shows a descending dysploid series comparable with that of the V. sativa complex. These conflicting views are mentioned again in part 7.3. Chooi (1971a) has also pointed out the striking difference in chromosome number and morphology between the closely allied V. narbonensis and V. faba. The former has the haploid number n=7, and its chromosomes are unusual within the group 'Sect. Vicia - Sect. Faba' in being relatively symmetrical (Fig. 40:11). V. faba, in contrast, has n=6 and a unique karyotype consisting of five acrocentric and one very long symmetrical chromosomes (Fig. 40:12). A full cytogenetical investigation of the other members of Sect. Faba - V. galilaea, V. hyaeniscyamus and V. bithynica - is obviously

Table 20. Chromosome numbers in Vicia.

SPECIES	ANNUAL (A) or PERENNIAL (P)	2n	DNA VALUE
Sect. Cracca			
V. unijuga	P	12, 24, 36	36
V. japonica	P	24	
V. amoena	P	12, 24	
V. dumetorum	P	14	56
V. pisiformis	P	12	50
V. sylvatica	P	14	65
V. cassubica	P	12	31
V. orobus	P	12	40
V. canescens subsp. variegata	P	10	
V. semiglabra	P	10	
V. biennis	A/biennial	14	22
V. cracca s.l.	P	14, 28	40 (2n = 28)
V. alpestris	P	28	
V. neglecta	A	12	35
V. benghalensis	A	14	26
V. villosa s.l.	A	14	
V. articulata	A	14	45
Sect. Ervum			
V. hirsuta	A	14	30
V. meyeri	A	14	47
V. disperma	A	14	25

Table 20, continued

SPECIES	ANNUAL (A) or PERENNIAL (P)	2n	DNA VALUE
V. tetrasperma	A	14	28
V. pubescens	A	14	20
Sect. Faba			
V. bithynica	A	14	34
V. narbonensis	A	14	55
V. faba	A	12	100
Sect. Vicia			
V. oroboides	P	14	
V. sepium	P	14	35
V. grandiflora	A	14	25
V. sativa complex:			
V. pilosa	A	14	19
V. amphicarpa	A	14	
V. angustifolia	A	12	23
V. macrocarpa	A	12	19
V. sativa	A	12	20
V. cordata	A	10	17
V. lathyroides	A	12	20
V. peregrina	A	14	71
V. michauxii	A	14	62
V. galeata	A	14	32
V. pannonica	A	12	51
V. hybrida	A	12	51

Table 20, continued

SPECIES	ANNUAL (A) or PERENNIAL (P)	2n	DNA VALUE
V. hyrcanica	A	12	51
V. melanops	A	10	86
V. anatolica	A	10	56
American species			
V. graminea	A	14	
V. americana	P	14	

Table 20 is compiled from data taken from Gunn (1968a), Mettin & Hanelt (1968), Hanelt & Mettin (1970b) and Chooi (1971a). The DNA values are those of Chooi; the figures are arbitrary units, and show the relative amount of DNA contained in each somatic cell, where the standard is V. faba: DNA value = 100. The figures are slightly simplified by being given to the nearest integer.

an important necessity.

Hanelt & Mettin (1970b) found that the average total length of chromosomes in the karyotype of several members of Sect. Cracca is about 45μ. Among the annuals of Sect. Vicia they found species with very low values, and others with high values. Thus, the average total length of the karyotype in V. sativa was estimated at c. 25μ, while V. peregrina and V. anatolica have very long chromosomes. The subject of chromosome size and DNA content was studied in greater detail by Chooi (1971, a & b). This author measured the amount of DNA per cell in 45 species, using a photometric method; his results are reproduced in Table 20. Chooi found that DNA content is generally proportional to chromosome size. Within Vicia there is a six-fold variation in average DNA content per cell; Sects. Cracca and Ervum both contain a continuous range of values, but in Sects. Vicia and Faba the species fall into two disjunct groups which are characterised, respectively, by a low and a high amount of DNA per cell. These results support the findings of Hanelt & Mettin, mentioned above. Chooi argued that since the range of DNA content per cell is wider in the relatively specialised sections Vicia and Faba, than in the more primitive Sect. Cracca, morphological advancement has been accompanied by evolutionary increase in DNA content per cell. Senn (1938a) has commented that the Vicieae (excluding Cicer) have probably the largest chromosomes within the Papilionoideae, and so it is reasonable to suppose that this upward trend has continued within Vicia to culminate in some specialised annuals (V. faba, V. melanops,

V. anatolica, V. peregrina). On the other hand, there may simultaneously have been an evolutionary reduction in chromosome size and DNA content per cell, in annuals like V. sativa s.l. (Hanelt & Mettin, 1970b), and in Sect. Ervum (see Fig. 40:5 & 6, and Table 20).

Lathyrus. The basic chromosome number in Lathyrus is seven. All wild annual species apparently are diploid, and this is also the rule amongst perennials (Darlington & Wylie, 1955; Löve & Löve, 1971). Exceptions are L. pratensis, which has both diploid and polyploid races (Simola, 1964), and L. palustris, with 2n=42. The few S. American species which have been investigated were found to be diploid (Senn, 1938b), while polyploidy is thought to be quite common among the N. American members of this genus (Hitchcock, 1952).

Investigations of chromosome morphology in Lathyrus are much fewer than in Vicia. The two main works on this subject are those of Senn (1938a) and Davies (Ph. D. thesis, 1958). With the author's permission, the following summary is taken from the latter, where the karyotypes of about thirty species are described in detail. Although there is some difference between the complements of individual members of Lathyrus, the variation is slight. If the species are arranged in order of decreasing overall chromosome length, perennial species (e.g. L. pisiformis, L. latifolius) are found to have the longest complements, while annuals (e.g. L. clymenum, L. angulatus) have the shortest. This may be evidence that there has been an evolu-

Key to Fig. 41.

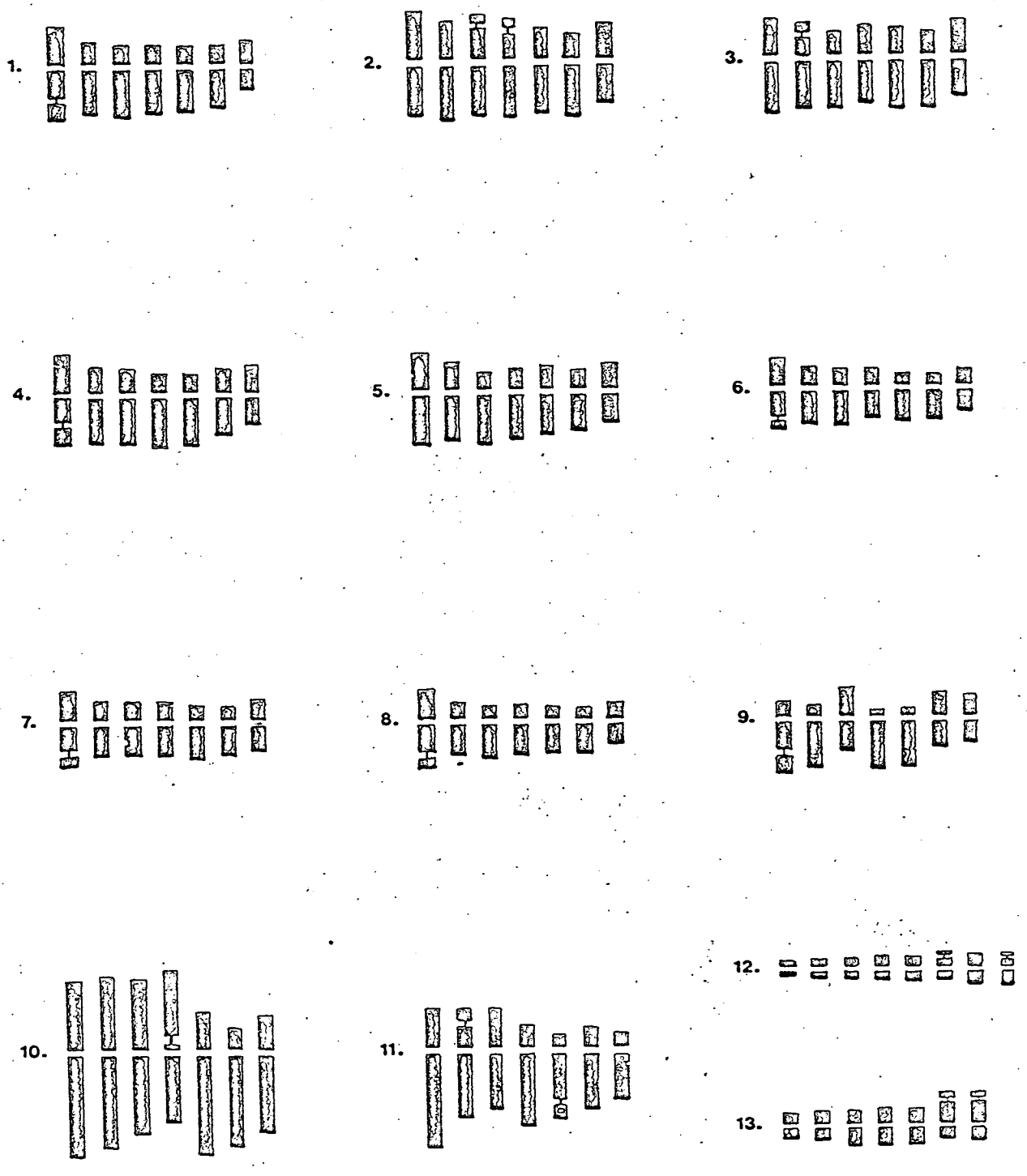
1. *Lathyrus vernus*
2. *L. pisiformis*
3. *L. latifolius*
4. *L. pratensis*
5. *L. hirsutus*
6. *L. angulatus*
7. *L. nissolia*
8. *L. aphaca*
9. *L. ochrus*
10. *Lens culinaris*
11. *Pisum sativum*
12. *Cicer arietinum*
13. *C. microphyllum*

Sources of karyotype date:

1. - 9. Davies (1958)
10. Mettin (1960)
11. Koller (1938)
12, 13. Iyengar (1939)

Scale: length of chromosomes - x 3,000;
width of chromosomes - not to scale.

Fig. 41. Karyotypes in Lathyrus, Lens, Pisum and Cicer.



tionary reduction in the average total chromosome length in Lathyrus. However, there is a complete gradation from one extreme to the other, and perennials are not sharply separated from annuals. The great majority of species have chromosomes with median or sub-median centromeres (Fig. 41). Davies agreed with Senn in finding that only in the small section Clymenum are there markedly asymmetrical chromosomes (e.g. L. ochrus, Fig. 41:9). In most species there is one chromosome with a secondary constriction per haploid complement; L. sativus and L. pisiformis are unusual in the genus in having two, while L. odoratus and L. hirsutus appear to have none.

Lens. The basic chromosome number in Lens, as reported by many authors, is seven. Literature dealing with the chromosome morphology of its species is very limited, and I have found only one description of the karyotype of L. culinaris, that of Mettin (1960) which is reproduced in Fig. 41:10. The idiogram shows that this species has very symmetrical chromosomes, and the overall length of the complement seems to be high in comparison with those of annuals of Lathyrus and of Vicia Sect. Ervum (the two areas of the Vicieae with which Lens has frequently been linked by taxonomists). However, since chromosome length is greatly influenced by variations in preparation techniques it is unwise to compare estimates of length by different authorities; one would very much like to see a karyological investigation of a representative selection of species from each genus of the tribe, performed as a single uniform experiment.

Pisum. In the first half of this century, Pisum was very popular as material for genetic studies (an attribute which the genus had acquired by being involved in Mendel's famous experiments), and there are consequently many papers describing the inheritance in Pisum of contrasted characters and of translocations between chromosomes, e.g. Håkansson (1929), Sansome (1933). Despite this, the karyotype as a whole has been rarely represented. Fig. 41:11 shows the idiogram of P. sativum, taken from Köller (1938). The complement comprises seven more-or-less symmetrical chromosomes, and has two secondary constrictions. The karyotypes of Vavilovia species are unfortunately unknown.

Cicer. Van der Maesen (1972) has recently given an account of cytogenetic investigations of Cicer up to the present, and has himself made a number of chromosome counts. Contandriopoulos et al. (1972) independently confirm some of these observations and provide other new counts. The results of these workers and of their predecessors are summarised in the following table.

Chromosome numbers reported in Cicer.

SPECIES	ANNUAL (A) or PERENNIAL (P)	2n	AUTHORITY
C. anatolicum	P	14	van der Maesen (1972)
		16	van der Maesen (1972)
			Contandriopoulos et al. (1972)
C. arietinum	A	14, 16	many authorities, see van der Maesen (1972)

C. bijugum	A	16	van der Maesen (1972)
C. chorassanicum	A	16	Podlech & Dieterle (1969)
C. cuneatum	A	16	van der Maesen (1972)
C. floribundum	P	14	Contandriopoulos et al. (1972)
C. heterophyllum	P	16	Contandriopoulos et al. (1972)
C. incisum	P	16	van der Maesen (1972), Contandriopoulos et al. (1972)
C. isauricum	P	16	Contandriopoulos et al. (1972)
C. judaicum	A	16	van der Maesen (1972)
C. microphyllum			
(as C. songaricum)	P	14	Iyengar (1939)
C. montbretii	P	16, 24	van der Maesen (1972)
		16	Contandriopoulos et al. (1972)
C. pinnatifidum	A	16	Avdulov (1937)
C. pungens	P	14	van der Maesen (1972)

This shows that the haploid chromosome number in Cicer varies from seven to eight, and the latter appears to be more common. There is no correlation between this variation and the perennial/annual habit, or with the region of origin of the species (van der Maesen, 1972). Fig. 41:12 & 13 illustrates idiograms of C. arietinum and C. microphyllum (as C. songaricum), taken from Iyengar (1939). The chromosomes all have median or submedian centromeres, and both complements are distinguished by the possession of two secondary constrictions. (This characteristic has not been confirmed by other workers.) The overall

lengths of the chromosome complements of these species appear to be markedly less than those of most members of the rest of the Vicieae.

7.3.

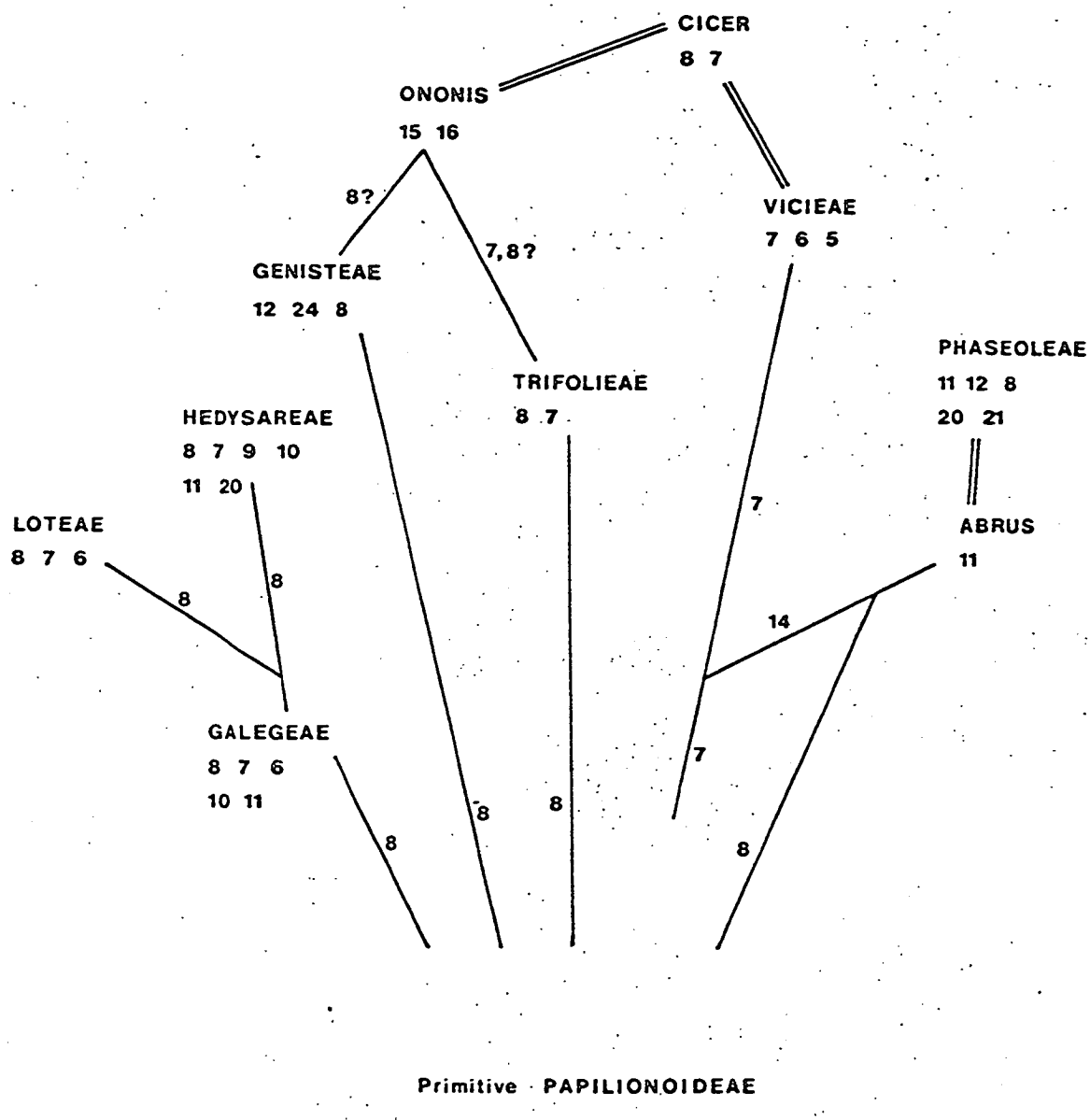
CHROMOSOME NUMBER RELATIONSHIPS IN THE PAPILIONOIDEAE

The chromosome numbers of the Papilionoideae were listed by Senn (1938b), who also discussed the value of these data in relation to phylogeny. Fig. 42 is a diagrammatic representation of his main conclusions, reproduced from this paper. The most common haploid chromosome number in the subfamily is eight, and I agree with Senn in accepting this as the most probable primitive base number. The Vicieae are very unusual in having predominantly x=7. The diagram shows that Abrus, which was for some time thought to be a member of the Vicieae (part 2.2), posseses n=11 like most of the Phaseoleae, a tribe with which it also has several morphological features in common.

The fact that 'n=8' is unknown in Vicia, Lathyrus, Pisum and Lens, but is predominant in Cicer, seems very significant. The numbers characteristic of Cicer provide a similarity between this genus and the Trifolieae and emphasise its distinctness from the rest of the Vicieae.

If it is true that a haploid complement of eight chromosomes is the primitive condition within the Papilionoideae, it seems very likely that the lower numbers in the Vicieae (7, 6, 5) have arisen by descending dysploidy. The evidence within Vicia itself is equivocal on this point, and different authors

Fig. 42. Hypothetical phylogenetic relationships in the Papilionoideae (after Senn, 1938).



The numbers are haploid chromosome numbers.
The lines indicate probable relationship; double lines show closer relationship than single ones.

have placed opposite interpretations on the facts (part 7.2).

As Fig. 42 shows, Senn followed Popov (1928) in believing that the relationship between Cicer and the rest of the Vicieae is a recent one and is not connected with the origin of the stock of Vicia and Lathyrus. He thought that Cicer arose as a hybrid genus (sic !) between Vicia and Ononis, and that the latter was derived at an even earlier period from a cross between the Genisteae and Trifolieae (see parts 2.7 and 9.2). A consideration of the chromosome numbers of Ononis does not shed much light on the situation. The genus is unusual within the subfamily in being apparently wholly polyploid, and the haploid number, according to the several authors who have reported chromosome counts, is 15 or 16.

In conclusion, a broad survey of chromosome numbers in the Papilionoideae shows that Vicia, Lathyrus, Lens and Pisum (and presumably also Vavilovia) together form a distinct and isolated group. The possession of the haploid number n=8 separates Cicer from these genera. On the other hand, the data is insufficient, in itself, to suggest an alternative taxonomic arrangement, or to make possible a sound phylogenetic hypothesis explaining the origin and relationships of these groups.

7.4.
BREEDING SYSTEMS

The flowers of the Vicieae are well adapted to pollination by bees, as described in part 4.3, but while many species are allogamous there is a strong tendency towards inbreeding

within the tribe. According to Hanelt & Mettin (1970b), perennials of Vicia Sect. Cracca are habitually cross-pollinated by Hymenoptera, and it is thought that self-incompatibility mechanisms may be present in these species. Certainly, solitary plants of many perennial members of the Vicieae grown at Edinburgh have very poor seed-set. In contrast, all annuals produce seeds in abundance; this is due partly to pollination by bees, and partly to self-fertilisation, the proportion of allogamy to autogamy varying with the species and with environmental circumstances. Plitmann (1967) carried out bagging experiments on annual members of Vicia and found that many produced seeds autogamously; in some the flowers tended to degenerate; and in a few no fruit were formed. V. faba was among the latter category. However, Hanelt & Mettin (1970b) found that outcrossing in this species was only 30-50%, and showed that the plants were not self-incompatible. It seems probable that most, if not all, annuals of this tribe are self-compatible, and as the anthers mature while the flower is still in bud and they are clustered round the stigma, self-pollination is very likely to occur. According to Proctor & Yeo (1973), the stigma becomes receptive when its papillae have been damaged, which is usually effected by a visiting insect; this would explain why V. faba did not set seed from bagged flowers although it was self-pollinated and self-compatible. A few species (e.g. Vicia sativa subsp. amphicarpa, V. pubescens, Lathyrus gloeospermus) have inconspicuous flowers with vestigial corollas, and are obviously cleistogamous; but cleistogamy is probably quite a common phenomenon among annuals,

even those with attractive flowers (e.g. Lathyrus nissolia).

7.5.
HYBRIDISATION

There are many reports of successful crosses having been made or found between members of the Vicieae, including even intergeneric hybrids; a list is given in Plitmann (1967). However, having reviewed the literature, Schelhorn (1940) concluded that few of these claims are reliable and that hybridisation within the Vicieae is in general very restricted. More recent, carefully controlled experiments have confirmed this opinion. Senn (1938a) used seventeen species of Lathyrus, and Pisum sativum, in 458 attempts at interspecific and intergeneric crosses. In a very few cases pods were formed, sometimes containing shrunken seeds, but no F1 hybrid offspring were produced. Davies (1958) also attempted to cross species within Lathyrus. In some instances the style of the maternal parent was cut short to facilitate the growth of the pollen tubes and increase the chance of fertilisation. In most cases hybridisation proved impossible, but there were a few successes: L. odoratus x L. hirsutus, which had been reported by previous workers; L. clymenum x L. articulatus; and L. clymenum x L. ochrus. It is interesting to note that L. odoratus and L. hirsutus have traditionally been placed in different sections (Lathyrus and Cicercula, respectively), but that Davies found they share a karyotype which is apparently unique within Lathyrus in having no chromosomes with a secondary constriction (see part 7.2 and Fig. 41:5). L. clymenum

and L. articulatus are phenetically so similar that Davis (1970) reduced them to subspecies of L. clymenum, and it is not surprising that they are capable of hybridisation. On the other hand, although L. ochrus is in Sect. Clymenum, it is very distinct from L. clymenum. According to Davis (1970), two closely-related members of Sect. Lathyrostylis, L. variabilis and L. spathulatus, are found to hybridise in nature.

In contrast to the situation among Old World members of Lathyrus, those native to N. America are capable of considerable interspecific hybridisation. This was shown by Hitchcock (1952), who recorded successful crosses between both diploid and tetraploid species pairs; examples are L. splendens x L. jepsonii and L. lanszwertii x L. arizonicus. He concluded that such hybridisations occur quite frequently in nature, and account for the difficulty of specific delimitation in this area. There is no information about hybridisations among S. American species of Lathyrus, but as they form a complex parallel to that of the northern continent, it seems likely that crossing is possible.

Within Vicia hybridisation is thought to occur only rarely, and then between the members of the taxonomically difficult complexes, e.g. V. cracca agg., V. villosa agg. and V. sativa agg. Hanelt & Mettin (1964) showed that hybridisation is possible between most of the microspecies of the V. sativa complex, but it is difficult in some combinations.

The case of the reported hybrid between Lens culinaris and Vicia sativa is particularly interesting as an example of a long-perpetuated misidentification. This 'hybrid', known as

Vicia leganyana, was studied by many workers including Moritz & Vom Berg (1931), who confirmed its postulated origin using serological methods.. However, more recently Mettin (1960) attempted to resynthesise V. leganyana, but failed. He found that the karyotype of the 'hybrid' was essentially similar to that of V. sativa and consequently quite unlike that of Lens culinaris (Figs. 40:8 and 41:10). Mettin concluded that V. leganyana is merely a flat-seeded mutant form of V. sativa, possibly adapted as a weed of lentil crops. In fact, this particular example of parallel mutations in related species was recognised by Vavilov (1922) as one of the best illustrations of his 'Law of Homologous Series in Variation'.

Chapter 8

THE DELIMITATION OF THE TRIBE VICIEAE

8.1. Discussion.

8.2. Description of the tribe Vicieae.

8.1.

DISCUSSION

The tribe Vicieae was first characterised by De Candolle (1825), who recognised three 'key' attributes:

1. Germination hypogeal.
2. Primordial leaves alternate, not opposite.

(These two characters are reflections of the same condition, and essentially represent only one.)

3. Leaves paripinnate and tendrillous.

It included seven genera, whose members are nowadays classified within Vicia, Lathyrus, Lens, Pisum, Vavilovia and Cicer (see part 2.2).

The delimitation of the tribe has remained constant since then, apart from the temporary inclusion of Abrus; but despite this apparent stability, its naturalness has occasionally been questioned, and in every case the doubt has centered upon Cicer. De Candolle himself remarked upon the similarity between Cicer and Ononis, and Gams (1924) stated that he considered this affinity was stronger than the link between Cicer and other members of the Vicieae. Popov (1928), in his monograph of Cicer, showed this phenetic relationship very clearly; but his hypothetical interpretation of the problem is wholly unacceptable in the light of present knowledge (cf. part 2.7.). The question of the delimitation of the Vicieae is therefore still open to debate.

Table 21 is a list of all the characters which link, or

show a contrast between, Cicer and the rest of the Vicieae. The 'differences' were simple to compile from a perusal of Chapters 3 to 7, but the 'similarities' presented some difficulty, for the following reason. A character found in the same state in Cicer and the rest of the tribe is only relevant here if it occurs in a different state in a taxon outside the tribe which is considered to be closely related to the Vicieae. The number of 'similarities' can be swelled or diminished, depending on judgments about a wide area of the Papilionoideae. For example, if the pulvinate-leaved tribe Phaseoleae were considered to be a candidate for affinity with Cicer, it would be worth noting "leaves epulvinate" as a feature consolidating the Vicieae. In practice, only the Trifolieae and Ononis appear to be close neighbours, and so the 'similarity' characters have been chosen with these groups in mind.

The most striking aspect of Table 21 is the large number of contrasting characters which distinguish Cicer from the rest of the Vicieae. This is particularly significant considering that Vicia, Lathyrus, Lens, Pisum and Vavilovia comprise some 300 species and a wide spectrum of variation; despite this range, there are relatively few characters which divide the tribe in any direction besides Cicer versus the rest.

Some of the characters should be qualified here, in addition to their description in an earlier chapter. It was mentioned in parts 2.7 and 4.2.4 that variation in the form of filaments and anthers was considered by Bentham & Hooker (1865)

Table 21. Comparison between Cicer and the rest of the Vicieae.

	CHARACTER		REFERENCE
	SIMILARITIES		
1.	Germination hypogeal.		3.1, Fig. 25.
2.	Mature leaves usually tendrillous.		3.2.
3.	Mature leaves usually multijugate.		3.5.
4.	Stipules free from petiole.		3.6.
5.	Smooth-walled simple hairs present.		3.7, Fig.5, Table 9.
6.	Flowers contain unusual 3,5-diglucosides.		6.2.
7.	Seeds contain legumin and vicilin.		6.4.2.1.
	DIFFERENCES		
	Cicer	Rest of Vicieae	
8.	Juvenile leaves imparipinnate.	Juvenile leaves paripinnate.	3.1, Fig.1.
9.	Venation craspedodromous.	Venation brochidodromous.	3.4, Fig.2.
10.	Leaflets serrate.	Leaflets entire.	3.5, Fig.2.
11.	Long-stalked glandular hairs present.	Long-stalked glandular hairs absent.	3.7, Fig.5, Table 9.
12.	Vexillum ovate, without strong folds or bosses.	Vexillum various, often sharply folded and bossed.	4.2.3.1, Figs. 10 to 18.
13.	Wings free from keel.	Wings adnate to keel.	4.2.3.1.

Table 21, continued

	Cicer	Rest of Vicieae	
14.	Vexillary stamen free from staminal tube.	Vexillary stamen lightly fused to staminal tube.	4.2.4, Figs. 10 & 18.
15.	Style terete, glabrous.	Style dorsally or laterally compressed, pubescent below stigma.	4.2.5, Figs. 18 & 21.
16.	Pod inflated.	Pod compressed or rarely sub-torulose, never inflated.	4.4, Figs.22 & 23.
17.	Seeds beaked above hilum.	Seeds not beaked.	4.5.2, Fig. 24.
18.	Post-chalazal vascular bundle bifurcated.	Post-chalazal vascular bundle undivided.	4.5.4, Fig. 24.
19.	First plumular leaf varies in position.	First plumular leaf always on convex side of seedling.	5.2.1, Fig. 25.
20.	Radicle has variable direction of growth.	Radicle has constant direction of growth.	5.2.1, Fig. 25.
21.	Cotyledons inserted at 180° on seedling axis.	Cotyledons inserted at 120° on seedling axis.	5.2.1.
22.	Transition region is in hypocotyl.	Transition region is in epicotyl.	5.2.2.
23.	No cortical bundles in the stem.	Cortical bundles present in stem.	5.2.4, Figs. 28 & 29.
24.	Leaf insertions separated.	Leaf insertions interlocked.	5.5, Figs. 34 & 35.
25.	Haploid chromosome number: n = 8 (sometimes 7).	Haploid chromosome number: n = 7 (sometimes 6, 5).	7.3.

to be important evidence linking Ononis with the Genisteae rather than the Trifolieae, and that Popov (1928) also used characters derived from the androecium to link Cicer with Ononis rather than with Vicia. However, since dilated filaments (part of the 'androecial syndrome' of Cicer and Ononis) are found in Pisum and Vavilovia and, rarely, in Trifolium, I have not brought this data into the debate.

Character 24, which concerns patterns of stem vasculature, needs to be substantiated by further studies, and therefore has only slight value here.

The results of my serological experiments are not shown in the table. As was discussed in part 6.4.2.4, Cicer appeared to be serologically quite distinct from all the genera with which it was compared, both in the Vicieae and other tribes, while the other members of the Vicieae showed a strong group affinity. There appeared to be a closer serological relationship between Cicer and Medicago (in the Trifolieae) than between Cicer and Vicia, etc. - but this conclusion was based on very limited evidence. The heterologous reactions produced by Ononis antigen to antisera of both Cicer and Lens were indistinct, but it is not known whether this was due to lack of affinity or to poor experimental material.

When the evidence of all the characters listed in Table 21 is weighed up, the Vicieae are revealed as a very heterogeneous group. If, however, Cicer is removed, the range of variation within the tribe is significantly reduced; its

delimitation from all other taxa of the same rank becomes much clearer; and its constituent genera form an association of unquestionable affinity. The effects of this alteration obviously result from the achievement of a 'natural' group, in contrast to the traditionally-defined Vicieae which were held together, not by the total of their attributes, but by two heavily-weighted 'key' characters (hypogeal germination and the presence of tendrils). I consider, therefore, that Cicer should be rejected as a member of the tribe, and that the Vicieae, as a natural unit, should comprise Vicia, Lathyrus, Lens, Pisum and Vavilovia.

8.2.

DESCRIPTION OF THE TRIBE VICIEAE

Perennial and annual herbs with erect or more usually climbing or sprawling habit; rootstock rarely tuberous. Indumentum of simple, smooth-walled hairs and short-stalked glandular hairs. Stems with cortical vascular bundles in the internodes, often winged; primary shoot almost always of limited growth, plants proliferating from basal nodes. Leaves alternate, distichous, hypostomatic, amphistomatic or epistomatic, paripinnate (very occasionally imparipinnate), tendrillous or mucronate; leaflets many-paired to unijugate, epulvinate; very rarely leaves phyllodic or reduced to a tendril (in Lathyrus); stipules semisagittate or hastate, sometimes with nectariferous spot. Vernation of leaflets conduplicate or supervolute. Venation brochidodromous, veins pinnate or parallel. Inflor-

escence rarely a panicle, usually a secund, axillary raceme or sometimes 1-flowered. Vexillum oblong, platynychioid or stenonychioid, sometimes pouched. Staminal tube diadelphous (vexillary stamen lightly adhering), truncate or oblique at apex; anthers introrse, versatile, of equal size, rarely alternate filaments dilated at apex. Style borne at right angle to ovary, usually compressed dorsally or laterally, always pubescent (distribution of hairs various), sometimes spathulate, sometimes contorted; stigma terminal, occasionally double. Legume more-or-less linear, compressed, 2-many-seeded, usually dehiscent, sometimes winged, rarely with woolly or membranous partitions between seeds. Seeds compressed-spherical, with long to short hilum; testa smooth or variously rough-textured; lens near hilum or rarely opposite; vascular bundle not branched, continuing past the chalaza; endosperm absent. Germination hypogeal; first scale-leaf borne on side of plumule away from cotyledons.

Chapter 9

THE STATUS AND RELATIONSHIPS OF CICER WITHIN THE PAPILIONOIDEAE

9.1. Discussion.

9.2. Phylogenetic speculation on the origin of *Cicer*.

9.1.

DISCUSSION

Having excluded Cicer from the Vicieae, an alternative and more justifiable taxonomic position must be found for this genus within the Papilionoideae. The only other groups to which Cicer shows a strong affinity are the Trifolieae and Ononis, which Hutchinson (1964) has recently separated from the former and placed in a tribe of its own (see part 2.7). Table 22 lists the characteristics of Cicer and indicates the extent of its phenetic similarity with these taxa.

Several other features should be mentioned here in addition to those summarised in the table. The members of the Trifolieae (sensu Hutchinson) are exclusively trifoliolate, except for Trifolium Sect. Lupinaster, whose species have palmately 7- and 5-foliolate leaves. In Ononis the majority of species have trifoliolate leaves at the base of the plant and reduced, unifoliolate leaves above which form bracts subtending the flowers; O. rotundifolia is unusual in having multijugate leaves. In contrast, most species of Cicer have many-paired leaves and only C. chorassanicum is trifoliolate. Thus a particular number of leaflets per leaf is strongly characteristic (differential) for each of these three groups, but is not strictly diagnostic.

The genera Cicer and Ononis share tendencies towards woodiness and a xerophytic production of spines from stipules, leaflets and (in Cicer) from the leaf-rhachis. The Trifolieae, on the other hand, in general comprise herbaceous species.

One of the features thought most important in the past in demonstrating a connection between Cicer and Ononis was the similarity of their androecia (characters 11 and 12). However, as was pointed out in part 4.2.4, these traits are found to a slight extent in neighbouring groups (Pisum and Trifolium) and their significance in indicating close taxonomic relationships must not be over-estimated.

As was described in part 5.2.1, I found that the position of the first leaf in germinating seeds of Cicer pinnatifidum and Trigonella foenum-graecum varies in relation to the hilum, whereas in the Vicieae s.s. it is constant. The behaviour of Ononis and the rest of the Trifolieae in this respect is unknown, and it might perhaps be of some significance in the present context.

The limited serological experiments which I carried out using Cicer arietinum antiserum indicated that while Cicer is very distinct from all neighbouring taxa, its seed storage proteins show a greater affinity with those of Medicago orbicularis than with those of members of the Vicieae. The double-diffusion spectra obtained using Ononis antigens were very faint, but the reasons for this were uncertain (see part 6.4.2.4). These results are most interesting, but it would be unwise to give them much weight in the present debate since confirmation by further experiments is necessary.

Table 22 shows clearly the strong affinity which Cicer has with both the Trifolieae and Ononis; the number of characters which link Cicer and the true Vicieae are, by compari-

Table 22. Characters of the genus Cicer.

		CHARACTER	REFERENCE
Ci.	1.	Germination hypogeal.	3.1, Fig. 25.
Ci.	2.	Mature leaves usually paripinnate and tendrillous.	3.1, 3.2.
Tr. On.	3.	Leaflets serrate, with craspedodromous venation.	3.4, Fig.2.
Ci.	4.	Stipules free from petiole.	3.6.
Ci.	5.	Smooth-walled simple hairs present.	3.7, Fig. 5, Table 9.
Tr. On.	6.	Long-stalked glandular hairs present.	
(Tr.)Ci.	7.	Multicellular hairs absent.	
Tr. On.	8.	Vexillum obovate with no strongly-marked fold lines.	4.2.3.1, Fig. 18.
Tr. On.	9.	Wings free from keel.	
Tr.	10.	Androecium completely diadelphous.	4.2.4, Fig. 18.
(Tr.) On.	11.	Filaments dilated below anthers.	
On.	12.	Anthers alternately basifixed and versatile.	
Tr.	13.	Anthers uniform in size.	
Tr. On.	14.	Style terete, glabrous.	4.2.5.
On.	15.	Legume inflated.	4.4.
Tr. On.	16.	Seeds beaked above hilum.	4.5.2, Fig. 24.
Ci.	17.	Seeds not containing endosperm.	4.5.3.
Ci.	18.	Post-chalazal vascular bundle long, dichotomising.	4.5.4. Fig. 24.
Tr. On.	19.	Hilum small, almost circular.	4.5.6.
Tr. On.	20.	Cotyledons inserted at 180 on seedling axis.	5.2.1.
Tr. On.	21.	No cortical bundles in stem.	5.2.4.

Table 22, continued.

		CHARACTER	REFERENCE
Ci.	22.	Canavanine absent from seeds.	6.3.
Tr.	23.	Members diploid (as far as known).	7.3.
Tr.	24.	Haploid chromosome number: n = 8 (sometimes 7).	

Key: Tr. character-state typical of the Trifolieae;
On. character-state typical of Ononis;
Ci. character-state peculiar to Cicer.
Parentheses show a less definite association of the character-state and the taxon.

son, relatively few (cf. Table 2). Even so, Cicer is well defined from both the Trifolieae and Ononis by at least seven significant features including its hypogeal germination and the tendrillous leaves which have stipules free from the petiole. Despite earlier claims of a special relationship betwen Cicer and Ononis (by De Candolle, 1825 and Popov, 1928), the evidence in fact shows Cicer to have equal phenetic similarity with the Ononideae and the Trifolieae.

Cicer's taxonomic position must be influenced not only by the number of features it has in common with various alternative groups, but also by the present delimitation and variability of those taxa and the effect which its inclusion within one of them would have on the hierarchy.

The Trifolieae form a very well-defined, natural tribe comparable with the true Vicieae; and the Ononideae, since it contains only Ononis and the monotypic Passaea, is similarly limited in its internal variability. In these circumstances, neither tribe could absorb Cicer without profoundly altering its definition. The differential characters which distinguish between the Trifolieae and the Ononideae are of less weight than those separating these tribes from Cicer, so that if the creation of the Ononideae is considered justified, the inclusion of Cicer within the Ononideae cannot be upheld.

These arguments show that Cicer cannot properly be included within the Trifolieae s.l. any more than within the Vicieae. The most satisfactory course is to place Cicer in

a distinct tribe of its own. A taxon of this rank already exists, because Alefeld (1859), in his treatment of the Vicieae, raised this tribe to a subfamily and created within it the three tribes Ciceridae, Viciidae and Orobidae. I maintain that the Ciceridae should now be brought out of obscurity to take its place in the hierarchy with the Vicieae s.s., the Trifolieae and the Ononideae; it should be called the Cicereae Alefeld.

9.2.

PHYLOGENETIC SPECULATION ON THE ORIGIN OF CICER

Taxonomists have long recognised that Cicer is phenetically intermediate between the Vicieae and the Trifolieae s.l.; in particular, between Vicia and Ononis (cf. part 2.7). The theory which Popov (1928) put forward to explain Cicer's origin was based directly on this observation. He thought that Ononis and Vicia, isolated from each other by the Tethys sea until the Miocene epoch., then came into contact and by direct hybridisation produced Cicer; moreover, this author traced his sections back to F2 generation segregants of the original cross! This concept is completely untenable in the light of present knowledge of genetics, and even within the framework of the hypothesis itself; thus Popov envisaged on one hand that distinct genera interbred freely in the past; on the other, that second generation offspring of a cross maintained their identity, with only internal evolution, to the present! In fact, as was shown in section 7.5, interspecific hybridisation in the Vicieae

is rare and difficult, and inter-generic or intertribal crossing certainly impossible. Despite the obvious fallacy of Popov's ideas, they apparently have been accepted by some later taxonomists: he is referred to by Simola (1968a & 1969), and by Senn (1938b) who incorporated the hypothesis into his own phylogenetic tree of the Papilionoideae (Fig. 42).

Since the possibility of a hybrid origin for Cicer is excluded, the genus must have arisen monophyletically by a process of divergent evolution. In this case it is important to decide whether the phenetic similarity between Cicer and the two tribes Vicieae and Trifolieae is a reflection of phylogeny on both sides, or whether Cicer is related to one tribe by descent and only connected with the other by a coincidental convergence of characters.

Tables 21 and 22 show, respectively, the features which Cicer shares with each of the two tribes. In both cases the characters concerned are of great taxonomic weight: the unique combination of the presence of tendrils and hypogeal germination is surely indicative of a phylogenetic link with the Vicieae; the rare type of leaf venation and glandular indumentum similarly connect Cicer with the Trifolieae. In addition, evidence from serology supports a strong relationship between Cicer and both tribes. If Cicer did not exist, however, it is doubtful whether the Vicieae and Trifolieae would be considered closely related; they have very few common features, within the context of the whole subfamily. Each tribe is a well-defined entity, separated from others by its characteristic

syndrome of traits.

These facts suggest that during the evolution of this part of the Papilionoideae, far more extinction has occurred than is often contemplated. The tribes are well-defined because they are the sole survivors among many once-existing branches which arose from a common stock. Cicer is another such survivor; presumably it is at least as old as the Vicieae and Trifolieae, because it has characteristics of each; but as it is comparatively small in number of species, geographical range and diversity, taxonomists have found it more convenient to place Cicer within a neighbouring tribe than to recognise its true status.

Chapter 10

THE DELIMITATION OF GENERA WITHIN THE VICIEAE

10.1. Introduction.

10.2. The delimitation of *Vicia* and *Lathyrus*: the problem of the 'oroboid' species.

10.3. The delimitation and relationships of *Lens*.

10.4. The new genus *Anatropostylia*.

10.5. The relationship of *Pisum* and *Vavilovia* to the rest of the Vicieae.

10.6. Key to the genera of the Vicieae (emended definition).

10.1.

INTRODUCTION

From the discussion in Chapter 8 it was concluded that the tribe Vicieae should properly comprise the five genera Vicia, Lathyrus, Lens, Pisum and Vavilovia, but should exclude Cicer. The delimitation of these taxa in the past was dealt with in Chapter 2; now their validity will be re-examined in the light of all the data presented in Chapters 3 to 7.

The 'key' characters used to separate the genera within the Vicieae were summarised in Table 2. They are: the shape of the style and the distribution of hairs on it; the nature of the staminal tube; and the type of leaflet vernation. My own studies have confirmed the special usefulness of these characters, and have also shown the occurrence of many other kinds of discontinuous variability within the tribe which together add weight to traditional generic concepts in the Vicieae. This can best be illustrated by taking one by one the various areas of the group which have caused controversy in the past.

10.2.

THE DELIMITATION OF VICIA AND LATHYRUS: THE PROBLEM OF THE 'OROBOID' SPECIES

The two largest genera of the Vicieae, Vicia and Lathyrus, can generally be distinguished by many characters apart from the 'key' features mentioned above. For example, members of Vicia usually have multijugate leaves while those of Lathyrus have few

leaflets; winged stems and parallel venation are found commonly in Lathyrus but never in Vicia; Vicia usually has dense, many-flowered racemes, in contrast to the often 1- or 2-flowered inflorescences of Lathyrus. However, none of these attributes is diagnostic, and both genera comprise a wide range of variation in morphological and other characters.

Within each genus there is a group of species which closely resemble one another; they have etendrillous leaves with exceptionally broad leaflets and dense, many-flowered racemes. Species of this facies have been referred to as 'oroboid', since Linnaeus placed them together in the genus Orobus (see part 2.2). Examples of these are: Vicia crocea, V. unijuga, V. pseudo-orobus (Sect. Cracca); V. oroboides (Sect. Vicia); and Lathyrus aureus, L. vernus, L. davidii (Sect. Orobus). The geographical distributions of the oroboid species in Vicia and Lathyrus are very alike; in each case all members are natives of the Old World, are found almost exclusively in the Euro-Siberian region, and are concentrated in E. Europe and E. Asia. The similarity between Vicia and Lathyrus at this point is so striking that it has always cast doubt upon the separation of the two genera.

Table 23 summarises the features which link together and distinguish between the oroboid members of Vicia and Lathyrus. The last two characters in the table, which are new additions to the traditional 'key' characters, must be qualified. Members of Vicia Sect. Cracca typically have stipitate fruits, while those of Sect. Vicia are sessile. Lathyrus almost always has non-stipitate fruits. All oroboid species, except for V.

Table 23. The characteristics of the oroboid species.

	CHARACTER	REFERENCE
	SIMILARITIES	
1.	Erect, bushy habit.	4.1.
2.	Leaves etendrillous.	3.2.
3.	Leaflets large and broad, few pairs per leaf.	3.5, Figs. 3:1-5 & 4:1-3.
4.	Venation of leaflets reticulate (pinnate-brochidodromous).	3.4.
5.	Leaves hypostomatic.	3.8, Tables 8 & 11.
6.	Racemes dense, many-flowered.	4.1.
7.	Calyx teeth unequal	4.2.2.
8.	Vexillum oblong (type A).	4.2.3.1, Figs. 19:1 & 20:1.
9.	'Kink' in upper edge of wing petals but only some members of Lathyrus).	4.2.3.1.
10.	Seeds with long hilum.	4.5.6, Tables 13 & 14.
11.	All chromosomes with approximately median centromeres (except V. oroboides).	7.2. Fig. 40:7.
	DIFFERENCES	
	Vicia / Lathyrus	
12.	Leaflet vernation con-duplicate. / Leaflet vernation supervolute.	3.3.
13.	Staminal tube ending obliquely. / Staminal tube ending squarely.	4.2.4, Figs. 10:F, 13:F.

Table 23, continued.

DIFFERENCES

	Vicia	Lathyrus	
14.	Style pubescent all round.	Style pubescent on adaxial face.	4.2.5, Figs. 10:G, 12:F.
15.	Fruit stipitate (except V. oroboides).	Fruit sessile.	4.4, Fig. 22:1 & 7, Fig. 23:1.
16.	Seeds containing canavanine.	Seeds not containing canavanine.	6.3.

This character is not known for all relevant species.

oroboides, can therefore be separated into genera by this difference. The distribution of the free amino acid canavanine within the Vicieae is of great interest and is relevant to the present problem, but unfortunately not all the oroboid species have been screened for this character and so its inclusion in the list must be tentative. It is regrettable that my serological experiments were not extensive enough to make any contribution towards solving the problem of the oroboid species, for this is one area of the tribe where additional information is most needed. A serological project centred upon the oroboid members of Vicia and Lathyrus would almost certainly give worthwhile and interesting results.

The similarities shared by the oroboid species are partly obvious traits of gross morphology which contribute to the characteristic facies of this assemblage (Table 23:1 - 4,6), and partly character-states which have been shown to be relatively primitive within the two genera (7,8,10 & 11). In contrast, the characters which separate Vicia and Lathyrus are functionally unrelated and comparatively obscure, and in each pair of states there is evidence of specialisation within one or other genus. This difference in quality between the 'similarity' and 'difference' characters is a significant factor when one is attempting to make a taxonomic judgment about the species concerned, for it throws a bias across the evidence. It suggests that although the 'differences' are outnumbered by the 'similarities', they are in fact of proportionally greater importance.

It seems quite possible that the vegetative oroboid facies

was evolved independently in each genus, phylogenies proceeding in a parallel manner to produce a bushy habit and similar types of leaf in response to similar mesophytic temperate forest habitats. The fact that V. oroboides (an otherwise typical member of Sect. Vicia) also possesses these vegetative features supports this idea, since it suggests that even within Vicia the oroboid group is polyphyletic. On the other hand, the consistent correlation of the four or five contrasting character-pairs in separating Lathyrus and Vicia is worthy of considerable taxonomic weighting. On balance, I consider that the maintenance of these two genera as discrete taxa is fully justified.

10.3. THE DELIMITATION AND RELATIONSHIPS OF LENS

As was described in Chapter 2, there has been more controversy in the past over the nature and position of Lens than about any other part of the Vicieae. The history of its classification is summarised in Table 5, which shows the subsequent treatment by various taxonomists of Linnaeus' genus Ervum; but that this is not the complete story can be seen from Table 4, where lentils are grouped as a subgenus of Lathyrus. Very recently Radzhi (1971) has returned to Linnaeus' original arrangement, placing ervoid species of Vicia together with Lens in Ervum.

The problem of Lens in some ways parallels that of the oroboid members of Lathyrus and Vicia: here again the taxonomist is faced with a conflict between, on one hand, characters

Table 24. Comparison between Lens and Vicia Sect. Ervum s.l.

	CHARACTER		REFERENCE
	SIMILARITIES		
1.	Plants small; weeds.		
2.	Leaves with few pairs of small, ovate leaflets.		3.5.
3.	Vernation of leaflets conduplicate.		3.3.
4.	Leaves epi-amphistomatic		3.8, Table 11.
5.	Inflorescence few-flowered.		4.1.
6.	Flowers small, pale and inconspicuous (except *Lens montbretii*).		4.2.3.1, 4.2.3.2.
7.	Staminal tube ending obliquely.		4.2.4.
8.	Haploid chromosome number : n = 7.		7.2.
	DIFFERENCES		
	Lens	*Vicia* Sect. *Ervum*	
9.	Calyx teeth much longer than tube.	Calyx teeth equal to or shorter than tube.	4.2.2, Fig. 16.
10.	Standard stenonychioid (type C), with bosses.	Standard various shapes, never bossed (except *V. caesarea*).	4.2.3.1, Fig. 16, Table 12, Fig. 19.
11.	Style dorsally compressed, pubescent on adaxial side.	Style compressed dorsally or laterally, or terete, ± pubescent all round.	4.2.5. Fig. 16 Table 12.
12.	Fruit characteristically shaped.	Fruit never as in *Lens*.	4.4. Fig. 22.
13.	Seeds flattened, lenticular.	Seeds never lenticular (except *V. caesarea*).	4.5.2.

Table 24, continued.

DIFFERENCES

	Lens	Vicia Sect. Ervum	
14.	Chromosomes relatively long.	Chromosomes relatively short.	7.2, Figs. 41:10 & 40:5 & 6.
	This character is not known for all relevant species.		
15.	Seeds not containing canavanine.	Seeds containing canavanine.	6.3.
	This character is not known for all relevant species, e.g. Lens montbretii and Vicia caesarea.		
16.	Evidence from serological experiments suggests that as far as storage proteins of seeds are concerned, Lens is more closely related to other parts of the Vicieae (Pisum and Lathyrus) than to Vicia Sect. Ervum.		6.4.2.4.

which impart a facies strongly reminiscent of another taxon, and on the other, some obscure and unrelated traits which suggest that the group in question is really distinct and that its superficial similarity to the other taxon is misleading. These two kinds of evidence for the relationships of Lens are set out in Table 24.

Although a phenetic classification should be based solely on facts (characteristics of the plants concerned), yet it is difficult to ignore phylogenetic considerations when the different judgments one might make, given the available evidence, have strongly contrasted evolutionary implications. In the case of the oroboid species, the characters which link together this group are all of a relatively primitive nature; the plants are outcrossing perennials growing in stable deciduous woodland environments. Although it is decided to classify them separately in Vicia and Lathyrus, we may still maintain that, in accordance with their primitive position within the tribe, the oroboid species are quite closely related. (This topic is treated in more detail in Chapter 15.)

The taxonomic decisions one makes about Lens have much more fundamental consequences in terms of one's concept of evolution in the Vicieae. Lens comprises highly specialised, weedy annuals. If it is judged to be a recent segregant from the 'ervoid' part of Vicia, as is implied in Table 5, then Lens automatically can have no close relationship with Lathyrus. On the other hand, if the type of style is thought worthy of special weighting and Lens is placed close to Lathyrus (as in Visiani's

scheme, Table 4), then all similarities between Lens and Vicia Sect. Ervum must be coincidental and due to parallel evolution. Vicia and Lathyrus are both large and diverse genera comprising perennial and annual species; if it is accepted that the more primitive members of these genera are to be found among the perennials, then it is impossible that the two are closely linked by Lens. The third possibility exists that Lens has been isolated from the rest of the tribe for a long time and is equivalent in age to the other genera. If this is the case, then Lens must be a highly depauperate group, for no close relations now exist which are perennial or which inhabit other than disturbed environments.

The species of Lens cannot be neatly delimited from ervoid members of Vicia because of the occurrence of two species (Vicia caesarea and Lens montbretii) which possess somewhat intermediate characteristics. The relevant features of these taxa are listed in Tables 25 and 26, respectively. Table 25 shows that V. caesarea has an approximately equal phenetic relationship with members of Lens and Vicia; its generic position must therefore depend on how its characteristics are weighted by the taxonomist. Characters 1 and 3 are equivocal, since the type of calyx and wing varies so widely in Vicia Sect. Ervum; the lenticular seed seems an important feature, but since this also occurs in V. lunata and even in a variety of V. sativa (cf. part 7.5), it may not necessarily indicate a connection between V. caesarea and Lens. The shape of the standard argues in favour of such a relationship; on the other hand, the serological

Table 25. Characters of Vicia caesarea.

		CHARACTER	REFERENCE
Ca. (Le.)	1.	Calyx teeth ± equalling tube, lowermost shortest.	4.2.2.
Le.	2.	Standard stenonychioid (type C), slightly bossed.	4.2.3.1, Fig. 19:10.
Le. Vi.	3.	Upper edge of wing not 'kinked'.	4.2.3.1.
Vi.	4.	Style dorsally compressed, pubescent all round.	4.2.5.
Ca.	5.	Fruit characteristically shaped, subtorulose.	4.4, Fig. 22:19.
Le. (Vi.)	6.	Seeds lenticular.	4.5.2.
Vi.	7.	Evidence from serological experiment suggests V. caesarea is less closely related to Lens than is V. ervilia.	6.4.2.4, Fig. 39:9.

Key: Le. character-state typical of Lens.
Vi. character-state typical of Vicia.
Ca. character-state peculiar to V. caesarea.
Parentheses show a less definite association of the character-state and the taxon.

Table 26. Characters of Lens montbretii.

		CHARACTER	REFERENCE
(Le.)	1.	Calyx teeth equal, about 2 x length of tube.	4.2.2.
Le.	2.	Standard stenonychioid (type C), bossed.	4.2.3.1.
(Vi.) Mo.	3.	Flower whitish, attractive.	4.2.3.2.
Vi.	4.	Upper edge of wing petal 'kinked'.	4.2.3.1.
Le.	5.	Style dorsally compressed, pubescent on adaxial face.	4.2.5.
Mo.	6.	Fruit golden-brown sericeous	4.4.
(Le.)	7.	Fruit in shape somewhat resembling that of Lens culinaris.	4.4.
Le.	8.	Seeds lenticular.	Davis (1970).

Key: Le. character-state typical of Lens.
Vi. character-state typical of Vicia.
Mo. character-state peculiar to L. montbretii.
Parentheses show a less definite association of the character-state and the taxon.

evidence, and most of all the type of style, suggest that V. caesarea is correctly placed in Vicia. At present it seems justified to leave this species in Vicia, but more characters are required for confirmation; it would be most interesting to know the karyotype of V. caesarea and to have an analysis of free amino acids in the seed. The characters of Lens montbretii are largely consonant with its recent transfer from Vicia (see part 2.5). The features which make it distinct from the other members of Lens do not argue very strongly in favour of a relationship with Vicia, but are partly expressions of the larger, more attractive flower of this species and partly traits which are peculiar to it alone. It is unfortunate that I could not obtain any seed of L. montbretii for serological experiments; more information about this species, especially chemical and genetical data, would be most useful.

The sum of evidence available on which to judge the delimitation and position of Lens appears to me insufficient, but on balance I support the view that this genus is a well-defined group and is not closely allied to Vicia Sect. Ervum. The main reason for this decision lies in the floral structure of Lens: although its flowers are inconspicuous, in detail they are not degenerate, cleistogamous versions of a vicioid type (like those of most members of Sect. Ervum), but delicate miniatures having characteristic features of their own and in some respects resembling flowers of Lathyrus. These points are listed in Table 27.

In constructing a phenetic classification of the Vicieae, the relationship of Lens to the other genera is not so important

Table 27. Characters of the genus Lens.

		CHARACTER	REFERENCE
Vi.	1.	Leaves multijugate.	3.5.
Vi. Pi.	2.	Leaflet vernation conduplicate.	3.3, Table 2.
Le.	3.	Calyx teeth much longer than tube.	4.2.2, Fig. 16.
La. Pi. Va.	4.	Standard stenonychioid (type C), with bosses.	4.2.3.1, Fig. 16.
La. Pi. Va.	5.	No 'kink' in upper edge of wing petal (except in L. montbretii).	4.2.3.1, Fig. 16.
Vi.	6.	Staminal tube ending obliquely.	4.2.4, Fig. 16, Table 2.
La.	7.	Style dorsally compressed, pubescent on adaxial side.	4.2.5, Fig. 16, Table 2.
Le.	8.	Fruit characteristically shaped.	4.4, Fig. 22:20.
Le. (Vi.)	9.	Seeds lenticular.	4.5.2.
La. Pi.	10.	Seeds not containing canavanine.	6.3.
La. Pi.	11.	Evidence from serological experiments suggests that Lens is more nearly related to Pisum or Lathyrus than to Vicia.	6.4.2.4.

Key: Vi. character-state typical of Vicia.
La. character-state typical of Lathyrus.
Pi. character-state typical of Pisum.
Va. character-state typical of Vavilovia.
Le. character-state peculiar to Lens.

as its delimitation; the former is, however, a more interesting and difficult subject. Of the three alternatives outlined on p. 347, I consider the third to be most likely, viz. that Lens is an old genus, more-or-less equal in status with Vicia, Lathyrus and Pisum. Lens combines characteristics of all of these genera (Table 27), but, as it is impossible to decide which features are most important in guiding phylogenetic speculation, the question of its nearest relatives must be left unanswered.

10.4.

THE NEW GENUS ANATROPOSTYLIA

Vicia koeieana, the single member of Sect. Anatropostylia, is an isolated annual species with many striking features. The history of its taxonomic treatment was outlined in part 2.3.1, and its position will be reassessed here in the light of data presented in earlier chapters.

The characters of V. koeieana are listed in Table 28. The general facies of this species is suggestive of Vicia or Lens, but even vegetatively it is immediately recognisable by its aristate leaflets and finely laciniate stipules. The flowers are quite untypical of Vicia, in both colour and morphology, except that the staminal tube ends obliquely; they are more like those of Lathyrus or Lens, but unique in the exact shapes of petals and gynoecium. The distribution of hairs on the style resembles that found in Lathyrus and Lens, but the style is sinuous and terete, and appears to arise from the lower suture

of the legume. The fruits and seeds are also very distinctive; the pods are narrowly cylindrical and subtorulose, with papery, strongly reticulate-veined valves; the seedshave a finely verrucose testa. Rough seeds are otherwise unknown in Vicia (except in V. cuspidata and V. lathyroides, members of Sect. Vicia), and although they do occur in Lathyrus, the patterning in these cases is smoothly papillate or rugose.

Table 28 shows that V. koeieana has no overriding phenetic similarity with any one of the genera of the Vicieae but combines features of each of them. In addition, it possesses several new characters. Its present position in Vicia is anomalous, since it provides the only exception to one of the 'key' characters of the genus - the distribution of hairs on the style. For these reasons I consider that Sect. Anatropostylia should be raised to the status of a genus. The new genus Anatropostylia (Plitmann) Kupicha has been published (Kupicha, 1973), and a reprint of the paper is placed at the end of the thesis (Appendix 2). The relationship of Anatropostylia koeieana to the rest of the Vicieae is even more problematical than the previously-discussed question of Lens. Since only a single species is involved, none of the characters on which judgment is based shows any significant variation. There is therefore no way of deciding, a posteriori, which of the features of A. koeieana are relevant in a concept of the genus Anatropostylia, relative to the characters used in delimiting the polytypic genera.

The characters listed in Table 28 do not provide any firm guidance as to the position of this genus within the tribe; it may be as old as the other genera, or it may equally well be

Table 28. Characters of the genus Anatropostylia.

		CHARACTER	REFERENCE
Vi. Le.	1.	Leaves multijugate.	3.5.
Vi. Le. Pi.	2.	Leaflet vernation conduplicate.	3.3, Table 2.
An.	3.	Leaflets aristate.	3.5, Fig. 3:44.
An. (Vi.)	4.	Both stipules at each node laciniate.	3.6.
Vi. La. Pi. Va.	5.	Calyx teeth shorter than to equalling tube.	Fig. 15.
La.	6	Corolla bright lemon-yellow.	4.2.3.2.
La. Le. Pi. Va.	7.	Vexillum stenonychioid, with 2 bosses.	4.2.3.1, Fig. 15.
La. Le. Pi. Va.	8.	No 'kink' in upper edge of wing petal.	Fig. 15.
Vi. Le.	9.	Staminal tube ending obliquely.	4.2.4, Fig. 15.
La. Le.	10.	Style dorsally compressed, pubescent on adaxial side, not folded abaxially.	4.2.5, Fig. 15.
An.	11.	Legume subtorulose, characteristically shaped, with papery, reticulate-veined valves.	4.4, Fig. 22:6.
An.	12.	Style appearing to arise from lower suture of legume.	4.4, Fig. 22:6.
An.	13.	Seeds finely scabrid-tuberculate.	4.5.2.
Vi.	14.	Evidence from serological experiment suggests that (as far as seed storage proteins are concerned) A. koeieana is less closely related to Lens than is V. ervilia.	6.4.2.4.

Key: Vi. - character-state typical of Vicia; La. - of Lathyrus; Le. - of Lens; Pi. - of Pisum; Va. - of Vavilovia. An. - character-state peculiar to Anatropostylia.

a relatively recent segregant from Lathyrus, Vicia or Lens. More information is needed about A. koeieana: for example, whether or not the seeds contain canavanine, the karyotype, and data from more serological experiments.

10.5. THE RELATIONSHIP OF PISUM AND VAVILOVIA TO THE REST OF THE VICIEAE

The 'key' characters which traditionally delimit Pisum from the rest of the tribe are shown in Table 2. Vavilovia agrees with Pisum in all these characters (as far as is known; the leaflet-vernation of Vavilovia has not yet been observed), and there is no doubt that these two ditypic genera are closely related. On the other hand, their separation also seems well justified, based as it is on several striking vegetative features (part 2.6).

Within Pisum and Vavilovia are found characteristics which link them with each of the other genera of the tribe. Thus, the presence of leaves with only one to three pairs of large, broad leaflets, the colour of the flowers, the shape of the vexillum and the truncate staminal tube all suggest an association with Lathyrus; the conduplicate leaflet vernation in Pisum is similar to that of Vicia and Lens; and serological evidence suggests that Lens is rather closely related to Pisum. On balance, it seems that Pisum and Vavilovia together form a small, heterogeneous group which is quite distinct from the rest of the Vicieae and which does not show an overriding affinity with any

of the other genera. This degree of isolation, and the fact that two genera can be recognised within such a small circle of related species, suggest that Pisum and Vavilovia are the survivors of a depauperate branch of the Vicieae which diverged from the rest of the tribe at an early stage in its evolution.

This concept of the origin and taxonomic relationships of Pisum and Vavilovia seems to me quite firmly based. Certainty in this area indirectly supports my hypothesis about the position of Lens (part 10.3), for it seems reasonable that other branches of the tribe may have developed in a way parallel to that of the Pisum-group, at first being linked to the main body of species in the tribe by intermediates, but later becoming isolated as these bridging taxa died out. Lens, and even Anatropostylia, may be relict groups of this kind.

In this context it is also relevant to refer to part 15.3, where I discuss the factors which affect the rates of evolution of perennials and annuals. It is concluded that annuals tend to evolve faster than perennials, because the gene pools of their populations can fluctuate severely from year to year, leading to genetic drift. The distinctness of the small annual genera Pisum, Lens and Anatropostylia may possibly be the result of phylogenies in which rapid changes of this kind played an important part.

10.6.
KEY TO THE GENERA OF THE VICIEAE (EMENDED DEFINITION)

1. Staminal tube ending obliquely; stipules never hastate
   2. Style dorsally compressed, pubescent only on adaxial face; annuals
      3. Legume subtorulose; seeds warty, subglobose; flowers bright yellow; stipules laciniate — Anatropostylia
      3. Legume compressed; seeds smooth, lenticular; flowers and stipules not as above — Lens
   2. Style with wide variation in shape and indumentum distribution, but never as above; annuals and perennials — Vicia

1. Staminal tube truncate, or if oblique then stipules hastate
   4. Leaflets with conduplicate vernation *; style folded so that the margins meet abaxially
      5. Annuals; leaves tendrillous, usually with more than one pair of leaflets; stipules large, foliaceous; keel petals cristate — Pisum
      5. Perennials; leaves mucronate to shortly tendrillous, unijugate; stipules small; keel petals not cristate — Vavilovia
   4. Leaves with supervolute vernation; style flat — Lathyrus

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* The leaflet-vernation of Vavilovia is unknown and so this character, though useful in distinguishing Pisum and Lathyrus, needs confirmation in this key.

Chapter 11

THE INFRA-GENERIC CLASSIFICATION OF VICIA

11.1. Introduction.

11.2. Description of *Vicia*.

11.3. Conspectus of taxa within *Vicia*.

11.4. Key to subgenera and sections.

11.5. Subgeneric and sectional descriptions.

11.1.

INTRODUCTION

Contemporary taxonomists dealing within Vicia tend to divide this genus into three or four groups whose status varies, according to author, from sectional to subgeneric rank. These groups are 'Cracca', 'Vicia', 'Ervum' and sometimes 'Faba' (cf. Ball, 1968; Davis & Plitmann, 1970: Radzhi, 1970). I consider, however, that primary divisions of this kind do not give a balanced reflection of broad relationships within the genus. Rather, there appears to be a striking dichotomy of character-states within Vicia which can best be expressed in the formation of just two subgenera, Subgen. Vicia (typified by V. sativa) and Vicilla. The first includes 'Vicia' and 'Faba', the second 'Cracca' and 'Ervum'. The name 'Subgen. Cracca (Vis.) Gams' cannot be used for the latter, because it is pre-dated by the subgenera of Vicia published by Rouy in 1899: Subgen. Vicilla, Pseudervoidea and Ervoidea. V. cracca, the lectotype of Sect. Cracca Vis., was a member of Subgen. Pseudervoidea; but, as one is free to choose, I prefer to use the more euphonious name Vicilla for the subgenus. Its lectotype is V. pisiformis.

Subgen. Vicia is the smaller taxon and can be circumscribed in a more positive way than Subgen. Vicilla, as its members all possess several features which could be regarded almost as forming a syndrome. There is also a wealth of taxonomically useful evidence providing differential characters within the subgenus, and its sectional classification is comparatively straightforward. Subgen. Vicilla provides an interesting con-

trast. The range of variation within the group is very wide so that it is difficult to define, and there is only a small degree of correlation between variation in different characters. This situation presents difficulties for the taxonomist. If he choses variation in a single part of the plant as the basis for sectional grouping, e.g. the use of the stylar shape and indumentum-distribution, then the groups are conveniently large but certainly unnatural. If, however, only convincingly natural assemblages of species (i.e. groups which share several traits) are accepted as sections, a too finely divided system is produced. I have tried to keep a balance between these two extremes, but perhaps leaning towards the latter alternative. The perennial species tend to fall into the larger sections while several of the annuals, whose morphological diversity is more extreme and disjunct, have been placed in monotypic or ditypic sections. The taxonomic structure which is produced has the same general pattern as that of the whole tribe.

The geographical distribution of a taxon is intimately connected with its phylogeny and its taxonomic relationships, but it is dangerous to use this information as a basis for classification since a circular argument can very easily be followed. On the other hand, patterns of distribution provide an extra dimension in which to judge phenetically delimited taxa. I have therefore delayed using geographical details, except in the most general way, until the infra-generic structure of Vicia has been introduced in full.

Some mention is made of the ecological aspects of the

different taxa, but on the whole these are not very significant in clarifying the taxonomic structure of the Vicieae, except on the broadest scale where the development of floras and phytochoria are being considered, as in part 13.5. The environment is both the home of a species and the source of the selection pressures which shape its evolution. While it is true that special ecological adaptations are sometimes characteristic of higher taxa (e.g. the Ericaceae are associated with acid soils, the Chenopodiaceae are able to tolerate high salt concentrations), it is also frequently found that speciation is linked with divergent adaptation to different environments. Both of these situations can be recognised in the Vicieae. Some sections of Vicia and Lathyrus comprise only woodland species, a few are entirely alpine, while many are confined to disturbed habitats. On the other hand, the trends which have allowed groups to diversify from one to another of these different habitats have apparently often recurred in the Vicieae, and in this tribe the fact that two taxa are adapted to the same type of environment is no proof of close phylogenetic relationship.

I have tried to make the species lists as comprehensive as possible, and in the areas of Europe, most of S.W. Asia and N. America I am confident that this has largely been achieved, because both fine modern revisions and plenty of herbarium material are available. I am less sure about species of Caucasia, C. & E. Asia, S. America (especially Chile) and N. Africa. Many more species names are published for these regions than I have listed, but I am convinced that most of them are superfluous.

The sequence of subgenera and sections is based on the concept of relative primitiveness and specialisation in Vicia which will be discussed in part 15.2; the order represents an evolutionary progression, with the least advanced groups placed first. In each section the species are listed in alphabetical order unless a more natural sequence or a more convenient informal subgrouping has been decided upon. Thus, the largest section, Cracca, is divided 'naturally' into New and Old World groups and the latter then subdivided 'artificially' into perennials and annuals. The members of these two Eurasian groups are arranged with most similar species as neighbours (e.g. V. ciceroidea-V. rafigae-V. multijuga; V. hirsuta-V. meyeri); The N. American species are listed alphabetically. The members of Sects. Vicilla, Atossa, Vicia and Faba are placed in a natural array; in all other polytypic sections the order is alphabetical. I have not recognised any subsections, although Sects. Vicilla, Cracca, Atossa, Vicia, Faba and Hypechusa could probably all be further subdivided. The nearer to the species level one comes in the creation of a hierarchy of taxa, the more delicate and difficult is the achievement of a natural system, and therefore I feel I cannot decide on a formal subsectional classification without a really intensive investigation of all members of each section. This would be a useful project, especially in Sect. Cracca.

In the sectional discussions in part 11.5, I often refer to characters which are described and investigated more fully in Chapters 3 to 7. In order to avoid constantly interrupting the sentences with references in parenthesis, these are placed

in the left-hand margin in line with the relevant remark.

11.2.

DESCRIPTION OF VICIA L.

Perennial or annual herbs with erect or more usually climbing or sprawling habit; rootstock never tuberous. Stems always unwinged, usually with complete replacement of cortical vascular bundles at the nodes, occasionally with partial replacement. Leaves hypostomatic to epistomatic, paripinnate or very rarely imparipinnate, tendrillous or mucronate, usually with several to many pairs of leaflets, rarely unijugate; stipules semi-sagittate or entire, sometimes toothed, rarely dimorphic; vernation of leaflets conduplicate (supervolute in V. biennis); venation brochidodromous, veins always pinnate. Inflorescence many- to 1-flowered, occasionally branched. Calyx usually with oblique mouth and teeth of unequal length ('irregular'), sometimes ± actinomorphic ('regular'). Vexillum oblong, stenonychioid or platynychioid, not bossed or pouched at the fold, very rarely pubescent on adaxial face. Alae usually with 'kink' in upper edge of limb. Staminal tube oblique at apex. Style linear, not contorted, dorsally or laterally compressed (rarely terete), distribution of pubescence various but style never hairy on adaxial side only. Legume often stipitate, sometimes hairy but hairs rarely tuberculate; pod sometimes containing 'woolly' parenchymatous tissue between the seeds. Seeds with short to long hilum; testa smooth or very rarely rough; lens near hilum or occasionally on opposite side of seed; canavanine sometimes

present.

11.3.

CONSPECTUS OF TAXA WITHIN VICIA

Authorities for subgenera and sections are given in part 11.5; those of the species are in the Index.

I. Subgen. Vicilla

Sections:	Species:	
1. Vicilla	1. V. unijuga	9. V. dichroantha
	2. V. crocea	10. V. amoena
	3. V. venosa	11. V. amurensis
	4. V. nipponica	12. V. japonica
	5. V. kulingiana	13. V. pisiformis
	6. V. pseudo-orobus	14. V. sylvatica
	7. V. hirticalycina	15. V. dumetorum
	8. V. venulosa	
2. Cassubicae	16. V. cassubica	21. V. sparsiflora
	17. V. dadianorum	22. V. multicaulis
	18. V. freyniana	23. V. semiglabra
	19. V. orobus	24. V. nigricans
	20. V. montenegrina	
3. Cracca	Old world members: perennials:	
	25. V. cracca agg.	28. V. ochroleuca
	26. V. pinetorum	29. V. atlantica
	27. V. sibthorpii	30. V. splendens

31. V. kotschyana
32. V. glareosa
33. V. sicula
34. V. alpestris
35. V. ciceroidea
36. V. rafigae
37. V. multijuga
38. V. glauca

Old World members: annuals:

39. V. villosa agg.
40. V. benghalensis
41. V. albicans
42. V. scandens
43. V. cirrhosa
44. V. chaetocalyx
45. V. filicaulis
46. V. monantha
47. V. leucantha
48. V. palaestina
49. V. hulensis
50. V. disperma
51. V. durandii
52. V. vicioides
53. V. lecomptei
54. V. hirsuta
55. V. meyeri

New World members:

56. V. acutifolia
57. V. caroliniana
58. V. exigua
59. V. floridana
60. V. hugeri
61. V. leavenworthii
62. V. ludoviciana
63. V. mexicana
64. V. minutiflora
65. V. pulchella
66. V. reverchonii

4. Variegatae — 67. V. argentea; 68. V. canescens agg.; 69 V. megalotropis

5. Pedunculatae — 70. V. altissima; 71. V. onobrychioides

6. Americanae — 72. V. americana

7. Subvillosae	73. V. subvillosa	
8. Biennes	74. V. biennis	
9. Cappadocicae	75. V. cappadocica	77. V. cretica
	76. V. cassia	
10. Ervum	78. V. laxiflora	80. V. tenuissima
	79. V. pubescens	81. V. tetrasperma
11. Ervoides	82. V. articulata	
12. Ervilia	83. V. ervilia (See V. quadrijuga, discussed on p. 367)	
13. Caesareae	84. V. caesarea	
14. Trigonellopsis	85. V. cypria	86. V. lunata
15. Australes	87. V. andicola	93. V. montevidensis
	88. V. bijuga	94. V. nana
	89. V. epetiolaris	95. V. platensis
	90. V. graminea agg.	96. V. pampicola
	91. V. linearifolia	97. V. setifolia
	92. V. macrograminea	98. V. stenophylla
16. Leucophaeae	99. V. leucophaea	
II. Subgen. Vicia		
17. Atossa	100. V. oroboides	102. V. balansae
	101. V. sepium	103. V. truncatula

18. Vicia	104. V. pyrenaica	107. V. barbazitae
	105. V. sativa agg.	108. V. lathyroides
	106. V. grandiflora	109. V. cuspidata
19. Faba	110. V. faba	113. V. hyaemiscyamus
	111. V. narbonensis	114. V. bithynica
	112. V. galilaea	
20. Hypechusa	115. V. anatolica	121. V. hyrcanica
	116. V. assyriaca	122. V. lutea
	117. V. ciliatula	123. V. melanops
	118. V. esdraelonensis	124. V. noeana
	119. V. galeata	125. V. pannonica
	120. V. hybrida	126. V. sericocarpa
21. Peregrinae	127. V. aintabensis	129. V. mollis
	128. V. michauxii	130. V. peregrina

Other species

V. quadrijuga. This annual species is known only from the type, which was collected in N.E. Anatolia. The leaves are mucronate, with few pairs of leaflets; the inflorescence 1-2-flowered; and the flowers pale yellow, with irregular calyx, ovate standard and dorsally compressed, evenly pubescent style. The petals are of comparatively simple form, the vexillum without bosses or folds and the wings with a single process and no 'kink' in their upper edge. Davis (1970) suggests that V. quadrijuga is allied to V. ervilia, and its vegetative and floral characters support this idea. The delimitation of the small 'ervoid'

sections of Vicia is particularly critical and precise, and depends largely on legume characters because the flowers tend to be reduced. Since the mature fruit of V. quadrijuga is unknown, I have not placed this species in Sect. Ervilia but consider that a firm decision about its taxonomic relationships should be delayed until it is better known.

V. dennesiana. This very distinctive perennial, which was endemic to the Azores, recently became extinct. The plants are stout, with creeping branches. The leaves are tendrillous, multijugate and epistomatic, the leaflets fairly large and broad. The inflorescence is dense, of large brownish flowers in which the standard is oblong and the style laterally compressed and evenly pubescent. V. dennesiana cannot be placed in any of the sections recognised here; its features suggest affinity with Sects Vicilla, Cassubicae and Cracca. It is mentioned again in part 15.4.

11.4.

KEY TO THE SUBGENERA AND SECTIONS OF VICIA

1. Stipules with nectariferous spot on abaxial surface; inflorescence much shorter than subtending leaf, usually few-1-flowered — Subgen. Vicia

2. Calyx subregular; sutures of legume parallel

3. Leaves usually with more than 3 pairs of leaflets (if fewer, then leaflets less than 1 cm long); veins of leaflets prominent and straight — Sect. 18. Vicia

3. Leaves with 1-3 pairs of leaflets which are more than 2 cm long; veins not prominent, curving towards leaflet apex Sect. 19. Faba

2. Calyx irregular; sutures of legume not parallel

4. Inflorescence several-flowered; vexillum oblong

5. Perennial; lens of seed close to hilum Sect. 17. Atossa

5. Annual; lens of seed opposite hilum Sect. 20. Hypechusa

4. Inflorescence 1-2-flowered; vexillum stenonychioid (i.e. with banner wider than claw)

6. Flowers yellow or white; lens of seed opposite hilum Sect. 20. Hypechusa

6. Flowers purplish; lens of seed close to hilum Sect. 21. Peregrinae

1. Stipules without nectariferous spot; inflorescence usually equalling or exceeding subtending leaf; usually many-flowered Subgen. Vicilla

7. Vexillum oblong

8. Perennials with many-flowered inflorescences; if stipules dimorphic, neither of the pair laciniate

9. Leaves hypostomatic, usually with few pairs of leaflets Sect. 1. Vicilla

9. Leaves epistomatic, usually with many pairs of leaflets Sect. 2. Cassubicae

8. Annual, with few-flowered inflorescences;

stipules strongly dimorphic, one of the pair finely laciniate — Sect. 11. Ervoides

7. Vexillum platynychioid, stenonychioid or ovate

10. Vexillum platynychioid (i.e. pandurate, 'waisted')

11. Style laterally compressed — Sect. 3. Cracca

11. Style dorsally compressed

12. Perennials; style glabrous adaxially, densely bearded on abaxial side — Sect. 4. Variegatae

12. Annuals; style pubescent all round, tufted on abaxial side — Sect. 9. Cappadocicae

10. Vexillum stenonychioid to ovate

13. Perennials

14. Style terete, bearing a dense ring of hairs clearly separated from the stigma — Sect. 16. Leucophaeae

14. Style dorsally compressed, pubescent near the stigma

15. Leaves imparipinnate — Sect. 7. Subvillosae

15. Leaves tendrillous

16. Style tufted abaxially

17. Flowers 1 cm or less in length; plants of S. America — Sect. 15. Australes

17. Flowers 1.5 cm or more in length

18. Vexillum stenonychioid; plants of W. Mediterranean — Sect. 5. Pedunculatae

18. Vexillum oblong; plants of N. America Sect. 6. Americanae

16. Style evenly pubescent all round

19. Vernation of leaflets conduplicate; stipules conspicuously dentate (V. sylvatica) Sect. 1. Vicilla

19. Vernation of leaflets supervolute; stipules semi-hastate or lanceolate, entire Sect. 8. Biennes

13. Annuals

20. Style tufted abaxially; plants of S. America Sect. 15. Australes

20. Style not as above; plants of Eurasia

21. Leaflets with supervolute vernation; plants up to 1.5 m, with 5-15-flowered racemes Sect. 8. Biennes

21. Leaflets with conduplicate vernation; plants seldom exceeding 0.5 m, with few-flowered racemes

22. Legumes not subtorulose

23. Leaves with 2-4 pairs of linear leaflets; style c. 1 mm long, bearing a few minute hairs Sect. 10. Ervum

23. Leaves with 4 or more pairs of ovate leaflets; style c. 5 mm long, evenly and fairly densely

pubescent Sect. 14. Trigonellopsis

22. Legumes subtorulose

24. Seeds subglobose; calyx teeth equal; leaves mucronate Sect. 12. Caesareae

24. Seeds lenticular; upper calyx teeth longer than the lowest; leaves with a simple tendril Sect. 13. Ervilia

11.5.

SUBGENERIC AND SECTIONAL DESCRIPTIONS

I. Subgen. Vicilla (Schur) Rouy in Rouy & Foucaud, Fl. Fr. 5:205(1899). Syn: Vicilla Schur, Enum. Pl. Transs. 170 (1866); Vicia Subgen. Cracca (Vis.) Gams in Hegi, Ill. Fl. Mitteleur. 4(3): 1499(1924).

Plants perennial or annual. Stems always with complete replacement of cortical vascular bundles at the nodes. Leaves hypostomatic to epistomatic, paripinnate or rarely imparipinnate, tendrillous or mucronate; stipules rarely dimorphic, never with nectariferous glands. Inflorescence many- to 1-flowered, equally to longer than subtending leaf. Calyx teeth equal or unequal. Vexillum oblong, stenonychioid or platynychioid, always glabrous. Style rarely terete, usually dorsally or laterally compressed, the pubescence even all round, tufted abaxially or rarely in dorsiventral or lateral patches. Legume often ±

ipitate, not containing 'woolly' parenchyma; sutures of fruit
rely parallel. Seeds with long to short hilum; testa smooth;
ns always near hilum; canavanine usually present.
Lectotype: V. pisiformis L. (Gunn, 1969).

Sect. Vicilla (Schur) Aschers. & Graebner, Syn. Mitteleur. Fl.
2):916 (1909). Syn: Vicilla Schur, Enum. Pl. Transs. 170
866); Swantia Alefeld in Öst. Bot. Zeitschr. 9:365 (1859);
cia Sect. Crocea Radzhi in Novit. Syst. Pl. Vasc. (Leningrad)
230 (1970).
Plants perennial. Leaves hypostomatic, hypo-amphistomatic or
rely (in V. sylvatica) epi-amphistomatic, tendrillous or muc-
nate, usually with few pairs of large, broad leaflets; sti-
les rarely dimorphic (i.e. in V. crocea). Inflorescence
ny-flowered, sometimes a panicle; pedicels often subtended
bracteoles. Flowers deep orange-yellow or pale yellow, whitish
purple. Calyx irregular; vexillum oblong; style dorsally
mpressed or rarely terete, evenly hairy all round. Legume
ipitate. Seeds with medium to long hilum. - c. 15 species.
Lectotype: V. pisiformis L. (Gunn, 1969).
Geographical distribution: Europe (except S. Iberian penin-
la, Turkey-in-Europe & some Mediterranean islands), N. Anato-
a, Crimea, Caucasia, N. Iran, Asia eastwards to Japan. See
gs. 57 & 58.

3.1 The genus Vicilla Schur arose originally as a develop-
ment of Godron's treatment of Vicia s.l. Godron
(1849) had redefined Vicia in a narrow sense to in-
ble 4 clude only large-flowered species with dorsally

compressed styles; he excluded '*Cracca*' and '*Ervum*' as separate genera. In 1866 Schur circumscribed *Vicia* even more narrowly so that it comprised only species whose styles are tufted abaxially; species in which
.3.3 the styles are evenly hairy all round were placed in *Vicilla*. This genus included *V. pisiformis*, *V. sylvatica*, *V. cassubica* and *V. orobus*. Ascherson & Graebner (1909) later used *Vicilla* as a section within 'Sect.' *Cracca* (see parts 2.3.1 and 2.3.3), but they widened its definition to include some tufted-styled
.2.5 species (*V. dumetorum* and *V. altissima*) as well as adding to it new taxa from Asia (*V. unijuga*). Since then there have been few attempts to subdivide *Vicia*, most writers of Floras being content to treat Sect. (or Subgen.) *Cracca* as if it were a homogeneous group. Radzhi (1970) has recently engaged in this task, though he deals only with Caucasian species. He clas-
.3.1 sifies Subgen. *Cracca* into four sections, dividing the species which I include in Sect. *Vicilla* between two of them: *V. crocea* forms a monotypic section, while *V. cassubica*, *V. pisiformis* and *V. biennis* comprise Sect. *Cassubicae* Radzhi. These two sections are differentiated by the style being terete in *V. crocea* but dorsally compressed in the other species, and also by the relative lengths of keel and standard.

The lectotype of *Vicilla* Schur is *V. pisiformis*, and, as my first section is defined primarily on the

original 'key' character of this genus (style dorsally compressed, evenly hairy all round), it is reasonable to use Schur's name for it. The concept of Vicilla is considerably changed, however. The group includes only species with hypostomatic leaves, and hence V. cassubica and V. orobus are removed to another section. The members of Sect. Vicilla have more-or-less oblong vexilla and do not, therefore, include V. altissima and V. onobrychioides; the exclusion of these two species is further supported by their linear leaflets and their styles being tufted abaxially. I consider, however, that V. dumetorum should be placed within Sect. Vicilla despite its tufted style, on the grounds that its leaves are strongly hypostomatic, the leaflets relatively broad, and the vexillum oblong.

Sect. Vicilla includes all the 'oroboid' members of Vicia, with the exception of V. oroboides (Sect. Atossa, Subgen. Vicia). The species concerned are woodland plants with a predominantly eastern north temperate distribution. The most 'extreme' examples of this facies, V. venosa, V. crocea, V. unijuga and V. kulingiana, have etendrillous leaves with very large, broad, papery-coriaceous, reticulate-veined leaflets. The inflorescence is branched, its lateral shoots subtended by bracts and the pedicels by bracteoles.

Other species, though grouped as 'oroboid', pos-

sess characteristics linking them with more typical members of Vicia. V. pseudo-orobus has smaller, more numerous leaflets and tendrils; V. pisiformis also has tendrils and the leaflets, though large and broad, are more herbaceous in texture than those of V. unijuga. V. sylvatica is hardly oroboid: it has multijugate, epi-amphistomatic leaves with small leaflets; the flowers are less numerous and are borne in a loose raceme; and the vexillum is intermediate between oblong and stenonychioid. It possesses the key characters of the section but indicates a link between this group and other sections of Subgen. Vicilla.

Fig. 3:5 & 2

Table 11

Fig. 12

2. Sect. Cassubicae Radzhi in Novit. Syst. Pl. Vasc. (Leningrad) 7:230 (1970). Syn: Vicilla Schur, Enum. Pl. Transs. 170 (1866), pro parte excl. typ.

Plants perennial. Leaves epistomatic, tendrillous or mucronate or rarely imparipinnate; leaflets numerous, ovate. Inflorescence many-flowered, racemose, ebracteate. Flowers yellow, whitish, pink or purple. Calyx irregular; vexillum oblong; style dorsally compressed, evenly pubescent all round. Seeds with hilum of long to medium length. - c. 9 species.

Type: V. cassubica L.

Geographical distribution: Europe except some Mediterranean islands, N. Anatolia, Lebanon, N. Iran, Caucasia, Crimea, Asia eastwards to Japan; W. coast of N. America: Chile. See Figs. 59 & 60.

In its original form, Sect. Cassubicae Radzhi

2.3.3 had virtually the same delimitation as the genus Vicilla Schur, but with V. cassubica as its type. V. cassubica belongs to an assemblage of closely allied species with a distinctive facies: their leaves, like those of the oroboid group, are often etendrillous and membranous, but the leaflets are smaller and more numerous. In addition, I found that these species, in strong contrast to oroboid members of Vicia, have epistomatic leaves. This cryptic morphological character, which is unusual in woodland plants, supports the delimitation of a separate section. In floral characters members of Sect. Cassubicae resemble those of Sect. Vicilla, and the two groups are probably quite closely related.

Fig. 3:22 & 23

3.8 Table 11 Fig. 7:2 & 8

Fig. 19:2 Table 12 4.2.5

Sect. Cassubicae is predominantly an Old World group, but it contains one American species, V. nigricans (syn. V. gigantea). The latter is quite distinct from all other New World natives of Vicia: it is very much larger; it is the only species with a dorsally compressed and evenly hairy style; the leaves are epistomatic; and the plant blackens on drying. Moreover V. nigricans is the only member of the genus which is found in both N. and S. America.

Fig. 21:7 Table 11 3.5

V. nigricans has well-developed tendrils, but among the other members of the section there is a strong tendency towards reduction to mucronate leaves. V. freyniana, and some plants of V. semiglabra,

3.2

are unusual in having leaves with a terminal leaflet; this trait is found otherwise only in V. subvillosa and V. argentea (Sects. Subvillosa and Variegatae, respectively).

3. Sect. Cracca Vis., Fl. Dalm. 3:320 (1852). Syn: Cracca Medik. in Vorles. Churpf. Phys. Ges. 2:359 (1787), non L. (1753); Vicia a) Cracca S.F. Gray, Nat. Arr. Brit. Pl. 2:609 (1821); Cracca Sect. Ervoides Gren. & Godron, Fl. Fr. 1:471 (1949), pro parte excl. typ.; Endiusa Alefeld in Öst. Bot. Zeitschr. 9:359 (1859); Vicia Subgen. Pseudervoidea Rouy in Rouy & Foucaud, Fl. Fr. 5:232 (1899); Vicia Sect. Lenticula Aschers. & Graebner, Syn. Mitteleur. Fl. 6(2):905 (1909).

Plants perennial or annual. Leaves amphistomatic to epistomatic, usually tendrillous, multijugate. Inflorescence racemore, many- to few-flowered. Flowers large and brightly-coloured (yellowish, crimson and purple) to small and pale. Calyx irregular, often gibbous at the base; vexillum platynychioid; style laterally compressed; ± evenly pubescent all round, sometimes somewhat tufted abaxially. Seeds with long to short hilum. - c. 40 species.

Type : V. cracca L.

Geographical distribution: Europe, N. Africa, Canaries, Azores, S.W. Asia, Crimea, Caucasia, Transcaspia, Asia eastwards to Japan, N. America. See Figs. 63, 64 & 80.

Sect. Cracca is the largest taxon of this rank within Vicia and contains the widest range of varia-

bility. The 'core' of this section, as delimited here, includes those species which Godron (1849)
2.3.1 placed in the illegitimate genus Cracca (Table 4); the key character of this group was the laterally compressed style. Since that time, however, the as-
2.3.3 semblage of species which possess this feature has rarely been recognised as a unit. Two trends have brought this about: firstly, the tendency of taxonomists to group together all members of Vicia (or the Vicieae!) which have small, pale flowers; secondly, the decreasing interest which more modern authors have shown in the fine morphological details which their predecessors often recorded so carefully.

I have reinstated 'Cracca' with confidence that it is a natural group. This is due mainly to the dis-
4.2.5 Fig. 13 4.2.3.1 Fig. 19:4,5 Table 12 covery that the laterally compressed style is always accompanied by a pandurate (platynychioid) vexillum, while this form of standard is rare outside the group. The delimitation of Sect. Cracca by these two characters is simple, but it involves the disruption of some other generally recognised groups within Vicia. Foremost among these is 'Ervum'. As was described in part 2.3.1, and summarised in Table 5, the classification of ervoid members of Vicia is unsatisfactory and has long been in a state of flux. In its narrow-
Table 5 est definition, 'Ervum' (sensu Godron) contained only the lectotype of Linnaeus' genus, E. tetraspermum

(V. tetrasperma); in its broadest sense, 'Sect.' Ervum sensu Aschers. & Graebner also included V. ervilia, V. hirsuta, V. articulata and V. monantha. (Alefeld (1859) had a concept of Ervum totally out of line with all other authors' - in his sense the genus Ervum contained perennials, e.g. V. unijuga, as well as small-flowered annuals.) Recent authors, e.g. Ball (1968) and Davis & Plitmann (1970) have tended to take a wide view of the group. I consider that this modern treatment is artificial and unnatural; the ervoid species share certain general features but in detail they form a heterogeneous collection. This is illustrated not only by their floral structures but by the striking differences in their fruits. Several species which Hall places in Sect. Ervum, viz. V. leucantha, V. vicioides, V. durandii, V. disperma and V. bifoliolata (= V. filicaulis), have laterally compressed styles and pandurate vexilla, and are therefore transferred to Sect. Cracca. This applies also to V. monantha, which Ascherson & Graebner put in 'Sect.' Ervum, but not to V. articulata. V. hirsuta and V. meyeri are moved to Sect. Cracca with these species, but by association rather than by their own possession of the key characters. Their flowers are so small and simple (due, presumably, to the evolution of a predominantly autogamous breeding-system) that the form of their parts cannot be used as taxonomic

Table 5

4.4
Fig. 22

Table 12

4.2.3.1

7.4

4.2.5 evidence; the style is reduced to a minute, terete, few-haired process, while the standard is ovate.

Table 12

Fig. 22:16 & 17 The fruits of V. hirsuta and V. meyeri are, however, quite distinctive, and these species have many morphological similarities with the slightly more robust V. palaestina, which has the style and standard typical of Sect. Cracca. This association is strengthened by the finding that V. palaestina and V. hirsuta possess closely similar serological characteristics when antigens from their seeds are precipitated by Lens culinaris antiserum. Members of Sect. Cracca typically have legumes which are rhomboidal and more-or-less stipitate, and it is interesting to find that all the species which are here transferred from Sect. Ervum (sensu Ball) to Sect. Cracca can be distinguished from the residue by their fruits with non-parallel sutures.

Table 12

6.4.2.3 Table 18

Fig. 22:9

Fig. 22:10 - 13

A correlation between laterally compressed styles and platynychioid vexilla is found again in N. American representatives of Vicia. In other characteristics (leaf shape, stomatal distribution, shape of fruit, etc.) these species agree well with Old World members of Sect. Cracca and they are therefore united with them. These new members include V. caroliniana, V. pulchella, V. acutifolia, V. exigua and V. ludoviciana.

Table 12

Fig. 3:39 - 42 Table 11

Within Sect. Cracca there is a wide range of

morphological variation. The majority of species
4.1 have multijugate, tendrillous leaves and dense, attractive, many-flowered racemes, but there are several types of exceptions to this rule. For example, V.
3.2 sicula has etendrillous leaves and its leaflets are
Fig. 3:15 few, very long and coriaceous, and have inrolled margins. V. filicaulis is few-flowered, and the whole
3.5 plant is modified to produce an extremely slender
Fig. 3:29 climber with narrow leaflets and long, delicate, branched tendrils. The three closely related species V. ciceroidea, V. rafigae and V. multijuga are xerophytes with coriaceous leaflets and hard, circinnate or almost spinous tendrils. The style in these
Fig. 21:5 three is distinctive in bearing hairs only on the adaxial and abaxial edges, not on the sides.

4. Sect. Variegatae Radzhi in Novit. Syst. Pl. Vasc. (Leningrad) 7:230 (1970).

Plants perennial. Leaves hypo-amphistomatic to epistomatic, multijugate, often with dense indumentum; tendrils often reduced or absent. Inflorescence many-flowered. Flowers white to purplish. Calyx irregular; vexillum platynychioid; style dorsally compressed, densely bearded on the abaxial side. Seeds with hilum of medium length. - 3 species.

Type: V. variegata Willd. (≡ V. canescens Lab. subsp. variegata (Willd.) Davis).

Geographical distribution: Pyrenees, S. Italy, S., Inner & N.E. Anatolia, Caucasia, N. Iran, W. Syria, C. Asia. See Fig.61.

The members of Sect. Variegatae form an easily-recognised group whose superficial unity is confirmed by other more cryptic features. Radzhi (1970) was probably the first to describe accurately the style of these species; it is of a type unique to this section, being strongly dorsally compressed, glabrous on the inner surface and long-bearded abaxially. I have shown, moreover, that in Sect. Variegatae the vexillum is of the platynychioid type which occurs otherwise only in Sects. Cracca and Cappadocicae. Members of Sect. Variegatae, like those of Sects. Vicilla and Cassubicae, show a tendency towards reduction of the tendrils. Some members of the polytypic V. canescens have mucronate leaves, while in most plants of V. argentea they are imparipinnate.

2.3.1
4.2.5
Fig. 21:8
Table 12
Fig. 19:6
3.2

Sect. Variegatae is a disjunct group, comprising typically alpine species. Its members are found in the Pyrenees (V. argentea), S. Italy, Anatolia and Caucasia (V. canescens s.l.) and C. Asia (V. megalotropis). The evolution of some of these taxa has been accompanied genetically by a decrease in the chromosome complement: thus in V. canescens subsp. variegata 2n = 10. Descending dysploidy is recorded by Stebbins (1950) as one of the trends commonly followed during the phylogenesis of highly-evolved perennials in specialised habitats.

Fig. 61
Table 20

5. Sect. Pedunculatae Rouy in Rouy & Foucaud, Fl. Fr. 5:221 (1899).

Plants perennial. Leaves epi-amphistomatic, multijugate and tendrillous, with linear leaflets. Inflorescence a loose raceme of several relatively large flowers. Flowers whitish to purple. Calyx irregular; vexillum stenonychioid; style dorsally compressed, pubescent all round but tufted abaxially. Seeds with short to long hilum. - Ditypic.

Lectotype designated here: V. onobrychioides L.

Geographical distribution: S. Europe excluding Turkey-in-Europe, N.W. Africa. See Fig. 62.

4.2.5 Table 4 2.3.3 4.2.3.1 Table 12 Fig. 19:3 Table 11

V. onobrychioides, V. altissima and V. dumetorum have the same type of style as members of Subgen. Vicia, and were placed together with these species by some early taxonomists (e.g. Godron, 1849; Rouy, 1899). Later authors tended to overlook this character in favour of the stronger phenetic similarity between V. onobrychioides etc. and Sect. Cracca s.l. However, when faced with the task of dividing Subgen. Vicilla into natural sections, one must be careful in deciding how to treat anomalous species such as these. In the case of V. dumetorum, I considered that its oblong vexillum and hypostomatic leaves show a strong enough link with members of Sect. Vicilla to justify its inclusion there. V. onobrychioides and V. altissima, on the other hand, have standards with a broadened banner, the leaves are epi-amphistomatic,

Fig. 3:21 and the leaflets are linear rather than ovate. It seems probable that these taxa are quite closely related to members of Sect. Vicilla, but have diverged from them following two recognisable trends: towards a more xerophytic habitat, and towards a condition where the individual flower, rather than the inflorescence, has become the attractive unit.

6. Sect. Americanae Kupicha, sect. nov. Syn: Abacosa Alefeld in Bonplandia 9:102 (1861).

Plants perennial. Leaves epi-amphistomatic, multijugate, tendrillous. Inflorescence several-flowered; flowers comparatively large and borne in a loose raceme, purplish. Calyx irregular; vexillum oblong; style dorsally compressed, pubescent all round but tufted abaxially. Seeds with long hilum. - Monotypic.

Type: V. americana Muhl. ex Willd.

Geographical distribution: N. America excluding the S.E. States. See Fig. 74.

Gunn, 1968a V. americana is an extremely polymorphic species, but despite its internal diversity it seems to be taxonomically isolated, at least in the New World. It is quite distinct from the N. American members of Sect. Cracca s.s., and also from V. nigricans. The species which are most alike in morphology belong to the small W. Mediterranean Sect. Pedunculatae, but I hesitate to unite V. americana with this section without further study; it would be surprising if such a disjunct

group proved to be natural. Sects. Pedunculatae and Americanae can be distinguished by the different shapes of their vexilla, which are stenonychioid and oblong, respectively. In its stylar characters, V. americana resembles the S. American species of Vicia. It is possible that this fact holds a clue to the origin of Sect. Australes, but at present there are few other indications linking the two groups.

Table 12

4.2.5
Fig. 21:9

V. americana also occurs in E. Asia, but is represented here only by var. tridentata (Gunn, 1968a). The centre of variability of this species is certainly N. American, and its extension into China, though not necessarily due to man, may be relatively recent in evolutionary terms.

7. Sect. Subvillosae Kupicha, sect. nov.

Plants perennial. Leaves amphistomatic, imparipinnate; leaflets few per leaf, subulate, villous. Inflorescence bearing few, large, purple flowers. Calyx sub-regular; vexillum stenonychioid; style dorsally compressed, pubescent on adaxial and abaxial faces. - Monotypic.

Type: V. subvillosa Boiss.

Geographical distribution: Afghanistan north-east to Tien Shan. See Fig. 65.

V. subvillosa is a particularly beautiful and taxonomically interesting species. Like members of Sect. Variegatae, it inhabits screes at high altitudes

2.3.3

3.7 & 3.2
4.1
Table 12
Fig. 19:7
3.2
4.2.5
Fig. 21:6

and has leaves which are densely hairy and etendrillous; like V. onobrychioides, the flowers are individually large and attractive and the vexillum is stenonychioid. It possesses several characters peculiar to itself; the leaves have a terminal leaflet; the calyx is subregular; and the style has a unique distribution of indumentum.

It is interesting to compare V. subvillosa with other groups in the tribe Vicieae which share a similarly rocky, alpine habitat; for example, Sect. Variegatae in Vicia, Sect. Lathyrostylis in Lathyrus,

10:5

and the ditypic genus Vavilovia. All show a tendency towards loss of tendrils, and it seems reasonable to infer that during the evolution of these comparatively specialised perennials, this morphological effect may have arisen repeatedly and independently in response to similar environmental conditions.

8. Sect. Biennes Kupicha, sect. nov.

Plants annual or biennial. Leaves epi-amphistomatic, multijugate, tendrillous; leaflets linear, with supervolute vernation. Inflorescence dense, many-flowered. Flowers violet. Calyx irregular; standard stenonychioid; style dorsally compressed, evenly hairy all round. Seeds with hilum of medium length. - Monotypic.

Type: V. biennis L.

Geographical distribution: S.E. Europe, S. Russia, Caucasia. See Fig. 66.

2.3.3 Table 12 3.3

Although in facies closely similar to some members of Sect. Cracca s.s., V. biennis possesses several characters which argue strongly against such an association. Its flower differs from those of Sect. Cracca in having a stenonychioid standard and a dorsally compressed style; it is distinguished from those of Sect. Pedunculatae in having the style not tufted but evenly pubescent all round. V. biennis is unique within Vicia in having its leaflets curled, rather than folded, in bud; this feature is otherwise confined to, and diagnostic of, the genus Lathyrus. In other respects V. biennis is a typical member of Vicia and shows no particular affinity with Lathyrus, and I do not consider that its anomalous vernation is necessarily an indication of close phylogenetic relationship with the latter; this character may have arisen as an independent mutation.

9. Sect. Cappadocicae Kupicha, sect. nov.

Annuals. Leaves epi-amphistomatic, tendrillous; leaflets few- to several-paired, linear. Inflorescence 1-few-flowered. Flowers reddish-purple to violet. Calyx irregular and gibbous or subregular; standard platynychioid; style dorsally compressed, pubescent all round but tufted abaxially. Seeds with short hilum. - 3 species.

Type: V. cappadocica Boiss. & Bal.

Geographical distribution: Greece, Cyprus, S. & Inner Anatolia,

W. Syria, N. & N.W. Iran, Transcaucasia. See Fig. 67.

The members of this group are very similar in facies to some of the more delicate representatives of Sect. Cracca (e.g. V. monantha, V. glauca, V. leucantha).

4.2.3.1 Table 12 This impression is supported by the pandurate vexilla found in all members of Sect. Cappadocicae and by the gibbous calyces of V. cassia and V. cretica. The only conflicting characters lie in the gynoecium: instead of being laterally compressed and evenly hairy all round, the styles in Sect. Cappadocicae are dorsally

4.2.5 flattened and tufted on the outer face.

As Table 12 shows, this type of style occurs in many species of Vicia, not all of which are closely related. It is typical of Subgen. Vicia, and this is

2.3.1 one of the reasons why Radzhi (1970) places V. cappadocica with V. sativa and V. bithynica in Sect. Vicia. The subregular calyx and parallel-sutured pods of V. cappadocica provide further evidence to support this arrangement. Equally strong arguments, however, can be used against it: V. cappadocica does not have stipular nectaries; the peduncle is long (although this is sometimes also found in V. bithynica); the standard is pandurate; and the fruit is more-or-less stipitate. Due to this balance of conflicting factors,

2.3.3 V. cappadocica has given taxonomists considerable trouble in the past.

The distribution of the dorsally compressed,

tufted style within Vicia is of particular interest.

Table 1.2

It occurs without exception in the well-defined Subgen. Vicia and sporadically outside it: in S. American species (except V. nigricans), in the N. American V. americana, in V. dumetorum and in Sects. Peduncula-tae and Cappadocicae. The constancy of the trait in some cases (within Subgen. Vicia and on the S. American continent) suggests that it has special taxonomic and functional significance there, and so its occasional appearance in other places is given equally strong weighting. The justification of this depends on how easily and how often this type of style can evolve. Its distribution pattern, which is disjunct both geographically and taxonomically, does not support the theory that it has a monophyletic origin within Vicia, and although it is difficult to envisage how such a distinctive form could have arisen more than once, it seems likely that this is the case. Perhaps the abaxially tufted style has an advantage over the evenly hairy style in promoting cross-pollination. This idea is supported by the common occurrence of

4.2.5

abaxial tufts on the laterally compressed styles of Sect. Cracca. One can deduce, from its occurrence throughout the whole of Subgen. Vicia, that the tufted style is not a recent feature but was present at early stages in the evolution of Vicia. In the light of these considerations it seems justified to use

such stylar characters to provide guides for the division, if not the unification, of taxa.

10. Sect. Ervum (L.) Taubert in Engler & Prantl, Naturl. Pflanzenfam. 3(3):350 (1894). Syn: Ervum L., Sp. Pl. 738 (1753); Vicia Subgen. Ervum (L.) Rouy in Rouy & Foucaud, Fl. Fr. 5:245 (1899);

Lectotype: V. tetrasperma (L.) Moench (Alefeld, 1859).

Geographical distribution: Europe, N. Africa, Palestine, W. Syria, N. Iraq, Outer Anatolia, Crimea, Caucasia, Asia eastwards to China. See Figs. 68 & 80.

Plants annual. Leaves amphi- to epistomatic, tendrillous, with few pairs of small, elliptical leaflets. Inflorescence few-flowered. Flowers small and pale. Calyx subregular; vexillum oblong to ovate; style terete to (slightly) dorsally compressed, sparsely hairy all round. Fruits less than 2 cm long, not stipitate, with parallel sutures. Seeds with short hilum. - 4 species.

The history of classification of 'ervoid' members of Vicia was discussed in part 2.3.1. and also in this chapter under Sect. 3 Cracca. The species which I include in Sect. Ervum represent the 'core' of closely allied taxa related to V. tetrasperma, the lectotype of the genus Ervum L. This narrow view coincides with the concept of Godron (1849), but conflicts with the opinions of the majority of more recent authors. The species which comprise Sect. Ervum s.s. are united by

Table 4

Fig. 22:14 & 15 their fruit type: the legume is very small (less than 2 cm long), not stipitate, and has parallel sutures.

The ervoid species will always present a problem, 7.4 because their flowers are simple (probably reduced or degenerate through adaptation to autogamy) and the usual taxonomic guides - standard shape and stylar details - are more-or-less obliterated. I consider, however, that although it may not be possible to link members of the ervoid group with other sections of Vicia, this assemblage should not be treated as a 'dust-bin' section but should rather be subdivided into smaller groups (even if these are rather inconvenient) whose internal affinity is certain. These can then be 15.1 regarded as 'natural' taxa of equal status within the hierarchy, and further phylogenetic speculation about their mutual relationships need not disturb the classification. Sects. Ervoides, Ervilia and Caesarea are all of this type, having been segregated from the broad and nebulous ervoid group.

11. Sect. Ervoides Gren. & Godron, Fl. Fr. 1:471 (1849). Syn: Coppoleria Todaro in Atti Accad. Sci. Litt. Palermo ser. 2,1:14 (1845): Parallosa Alefeld in Öst. Bot. Zeitschr. 9:359 (1859); Vicia Subgen. Ervoidea (Gren. & Godron) Rouy in Rouy & Foucaud, Fl. Fr. 5:241 (1899).

Plants annual. Leaves epi-amphistomatic, multijugate, tendrillous, with narrow leaflets; stipules strikingly dimorphic.

Inflorescence 1(-2)-flowered. Flowers lilac. Calyx slightly irregular; vexillum oblong; style dorsally compressed, evenly pubescent all round. Legume subtorulose. Seeds with short hilum. - Monotypic.

Lectotype designated here: V. articulata Hornem.

Geographical distribution: Italy, Balkans, Corsica, Sardinia, Sicily, Crete, W. Turkey. See Fig. 69.

Tables 4 & 5

V. articulata has long alternated in position between the two broad groups 'Cracca' and 'Ervum', without having obvious strong affinities with any other species. It is isolated by two striking morphological features:

4.4

it has subtorulose fruits, and dimorphic stipules in

3.6

which one of the pair is simple, the other composed of many fine radiating branches. In its fruit V. articulata approaches V. ervilia and V. caesarea; in the

10.4

laciniate stipules, Anatropostylia (Vicia) koeieana. The floral characters, however, provide taxonomic evidence of a different persuasion: the standard is oblong, and the style is dorsally compressed and evenly pubescent as in the perennial (primitive?) Sects. Vicilla and Cassubicae. This type of flower is quite unlike those of Sect. Cracca or of Anatropostylia, but the gynoecium is perhaps comparable with that of V. ervilia. On balance it seems best to separate V. articulata as a monotypic section. V. ervilia may possibly be one of its nearest allies, but were they united in a single section this taxon would contain

Table 12

too wide a variability for its size.

12. Sect. Ervilia (Link) W. Koch, Syn. Fl. Germ. ed. 1:191 (1836). Syn: Ervilia Link, Enum. Hort. Berol. 2:240 (1822). Ervum Sect. Ervilia (Link) Ser. in DC., Prodr. 2:366 (1825); Vicia Subgen. Ervilia (Link) Rouy in Rouy & Foucaud, Fl. Fr. 5:248 (1899).

Plants annual. Leaves epi-amphistomatic, multijugate, mucronate; leaflets linear. Inflorescence with one to several small pale lilac flowers. Calyx subregular with equal teeth; vexillum ovate; style dorsally compressed, evenly pubescent all round. Fruits subtorulose. Seeds with short hilum. - Monotypic.

Type: V. ervilia (L.) Willd.

Geographical distribution: S. Europe, N. Africa, Palestine, W. Syria, N. Iraq, W. Iran, W. & S. Anatolia. See Fig. 70.

The isolated position of V. ervilia has been recognised almost since the beginning of classification of Vicia. It was segregated as a monotypic genus by Link (1822) and by Godron (1849), while in Taubert's scheme (1894) this taxon had the rank of a section within Vicia. Other authors have taken a wider view of Sect. Ervilia. In the sense of Seringe (1825) it included V. tetrasperma and V. articulata as well as the type species. Lastly, Plitmann (1967) has used Ervilia as a series within Sect. Ervum which includes V. ervilia and V. caesarea.

2.3.1

Table 4

Table 5

V. ervilia was placed within the ervoid assem-
Fig. 19:9 blage because it has small, pale flowers in sparse rac-
emes. It differs from other members in having a bushy
3.2 habit; tendrils are absent and the plant does not
support itself on neighbouring vegetation. In addi-
tion, the leaves have very many leaflets (8-20 pairs)
4.4
Fig. 22:18 and the fruit is subtorulose. V. ervilia is culti-
vated as a fodder crop in Mediterranean countries and
it is possible that some of its characteristics (e.g.
the etendrillous leaves) have been selected by man.

V. quadrijuga, which resembles V. ervilia in its habit and floral characters, but whose mature fruits are unknown, is discussed at the end of part 11.3.

13. Sect. Caesareae Kupicha, sect. nov.

Plants annual. Leaves amphistomatic, tendrillous, with few to several pairs of small elliptical leaflets. Inflorescence few-flowered. Flowers bicoloured, lavender-blue and white. Calyx subregular, with upper teeth longer than the lowest one; vexillum ovate, with two small pouches; style dorsally compressed, pubescent all round. Fruit subtorulose. Seeds lenticular, with short hilum. - Monotypic.

Type: V. caesarea Boiss. & Bal.

Geographical distribution: C. & adjacent S. Anatolia. See Fig. 71.

Since it is endemic to Turkey, V. caesarea has rarely been considered in relation to the rest of

Vicia and has had an uneventful taxonomic history. The synonymous V. vulcanica Hand. - Mazz. was described under the mistaken impression that it was perennial. Plitmann (1967) has recently placed it in Ser. Ervilia, within Sect. Ervum; it is linked with V. ervilia because they both have subtorulose legumes. In other characters, however, V. caesarea appears to be quite distinct from V. ervilia (i.e. in the presence of tendrils; the shape of the calyx and standard; and in the lenticular seeds), and I do not consider that the evidence justifies such a close association of the two species. In habit, V. caesarea is remarkably similar to Lens, and certain details of its morphology (e.g. the bossed standard and the flattened seeds) support this superficial impression. This was discussed more fully in part 10.3, where I concluded that V. caesarea should be retained within Vicia at present, but merits special study to confirm its position.

4.4
Fig. 22:19

4.2.2
Fig. 19:10
4.5.2

Table 25

14. Sect. Trigonellopsis Rech. fil. in Arkiv för Botanik 5(1): 260 (1959). Syn: Sellunia Alefeld in Öst. Bot. Zeitschr. 9:358 (1959).

Plants annual. Leaves multijugate, tendrillous, with broadly elliptical leaflets. Inflorescence few-flowered. Flowers bicoloured, bluish and yellowish. Calyx subregular; standard stenonychioid; style long and slender, dorsally compressed,

evenly hairy all round. Fruits sometimes (i.e. in V. lunata) somewhat inflated, with papery, indehiscent valves. Seeds with short hilum, lenticular in V. lunata. - Ditypic.

Type: V. lunata (Boiss. & Bal.) Boiss.

Geographical distribution: Cyprus, W. & S. Anatolia, W. Syria. See Fig. 72.

2.3.1 Sect. Trigonellopsis was originally monotypic and based on V. lunata. This species is distinct

4.4 from all others in having broadly crescentic fruits

Fig. 22:5 whose valves become papery and somewhat inflated on maturity. V. cypria has legumes of a more usual form, but shares with V. lunata several features which confirm their close relationship. The leaflets in both are rather distantly placed on the rachis and are broadly elliptical to emarginate or praemorse. The stipules in these species are sometimes fringed with slender laciniae, but I do not agree with Rechinger (1959) who considers them very similar to the deeply divided, fimbriate stipules of V. articulata and Anatropostylia koeieana. The flowers of V. lunata and V. cypria are similar, both in general appearance and detail. The vexilla are large and blue, forming a contrast with the yellow wings and keel.

Fig. 19:8 The standards are stenonychioid (a comparatively

Table 12 rare shape in Subgen. Vicilla), while the styles are distinctively long and slender.

15. Sect. Australes Kupicha, sect. nov.

Slender annuals and perennials. Leaves epi-amphistomatic, tendrillous, usually with few pairs of leaflets. Inflorescence few- to many-flowered. Flowers white to deep blue. Calyx subregular to irregular; vexillum stenonychioid to oblong; style dorsally compressed, pubescent all round but tufted abaxially. Seeds with short to long hilum. - c. 12 species.

Type: V. graminea Smith.

Geographical distribution: Mexico, Colombia, Peru; S. America S. of lat. 25° S. See Fig. 73.

Apart from V. nigricans, the S. American members of Vicia form a closely-related complex of species whose boundaries are often difficult to determine and may possibly be affected by hybridisation. Although their stylar characters suggest an affinity with Subgen. Vicia there is no other evidence for this; stipular nectaries are absent and the inflorescence is usually borne on a long peduncle. In habit V. graminea s.l. is reminiscent of the W. Mediterranean V. filicaulis, but floral details (stenonychioid standard and tufted, dorsally compressed style) show that the former is not a member of Sect. Cracca. I agree with Hanelt & Mettin (1970b) that the affinities of S. American species of Vicia lie more with Subgen. Vicilla than with Subgen. Vicia, and I consider them sufficiently distinct, as a group, to merit classification in an independent section.

Table 12

16. Sect. Leucophaeae Kupicha, sect. nov.

Plants perennial. Leaves epi-amphistomatic, tendrillous, with few pairs of leaflets. Inflorescence 1- to 2-flowered. Flowers yellowish. Calyx subregular; vexillum stenonychioid; style terete, arcuate, with a dense ring of hairs at some distance from the stigma. Seeds with hilum of medium length. - Monotypic.

Type: V. leucophaea Greene.

Geographical distribution: New Mexico. See Fig. 73.

In habit, V. leucophaea resembles the N. American members of Sect. Cracca, but it differs from them in floral details. The standard is stenonychioid rather than pandurate, and the style has a form unique within the genus. V. leucophaea could be compared with V. subvillosa: both are taxonomically isolated perennials inhabiting restricted mountainous localities; both have villous leaves and few-flowered racemes in which the individual blooms are conspicuous.

Table 12
4.2.5
Fig. 21:10

II. Subgen. Vicia.

Plants perennial and annual. Stems sometimes with partial replacement of cortical vascular bundles at the nodes. Leaves hypostomatic to hypo-amphistomatic, paripinnate, usually tendrillous, occasionally mucronate; stipules monomorphic, always with a glandular nectariferous pit on the abaxial side. Inflorescence several- to 1-flowered, always shorter than the subtend-

ing leaf; flowers sometimes ± sessile in leaf axil. Calyx regular or irregular. Vexillum oblong or stenonychioid, rarely pubescent on the adaxial side. Style dorsally compressed, hairy all round or only on abaxial side, always tufted abaxially. Legume not stipitate, containing ± well-developed 'woolly' parenchymatous tissue between the seeds; pods rhomboidal or linear. Seeds with long to short hilum; testa smooth or very rarely rough; lens near hilum or on opposite side of the seed; canavanine absent.

Lectotype: V. sativa L.

17. Sect. Atossa (Alefeld) Aschers & Graebner, Syn. Mitteleur. Fl. 6(2):949 (1909). Syn: Vicioides Moench, Meth. 135 (1794); Atossa Alefeld in Bonplania 9:100 (1861); Vicia Sect. Pedunculatae Rouy in Rouy & Foucaud, Fl. Fr. 5:221 (1899), pro parte excl. typ.; Vicia Sect. Sepium Radzhi in Novit. Syst. Pl. Vasc. (Leningrad) 7:235 (1970).

Plants perennial. Stems with complete replacement of cortical vascular bundles at nodes. Leaves hypostomatic, tendrillous or mucronate; leaflets few- to several-paired. Inflorescence pedunculate, several-flowered. Flowers pale yellow or bluish-purple. Calyx irregular; vexillum oblong, glabrous. Legume with sutures not parallel. Seeds with hilum encircling over half the circumference; lens near hilum; testa smooth. - 4 species.

Lectotype: V. sepium L. (Gunn, 1969).

Geographical distribution: Europe except Sardinia and Turkey-

in-Europe; N. Anatolia, Crimea, Caucasia, N. Iran, Asia eastwards to the Pacific. See Figs. 75 & 80.

The species of this small and rather heterogeneous group inhabit deciduous woods or hedgerows, and share with other more distantly related members of the tribe several characteristics which appear to be correlated with a mesophytic habitat. While V. sepium has a scrambling habit, the other species tend to grow erect and free from supporting vegetation; V. truncatula and V. oroboides have etendrillous leaves. As has been mentioned in earlier chapters, V. oroboides is remarkable for its resemblance to 'oroboid' members of Vicia Sect. Vicilla and Lathyrus Sect. Orobus. I consider, however, that the facies of this phenetic assemblage has probably evolved separately several times; there is no doubt that V. oroboides is a true member of Subgen. Vicia since it possesses all the key characters of this well-defined group. Members of Sect. Atossa have strongly hypostomatic leaves; this trait, among others, serves to distinguish V. truncatula and V. balansae from the species of Sect. Cassubicae (e.g. V. orobus, V. cassubica) which are very similar in habit. Like many woodland species, members of Sect. Atossa have dense inflorescences which are conspicuous in number of flowers rather than by the attractiveness of each bloom. The flowers themselves do not have widened

3.2
2.3.3
10.2
Table 23
Fig. 3:3
3.8
Table 11
Fig. 7:3 & 4
4.1

Fig. 14
Fig. 19:12
Table 12
Table 13

banners, as in the majority of the subgenus, but oblong vexilla. (A correlation between the congested inflorescence and oblong standards is also found in Sect. Hypechusa, and in Lathyrus Sect. Orobus.) Finally, the long hila of the seeds of Sect. Atossa are also typical of other perennials of the tribe Vicieae.

18. Sect. Vicia. Syn: Cujunia Alefeld in Bonplandia 9:101 (1861); Vicia Sect. Subsessiles Rouy in Rouy & Foucaud, Fl. Fr. 5:208 (1899).

Plants annual or perennial. Stems with complete replacement of cortical vascular bundles at the nodes. Leaves hypoamphistomatic, tendrillous; leaflets many- to several-paired. Inflorescence 1-2-flowered; flowers sessile in the leaf axils, pale yellow, purple or lavender. Calyx teeth equal; vexillum stenonychioid, glabrous. Legume with parallel sutures. Seeds with hila very long to very short; lens near hilum; testa rough or smooth. - c. 6 species.

Lectotype: V. sativa L.

Geographical distribution: Europe, N. Africa, S.W. Asia, Crimea, Caucasia, Transcaspia, Asia eastwards to Japan. See Figs. 76 & 80.

Sect. Vicia comprises an undoubtedly natural group of species and yet contains a fairly wide range of character-variation. On one hand there is the only perennial member, V. pyrenaica, endemic to the Sierra

Nevada and the Pyrenees; on the other, the polymorphic cosmopolitan weed V. sativa, the type of the genus, which has been divided into five or more microspecies or subspecies.

Ball, 1968

Members of this section can often be recognised by their foliage: the leaflets, although variable in dimensions, are usually emarginate and mucronate, and have prominent, straight lateral veins. V. grandiflora has seeds in which the hilum occupies over half the circumference; in Old World species of Vicia this trait is otherwise confined to perennials (as in Sect. Atossa), but it is common in American species, including the annuals. Ascherson & Graebner (1909) attempted to divide 'Sect. Euvicia' (equivalent with Subgen. Vicia) into two groups based on hilum length; in this arrangement V. grandiflora was placed with V. sepium. However, apart from its anomalous seeds and its yellow flowers, V. grandiflora is a typical member of Sect. Vicia. The two small species V. lathyroides and V. cuspidata are unusual within the genus in having rough-coated seeds; they can be distinguished from each other by the different patterning of the testa surface.

3.5

Fig. 3:11, 36 & 37

Table 13

2.3.1

4.5.2

The present taxonomic arrangement is not supported by the distribution of free amino acids found in some members of the subgenus. Seeds of V. sativa, V. grandiflora and V. sepium were reported to contain

6.3

the lathyrogenic substance β-cyanoalanin, but this was absent from V. lathyroides. The latter and all other species tested had relatively large quantities of arginine in their seeds instead. Unfortunately V. oroboides, V. truncatula and V. balansae were not screened for this character, so it is not possible to judge the full implications of its distribution pattern.

19. Sect. Faba (Miller) Ledeb., Fl. Ross. 1:664 (1842). Syn: Faba Miller, Gard. Dict. ed. 4 (1754); Arachus Medik. in Vorles. Churpf. Phys. Ges. 2:360 (1787); Vicia Sect. Arachus (Medik.) Tutin in Clapham et al., Fl. Brit. Is. 447 (1952).

Plants annual. Stems with complete replacement of cortical vascular bundles at the nodes. Leaves hypo-amphistomatic, tendrillous or mucronate, with few (1-3) pairs of large leaflets. Inflorescence 1-2-flowered; flowers pedunculate or sessile in the leaf-axils, whitish or purple. Calyx regular; vexillum stenonychioid, glabrous. Legume with parallel sutures. Seeds with short hilum; lens near hilum; testa smooth. - 5 species.

Type: V. faba L.

Geographical distribution: W. & S. Europe, N. Africa, Palestine, W. Syria, Syrian Desert, N. Iraq, W. Iran, S. Anatolia, Crimea. See Fig. 77.

V. faba itself occurs only in cultivation, or as an escape, but although its precise origins are unknown there are closely similar wild relatives (V. narbonensis and the recently described V. haemiscyamus

and V. galilaea). The characters which are associated
3.2, 3.1 with its role as a crop plant (absence of tendrils,
Fig. 3:24 stout habit, very large leaves) have been very heavily
weighted in the past; Fedtschenko (1948) even made
2.3.1 V. faba the basis of a monotypic subgenus equivalent
in status with the rest of the genus! I consider,
however, that V. faba and V. narbonensis are in most
respects typical members of Subgen. Vicia, and their
possession of all its key characters is surely of much
greater significance, in the construction of a natural
classification, than features which were probably
selected by man.

2.3.3 V. bithynica has only recently been associated
with the V. faba group; it is a distinctive species
with an unsettled taxonomic history. In habit V.
bithynica stands apart from other members of Sect.
Faba; it is more slender and has well-developed ten-
4.1 drils, and the flowers are often borne on a long
peduncle and pedicel. However, the characters which
it shares with them suggest that Sect. Faba, as
defined here, is probably a natural group. In its
4.4 regular calyx, parallel-sided pods and dentate stip-
Fig. 22:4 ules, Sect. Faba appears to have some affinity with
Sect. Vicia.

20. Sect. Hypechusa (Alefeld) Aschers. & Graebner, Syn. Mitteлleur. Fl. 6(2):957 (1909). Syn: Hypechusa Alefeld in Bot.

Zeitung 18:165 (1860); Vicia Sect. Subsessiles Rouy in Rouy & Foucaud, Fl. Fr. 5:208 (1899), pro parte excl. typ.; Vicia Sect. Pedunculatae Rouy, op. cit. 221, pro parte excl. typ.

Plants annual. Stems with partial replacement of cortical vascular bundles at the nodes. Leaves epi- or hypo-amphistomatic, tendrillous; leaflets many-paired. Inflorescence many- to 1-flowered, flowers pedunculate or sessile in leaf-axils, yellowish or very rarely purplish. Calyx irregular; vexillum oblong or stenonychioid, occasionally pubescent on adaxial side. Legume rhomboidal (sutures not parallel). Seeds with medium to short hilum; lens on opposite side of the seed from the hilum; testa smooth. - 12 species.

Lectotype: V. lutea L. (Gunn, 1969).

Geographical distribution: W., S. & C. Europe, Crimea, N. Africa, W. Syria, S.W. Asia, Caucasia, Transcaspia. See Fig. 78.

2.3.1 This group was first distinguished by Alefeld (1860) as a genus of the Subtribe Viciosae (equivalent with Subgen. Vicia); it was based on the lens position, on flower colour, and on the absence of spongy tissue within the legume. Boissier (1872) was the only taxonomist to follow Alefeld in recognising this assemblage as a unit; Ascherson &

4.5.5 Graebner (1909) also made use of the lens-position character, but in conjunction with the non-correlated variation in hilum length, and the delimitation of 'Hypechusa' was consequently altered. Recent authors

have usually ignored variation in lens position in Vicia. For example, Plitmann (1967) divides the species of Sect. Hypechusa between four groups without suggesting that these possess a sign of close relationship within the hierarchy. Hypechusa is reinstated here as a section chiefly because of the discovery of another character confined to the group - a variation in nodal anatomy. Its members are probably unique within the tribe in that the replacement of cortical vascular bundles at the nodes of the mature plant is partial rather than complete.

5.3.2
Fig. 31
Table 15

This section comprises some very attractive plants and considerable morphological variation. Most of the species have sessile flowers, solitary or twinned in the leaf axils, and the vexilla in these flowers have a wide banner and narrow claw. A few species, however, have several-flowered inflorescences on short peduncles (e.g. V. pannonica and V. melanops), and in these the vexillum is oblong. These characteristics belong to a syndrome which is generally typical of perennial woodland species of the tribe; their presence here in weedy annuals is therefore particularly interesting and suggests that these species are primitive within Sect. Hypechusa.

Fig. 19:13

Other distinctive characters which occur within the section may be mentioned: V. pannonica, V. hybrida and V. anatolica are unique within the tribe in having

4.2.3.1 3.7 4.4 pubescent standards; V. lutea has pods bearing long tuberculate-based hairs; and the wing petals of V. melanops are greenish-yellow with a conspicuous velvety black spot. Alefeld considered that the fruits on Sect. Hypechusa do not contain spongy tissue, but this distinction cannot be supported. All members of Subgen. Vicia seem to have 'woolly' mesophyll in their pods, but in some species it is more strongly developed than in others.

21. Sect. Peregrinae Kupicha, sect. nov. Syn: Tuamina Alefeld in Bonplandia 9:102 (1861); Vicia Sect. Subsessiles Rouy in Rouy & Foucard, Fl. Fr. 5:208 (1899), pro parte excl. typ.

Plants annual. Stems with complete replacement of cortical vascular bundles at the nodes. Leaves weakly epi-amphistomatic, tendrillous, multijugate. Inflorescence 1-flowered, not pedunculate but flowers borne on fairly long pedicels. Flowers whitish, pale yellow or dark violet. Calyx irregular; vexillum stenonychioid, glabrous. Legume rhomboidal (sutures not parallel). Seeds with very short hila; lens near hilum; testa smooth. - 4 speeies.

Type: V. peregrina L.

Geographical distribution: S. Europe, N. Africa, Crimea, S.W. Asia eastwards to Afghanistan. See Fig. 79.

This section is based on a group delimited by Boissier (1872). Its species are not very striking, morphologically, but form a convenient assemblage

which is probably also a natural one. Members of

Fig. 3:35 Sect. Peregrinae often have very narrow leaflets. Their flowers are characteristically not completely

4.1 sessile but are borne on short pedicels; the peduncle is absent. V. michauxii is unusual within the

4.5.2 genus in having large seeds which are up to 1 cm long.

Chapter 12

THE INFRA-GENERIC CLASSIFICATION OF LATHYRUS

12.1. Introduction.

12.2. Description of *Lathyrus*.

12.3. Conspectus of taxa within *Lathyrus*.

12.4. Key to sections.

12.5. Sectional descriptions.

12.1.

INTRODUCTION

The historical development of the classification of Lathyrus was a simple process, compared with that of Vicia. An ever-increasing number of distinct infra-generic groups were recognised, leaving a dwindling residue of taxonomically difficult species (see part 2.4.1). The pattern is complicated only by differences of opinion about the status of these taxa, and by the recent attempts by Bässler (1966) and Czefranova (1971) to create a hierarchy of subgenera, sections and series within Lathyrus.

The classification which I propose consists of 13 sections; I describe three new ones (Viciopsis, Linearicarpus and Notolathyrus) and sink Sect. Cicercula into Sect. Lathyrus. I have not recognised any subgenera, and disagree, in this respect, with the systems of Bässler and Czefranova. Bässler (1966), who dealt only with Subgen. Orobus, included in this group the sections Orobus, Lathyrostylis, Pratensis (sensu Davis, 1970), Orobon and Neurolobus. Subgen. Orobus sensu Bässler can be defined only with difficulty and I consider it unnatural, since it divides two apparently closely related section-pairs (Orobon and Lathyrus; Pratensis and Aphaca). Czefranova (1971) classified Lathyrus into 6 subgenera. Four of these are equivalent to Sects. Clymenum, Nissolia, Cicercula and Aphaca; Subgen. Orobus contained the species which I place in Sects. Orobus, Lathyrostylis, Pratensis and Neurolobus; and Subgen. Lathyrus included Sects. Lathyrus, Orobon and Orobastrum. Several aspects of this grouping can be criticised. Firstly, there is little evi-

dence to suggest that Sect. Orobastrum (sensu Davis, 1970) is more closely related to Sects. Orobon and Lathyrus than to any other part of the genus. Secondly, I consider that Sects. Cicercula and Lathyrus, Sects. Nissolia and Orobastrum and Sects. Aphaca and Pratensis, each form a related pair, and it is unnatural to separate the components of these pairs into different subgenera.

For the reasons given in part 11.1, I have not recognised series within any of the sections of Lathyrus. Bässler (1973) has published a revised series classification of Sect. Orobus, and a synopsis of this is given in Table 35 (Addendum). Apart from this group, Sects. Lathyrus and Notolathyrus contain the widest ranges of variation and each deserves infra-sectional classification. I have indicated the lines which this structure might follow in Sect. Lathyrus by arranging the species in a natural order, grouping them informally in part 12.5 into three habit-types, and emphasising the character-trends in this section. The Eurasian members of Sect. Orobus, and species of Sect. Lathyrostylis, are similarly listed with most closely related species as neighbours; the members of other polytypic sections are tabulated alphabetically.

The remarks which I made in part 11.1 about the completeness of species lists, and about geographical distribution and ecological considerations, all apply equally to Lathyrus.

12.2.

DESCRIPTION OF LATHYRUS L.

Perennial or annual herbs with erect or more usually climbing or sprawling habit; rootstock occasionally tuberous. Stems winged or unwinged, always with complete replacement of cortical vascular bundles at the nodes. Leaves hypostomatic to epi-amphistomatic, paripinnate (except in the phyllodic L. nissolia), tendrillous or mucronate; leaflets unijugate to multijugate; leaves occasionally phyllodic or reduced to stipules and a tendril; stipules semi-sagittate or hastate; vernation of leaflets supervolute; venation brochidodromous, veins pinnate or parallel. Inflorescence many- to 1-flowered. Calyx regular or irregular. Vexillum oblong to stenonychioid, usually bossed or pouched at the fold. Alae very rarely with 'kink' in upper edge of limb. Staminal tube usually truncate at apex, rarely oblique. Style dorsally compressed, pubescent on adaxial face, sometimes spathulate and/or contorted; stigma sometimes double (i.e. the style has two separate adjacent stigmatic areas at its apex). Legume sometimes winged, occasionally bearing glandular or tuberculate hairs, rarely villous, rarely with membranous or woolly speta between the seeds. Seeds with long to short hila; testa rough or smooth; lens always near hilum.

12.3.

CONSPECTUS OF TAXA WITHIN LATHYRUS

Authorities for sections are given in part 12.5, and those for the species in the Index.

Section:	Species:
1. Orobus	Old World members:
	1. L. davidii
	2. L. gmelinii
	3. L. krylovii
	4. L. emodi
	5. L. vaniotii
	6. L. libani
	7. L. aureus
	8. L. occidentalis
	9. L. laevigatus
	10. L. transsilvanicus
	11. L. humilis
	12. L. vernus
	13. L. frolovii
	14. L. komarovii
	15. L. venetus
	16. L. alpestris
	17. L. incurvus
	18. L. niger
	19. L. japonicus
	20. L. pisiformis
	21. L. palustris
	22. L. dielsianus
	23. L. wilsonii
	24. L. quinquenervius
	25. L. linifolius
	26. L. dominianus
	New World members:
	27. L. arizonicus
	28. L. bijugatus
	29. L. brachycalyx
	30. L. delnorticus
	31. L. eucosmus
	32. L. graminifolius
	33. L. jepsonii
	34. L. laetiflorus
	35. L. lanszwertii
	36. L. leucanthus
	37. L. littoralis
	38. L. nevadensis
	39. L. ochroleucus
	40. L. parvifolius
	41. L. pauciflorus
	42. L. polymorphus
	43. L. polyphyllus
	44. L. rigidus
	45. L. splendens
	46. L. sulphureus

	47. L. torreyi	50. L. vestitus
	48. L. tracyi	51. L. whitei
	49. L. venosus	52. L. zionis
2. Lathyrostylis	53. L. pannonicus	62. L. cyaneus
	54. L. satdaghensis	63. L. armenus
	55. L. karsianus	64. L. digitatus
	56. L. bauhinii	65. L. brachypterus
	57. L. filiformis	66. L. variabilis
	58. L. pallescens	67. L. tukhtensis
	59. L. pancicii	68. L. spathulatus
	60. L. nivalis	69. L. elongatus
	61. L. boissieri	70. L. cilicicus
3. Lathyrus	71. L. mulkak	86. L. hirsutus
	72. L. cirrhosus	87. L. chrysanthus
	73. L. grandiflorus	88. L. chloranthus
	74. L. rotundifolius	89. L. trachycarpus
	75. L. tuberosus	90. L. lycicus
	76. L. undulatus	91. L. phaselitanus
	77. L. heterophyllus	92. L. sativus
	78. L. latifolius	93. L. amphicarpos
	79. L. sylvestris	94. L. cicera
	80. L. tingitanus	95. L. stenophyllus
	81. L. tremolsianus	96. L. marmoratus
	82. L. annuus	97. L. blepharicarpus
	83. L. hierosolymitanus	98. L. lentiformis
	84. L. cassius	99. L. gorgoni
	85. L. odoratus	100. L. pseudo-cicera

4. Orobon	101. L. roseus	
5. Pratensis	102. L. binatus	105. L. laxiflorus
	103. L. czeczottianus	106. L. layardii
	104. L. hallersteinii	107. L. pratensis
6. Aphaca	108. L. aphaca	109. L. stenolobus
7. Clymenum	110. L. clymenum	112. L. ochrus
	111. L. gloeospermus	
8. Viciopsis	113. L. saxatilis	
9. Orobastrum	114. L. setifolius	
10. Linearicarpus	115. L. angulatus	118. L. tauricola
	116. L. inconspicuus	119. L. vinealis
	117. L. sphaericus	120. L. woronowii
11. Nissolia	121. L. nissolia	
12. Neurolobus	122. L. neurolobus	
13. Notolathyrus	123. L. americanus	131. L. macropus
	124. L. berterianus	132. L. macrostachys
	125. L. cabrerianus	133. L. magellanicus
	126. L. campestris	134. L. multiceps
	127. L. hasslerianus	135. L. nigrivalvis
	128. L. hookeri	136. L. paraguayensis
	129. L. linearifolius	137. L. paranensis
	130. L. longipes	138. L. parodii

139. L. pubescens
140. L. pusillus
141. L. subandinus
142. L. subulatus
143. L. tomentosus
144. L. tropicalandinus

12.4.

KEY TO THE SECTIONS OF LATHYRUS

1. At least some of the leaves phyllodic; annuals
  2. All leaves phyllodic; phyllodes with parallel-brochidodromous venation; fruits not winged — Sect. 11. Nissolia
  2. Lower leaves phyllodic, upper ones with leaflets; phyllodes with pinnate-brochidromous venation; fruits winged — Sect. 7. Clymenum
1. None of the leaves phyllodic; annuals and perennials
  3. Stipules hastate (in adult leaves)
    4. Leaves (except in seedling) without leaflets — Sect. 6. Aphaca
    4. All leaves with leaflets
      5. Leaves with two or more pairs of pinnate-veined leaflets — Sect. 1. Orobus
      5. Leaves unijugate, leaflets parallel-veined
        6. Leaves hypo-amphistomatic; wing petals with 'waisted' limb; perennials (plants of Old World) — Sect. 5. Pratensis

6. Leaves epi-amphistomatic; wing petals not 'waisted': annuals and perennials (plants of New World) Sect. 13. Notolathyrus

3. Stipules semi-sagittate

7. Style contorted; banner of vexillum much broader than claw (i.e. standard stenonychioid)

8. Tendrils absent; perennials

9. Leaves unijugate, hypostomatic; leaflets broadly ovate, with pinnate-brochidodromous venation Sect. 4. Orobon

9. Leaves 1-7-paired, epi-amphistomatic; leaflets lanceolate, with parallel-brochidodromous venation Sect. 2. Lathyrostylis

8. Tendrils present or if absent then plants annual Sect. 3. Lathyrus

7. Style not contorted, or if so then banner of vexillum narrower than claw (L. sulphureus)

10. Annuals

11. Leaves with two or more pairs of leaflets

12. Leaflet venation pinnate-brochidodromous Sect. 8. Viciopsis

12. Leaflets venation parallel-brochidodromous Sect. 10. Linearicarpus

11. Leaves unijugate

13. Legumes strongly stipitate Sect. 9. Orobastrum

13. Legumes not stipitate

14. Stems winged; leaves hypo- amphistomatic (L. gorgoni & L. pseudocicera) Sect. 3. Lathyrus

14. Stems not winged; leaves epi-amphistomatic Sect. 10. Linearicarpus

10. Perennials

15. Leaves unijugate

16. Stems strongly winged; flowers less than 1 cm long; plants of Crete Sect. 12. Neurolobus

16. Stems not or only weakly winged; flowers more than 1.5 cm long; plants of S. America Sect. 13. Notolathyrus

15. Leaves with two or more pairs of leaflets

17. Legumes tomentose; plants of S. America Sect. 13. Notolathyrus

17. Legumes ± glabrous; plants of N. America and Eurasia

18. Leaflets epi-amphistomatic, parallel-veined; leaf rachis entendrillous; stem not winged Sect. 2. Lathyrostylis

18. Leaflets usually hypostomatic and pinnate-veined; leaf rachis tendrillous or etendrillous; stem winged or unwinged (if leaves epi-amphistomatic then stem winged & tendrils present;

if leaves parallel-veined then
stem winged and/or leaves
hypostomatic) Sect. 1. Orobus

12.5.

SECTIONAL DESCRIPTIONS

1. Sect. Orobus (L.) Godron in Gren. & Godron, Fl. Fr. 1:485 (1849). Syn: Orobus L., Sp. Pl. 728 (1753); Lathyrus Subgen. Orobus (L.) Peterm., Deutschl. Fl. 155 (1849); Lathyrus Sect. Orobastrum Boiss., Fl. Or. 2:601 (1872), pro parte excl. typ.; Lathyrus Sect. Lathyrobus (Tamamsch.) Czefr. in Novit. Syst. Pl. Vasc. (Leningrad) 8:192 (1971).

Plants perennial, sometimes with tuberous rootstocks. Stems usually wingless but occasionally winged. Leaves hypostomatic to amphistomatic, multijugate, with or without tendrils; leaflets broadly ovate to lanceolate; venation pinnate to (rarely) parallel; stipules semi-sagittate or occasionally hastate. Inflorescence many- to several-flowered, dense to comparatively lax (racemes 1-2-flowered in L. torreyi). Flowers brownish-yellow or bluish- or reddish-purple. Calyx teeth unequal; vexillum oblong to stenonychioid (in L. sulphureus the banner is narrower than the claw), usually bossed at the fold; wings rarely with 'kink' in upper edge of limb; style not contorted (except in L. sulphureus), not spathulate. Legumes linear, not stipitate, occasionally gland-dotted. Seeds smooth, with relatively long hilum. - c. 50 species.

Lectotype: L. linifolius (Reichard) Bässler (synonymous with Orobus tuberosus L. and Lathyrus montanus Bernh.) Green, 1929. See Addendum.

Geographical distribution: Europe, N.W. Africa, Anatolia (except the S.W.), W. Syria, N. Iraq, N. Iran, Russia, E. Asia, Japan, N. & C. America. See Figs. 82-84, 97.

The status of Sect. Orobus, and its delimitation,
2.4.1. have undergone constant change throughout its taxonomic history. The genus Orobus L. originally contained only etendrillous perennial species. Later Döll (1843) considered that the group should comprise all members of the Lathyrus affinity which did not possess a twisted style, thus greatly widening its
3.2 compass. This idea was followed to some extent by Boissier (1872), but he refined Orobus by excluding all tendrillous species. Much more recently, Tutin (1956) has made the novel suggestion (which has not
3.4 been followed in practice) that Orobus should be a genus including only species with pinnately-veined leaflets. In one of the latest regional treatments of Lathyrus (Davis, 1970), Sect. Orobus has the same
2.4.1 delimitation as the genus Orobus sensu Boissier, with the exclusion of species with spathulate styles; the latter are placed in Sect. Platystylis (= Sect. Lathyrostylis). The N. American species of Lathyrus have never been dealt with taxonomically in the context of the whole genus, but Bässler (1966) has suggested the

2.4.2 strong relationship between them and the Old World members of Sect. Orobus. The present treatment of this group is a direct descendant of earlier taxonomic arrangements, and closely resembles the most recent accounts. The Eurasian species are listed in the order given by Bässler (1973), and a synopsis of their series classification, very recently published by this author, is given in Table 35 in the Addendum. Sect. Orobus is probably a natural assemblage, but it contains a diversity of vegetative and floral forms and many of its members appear to be rather distantly related.

Table 23 3.5 Fig. 4:1, 2 3.4 Table 8 3.8 Fig. 6:1 Table 8 3.2 Table 8 4.1 Fig. 10 Fig. 20:1

The Old World representatives include a number of 'oroboid' species characterised by an erect, bushy habit and leaves with few pairs of large, broad, pinnately-veined leaflets. The epidermal cells of the leaf are isodiametric, with very wavy walls, and stomata occur only on the lower leaf surface. The oroboid syndrome is most complete in L. aureus, L. libani, L. niger, L. transsilvanicus, L. gmelinii and L. laevigatus, for these have etendrillous leaves and Vicia-like inflorescences in which the flowers are numerous, borne in a close, secund raceme, and the vexillum is oblong rather than stenonychioid and is not bossed. Species with this facies are linked to the rest of Sect. Orobus by members with intermediate characteristics. Thus L. davidii closely resembles

3.2 L. aureus, but has strongly developed tendrils. L. vernus and L. venetus have typically oroboid leaves but laxer inflorescences in which the flowers are individually more attractive; however, these two species appear to be unique within Lathyrus in the 4.2.3.1 possession of wing petals with a 'kink' in the upper edge, a feature otherwise associated with Vicia.

A few species which are included in Sect. Orobus approach rather closely to members of Sect. Lathyrostylis. The most problematic species of this type is L. alpestris, native to the Balkan peninsula, which has unwinged stems and etendrillous leaves with parallel-veined, lanceolate leaflets; in facies it is thus very reminiscent of Sect. Lathyrostylis. Bässler (1973) records that the leaves are hypostomatic, and this provides some support for its present taxonomic position. However, L. quinquenervius, a species nearly related to L. palustris and distinguished from members of Sect. Lathyrostylis by its winged stems and tendrils, has epi-amphistomatic leaves. The circumboreal L. palustris has winged stems, tendrillous Table 8. Fig. 4:4 leaves with an intermediate type of venation, and a looser inflorescence than the oroboid species and vexilla which are stenonychioid. In these characters it forms a link between the N. American and the Old World members of Sect. Orobus.

L. linifolius (= L. montanus) stands apart from

3.10 Table 8 other members of Sect. Orobus, having a tuberous rootstock, winged stems and etendrillous leaves with parallel-veined, lanceolate leaflets. L. japonicus and L. pisiformis comprise another somewhat isolated

3.6 group, characterised by the presence of hastate stipules.

The American representatives of Sect. Orobus number about 30, and although some morphologically distinct species are present (e.g. L. splendens with few, very large flowers; L. torreyi with mucronate, multijugate leaves and 1-2-flowered inflorescences), many of the taxa form complexes whose limits are confused

7.5 by interspecific hybridisation, a phenomenon unusual within the Vicieae. Besides L. palustris, only L.

3.9 delnorticus and L. jepsonii have winged stems. Most species are climbers, having tendrillous leaves with

Fig. 4:22 Fig. 4:23 many pairs of broad, pinnately-veined leaflets. A few (e.g. L. polymorphus and L. arizonicus) are more bushy, lacking tendrils and having linear leaflets. The in-

4.1 florescence usually comprises several to many, often

Fig. 20:13 & 14 4.2.5 showy flowers, with stenonychioid vexilla. L. sulphureus is unusual in Sect. Orobus in having a twisted style. This character is variable within the species: sometimes the style is not contorted, and when twisting occurs its direction varies. It seems most unlikely that this species is at all closely connected with members of other sections (e.g. Sects. Lathy-

rostylis and Lathyrus) in which a twisted style is commonly or typically present. The flower of L. sul-
4.2.3.1 phureus is also most distinctive in possessing a standard in which the claw is broader than the banner.
Table 8 In epidermal characters, N. American members of Sect.
3.8 Orobus resemble the non-oroboid Eurasian species. The leaves are hypo-amphistomatic to amphistomatic, and the epidermal cells are elongated, with slightly wavy walls. This type of leaf is correlated with a
4.1 loose inflorescence and the stenonychioid, bossed
4.2.3.1 standard.

2. Sect. Lathyrostylis (Griseb.) Bässler in Feddes Rep. 82:443 (1971). Syn: Platystylis Sweet, Brit. Fl. Gard. ser. 1,3:239 (1828); Orobus Sect. Lathyrostylis Griseb., Spic. 1:74 (1843); Lathyrus Sect. Platystylis (Sweet) Bässler in Feddes Rep. 72:88 (1966).

Plants perennial, sometimes with tuberous rootstocks. Stems not winged. Leaves epi-amphistomatic, with 1-7 pairs of leaflets, pinnate to subdigitate, etendrillous; leaflets narrowly linear-lanceolate to elliptical; venation parallel; stipules semi-sagittate. Inflorescence lax, several-flowered. Flowers in a wide range of colours. Calyx teeth equal or unequal; vexillum stenonychioid, bossed; style linear or more usually moderately to strongly spathulate at the apex, sometimes contorted. Legumes linear, not stipitate, not gland-dotted. Seeds rough or smooth, with relatively long hilum. - c. 18

species.

Type: L. digitatus (Bieb.) Fiori.

Geographical distribution: Central & S. Europe (except extreme W.), N.W. Africa, Anatolia, W. Syria, Iraq, W. Iran, Caucasia, Russia. See Figs. 85 & 97.

Sect. Lathyrostylis, although fairly large, is remarkable for its relative uniformity; its species all share a distinctive habit and have several less obvious characteristics in common. It is undoubtedly a natural group. In spite of this, it has only recently been given general taxonomic recognition (Bässler, 1966; Davis, 1970), because the large majority of its members are endemic to S.W. Asia and have rarely been included in studies of the genus. Boissier (1872) divided those species which he recognised between Lathyrus and Orobus, because some (i.e. L. nervosus - a synonym of L. boissieri) were found to have twisted styles, while others (e.g. O. cyaneus and O. armenus) had straight styles and no tendrils.

2.4.1
Table 6
3.2

Members of Sect. Lathyrostylis are perennials which grow erect, their rigid stems requiring no support from neighbouring vegetation. The rootstocks of L. pannonicus, and possibly other species, bear clusters of tubers. (The occurrence of these storage organs ought to be elucidated by better collecting techniques.) The leaves are always etendrillous. Most species have unijugate leaves in the lower part

3.10
3.2
Table 8

of the plant and bijugate ones above; L. elongatus
3.5 is unusual in having uniformly unijugate leaves;
while L. armenus, L. pancicii, L. pannonicus and L.
satdaghensis have more numerous leaflets, in the
latter up to seven pairs per leaf. The leaflets are
Fig. 4:6 & 7
3.4 narrowly lanceolate to elliptical, with strongly parallel venation. The petiole and rachis of the leaf are frequently both very short so that the leaflets are
3.5 crowded together, giving a subsessile, subdigitate appearance. Sect. Lathyrostylis is distinctive in
Table 8
3.8
Fig. 6:5 having leaves with a higher proportion of stomata in the upper epidermis than in the lower (epi-amphistomatic).

4.1 The inflorescence bears several flowers which are often large and beautiful; apart from the differences in leaf form, it is this part of the plant which provides the main source of variation between species. Flower colour varies from deep blue, through
4.2.3.2 lilac, magenta and pink, to yellow and cream; the corolla is often bicoloured. In L. boissieri the leaves at the apex of the flowering stem are reduced in size, and secondary shoots arise in the axils of earlier peduncles. This condition suggests a transition towards (or away from) a compound type of in-
4.1 florescence, otherwise seen only in some 'oroboid' members of Vicia Sect. Vicilla. The form of the corolla of this group is similar to that found in the

non-oroboid species of Sect. Orobus: the vexillum is
Fig. 20:3 stenonychioid and bossed, and the wings are joined to the keel by a strongly-developed interlocking arrangement. In about half the species (e.g. L. pallescens,
4.2.5 L. elongatus, L. cilicicus, L. filiformis, etc.) the
Fig. 21:1 style is spathulate, terminating in a wide stigma.
Fig. 21:2 In other species (L. cyaneus, L. satdaghensis) the style is almost parallel-sided as in Sect. Orobus.
4.2.5 Twisted styles are found occasionally in Sect. Lathyrostylis, and it seems that this character is variable within most of the species where it occurs (as obser-
Fig. 21:2 ved in L. satdaghensis, L. boissieri, L. spathulatus, L. filiformis). It is also probable that the contortion is irregular in its direction, unlike the situation in Sect. Lathyrus. The fruits of Sect. Lathyrostylis are uniform in shape, and similar to those of Sect. Orobus.

The limited geographical distribution and narrow range of variability of this section, combined with its large size, suggest that many of its species are of comparatively recent origin, and that the group is still actively evolving. The taxonomy of the sec-
7.5 tion is difficult, and hybridisation is thought to occur between some of the species.

3. Sect. Lathyrus. Syn: Cicercula Medik. in Vorles. Churpf. Phys. Ges. 2:358 (1787); Lathyrus Sect. Cicercula (Medik.)

Gren. & Godron, Fl. Fr. 1:481 (1849); Lastila Alefeld in Bonplandia 9:146 (1861); Navidura Alefeld, op. cit. 147.

Plants annual and perennial, rarely with tuberous rootstock (i.e. in L. tuberosus). Stems usually winged. Leaves hypoamphistomatic, unijugate and tendrillous (rarely with 2-3 pairs of leaflets or etendrillous); leaflets suborbicular to narrowly lanceolate; venation pinnate, intermediate or parallel; stipules semi-sagittate. Inflorescence 1- to few-flowered. Flowers in a wide range of colours. Calyx teeth equal; vexillum stenonychioid, with very wide banner and short claw, not bossed; style contorted (always in the same sense) or very rarely straight. Legumes of variable morphology, sometimes glandular, tuberculate-hairy or with winged sutures. Seeds often with rough testa; hilum long to short. - c. 30 species.

Type: L. sylvestris L.

Geographical distribution: Europe (excluding Ireland), Canaries, N. Africa, Anatolia, Caucasia, Palestine, Lebanon, Iraq, Iran, Afghanistan, Transcaspia, Russia. See Figs. 86 & 97.

Very broadly speaking, Sect. Lathyrus includes three habit-types:

1. Delicate (though often tall-growing) perennials with narrowly winged or unwinged stems and thin, suborbicular, pinnate-veined leaflets: e.g. L. grandiflorus, L. tuberosus, L. rotundifolius.

2. Sturdy perennials and annuals with wide-winged stems and coarse, broadly lanceolate leaflets with

intermediate to parallel venation: e.g. L. latifolius, L. sylvestris, L. mulkak, L. odoratus, L. trachycarpus;

3. More delicate annuals with narrowly lanceolate leaflets and parallel venation: e.g. L. cicera, L. lentiformis, etc.

These habit-types are not well-defined; L. undulatus and L. lycicus are intermediate between the first two, L. annuus, L. hirsutus and L. sativus between the second and third. Against this background, variation in many characters can be traced, as follows.

3.5 Table 8 — All species have unijugate leaves with the exception of three perennials: L. mulkak, L. cirrhosus and L. heterophyllus (all rather coarse in habit, with thick, elliptical leaves). Only L. trachycarpus has etendrillous leaflets; apart from this sturdy species, it appears that the larger annuals and the perennials have the best-developed tendrils, while in the smallest annuals these organs are weak and unbranched.

3.5 Fig. 4:13 to 21 — Leaflet shape varies quite regularly from very broadly ovate in the delicate perennials, through broadly lanceolate in sturdy annuals and perennials, to narrowly lanceolate in most annuals. The type of venation is strictly correlated with leaflet-shape: suborbicular leaflets have pinnate venation, lanceolate ones are parallel-veined, and broadly lanceolate ones have an intermediate type.

The number of flowers in the inflorescence follows a parallel course of variation. The perennials and the sturdier annuals have both the largest flowers and the highest number of blooms per raceme. Among the perennials, examples include L. rotundifolius (with about 8 flowers on each peduncle), L. undulatus (with about 6), L. mulkak (c. 3); among the annuals, L. trachycarpus (c.5), L. chrysanthus (c. 4), L. annuus (c. 3) and L. hirsutus (c. 3). The more delicate annuals have only one or two flowers per inflorescence. Flower colour is very variable within Sect. Lathyrus; almost every shade is represented, from deep crimson in L. tingitanus to deep pink in L. latifolius, yellow in L. chrysanthus, blue in L. hirsutus and brick-red in L. cicera. The wild sweet pea (L. odoratus) has a purple standard and mauve wings, but its cultivated descendants have reproduced most of the colours found in the rest of the section, except yellow. As far as I know, L. odoratus and L. tuberosus are the only strongly scented members of the Vicieae; more field observations are needed on this subject.

4.1

4.2.3.2

The shape of the legume shows considerable variation within Sect. Lathyrus, especially among the annual species. All perennials have large, parallel-sided, linear pods like those of members of Sects. Orobus and Lathyrostylis, and the larger annuals,

4.4

Fig. 23:11 & 14

including L. annuus, L. chloranthus and L. cassius, have fruits of a similar shape. In the smaller annuals, however, they are usually shorter and broader and often possess specifically distinct characteristics. Several

Fig. 23:7, 8 & 9

species have pods with winged sutures (e.g. L. sativus, L. marmoratus and L. blepharicarpus). In L. blepharicarpus, as its name implies, the wings are fringed with ciliate hairs. L. amphicarpos (closely related to L. sativus) is remarkable within Lathyrus in having both aerial and subterranean fruits. The fruits of

Fig. 23:10

L. pseudo-cicera have a prominent longitudinal vein on each valve. Finally, the recently-discovered

Fig. 23:13

L. lentiformis takes this variation to an extreme, having a very small, papery-valved and indehiscent fruit containing only one or two seeds. A number of

4.4

species have legumes which bear tuberculate hairs;

Fig. 23:11 & 12

these are L. hirsutus, L. odoratus, L. trachycarpus, L. chrysanthus, L. chloranthus and L. lycicus. This

3.7

feature is not found elsewhere in Lathyrus but occurs in Vicia lutea. L. odoratus and L. cassius are apparently unique within the tribe in possessing glandular hairs of the kind shown in Fig. 5:B. In the for-

3.7

mer species they occur on the young shoots, in the latter on the fruit. Many species in this section

4.5.2

have seeds with a rough testa (e.g. L. tuberosus, L. sylvestris, L. hirsutus, L. chloranthus, L. annuus, L. lentiformis, etc.). Probably about the same pro-

portion of species have smooth seeds; these include L. tingitanus, L. sativus, L. marmoratus, etc.

4.2.5 All members of Sect. Lathyrus have a style which is contorted, always anticlockwise (Fig. 11), with the exception of the closely related species L. gorgoni and L. pseudo-cicera. In these two the style is straight and widened slightly below the stigma. The other characteristics of these species link them very strongly with annuals of Sect. Lathyrus (especially with L. cicera, L. hierosolymitanus, etc.) and there is little doubt of their taxonomic affinities.

The two sections Lathyrus and Cicercula, which are here reduced to synonymy, were originally separated by the type of style in each: in the former

2.4.1 it was said to be arcuate, in the latter canaliculate (Godron, 1849). In practice this distinction, which is exaggerated in the dried flower, appears to reflect merely the robustness of the style and hence the size of the flower. Large-flowered annuals (L. odoratus, L. trachycarpus and L. chloranthus) have 'arcuate' styles similar to those of all perennials, while the more delicate annuals have 'canaliculate' styles which collapse on drying. A sectional classification whose limits are based strictly on this distinction is probably unnatural, since there is little doubt that the wholly annual section Cicercula which results is not monophyletic but has more than one connection with

the presumably older and more primitive Sect. Lathyrus. For example, L. odoratus and L. hirsutus have
7.5 been successfully hybridised by several workers, an achievement rare in the Vicieae except between the most closely related taxa. It seems reasonable, on this evidence alone, to place these two species in the same section. Again, L. sylvestris (Sect. Lathyrus) and L. annuus (Sect. Cicercula) are very similar in general morphology, arguing strongly for a close taxonomic relationship.

Sect. Lathyrus (in the broad sense adopted here) contains a particularly interesting assemblage of species, many of which are also extremely beautiful. The many characters which vary throughout the group appear to be correlated to some extent, suggesting trends which may have been followed during its evolution. In the conspectus of taxa (part 12.2) I have tried to arrange the species in a natural order, basing the sequence on the trends and characters mentioned in these paragraphs.

4. Sect. Orobon Tamamsch. in Takhtadjan, Fl. Armenii 4:316 (1962).

Erect perennial with unwinged stems. Leaves hypostomatic, unijugate, etendrillous; leaflets suborbicular, pinnate-veined; stipules semi-sagittate. Inflorescence few-flowered; flowers deep pink. Calyx teeth equal; vexillum stenonychioid, with

very broad banner and short claw, not bossed; style contorted. Fruit linear. Seed smooth, with hilum of intermediate length. - Monotypic.

Type: L. roseus Stev.

Geographical distribution: Crimea, Caucasia, N.E. & E. Anatolia, N. & N.W. Iran. See Fig. 87.

L. roseus is a beautiful species unusual within the tribe in its tall bushy habit; its twiggy shoots grow up to 1.5 m, but die back each season. The characters of flower and fruit agree entirely with those of members of Sect. Lathyrus, and it is only the vegetative features which support the sectional isolation of L. roseus. The leaflets are similar in shape and venation to those of L. grandiflorus and L. tuberosus, and L. roseus probably has its closest relatives among the 'delicate' perennials of Sect. Lathyrus. Its leaves are, however, distinguished by having stomata only on the lower surface and in being etendrillous. The correlation of these two characters in L. roseus is particularly interesting, since it parallels the situation found in the various 'oroboid' groups of the Vicieae. As in the oroboid species, the epidermal cells of L. roseus are isodiametric and very strongly wavy-walled; in species of Sect. Lathyrus they are somewhat elongated and more faintly wavy-walled.

Fig. 20:8

3.9

Table 8

3.8

3.2

3.8

5. Sect. Pratensis Bässler in Feddes Rep. 72:90 (1966). Syn: Lathyrus Sect. Orobastrum Boiss., Fl. Or. 2:601 (1872), pro parte; Lathyrus Sect. Eurytrichon Bässler, loc. cit.

Perennials, often pubescent to villous, sometimes with creeping or tuberous rootstock. Stems not winged. Leaves hypoamphistomatic, unijugate, tendrillous or mucronate; leaflets broadly to narrowly elliptical, with parallel-brochidodromous venation; stipules hastate. Inflorescence several-flowered. Flowers yellow or bluish-purple. Calyx teeth equal; vexillum stenonychioid, bossed; wing petals with 'waist' in the limb; style linear, not contorted. Fruit linear, glabrous or hairy. Seeds smooth; hilum short. - c. 6 species.

Type: L. pratensis L.

Geographical distribution: Europe, N.W. Africa, Abyssinia, Lebanon, N. Iraq, Caucasia, eastwards to C. Europe & Himalayas. See Figs. 88 & 97.

The members of this small section form a well-defined group, sharing several distinctive characteristics. Their leaves are always unijugate, with elliptical, parallel-veined leaflets. L. pratensis and the closely related L. hallersteinii have well-developed, branched tendrils, but a reduction in this organ is found in the remaining species: in L. binatus and L. layardii it is short and simple, in L. czeczottianus and L. laxiflorus absent. Members of Sect. Pratensis are recognisable by the presence of large hastate stipules, and, as was shown in part

Table 8
Fig. 2:C
Fig. 4:12

2.4.1

3.2

3.6

5.4.1, the nodal anatomy of this group differs from that of most other species of Lathyrus. The stipules receive an augmented vascular supply (derived from both the lateral and median leaf traces), while the supply to the petiole is diminished, consisting merely
5.4.1 of part of the median trace. A vascular pattern of this type is found elsewhere only in L. aphaca and in some S. American species with hastate stipules. The flowers of this section are also distinctive. In general they resemble those of Sect. Orobus and Lathyrostylis, but differ in the presence of long, equal calyx segments and in the shape of the corolla wings.
4.2.3.1 These petals are narrowed abruptly to a 'waist' between the distal part of the limb and the region of attachment to the keel (Fig. 20:4). (The members of Sect. Aphaca also have flowers of this type.). L.
4.2.3.2 pratensis, L. hallersteinii and L. binatus have yellow flowers; in the remaining species they are bluish.

6. Sect. Aphaca (Miller) Reichenb., Fl. Germ. Exc. 533 (1832).
Syn: Aphaca Miller, Gard. Dict. ed. 4 (1754).

Glabrous annuals with unwinged stems. First two seedling leaves with a pair of elliptical, parallel-veined leaflets; leaves of mature plant without leaflets but with strong, simple tendril and large, hastate stipules. Inflorescence 1-2-flowered. Flowers bright yellow, cream or sulphur-coloured. Calyx teeth

equal; vexillum stenonychioid, bossed; wing petals with 'waist' in the limb; style linear, not contorted. Fruit linear. Seeds smooth, hilum short. - Ditypic.

Type: L. aphaca L.

Geographical distribution: W., C. & S. Europe, N. Africa, S.W. & C. Asia. See Fig. 89.

Sect. Aphaca comprises two species: L. aphaca, which is very variable and widespread, and the closely related L. stenolobus, endemic to the Amanus region. The two species are distinguished by the different shapes of their stipules and fruits.

3.6 Fig. 9:A The remarkable ontogeny of L. aphaca, in which the photosynthetic functions of the leaf become delegated from the leaflets to the stipules, makes it one of the most interesting species in the Vicieae. Despite its apparent morphological distinctness, however, L. aphaca has several significant features in common with members of Sect. Pratensis. Its earliest leaves are similar to theirs, having a pair of parallel-veined leaflets. In both sections the stipules are hastate (or sagittate), and the species share an unusual pattern of nodal anatomy which may provide the clue to understanding how the peculiar habit of L. aphaca has evolved (see part 5.4.1). L. aphaca and L. stenolobus have flowers similar in shape to those of Sect. Pratensis, sharing, in particular, the same wing-shape. Sect. Aphaca is kept

3.4 3.6 5.4.1 Fig. 32:4 Fig. 20:5

separate from Sect. Pratensis because of its annual habit, and because the latter group is very uniform, containing little diversity. The addition of L. aphaca and L. stenolobus to this compact section would greatly increase its variability and an unbalanced, heterogeneous group would result.

7. Sect. Clymenum (Miller) DC. ex Ser. in DC., Prodr. 2:375 (1825). Syn: Clymenum Miller, Gard. Dict. ed. 4 (1754); Lathyrus Sect. Gloeolathyrus Warburg & Eig in Feddes Rep. 25:351 (1928).

Annuals with strongly winged stems. Leaves hypo-amphistomatic; early ones entirely phyllodic and etendrillous, later ones with several pairs of leaflets, tendrillous; leaflets broadly ovate to lanceolate; venation (of leaflets and phyllodes) pinnate; stipules semi-sagittate or minute. In L. clymenum and L. ochrus inflorescence pedunculate, 1- to few-flowered; flowers purple, pink or yellow; vexillum stenonychioid, with two very prominent pouches at the fold; style spathulate at apex; stigma double, its halves separated by a sterile mucro or arista. In L. gloeospermus flower solitary, inconspicuous, sessile in leaf-axil, greenish-yellow, cleistogamous, with morphologically simple parts. Legume large, linear, broadly winged at sutures and sometimes on valves. Seeds smooth; hilum of medium length. - 3 species.

Lectotype: L. clymenum L. (as its synonym L. articulatus L.); cf. Gunn, 1969.

Geographical distribution: Mediterranean area. See Fig. 90.

The members of this small section possess several remarkable morphological features. They share a peculiar ontogeny, in which the early leaves are phyllodic and etendrillous; leaves produced at later nodes are also phyllodic, but have tendrils at the distal end; and finally, leaves of the mature plant bear leaflets but retain a very broadly winged petiole and rachis. This developmental sequence unfolds quite rapidly in L. clymenum and L. gloeospermus, but in L. ochrus leaflets are produced only by leaves at the end of the life-cycle. The venation of both phyllodes and leaflets is pinnate, and the leaves are hypoamphistomatic. The stipules, in the early leaves of these species, are borne on the edge of the phyllode at the point where it passes the node and continues down as the stem-wing. These organs are often very small, being represented by a minute tooth (Fig. 9:B & C). In the adult, leaflet-bearing leaves, however, stipules of normal form and size appear at the base of the petiole.

3.9

Fig. 9:B & C

Table 8
3.4

Fig. 6:2

Fig. 30:1

The flowers of L. clymenum and L. ochrus are distinctive in having hollow, finger-like pouches on the standard instead of the shallow bosses found in Sects. Orobus and Lathyrostylis. These species also have an unusual type of style. It is spathulate, as in some members of Sect. Lathyrostylis, but the apex is produced into a sterile fleshy mucro or arista which

4.2.3.1

Fig. 20:6

4.2.5

Fig. 21:3

divides the stigma into two halves. In contrast,
4.2.3.1 L. gloeospermus has very inconspicuous flowers; they are sessile, with rudimentary, greenish corollas and
7.4 reduced sex organs, and they develop cleistogamously. The strong tendency towards winging of petioles and stems exhibited in the vegetative parts of these species is reflected also in their fruits. L. clym-
4.4 enum and L. ochrus have pods with winged sutures,
Fig. 23:4 & 5 while the legumes of L. gloeospermus have narrow, leafy laminae on the valves as well.

Although the flowers of L. gloeospermus are very unlike those of L. clymenum and L. ochrus, all the differences can be attributed to a single factor: the adoption of cleistogamy in L. gloeospermus. This has obscured the normal floral features which the ancestors of this species must have possessed, and prevents a true comparison between the flowers of L. gloeospermus and the other members of the section. On the other hand the unusual ontogenetic sequence, and the presence of winged stems, winged legumes and hypo-amphistomatic, pinnate-veined, multijugate leaves, all provide evidence to support my decision to unite Sects. Clymenum and Gloeolathyrus.

Taxonomic treatment of annual species formerly placed in Sect. Orobastrum. The delimitation of Sect. Orobastrum has undergone considerable change since the group was first described

by Boissier in 1872. In the sense of this author it comprised tendrillous species of the Lathyrus affinity which did not belong to Sects. Aphaca, Clymenum or Nissolia, and which were also excluded from Sects. Lathyrus and Cicercula by the absence of a twisted style (see Table 6). Since then this negative concept has been modified, notably by Bässler (1966) who removed the perennial species to Sect. Orobus (L. japonicus and L. pisiformis) and Sect. Pratensis (L. pratensis), leaving behind only small-flowered annuals: L. setifolius, L. saxatilis, L. inconspicuus, L. sphaericus, L. vinealis, L. tauricola, L. woronowii and L. angulatus. Though small in number of species, this group embraces rather wide variation. Its members are highly evolved, showing reduction in several characters (e.g. in tendril development, number of leaflets, length of peduncle, etc.) and specialisation in others (diversity in legume shape, presence of septa between the seeds, etc.). While the majority of species form a group of undoubted affinity, L. saxatilis and L. setifolius are each isolated by the possession of several differential characteristics. I consider that this heterogeneity is properly reflected by the recognition of three sections instead of one, and these are described below. Since Czefranova (1971) has selected L. setifolius as the type of Sect. Orobastrum, this section, once the most diverse 'dustbin' group in Lathyrus, now become monotypic.

8. Sect. Viciopsis Kupicha, sect. nov. Syn: Lathyrus Sect. Orobastrum Boiss., loc. cit., pro parte excl. typ.

Annual, with unwinged stems. Leaves epi-amphistomatic, etendrillous, with 1-3 pairs of leaflets; leaflets ovate to linear, pinnate-veined; stipules semi-sagittate. Inflorescence 1-flowered. Flowers small, pedunculate, cream-coloured. Calyx teeth subequal; standard stenenychioid, bossed; style not contorted. Fruit linear-rhomboidal, not stipitate. Seeds smooth, with short hilum. - Monotypic.

Type : L. saxatilis (Vent.) Vis.

Geographical distribution: S. Europe, E. Anatolia, N.W. Africa. See Fig. 94.

L. saxatilis has had an unsettled taxonomic history. It was first described by Ventenat (1802) as a member of the genus Orobus, later being transferred to Lathyrus by Visiani (1852) and to Vicia by Tropea (1907). Fedtschenko (1948), in Fl. URSS, placed it in Vicia Sect. Vicia. The species is distinguished from members of Sects. Linearicarpus and Orobastrum, and in fact from all other annual species of Lathyrus, by its leaves which have up to three pairs of pinnate-veined leaflets. The leaves produced early in the life-cycle have ovate, emarginate leaflets and are very similar in appearance to those of Vicia Sects. Vicia and Hypechusa. Leaflets of later shoots are quite different in shape, being narrowly linear, but they are still pinnate-veined. The style of L. saxatilis is dorsally compressed and pubescent on the adaxial side, confirming its position within Lathyrus.

Table 6

Table 8

Fig. 4:9

4.4 The legume is linear, but shorter and broader than those of Sect. Linearicarpus; it resembles the fruit
Fig. 23:15 of some members of Sect. Lathyrus (e.g. L. cicera).

9. Sect. Orobastrum Boiss, Fl. Or. 2:601 (1872).

Annual, with narrowly winged stems. Leaves amphistomatic, unijugate, with an unbranched tendril; leaflets narrowly lanceolate, parallel-veined; stipules semi-sagittate. Inflorescence 1-flowered. Flowers pedunculate, brick-red. Calyx teeth equal; standard stenonychioid, bossed; style not contorted. Legume rhomboidal, strongly stipitate. Seeds rugose, with short hilum. - Monotypic.

Lectotype: L. setifolius L. (Czefranova, 1971).

Geographical distribution: Mediterranean region, Crimea, Transcaucasia. See Fig. 93.

In habit L. setifolius resembles the members of Sect. 10. Linearicarpus, but has winged stems. It is thus very similar to some of the annual species in Sect. Lathyrus. The flowers are brick-red, a
4.2.3.2 colour occurring in both Sect. Linearicarpus (e.g. L. sphaericus) and Sect. Lathyrus (e.g. L. cicera). The vexillum is short-clawed like those of Sect. Lathyrus, but is distinctly bossed. The fruit of
4.4 L. setifolius is its most characteristic feature;
Fig. 23:2 a pod of this shape is commonly found in Vicia Sect. Cracca, but is very unusual within Lathyrus. The most similar fruits occur in Sect. Lathyrus (e.g. L. lentiformis). Davies (1958) states that

4.2.5 L. setifolius has a twisted style. According to my own observations the style is in fact straight, but if it was confirmed that this character is variable within the species the taxonomic position of Sect. Orobastrum would have to be reconsidered, bearing in mind the almost equal phenetic affinity of L. setifolius with members of Sects. Linearicarpus and Lathyrus; it might be better placed within the latter.

10. Sect. Linearicarpus Kupicha, sect. nov. Syn: Graphiosa Alefeld in Bonplandia 9:128 (1861); Lathyrus Sect. Orobastrum Boiss., Fl. Or. 2:601 (1872), pro parte excl. typ.

Annuals with unwinged stems. Leaves epi-amphistomatic, unijugate or bijugate, mucronate or with simple tendril; leaflets narrowly lanceolate, parallel-veined; stipules semi-sagittate. Inflorescence 1-flowered. Flowers subsessile to pedunculate, brick-red, pale purple or yellowish, small. Calyx teeth equal; standard stenonychioid, bossed; style not contorted. Legume narrowly linear, sometimes with membranous septa between the seeds; valves sometimes prominently veined. Seeds rough or smooth, with short hilum. - c. 6 species.

Type: L. sphaericus Retz.

Geographical distribution: S., W. & C. Europe, N. Africa, Anatolia, Caucasia, Palestine, W. Syria, Iraq, Iran, Afghanistan. See Figs. 92, 97.

The members of this section share a characteristic habit and appear to be closely related. The

Table 8 species are distinguished by the presence or absence
Fig. 23:3 of tendrils, veins on the legumes, and partitions
4.4 between the seeds; the length of the peduncle, and
4.1 whether it is prolonged past the pedicel into an arista; and flower colour.

11. Sect. Nissolia (Miller) Reichenb., Fl. Germ. Exc. 533 (1832). Syn: Nissolia Miller, Gard. Dict. ed. 4 (1754).

Annual. Stems not winged. Leaves phyllodic throughout life-cycle, lanceolate, parallel-veined, etendrillous, epi-amphistomatic; stipules minute. Inflorescence 1-2-flowered. Flowers pink to brick-red, pedunculate. Calyx teeth subequal; vexillum stenonychioid, bossed; style linear, not twisted. Legume linear, prominently veined, very rarely with septa between the seeds. Seeds tuberculate, with short hilum. - Monotypic.

Type: L. nissolia L.

Geographical distribution: W., C. & S. Europe, N.W. Africa, Crimea, Caucasia, Anatolia, N. Iraq. See Fig. 95.

L. nissolia is unique within Lathyrus in having
3.9 entirely phyllodic leaves. Although a parallel tendency is found in Sect. Clymenum, there is little to indicate a close relationship between the two groups: the flower and fruit of L. nissolia are quite unlike those of Sect. Clymenum. On the other hand, the vegetative and reproductive characteristics of L. nissolia both provide evidence suggesting a connection with Sect. Linearicarpus. Thus the stem is unwinged (despite the apparently contrary tendency which has

led to the evolution of the phyllodic leaf), and the leaf itself is similar in shape, stomatal distribu-

Table 8 tion and venation to the leaflets in L. sphaericus, L. angulatus, L. inconspicuus, etc. The leaf of L. nissolia is, of course, not strictly homologous with a leaflet of another species, but it seems permissible to compare their attributes. The flower of

4.2.3.2 L. nissolia is similar in colour, shape and size with

Fig. 20:12 that of L. sphaericus, and its fruit, like that of the latter species, is long, parallel-sided and prominently veined in a 'herringbone' pattern. There are

4.4 usually no partitions between the seeds, but I have observed the presence of this character in a single case.

The relationship between L. nissolia and Sect. Linearicarpus appears to parallel that of Sects. Aphaca and Pratensis. In each case, a mono- or ditypic section is defined almost entirely on the basis of a striking vegetative character, while data from other vegetative and reproductive traits suggest an alliance with a larger neighbouring group.

12. Sect. Neurolobus Bässler in Feddes Rep. 72:91 (1966).

Perennial. Stems slender, broadly winged. Leaves amphistomatic, unijugate, tendrillous; leaflets elliptical, parallel-veined; stipules semi-sagittate. Inflorescence 1-2-flowered. Flowers bluish-violet. Calyx teeth subequal, style not con-

torted or spathulate at apex. Fruit linear, with prominent longitudinal veins. Seed unknown. - Monotypic.

Type: L. neurolobus Boiss. & Heldr.

Geographical distribution: W. Crete. See Fig. 91.

This little-known species appears to be of very
2.4.1 isolated taxonomic position (Bässler, 1966). Its unijugate leaves and parallel-veined leaflets suggest a connection with Sect. Pratensis; the wide-winged stems are reminiscent of Sects. Lathyrus and Clymenum; and the small flowers and strongly-nerved fruits resemble those of Sect. Linearicarpus. None of these groups, however, has a convincing claim to particular affinity with Sect. Neurolobus, and it is perhaps best regarded as a relict species.

13. Sect. Notolathyrus Kupicha, sect. nov.

Plants perennial (except for the annual L. pusillus). Stems winged or unwinged. Leaves epi-amphistomatic, usually unijugate (rarely multijugate), usually with a strong, branched tendril; leaflets broadly to narrowly lanceolate, with parallel venation; stipules semi-sagittate or hastate. Inflorescence several- to few-flowered. Flowers purplish, pink or yellow. Calyx teeth equal or unequal; vexillum steononychioid, bossed; (staminal tube ends obliquely in L. pusillus); style not contorted, often spathulate; stigma sometimes double. Fruits sometimes hairy sometimes with septa between seeds. Seeds with short to moderately long hilum. - c. 20 species.

Type: L. hookeri G. Don.

Geographical distribution: Temperate S. America (Chile, Argentina, Paraguay & Uruguay); Andes of Peru and Columbia; South-East U.S.A. See Fig. 96.

The S. American species of Lathyrus (including L. pusillus, which extends into N. America), form a fairly homogeneous group clearly distinct from members of Sect. Orobus to the north. The most striking difference is that the leaves of N. American species

Table 8

are multijugate while those of S. American species are unijugate; but there are many other traits by which the southern group shows itself to be more highly evolved and specialised.

Members of Sect. Notolathyrus have several features in common with the mainly Turkish section

Fig. 4:26
Table 8 to 29
3.8
Fig. 6:8
Fig. 21:4

Lathyrostylis. For example, the leaflets are lanceolate, have parallel venation, and are epi-amphistomatic. The stems are rarely winged. The style is often spathulate (e.g. in L. cabrerianus). However, unlike species of Sect. Lathyrostylis, S. American species have unijugate leaves (except for L. multi-

Table 8

ceps and L. macropus), usually with well-developed tendrils. Other interesting characters are found here. The calyx and fruit are frequently tomentose or

4.4

sericeous (e.g. in L. cabrerianus, L. macropus, L. pubescens and L. tomentosus). The stigma is some-

4.2.5

times double (e.g. in L. pubescens, L. subulatus and

L. tomentosus), although the style is not prolonged into a sterile mucro, as in some members of Sect. Clymenum. Some species have 'woolly' false septa between the seeds, rather as in Sect. Linearicarpus; examples are L. pubescens, L. americanus (= L. nervosus), L. subulatus and L. tomentosus. The majority of species have semi-sagittate stipules, but in L. hookeri, L. magellanicus and L. pusillus (syn. L. crassipes, L. arvensis) they are hastate in form. I found that the nodal anatomy of L. pusillus is of the same type as that of L. aphaca and L. pratensis, while the vascular pattern in L. americanus and L. hookeri resembles that of L. japonicus and Pisum sativum.

4.4

3.6

5.4.1

Fig. 32:5 & 6

Sect. Notolathyrus is an interesting group, both in itself and in the context of the whole genus. Its members share a relatively uniform habit which unites the section, but they possess a variety of highly specialised characteristics each of which would be given strong taxonomic weighting if found in Old World species of Lathyrus. Thus in Europe a species with parallel-veined, epistomatic leaflets and a spathulate style would be placed in Sect. Lathyrostylis; the presence of a divided stigma is exclusive to Sect. Clymenum; and septa between the seeds are found only in Sects. Linearicarpus and Nissolia. The occurrence of these features in Sect. Notolathyrus will be discussed in parts 15.3 and 15.4 in the

light of its geographical isolation and in relation to theories of evolution of the genus.

Chapter 13

HISTORY OF THE NORTHERN HEMISPHERE DURING THE MESOZOIC AND CENOZOIC ERAS

13.1. Introduction.

13.2. Outline of the geological history of the northern hemisphere during the Mesozoic and Cenozoic eras.

13.3. The development of the Mediterranean area during the late Mesozoic and Tertiary.

13.4. The climate of the northern hemisphere during the Mesozoic and Cenozoic eras.

13.5. The development of Angiosperm floras in the northern hemisphere from the late Mesozoic to the present.

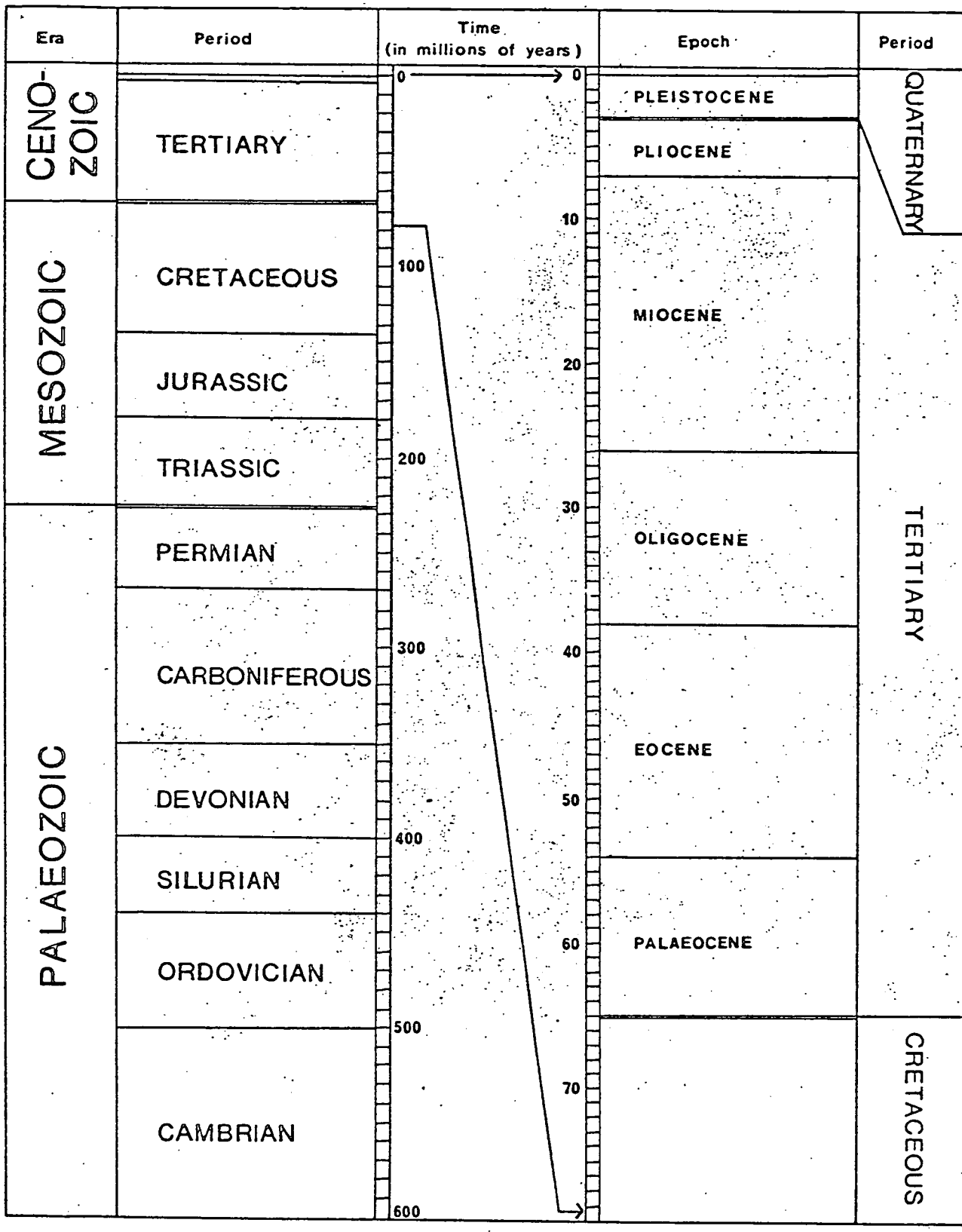
13.1.

INTRODUCTION

Macro-evolution is a very slow process which takes place on a time-scale similar to that required for the creation of oceans or the building of mountains. For this reason, present-day patterns of plant distribution cannot be fully interpreted without some knowledge of the geological and climatic changes which have occurred in the areas under consideration. The broad outlines of the geological development of the earth during Phanerozoic eras (the last 600 million years, represented in Table 29) are known in some detail, especially those of more recent times, and, as will be shown, the events of the last 100 million years are indeed relevant to any consideration of the evolution of the Vicieae. It must be emphasised that the attempt to reconstruct the earth's history is a very recent science, and one which is being actively developed at present. There is controversy about many of the details, and even some major points are debatable (e.g. the climate of Arctic regions during the early Tertiary). I have presented a rather black-and-white account, for the sake of brevity and clarity; but because the subject is so new, some of the statements may later be proved inaccurate.

The concept of plate tectonics. The idea that the continents have wandered about during geological history, and were once joined together as much larger land-masses, was first put forward seriously by Antonio Snider in 1858. Later, Taylor (1908)

Table 29. Time-scale and subdivisions of the Phanerozoic eras.



and Wegener (1910) both worked out elaborate hypotheses based on this assumption, which were supported by the distribution-patterns of fossils and glaciations. Their proposals were dismissed by their contemporaries, chiefly because at that time no force was known capable of moving the continental blocks in this way. However, more recently evidence from palaeomagnetism, stratigraphy and other sources has added much weight to the arguments in favour of continental drift, and although its energy-source is still not fully understood this phenomenon is now generally accepted (Holmes, 1965). The following brief summary of the modern concept of continental drift, its underlying causes and its consequences, is derived from the works of Tarling & Tarling (1971), Dietz (1972) and Smith et al. (1972).

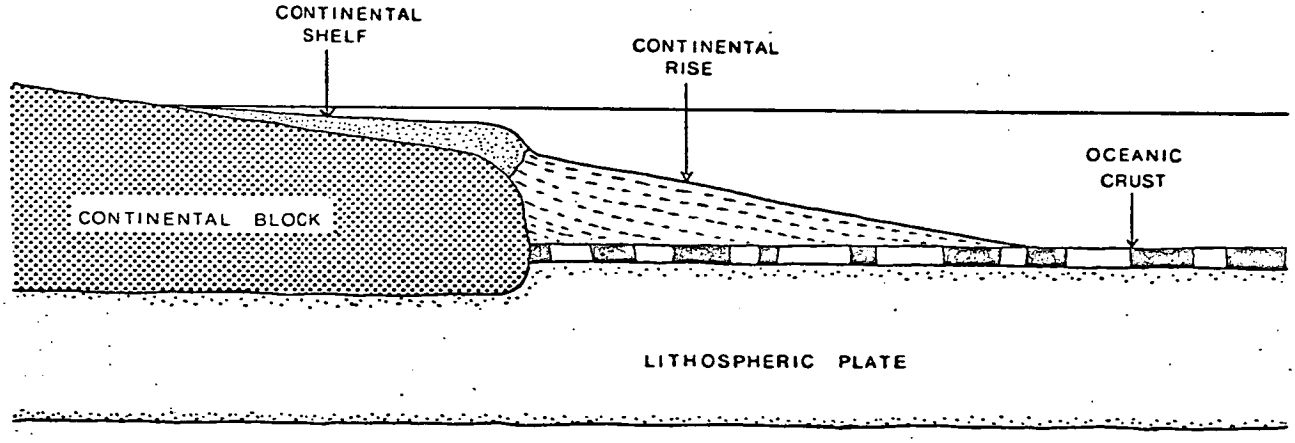
The earth's crust is believed to consist of 'islands' of relatively light rocks floating upon a continuous layer of more dense material. The former are represented by the continental blocks, the latter by the ocean floors. Beneath the continuous denser layer (the lithosphere) are slowly circulating convection currents which divide the lithosphere into a number of 'plates', depending on the patterns of the currents. The plates have three different kinds of margin: extensional, where a rising current causes the upwelling of lava along a rift to form new crust; compressional, where a descending current causes one plate to plunge beneath its neighbour; and translational, where adjacent plates move laterally relative to each other without gain or loss of surface area. A continent floating

upon a plate is automatically carried away from its extensional, and towards its compressional, margin.

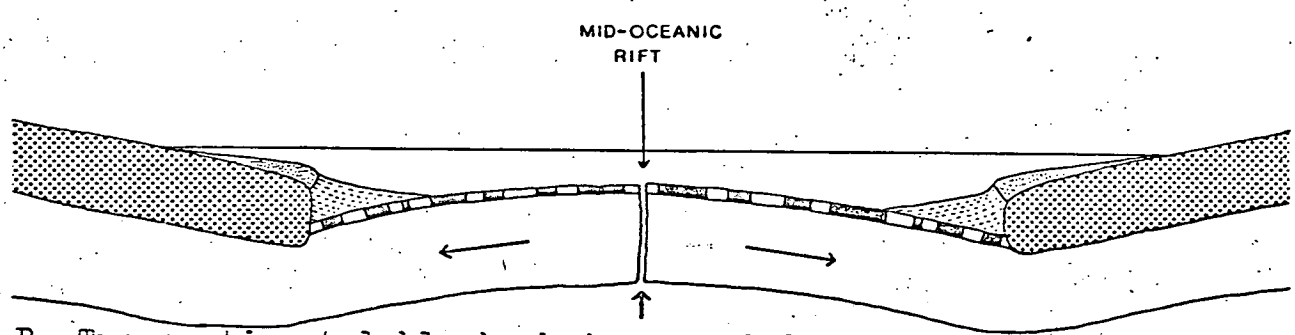
While the edge of a continental block is in a situation unaffected by the margins of its plate, the geology of this region is very stable. The only major development is a steady erosion of the land surface, with the resulting deposition of sediment on the continental shelf and continental rise; the continent thus becomes bordered by a deep geosyncline (Fig. 43:A). This process continues until the continental block is carried on its plate into the site of a descending convection current. When this happens the heavy crust of one plate is overridden by its neighbour, but the sediments of the geosyncline, being less dense, remain at the surface and are subjected to compression, folding and metamorphosis; they are thrust back against their mother-continent, to form a mountain-range along its margin. The subduction of a plate margin and the folding of sediments respectively cause both deep and shallow seismic activity; the new mountains are intruded by plutons of granite and other igneous rocks, and volcanoes of the andesitic type occur, their lavas highly charged with water from the ocean floor (Fig. 43:C).

It is evident that a continent is basically a permanent entity. Its land surface is destroyed by erosion, but this material is only temporarily lost, because it will eventually contribute to new mountain ranges which renew the continental block at its margins. If the pattern of convection currents is stable for long enough, several continents become welded together; evidence for this is provided by the presence of

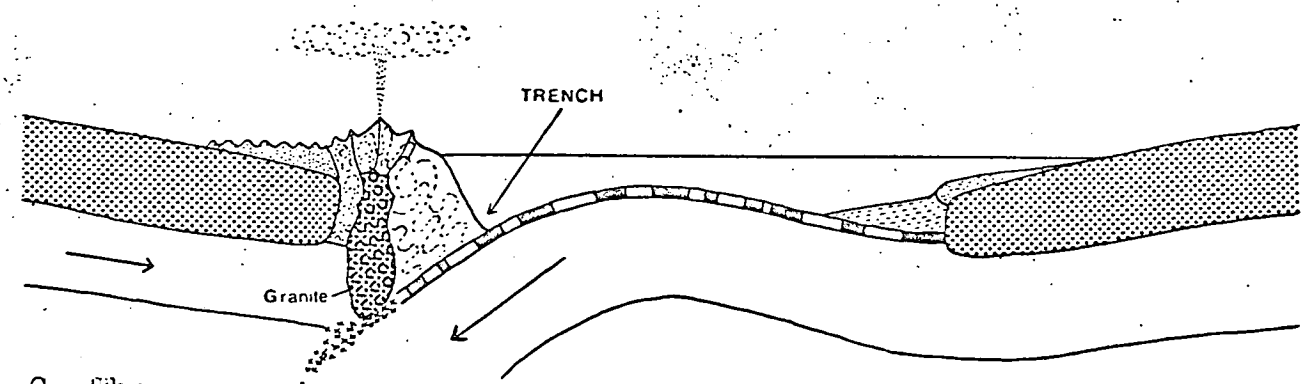
Fig. 43. Diagrams illustrating continental drift and orogenesis at plate margins (after Dietz, 1972).



A. Formation of geosynclinal sediments at the continent margin.



B. Two continental blocks being carried away from an extensional plate margin.



C. The orogenic consequences of plate subduction near a continental margin.

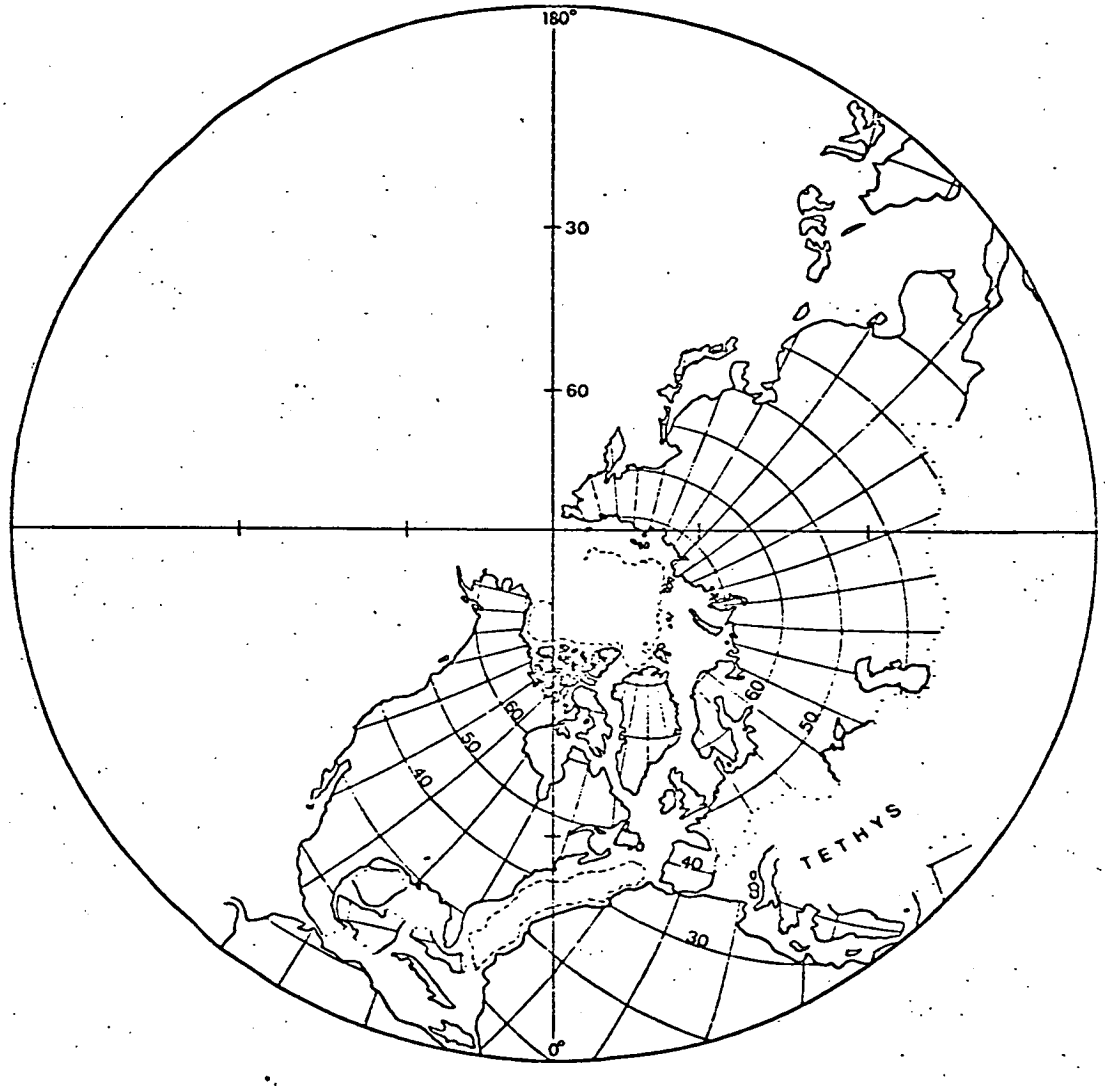
fold-mountains which are completely surrounded by older continental rocks (e.g. the Urals). The convection-current pattern does change, however, from time to time. The Atlantic, whose mid-oceanic ridge marks the extensional margins of two plates, is no older than the Jurassic period, and the Caledonian and Appalachian mountain ranges are thought to have originally been part of a single chain, itself the result of an earlier, Palaeozoic orogeny caused by the closing of a Proto-Atlantic.

13.2.
OUTLINE OF THE GEOLOGICAL HISTORY OF THE NORTHERN HEMISPHERE DURING THE MESOZOIC AND CENOZOIC ERAS

Geological evidence points to the conclusion that some 200 to 300 million years ago all the continental material of the earth was close together, forming a single land mass known as 'Pangaea'. During the Jurassic period Pangaea began to split up into fragments which drifted apart, eventually to form the continents of today (Dietz & Holden, 1970).

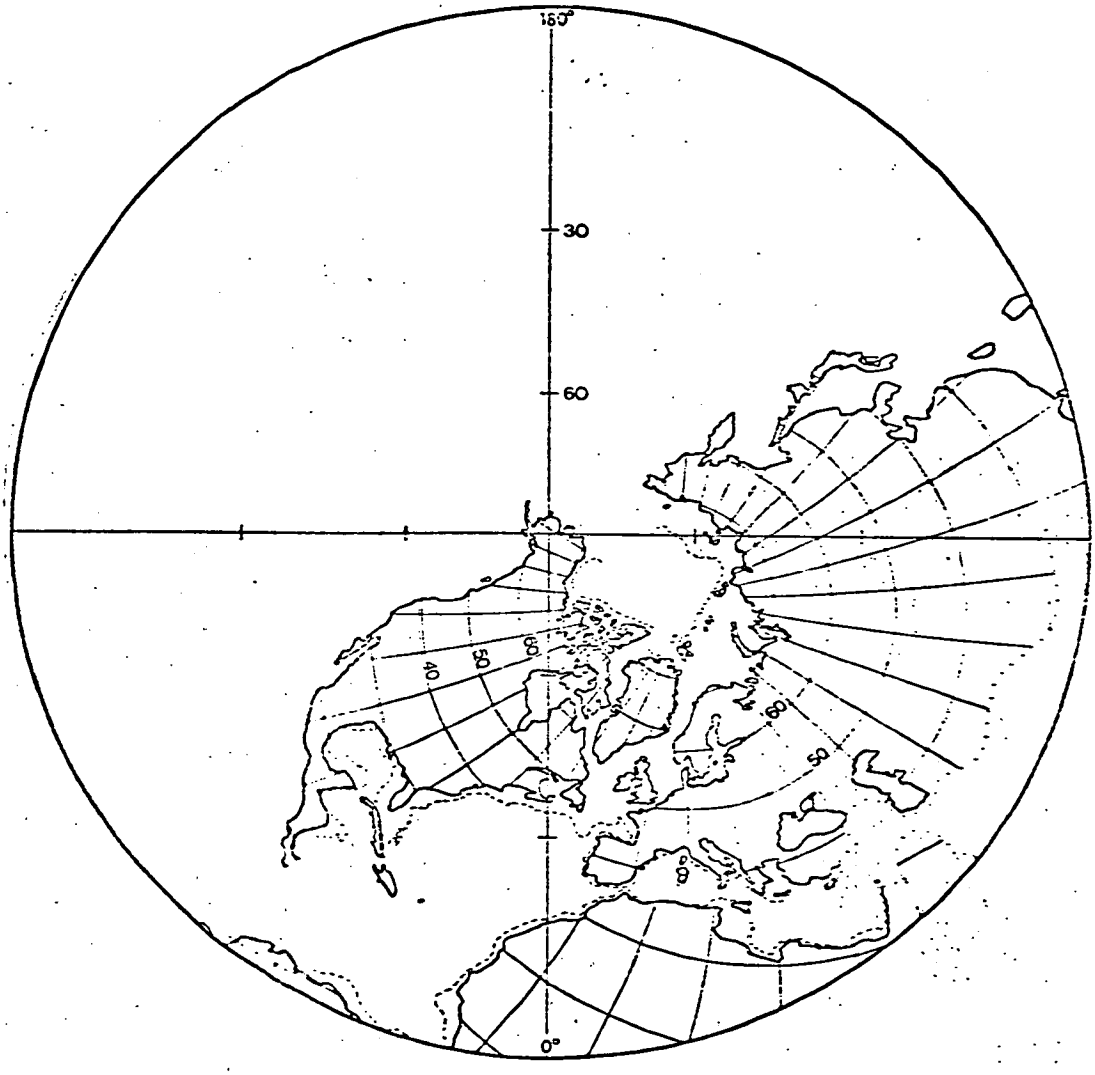
Fig. 44 shows the northern hemisphere in the Jurassic. N. America and Greenland were in contact with Western Europe, while N.W. Africa abutted onto America and S.W. Europe. Southern Asia differed greatly in shape and position from its contemporary state, since India existed as a distant continent in the southern hemisphere and Eurasia was separated from N. Africa and Arabia by a wide ocean known as Tethys. During the next 150 million years (until the late Tertiary) the western part of the

Fig. 44. The northern hemisphere during the Jurassic period.



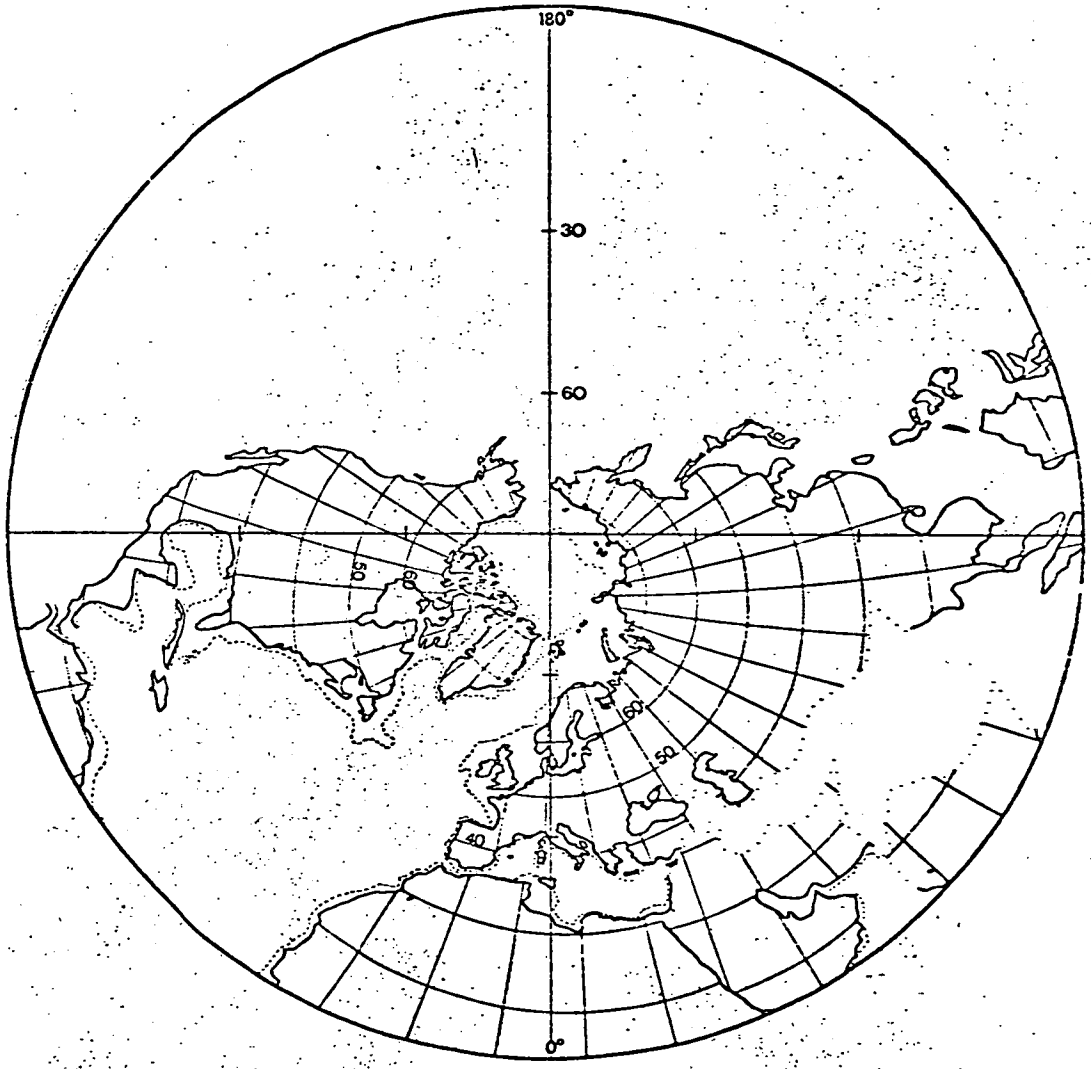
From Smith et al., 1972

Fig. 45. The northern hemisphere during the Cretaceous period.



From Smith et al., 1972

Fig. 46. The northern hemisphere during the Tertiary period (Eocene epoch).



From Smith et al., 1972

Tethys gradually closed up by an anti-clockwise rotation of Africa, while the N. American continent separated from Europe. This latter movement was achieved by the growth of the Atlantic, which opened up from the south, pivoting about Siberia.

At the beginning of the Tertiary period the westward drift of North America brought Alaska towards Siberia. Although the continental blocks did not collide, there was apparently a land connection between America and Asia, at least sporadically, during the Palaeocene and Eocene epochs. Evidence for this is provided by the mammalian fossil record, which shows that there was a sudden increase in similarity between the fauna of N. America and E. Asia at this time (Hallam, 1972). Fossil evidence also shows that there was a land connection between Europe and N. America until the early Eocene: up to this time the mammalian faunas of the two continents were closely similar, but from then onwards they diverged (Hallam, 1972). The broken line surrounding each continent in Fig. 46 (Eocene epoch) is the present-day 1000 metre line, and it roughly represents the edge of the continental shelf. The point at which Europe and N. America are thought to have finally separated is just north-east of Greenland (McKenna, 1972).

S. America originated in the early Mesozoic as a fragment of Pangaea which separated from Africa and drifted westwards independently of N. America; the isthmus of Panama was not formed until the Pliocene (Hallam, 1972). These events are summarised in Table 30.

13.3.

THE DEVELOPMENT OF THE MEDITERRANEAN AREA DURING THE LATE MESOZOIC AND TERTIARY

In Figs. 44 - 46 the continents of the past are represented by their modern outlines. This is necessary for the identification of the fragments of Pangaea, but misleading: firstly, much of the land now bordering the continents was formed during the last two eras by the compression of geosynclines; secondly, the relative levels of land and sea have changed considerably in this time.

In the Cretaceous period, much of the European continent was invaded by seas (Fig. 47). Their warm shallow waters were inhabited by the foraminiferal organisms whose shells built up the characteristic chalk formations of this period. The shelf seas of Europe and Africa were separated by the deep ocean Tethys. During the early Tertiary, however, the shelf seas retreated, until by the Oligocene the connections between the Arctic ocean and Tethys were severed (Fig. 48). At the same time, the northern edge of the African continent swung round towards Southern Europe, and Tethys progressively narrowed. The compressional margins of the European and African plates lay along a trench passing through the middle of this ocean from east to west (Dietz & Holden, 1970). The southern plate was subducted beneath the northern, and the geosynclinal sediments which had been deposited on the continental rise of S. Europe were metamorphosed and folded up into the Alpine mountain system (Fig. 50). The movement of Africa towards Europe occurred through-

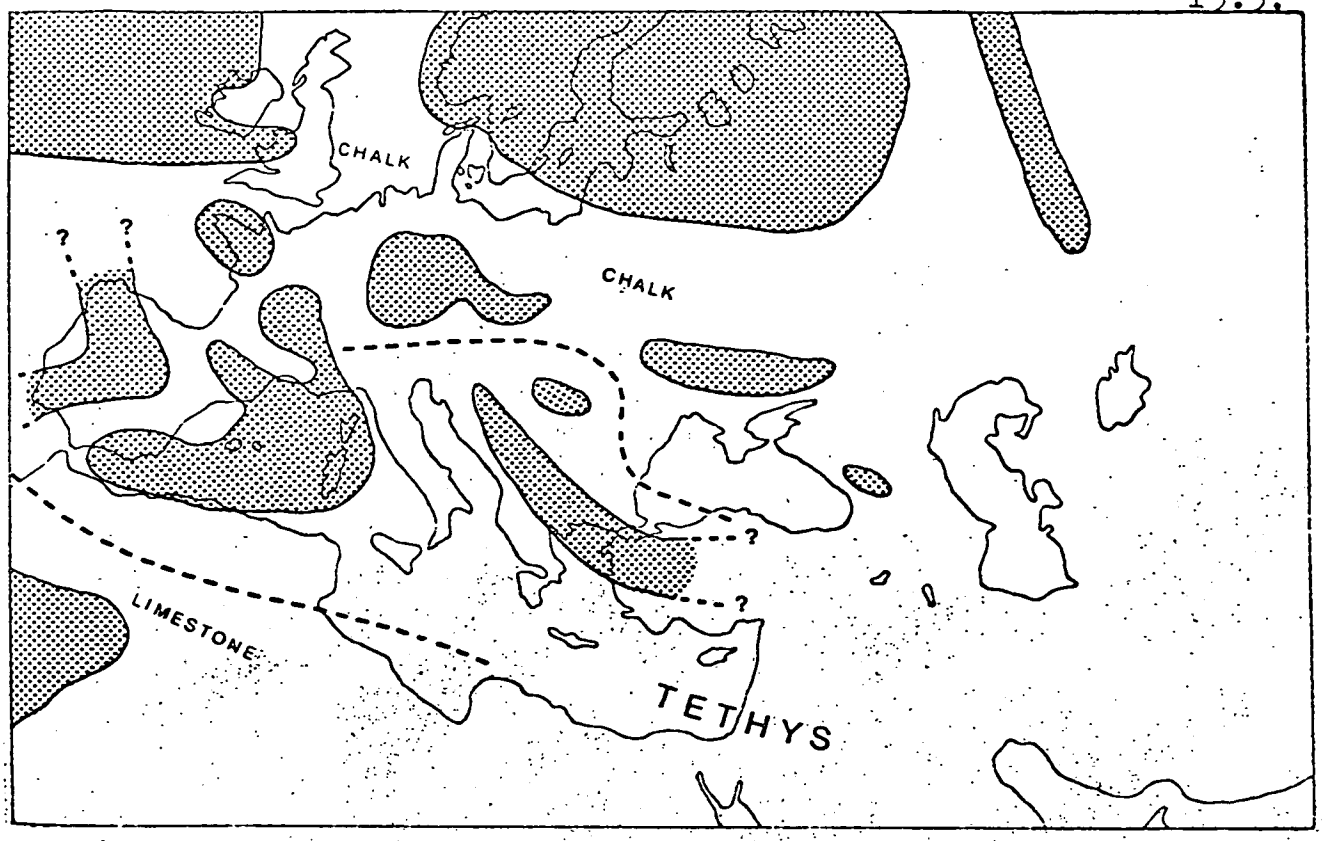


Fig. 47. W. Eurasia in the late Cretaceous (after Wills, 1951).

KEY: ----- limits synclinal sea of Tethys; land is stippled.

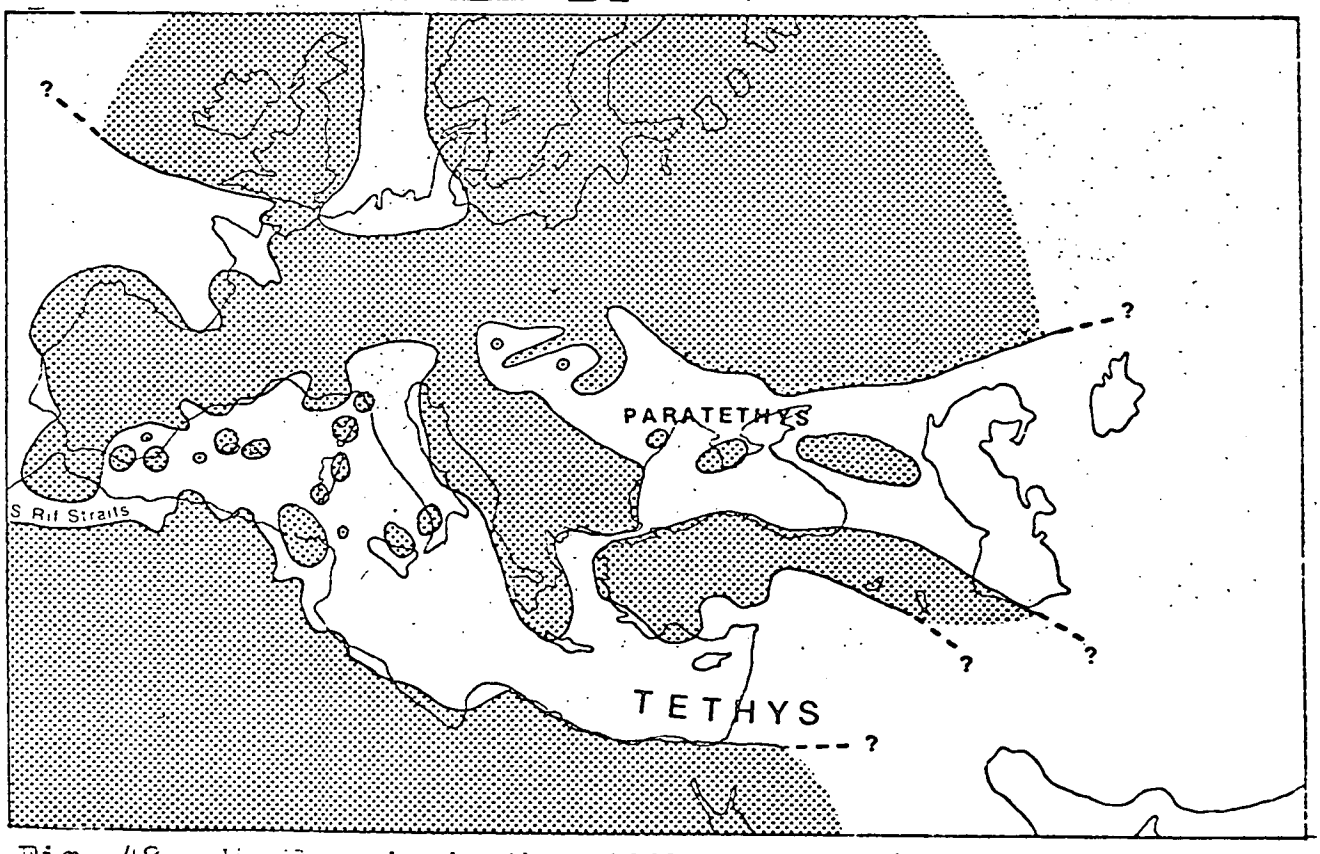


Fig. 48. W. Eurasia in the middle Miocene (after Wills, 1951; Ruggieri, 1967 and Kosswig, 1967).

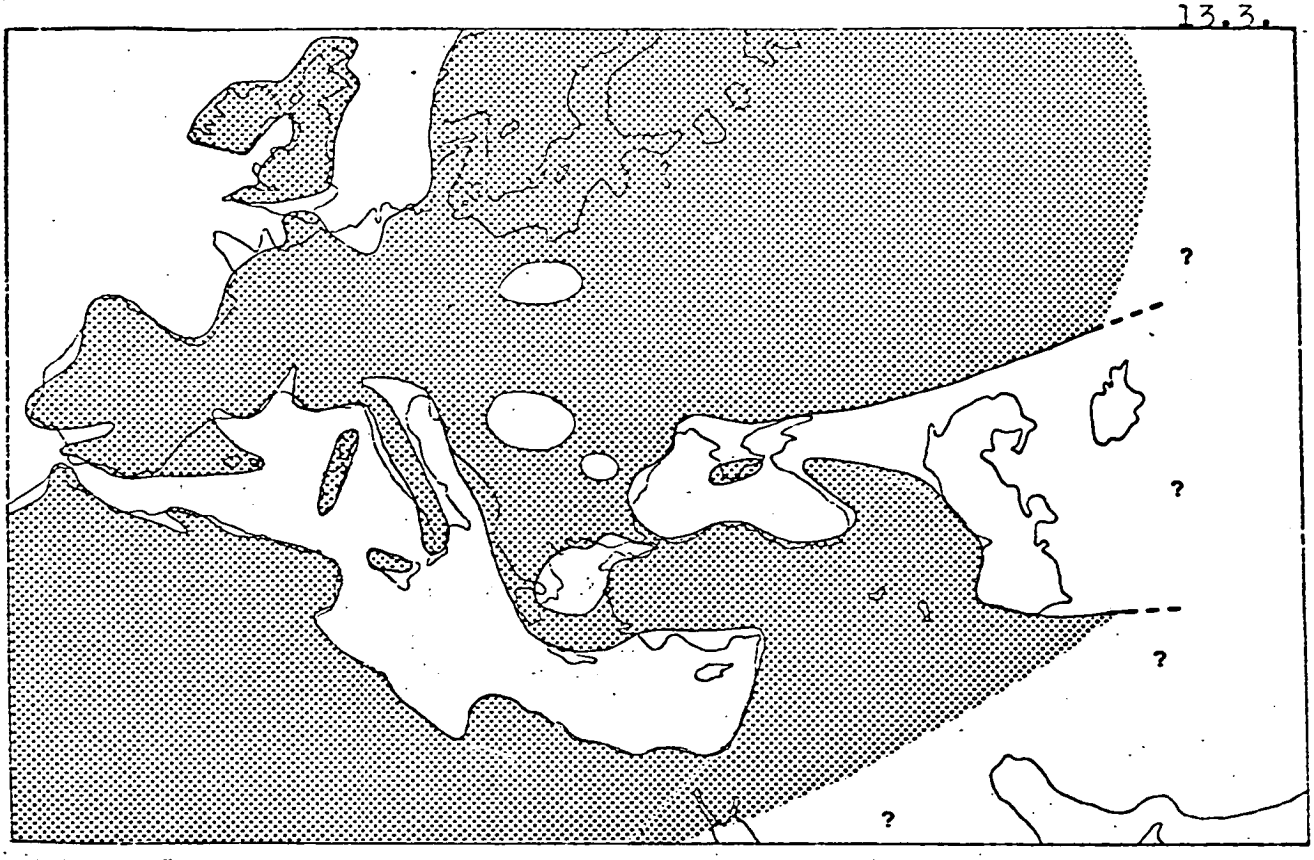


Fig. 49. W. Eurasia during the Pliocene (after Wills, 1951 and Kosswig, 1967).

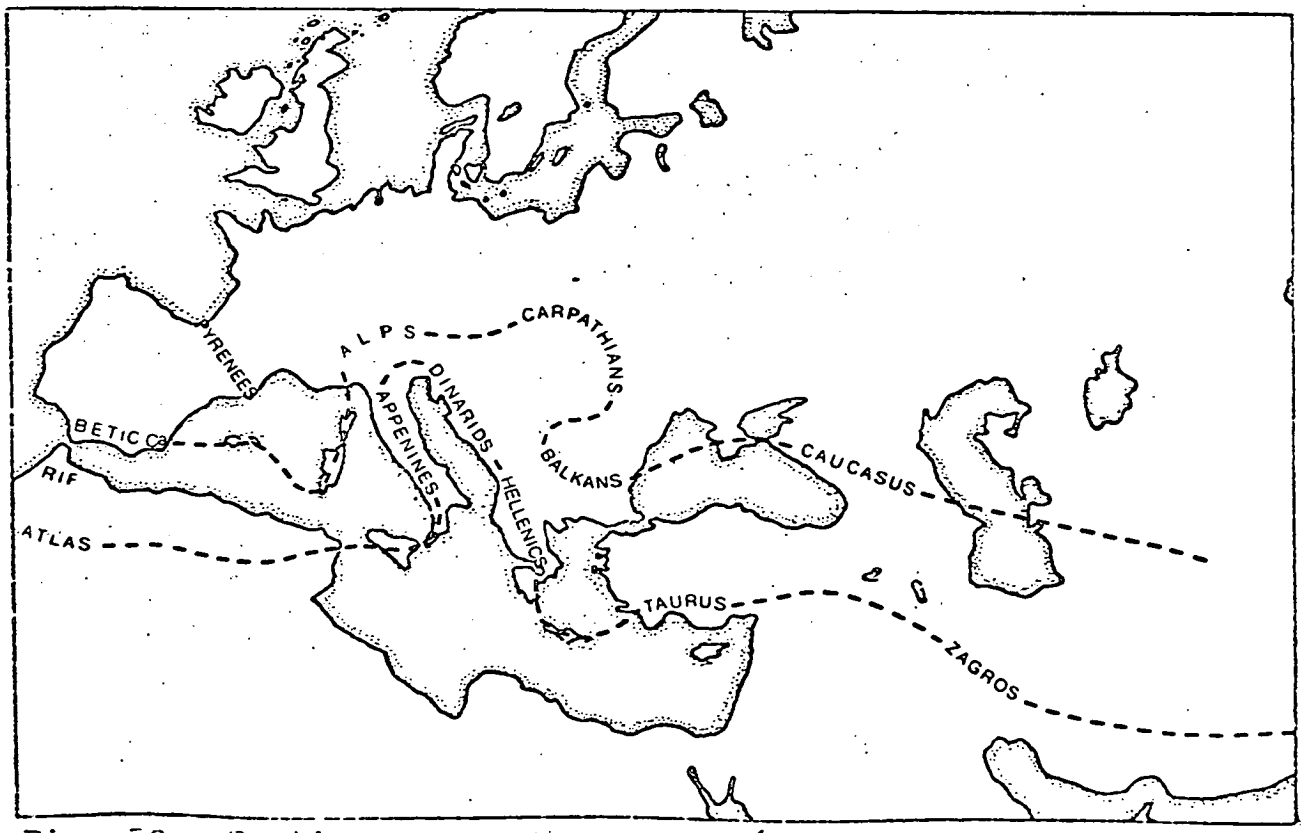


Fig. 50. Tertiary mountain systems (after Du Toit, 1937 and Holmes, 1965).

Table 30. Events in the northern hemisphere during the Tertiary period.

PERIOD	EPOCH	TIME (years x 10^6)	GEOLOGICAL EVENTS	CLIMATE
QUATERNARY	PLEISTOCENE		Ice Age	Pluvials & interpluvials
	PLIOCENE		S. America joined to N. America. Alpine orogeny at its peak.	
TERTIARY	MIOCENE	10	Mediterranean sporadically land-locked, with strong evaporation leading to saline desertic conditions.	
		20		
	OLIGOCENE	30	Tethys divided by S.W. Asia: Indian Ocean and Mediterranean Ocean formed.	Climate deteriorating
	EOCENE	40	Arctic Ocean cut off from Tethys. Alpine orogeny in progress. Tethys narrowing. Africa moving north to meet S.Europe.	
		50	Eurasia and N. America finally separated.	
	PALAEOCENE	60	N. Eurasia enjoys temperate, moist, oceanic climate, with arid belt from Spain to C. Asia. Gentle latitudinal climatic zonation.	

out the Tertiary, and it was not until the Pliocene epoch that orogenic activity reached its peak.

The connection between the 'Indian Ocean' and 'Mediterranean' regions of Tethys was finally broken in late Oligocene or early Miocene times (Takhtadjan, 1969). This is shown by two changes in the animal fossil record: firstly, the mammalian faunas of Africa and Asia, which had been very distinct, suddenly became more similar; secondly, the Pantethyan invertebrate fauna underwent a strong divergence into Indian Ocean and Mediterranean lines (Hallam, 1972).

The western end of Tethys was in contact with the Atlantic during most of the Tertiary, at first by two channels, then by the South Rif Straits (Fig. 48) and finally by the Straits of Gibraltar (Fig. 49). In the Miocene, however, the Mediterranean became completely land-locked on more than one occasion, and its waters apparently evaporated more-or-less completely, leaving the ocean floor a hot saline desert far below sea level (Hsü, 1972). See Table 30.

13.4.
THE CLIMATE OF THE NORTHERN HEMISPHERE DURING THE MESOZOIC AND CENOZOIC ERAS

In Figs. 44, 45 and 46 the continents bear the grid of present-day latitude and longitude, while the perpendicular lines intersecting in the centre of each map refer to the geographical co-ordinates which existed in the period being illustrated. The palaeolatitudes of the continents may thus be compared with their contemporary positions. During the

Jurassic period, Central Europe lay at about 30° North, i.e. approximately twenty degrees further south than at present. This area was at about the same latitude in the Cretaceous, while Western N. America became colder (Alaska was at the North Pole) and Siberia moved south. In late Mesozoic and early Tertiary times the Arctic Ocean was free from ice, being warmed by southern currents from Tethys and eventually also from the Atlantic. The eastern end of Tethys lay at the equator, and its waters were able to flow into the polar regions *via* the Eurasian shelf seas (Fig. 47).

Much of Eurasia was thus much warmer than at present. Judging by their fossil floras, the lands of north temperate latitudes had a moist, oceanic type of climate; while geological evidence suggests that during the late Cretaceous and early Tertiary there were broad arid zones in the subtropics, extending in the Old World from Spain eastwards to Central Asia and N. Indo-China, and in the New World from Mexico north to southwestern U.S.A.. (Takhtadjan, 1969). The mammalian fossil record supports the reconstruction of land positions, relative to the North Pole, shown in Fig. 46 (Eocene). It shows that animals were able to travel from America to Eurasia at that time, both by the 'De Geer' route (N. Norway to Greenland) and *via* Beringia; but the climate of the former was much more equable than that of the latter, and had a weaker 'filtering effect' on the migrating faunas (McKenna, 1972).

This situation persisted until about the end of the Eocene, when several factors combined to begin the long climatic deterior-

ation which culminated in the Quaternary Ice Age. The connection between the Arctic Ocean and Tethys was severed by a rise of the land-surface of Europe and Western Asia (Fig. 48); the latitude of Eurasia increased; and the Alpine orogeny began to build an east-west chain of mountains which prevented warm southerly airstreams from penetrating far north of the Mediterranean. The effects of climatic change in the Tertiary and Quaternary were most pronounced in Europe and Western Asia. The Mediterranean was finally separated from the Indian Ocean in the early Miocene, and at the end of this epoch it was sporadically also cut off from the Atlantic and evaporated almost completely. During these periods of isolation, the vast area of the Mediterranean basin may have resembled the Dead Sea region of today. The fresh waters of Paratethys shrank gradually into its contemporary fragments, the Black Sea and the Caspian.

During the Pleistocene the climate fluctuated between periods of severe cold (pluvial phases) and milder interludes (interglacials). There were four major glaciations, the ice at its maximum covering the area shown in Fig. 52. The European ice spread out mainly from Scandinavia and Scotland but there were secondary centres in the Pyrenees, Alps and mountains of Caucasia. In Asia a continuation of the Scandinavian ice sheet covered much of Siberia. The glaciation of N. America was even more extensive, the ice sheet extending to 40° N. in the eastern States. The ice of the last major glacial period began to retreat about 15,000 years ago (Schwarzbach, 1963).

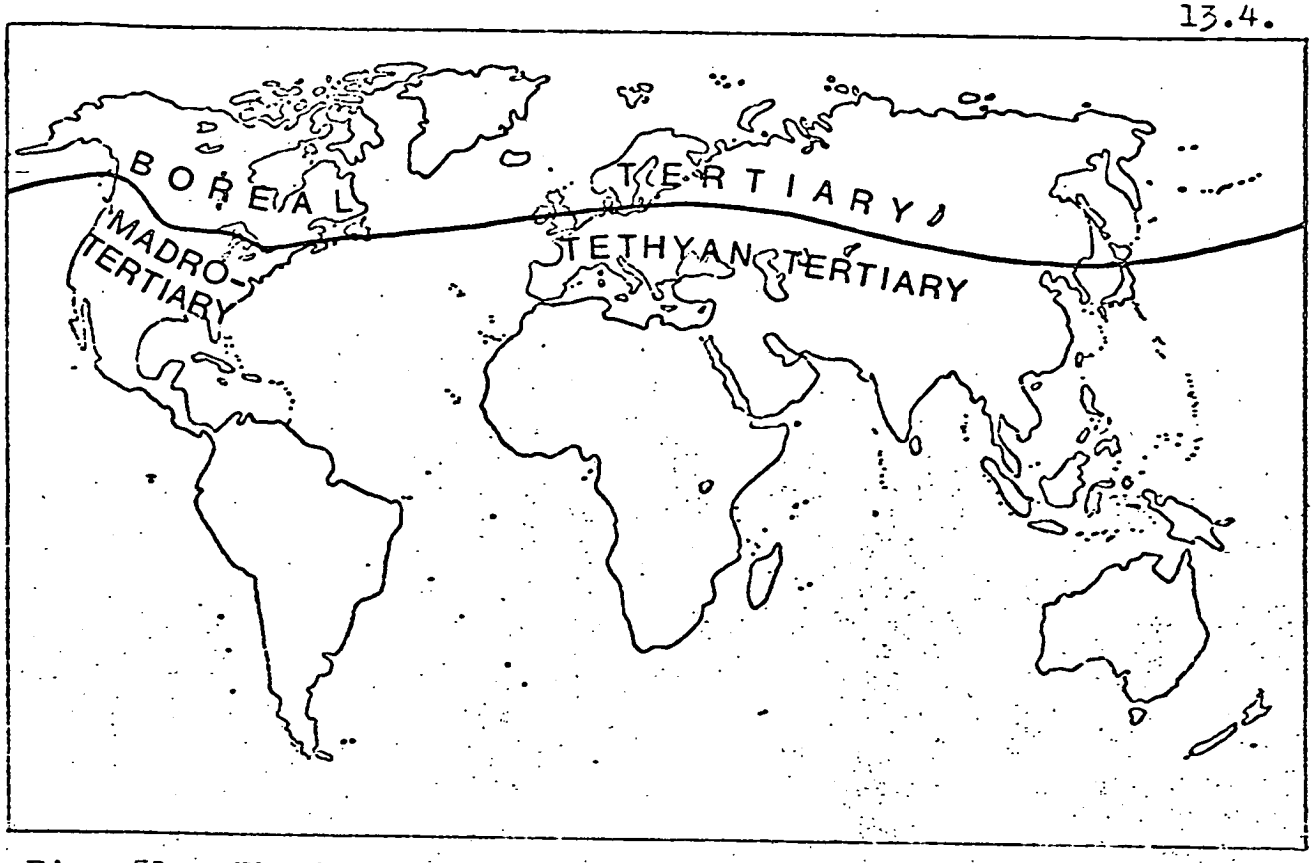


Fig. 51. The boundary between temperate and warm-temperate vegetation of the northern hemisphere in the early Tertiary (after Takhtajan, 1969).

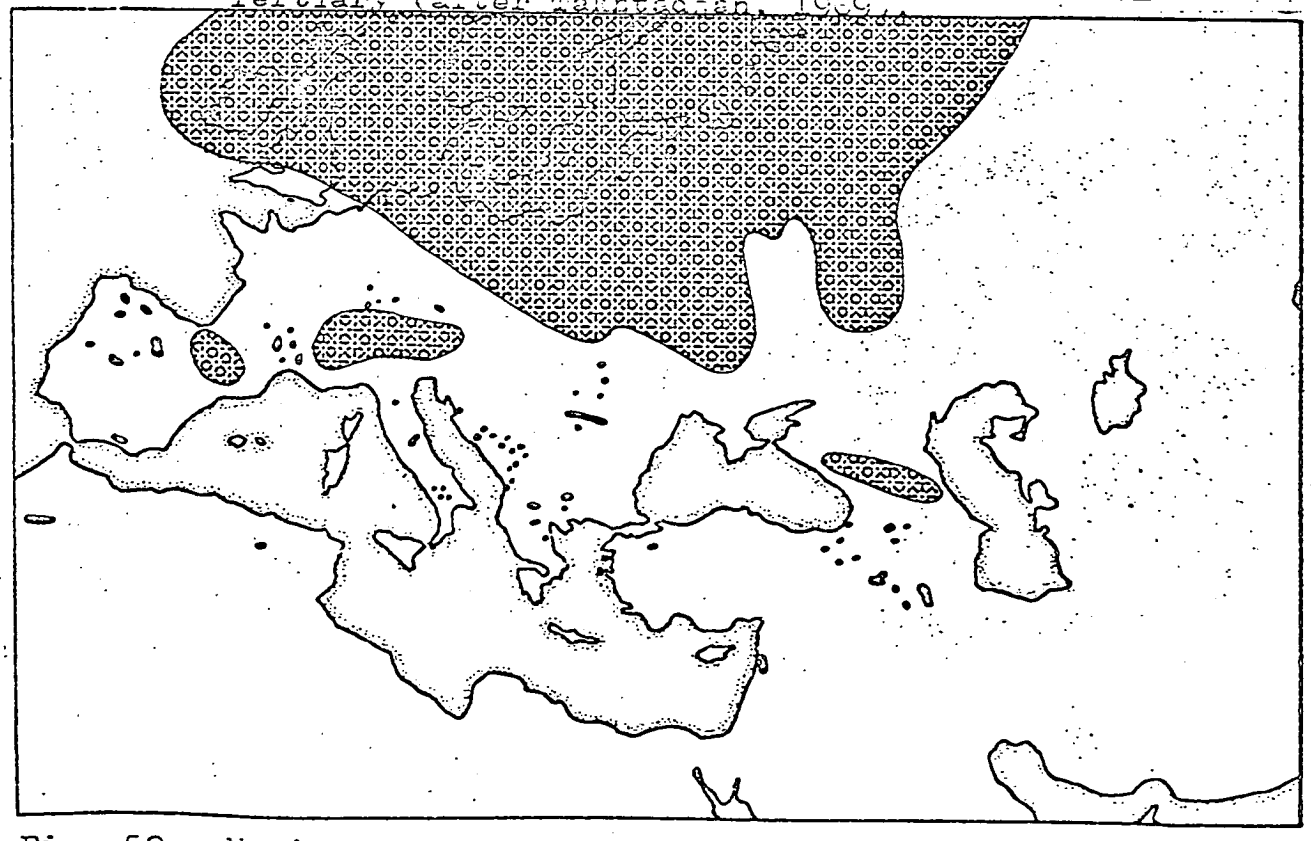


Fig. 52. Maximum extent of ice in W. Eurasia during the Pleistocene (after Wills, 1951 and Holmes, 1965).

13.5.

THE DEVELOPMENT OF ANGIOSPERM FLORAS IN THE NORTHERN HEMISPHERE FROM THE LATE MESOZOIC TO THE PRESENT.

The first stages in the evolution of Angiosperms are completely unknown. The first undisputed fossils of this group come from the Lower Cretaceous of Southern France, and yet by the middle of this same period flowering plant remains of great diversity are found widely distributed throughout the world (Takhtadjan, 1969). Takhtadjan has put forward the theory that the cradle of flowering plants was in tropical S.E. Asia, since this is the only region of the world where a rich assemblage of primitive forms can be found today living side by side with closely related but more specialised taxa. It is asserted, in support of this theory, that the extant flora of S.W. China is transitional in character between tropical and temperate, and that the elements which belong to these two vegetational types are phylogenetically related. It is proposed that the Angiosperms evolved at high altitudes in this area during the Jurassic period, and that later "their original vertical zonation was transformed, as it were, into a secondary latitudinal one" by northward migration into temperate lands.

Axelrod (1952) has divided the lowland flora of the late Cretaceous into latitudinal zones, viz. the Arcto-Cretaceous, Tropical-Cretaceous and Antarcto-Cretaceous. We are here interested only in the development of the first of these, which Takhtadjan subdivides into Boreal and Tethyan zones. The Holarctic floras of the Tertiary, which evolved from those of the preceding period, are known as Boreal-Tertiary and Tethyan-Tertiary.

Their mutual boundary delimits temperate vegetation to the north from subtropical to the south. The position of this boundary in Eocene times is shown in Fig. 51 (the northern subtropical flora of the New World is known as the Madro-Tertiary). The temperate flora of the Boreal-Tertiary consisted of a broad-leaved deciduous forest association, rich in species, the great majority of whose genera are still extant. These included Platanus, Alnus, Corylus, Betula, Tilia, etc., and the deciduous Gymnosperms Ginkgo, Metasequoia and Taxodium. The vast area covered by this flora appears to have had a very gentle climatic zonation. In the early Tertiary, trees flourished in what is now the Arctic, in a cool-temperate environment; this gave way southward to a warm-temperate zone, and this in turn to the subtropical Tethyan regime.

The flora of the Tethyan-Tertiary in Western Europe was chiefly of evergreen trees and shrubs; among the Angiosperms were many representatives of the Lauraceae, together with species of Quercus and other members of the Fagaceae. The climate of Europe was, as has been described, much influenced by the warm Tethys sea, and here the boundary between Boreal- and Tethyan-Tertiary floras was deflected northwards; in addition, tropical elements (e.g. the palm Nipa, and mangroves) penetrated the subtropical flora by migration along the northern shores of Tethys (Matthews, 1955). In the early Tertiary Europe was divided into a number of islands, and its vegetation was apparently fairly mesophytic in constitution; Central Asia, however, had a dry, continental climate and supported a xerophilous Tethyan-Tertiary

flora (Takhtadjan, 1969).

Until the late Eocene, the Holarctic flora (often referred to collectively as the Arcto-Tertiary) appears to have been relatively homogeneous, due to the easy circumpolar migration of its constituents. At about this stage the connections between N. America and Europe, and between Asia and Alaska, were finally broken; from then on the floras of the New and Old Worlds evolved independently.

Climatic changes now began to affect the latitudinal floral zonation of each continent, and from the Oligocene to the Pliocene there was a continuous southward migration of plant communities in Eurasia and N. America. In America and E. Asia the floras were able to move intact without being seriously affected during their migration, but the situation in Europe was very different. Here the southward movement of the subtropical/temperate floral zones coincided in time with the Alpine orogenesis. The floras were driven into an area which upset their balance in two directions: firstly, the habitats suitable for these forest associations became very restricted, which caused the extinction of many species; secondly, the range of new habitats available for colonisation increased, providing wide opportunities for evolution. As a result, species of Arcto-Tertiary woodland probably gave rise, by adaptive radiation, to new taxa inhabiting unstable slopes and screes, cliffs, high altitude regions and mountain pastures. These new species may have included many annuals, and also specialised perennials adapted to cryophytic, xerophytic or primary habitats.

The European floras of the Arcto-Tertiary were affected not only by the Alpine-Caucasian mountain barrier, but also by the Mediterranean ocean which completely prevented further southward migration. During the Miocene the saline desert conditions which existed from time to time in the Mediterranean basin must have been totally alien to European Arcto-Tertiary species, but they may have stimulated their descendants towards even more extreme xerophytic adaptation (Stebbins, 1952). In addition, the increasingly dry climate of Western Europe and the Near East permitted the xerophytic Tethyan-Tertiary flora of Central Asia to migrate westwards along the newly-formed land connection between Arabia and Asia.

The distribution of Holarctic phytochoria at the end of the Tertiary was very similar to that of the present, but in the intervening period the floras of the northern hemisphere were severely affected by the Pleistocene Ice Age. At the peak of each glacial phase most of Europe north of the Alps was occupied by tundra and steppe vegetation, and woodland survived only in narrow belts round the Mediterranean and in N. Anatolia. The Mediterranean flora itself was displaced into N. Africa and the Near East (Schwarzbach, 1963). In interglacial periods the floras migrated back to occupy more-or-less their present pattern of distribution. An analysis of the pollen in Pleistocene deposits of Caucasia has shown how the flora of each interglacial was more impoverised than its predecessor (Tumajanov, 1971), and this finding is reproduced in many other parts of Europe (cf. Matthews, 1955). A large proportion of species failed to find

refugia during the severest phases and became extinct; others, which occurred in Europe before the Pleistocene, are now found only in S.E. Asia or the south-east of N. America. Many species survived only as small populations; many had their distribution area divided into widely disjunct fragments.

Although the Tertiary floras were greatly impoverished by the rigours of the Pleistocene, their descendants are still clearly apparent. Takhtadjan, recognising this, divides the Holarctic Kingdom into the regions shown in Fig. 53. The vegetation of the Boreal Subkingdom (excluding the Arctic and Subarctic) is composed of two elements; boreal coniferous forest and broad-leaved deciduous nemoral forest (Kornaś, 1972). The latter is a descendant of the Boreal-Tertiary flora, and, since its fragments have been isolated on the continents of America, Europe and Asia since the early Tertiary, there is a considerable degree of differentiation between them. This can be recognised in the occurrence of species pairs (e.g. Platanus occidentalis - eastern U.S.A. and P. orientalis - E. Mediterranean) which, though still potentially interfertile, are morphologically and ecologically divergent (Davis & Heywood, 1963). The main contemporary refugia of Boreal-Tertiary relicts are in south-eastern N. America, S.E. Asia, and in the Euxine province of the Euro-Siberian region. The last of these three, which includes the Balkans, Crimea, Caucasia, N. Anatolia and Hyrcania (N. Iran), is the poorest, mainly because its species were steadily depleted during the Pleistocene. The flora of Caucasia is particularly interesting and complex, for besides its important Boreal-Tertiary element it contains small

enclaves of broad-leaved evergreen Tethyan-Tertiary species (e.g. Rhododendron ponticum, Buxus sempervirens, Ilex colchica). It is also penetrated at high altitudes by conifers belonging to the boreal forest of Euro-Siberia (Tumajanov, 1971).

The boreal forests are thought to be of recent origin, compared with the deciduous Angiosperm forests to the south, because they show so little taxonomic differentiation throughout the Holarctic zone. It is postulated (Kornaś, 1972) that they belong to an old formation, perhaps dating back to the early Tertiary, which originated in a moutainous area bordering the North Pacific. This later spread widely to fill the niche left by the retreating Arcto-Tertiary flora. The deciduous trees (oak, beech, willow, alder) which today form the natural climax forests of Central Europe represent the most cold-resistant species of the Boreal-Tertiary. These were able to survive the Ice Ages and recolonise areas of the continent which had been either buried beneath ice or bore only tundra or steppe vegetation.

The regions of the Tethyan Subkingdom are occupied by floras which are taxonomically much more divergent than those of the Boreal Subkingdom, due to the greater duration of their isolation. In Western Eurasia there are three main descendants of the Tethyan-Tertiary phytochorion: the Macaronesian, the Irano-Turanian and the Mediterranean. The islands of the Canaries, Madeira and the Azores are volcanic mountains whose upper slopes, being daily shrouded in mist, provide a warm, humid environment. Here survives a distinctive forest flora,

dominated by members of the Lauraceae, whose associated species (both Angiosperm and Pteridophyte) were widely distributed in Europe in the early Tertiary (Takhtadjan, 1969).

The Irano-Turanian phytochorion is believed to have evolved in Central Asia since the late Mesozoic. At the end of the Tertiary period this flora migrated westwards south of the Caspian, and penetrated into E. Central Anatolia which had very recently become dry land (Kosswig, 1967; Davis, 1971). Here, being newly arrived in fresh territory, and closely bounded by two other phytochoria (Mediterranean and Euro-Siberian), its elements underwent a fresh burst of evolution.

The Mediterranean phytochorion is one of the youngest floras of the northern hemisphere. It is classified as part of the Tethyan Subkingdom as it is considered to be descended largely from subtropical elements, but Boreal-Tertiary ancestors were no doubt also involved, especially in the east (Takhtadjan, 1969). It is also strongly affected by infiltrations of Irano-Turanian elements. The delimitation of the Mediterranean and Irano-Turanian phytochoria is still a matter of controversy; according to Zohary (1973), the Middle and High Atlas regions of N.W. Africa, which he terms the 'Mauritanian Steppe Province', is Irano-Turanian territory. The Mediterranean flora comprises xerophilous evergreen shrubs and trees (e.g. Quercus ilex, Pistacia lentiscus), endemic conifers (e.g. Pinus pinea) and a rich herbaceous element in which annuals and bulbous or tuberous species, some, no doubt, of Irano-Turanian origin, play an important part.

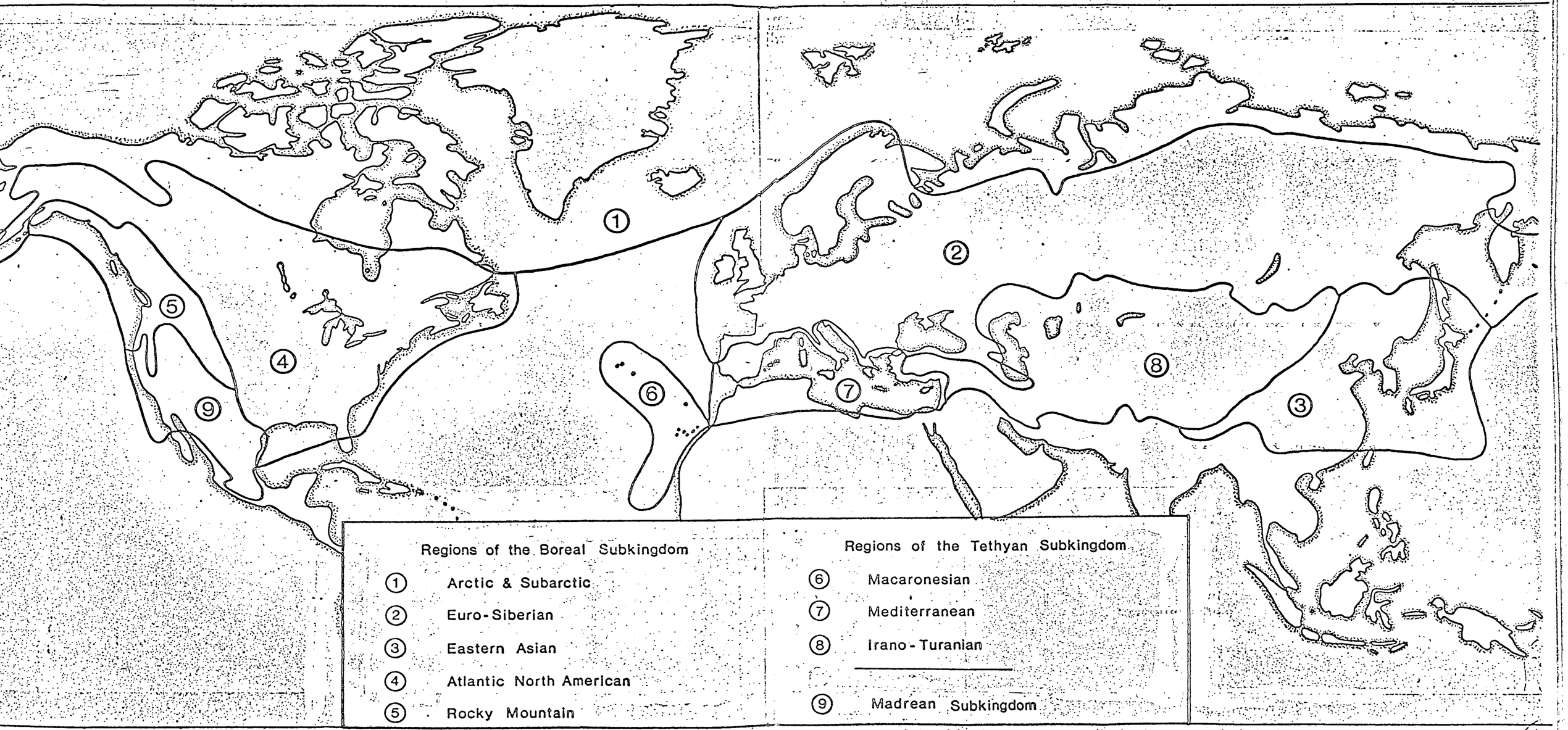


Fig. 53. Phytogeographical classification of the north temperate regions (after Takhtadjan, 1969).

Chapter 14

THE GEOGRAPHICAL DISTRIBUTION OF THE VICIEAE

14.1. Introduction: mapping methods.

14.2. The maps.

14.3. The interpretation of patterns of geographical distribution.

14.1.

INTRODUCTION: MAPPING METHODS

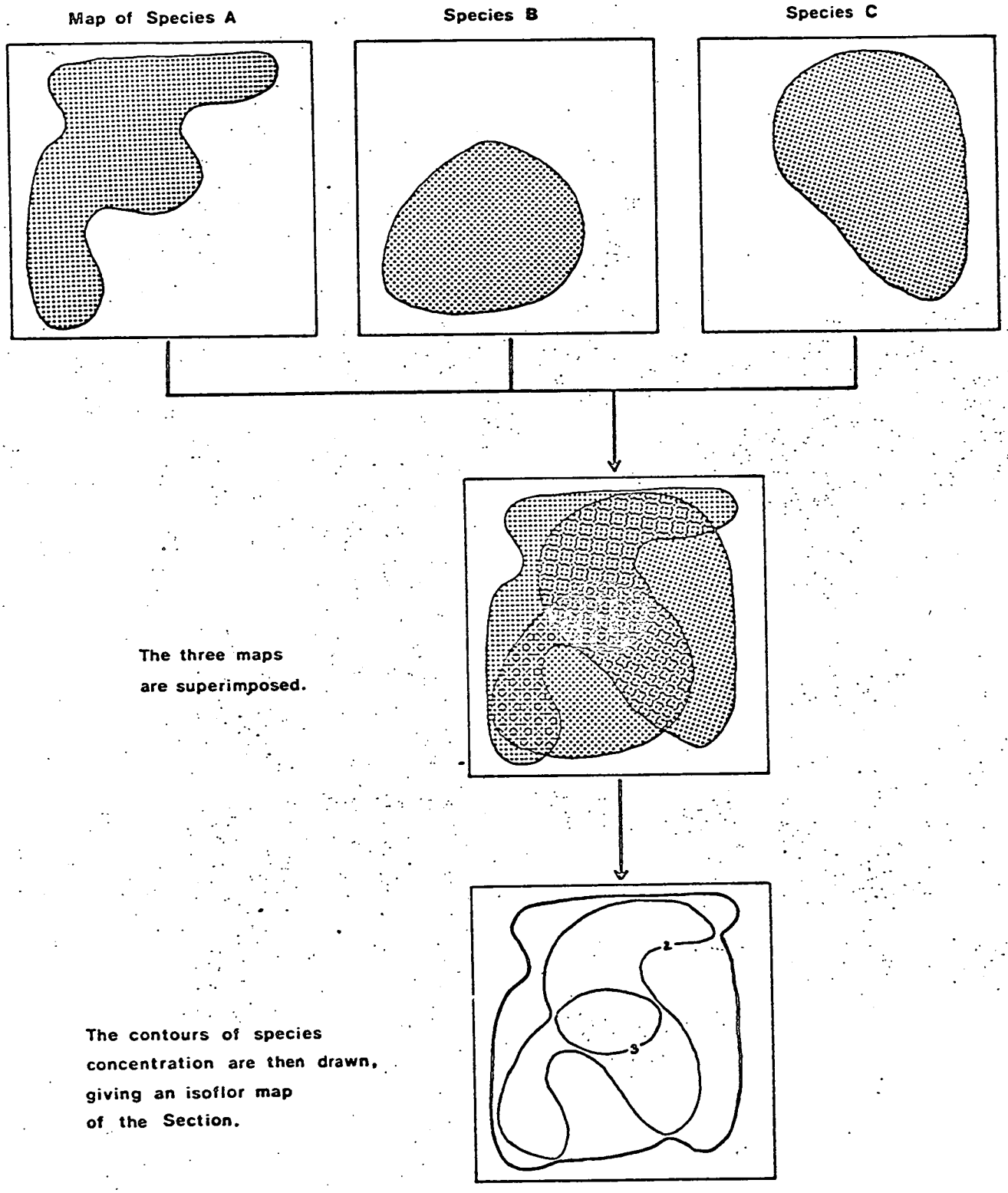
As a basis for constructing the maps of genera and sections which are shown in the following pages, I first plotted the distribution of each species of the Vicieae on a small-scale map of the World (like the one in Fig. 60). The isoflor maps of sections do not show the actual distribution of individual species (except where the section is monotypic), but each line is a contour delimiting a greater concentration of species from a lesser. Thus, while only a single species of the section occurs at any point between the bold outermost line and the next adjacent inside line, this may be a different member of the section in different parts of its perimeter. Only two species occur at any point between the second and third lines, and so on. The isoflor maps were made by taking the individual species maps for all the members of a particular section, and transferring the outline of every species onto a single map. This procedure is shown diagrammatically in Fig. 54. The outline maps for each section and genus were made in the same way, but omitting all details except the boundary line.

The information about the geographical distributions of species was gleaned from monographic works and regional floras *, and from herbarium material, and it is more accurate

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* chiefly Ball (1968); Bobrov (1948); Burkart (1935, 1942 & 1966); Davis (1970); Davis & Plitmann (1970); Fedtschenko (1948); Hermann (1960); Quézel & Contandriopoulos (1965); Tutin (1962); Hitchcock (1952) and Lems (1960).

Fig. 54. Method of construction of the isoflor map of a section containing three species.



and detailed in some areas than in others. The N. American, European and S.W. Asian areas are reliably covered, but data on E. Asian and S. American distributions are more generalised. The maps are intended to show patterns of distribution rather than precise details, and so this degree of inaccuracy does not detract from their effectiveness. In any case, an isoflor map, however full the data on which it is based, automatically blurs reality. The distribution of a plant species, with its special ecological requirements, cannot be satisfactorily shown on a map by surrounding an area with a line; and also, where many isoflors have to be drawn close together, the implied distribution of species in that particular area is certainly false.

14.2.
THE MAPS

The first map shows the distribution of genera in the tribe; the rest are devoted to Vicia and Lathyrus. For each of these large genera, the first map shows its iso-sectional distribution while the last is the complementary map giving actual outlines for each section. This large folding map is placed last in each genus, after the isoflor maps of individual sections, so that the full distribution of each section can be seen if required.

The treatment of cultivated species and aliens is as follows; Taxa which are widely cultivated, but which also occur as naturalised and wild plants, are mapped according to the range within which they are thought to be wild or fully

naturalised: e.g. Pisum sativum (Fig. 55), Vicia ervilia (Fig. 70). However, the broad bean (Vicia faba), which is known only in cultivation, is not mapped (Fig. 77). Undoubtedly alien species are omitted; for example, over half the representatives of Vicia in N. America are introduced from the Old World *, but these are not shown in the isoflor maps.

The maps do not give information about the terrain or climate of the different regions. These additional factors are extremely interesting and relevant to the geography of individual species, as they provide ecological data which may help to interpret patterns of distribution. However, their usefulness is limited when sections or genera are being studied as units, because the species which constitute each group often have divergent ecological requirements, so that these factors will tend to cancel each other out when the species are mapped together. From the point of view of sections and genera, it is more useful to compare their isoflor maps with Fig. 53, which outlines the phytochoria of the north temperate regions. These phytogeographical divisions are based on a complex of attributes which includes broad climatic differences between regions and also incorporates the floristic differentiation and

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* V. unijuga, V. cracca, V. villosa, V. benghalensis, V. monantha, V. articulata, V. ervilia, V. hirsuta, V. disperma, V. tetrasperma, V. oroboides, V. sepium, V. sativa, V. lathyroides, V. grandiflora, V. lutea, V. pannonica, V. narbonensis, V. faba.

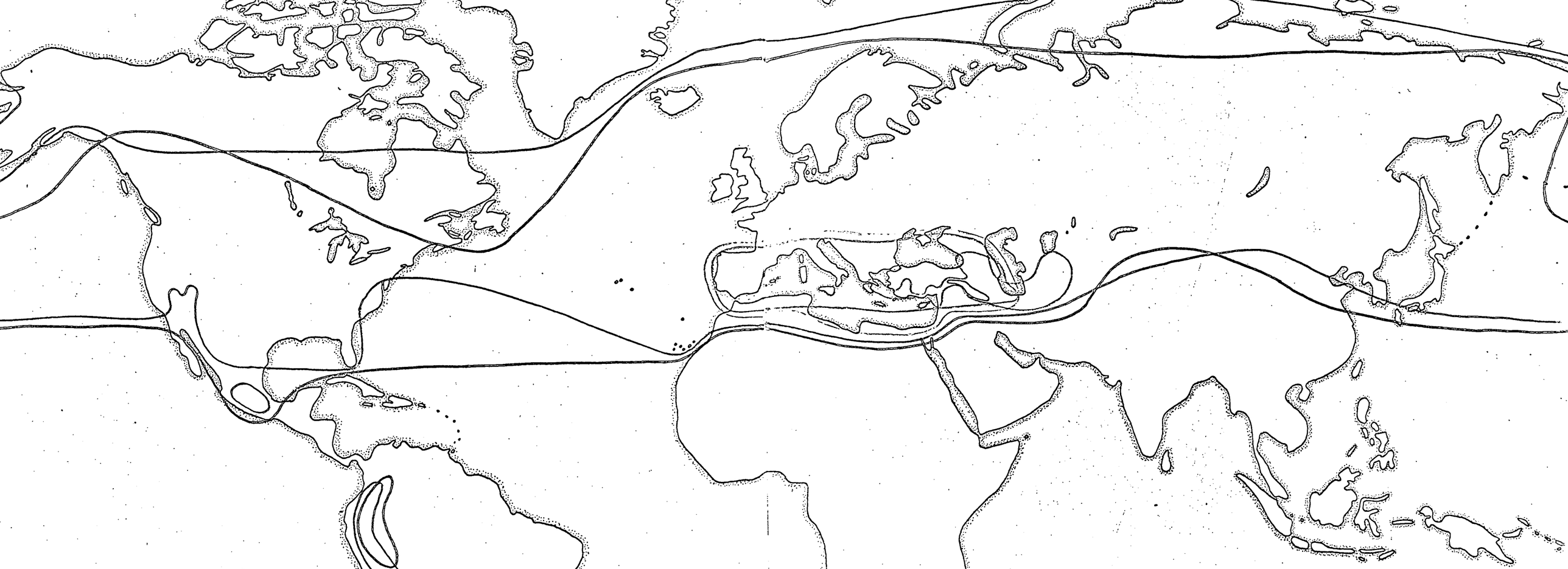


Fig. 55. Map showing distribution of the genera of the Vicieae.

KEY:

Vicia

Lathyrus

Lens

Pisum

Vavilovia

Anatropostylia

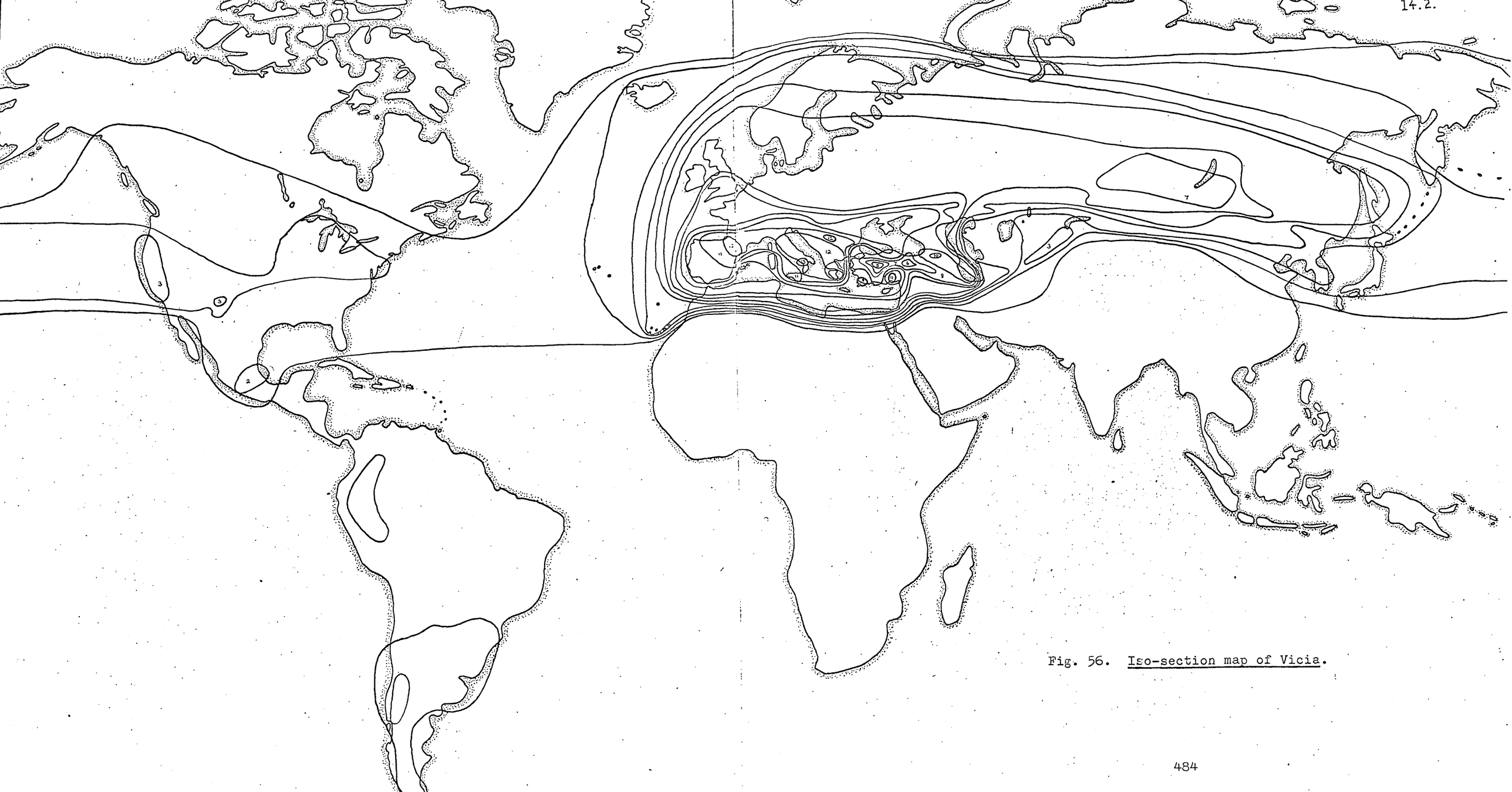


Fig. 56. Iso-section map of Vicia.

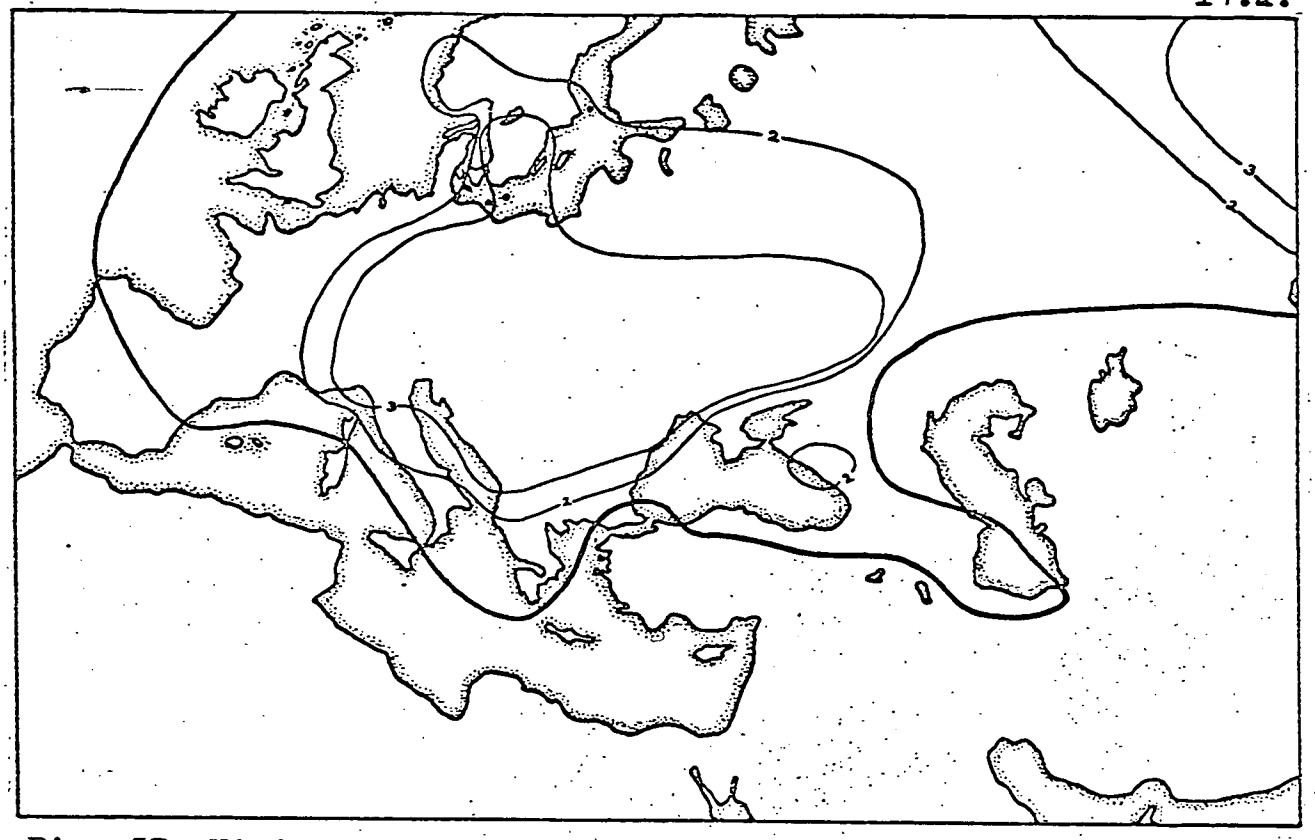


Fig. 57. Vicia Sect. Vicilla in Europe and S.W. Asia.

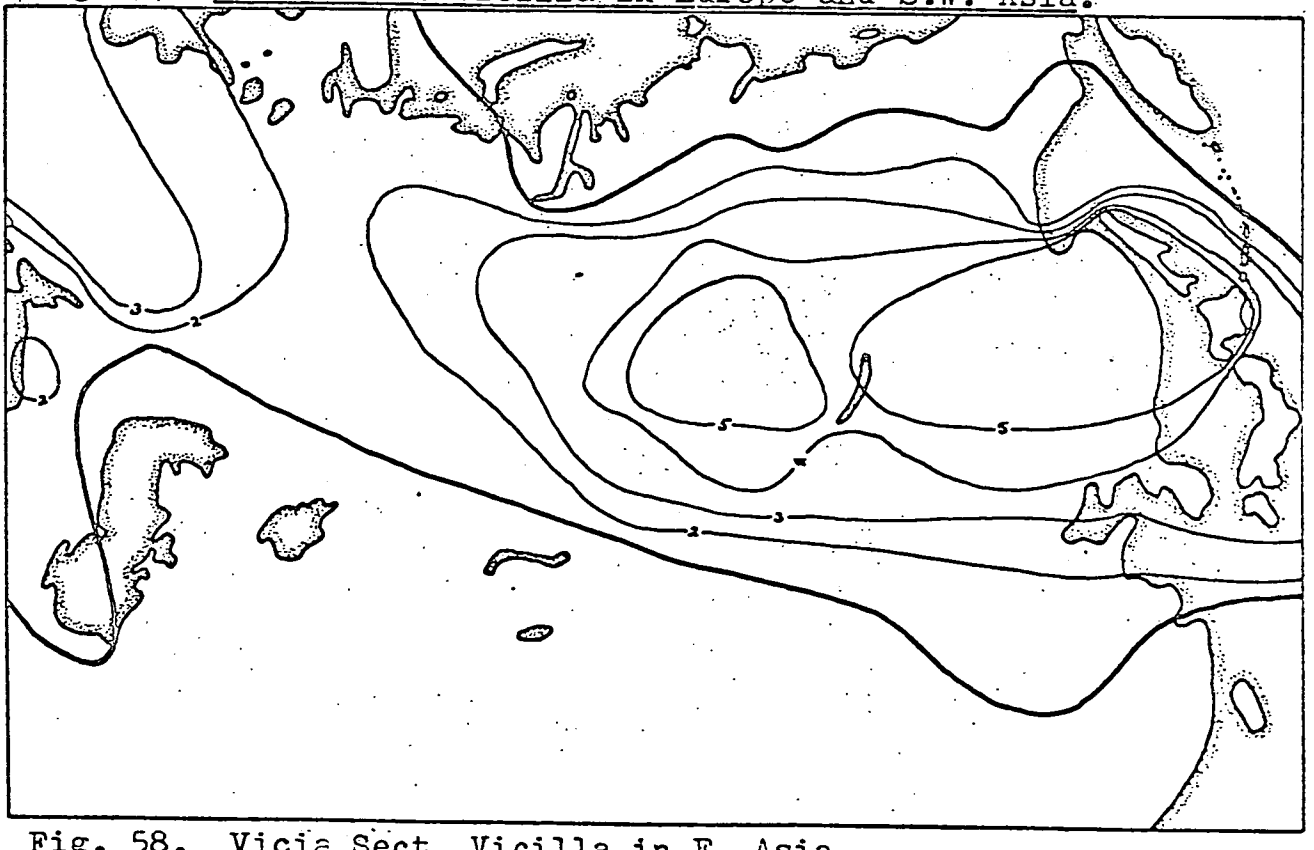


Fig. 58. Vicia Sect. Vicilla in E. Asia.

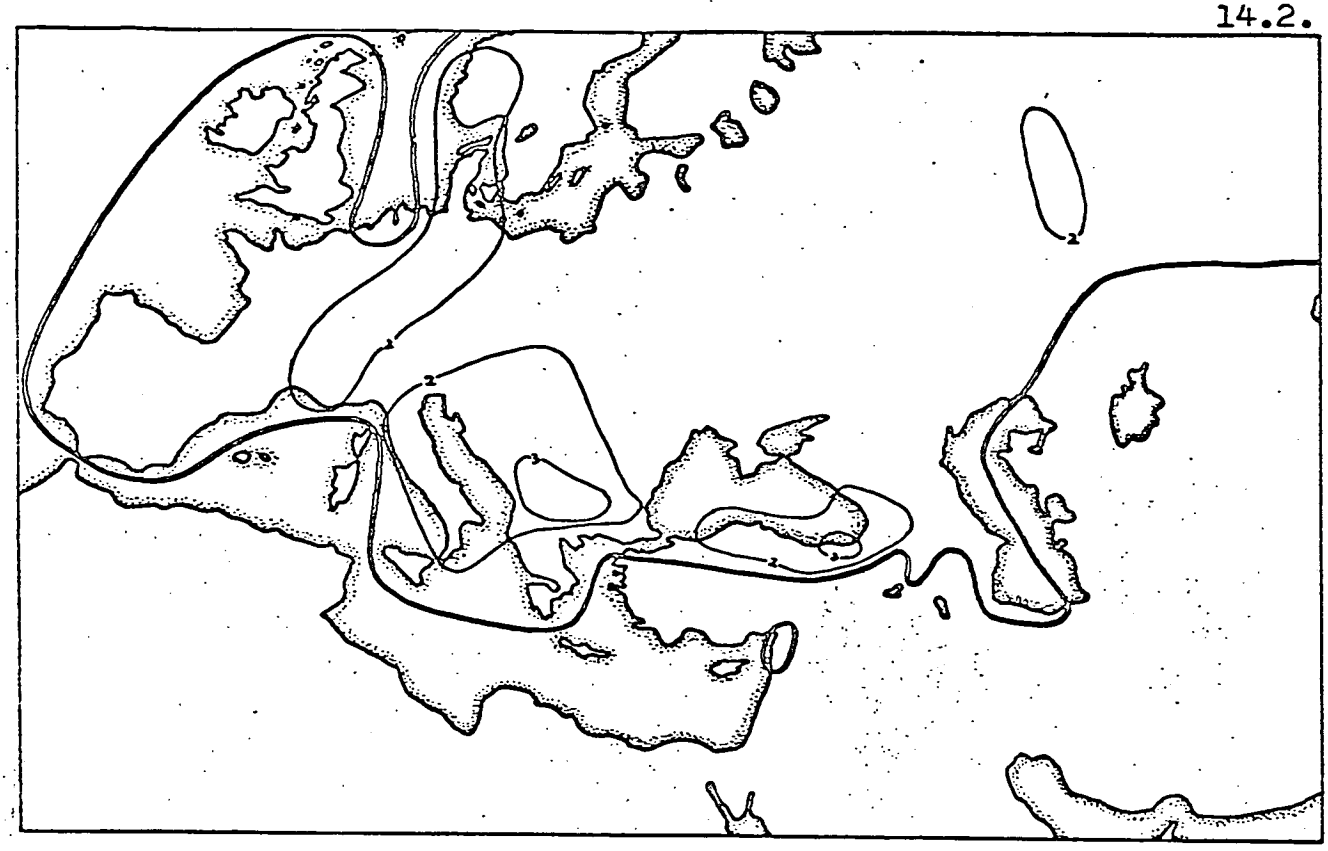


Fig. 59. Vicia Sect. Cassubicae in Europe and S.W. Asia.

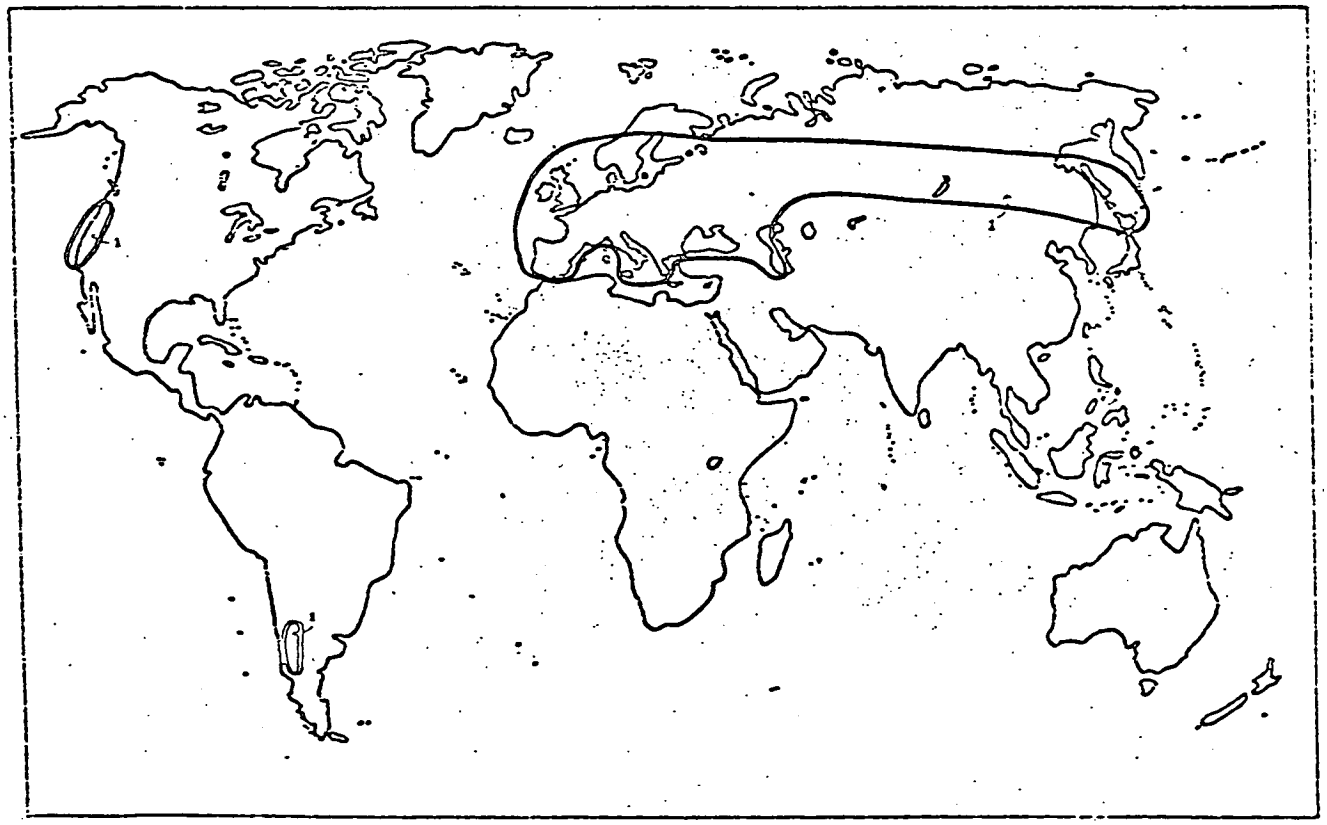


Fig. 60. Vicia Sect. Cassubicae: World distribution.

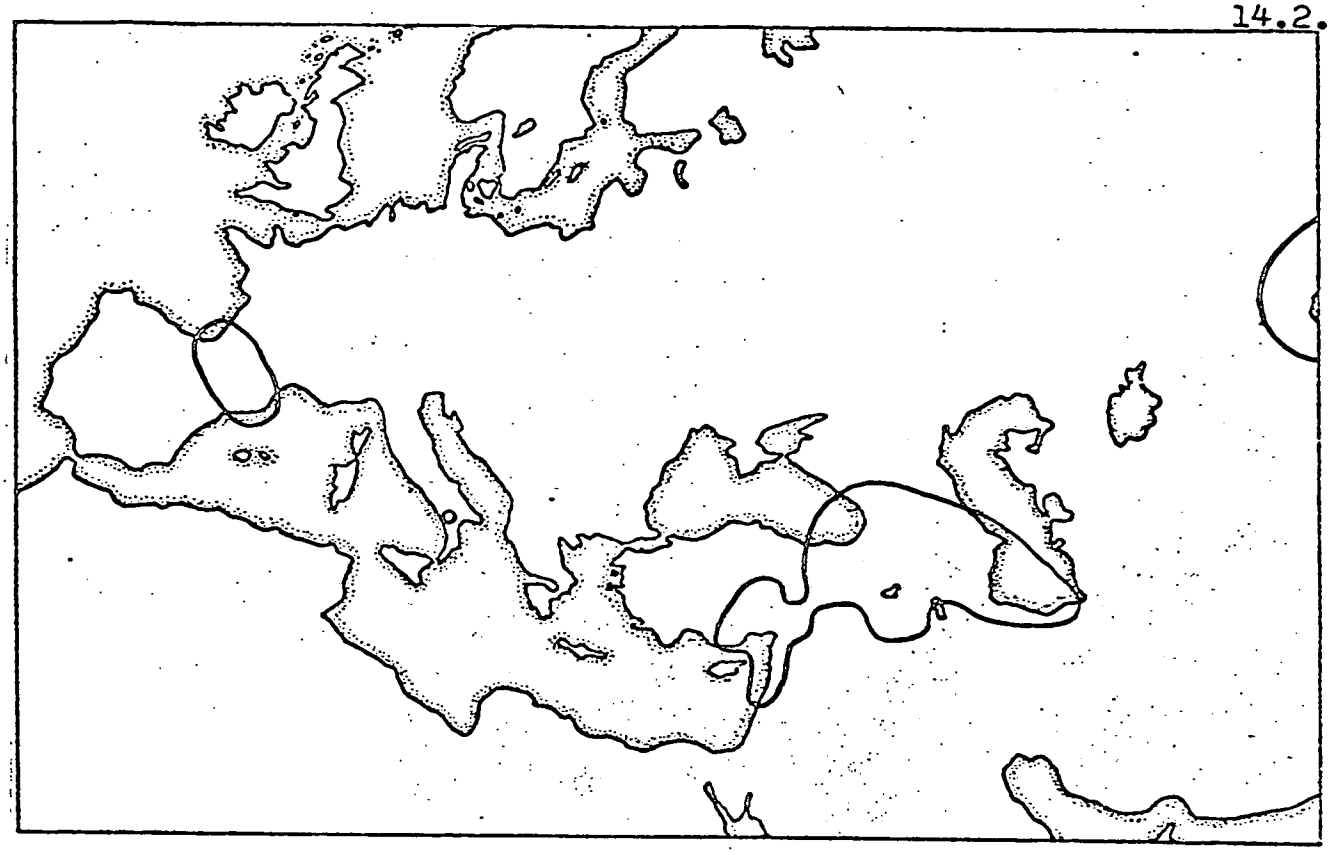


Fig. 61. Vicia Sect. Variegatae

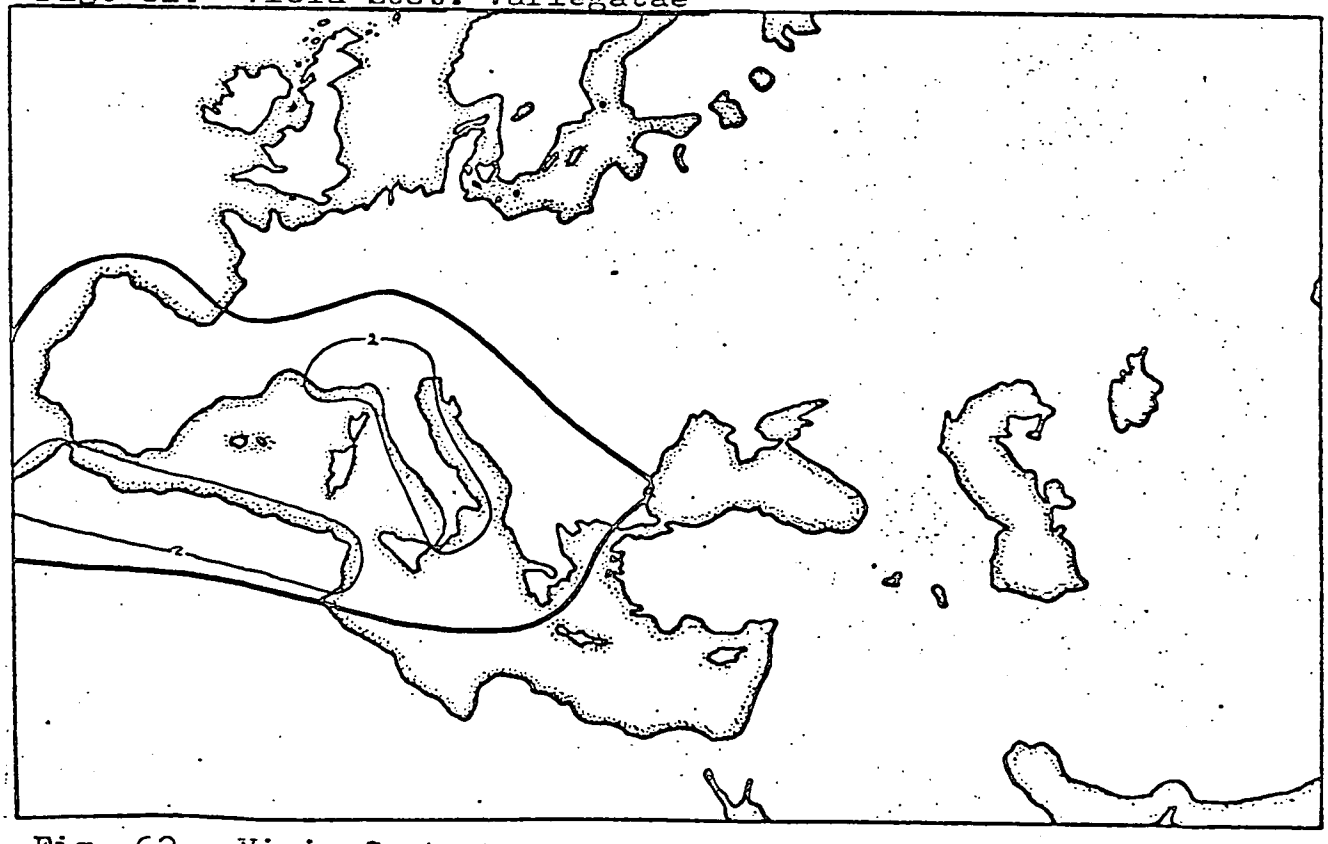


Fig. 62. Vicia Sect. Pedunculatae.

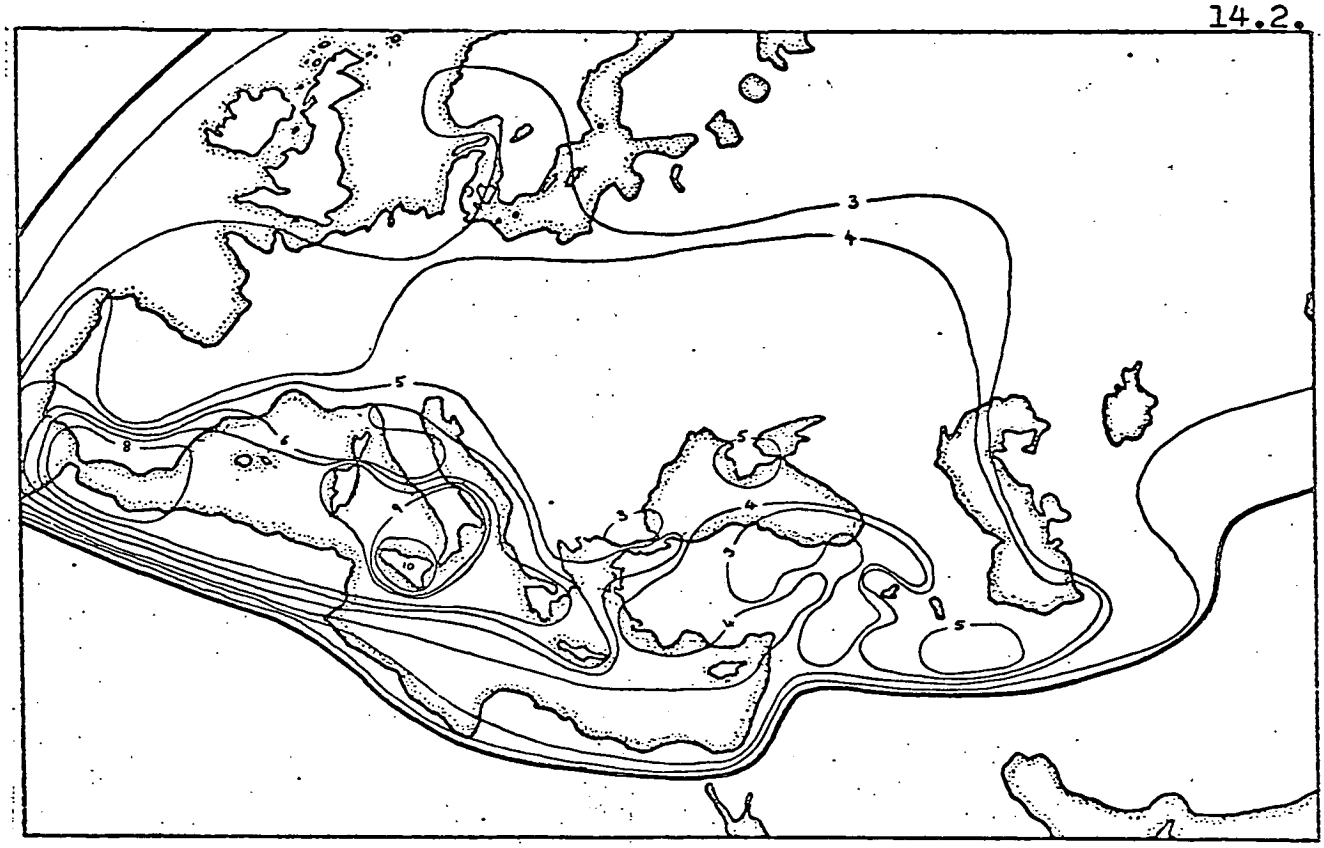


Fig. 63. Vicia Sect. Cracca in Europe, N. Africa and S.W. Asia.

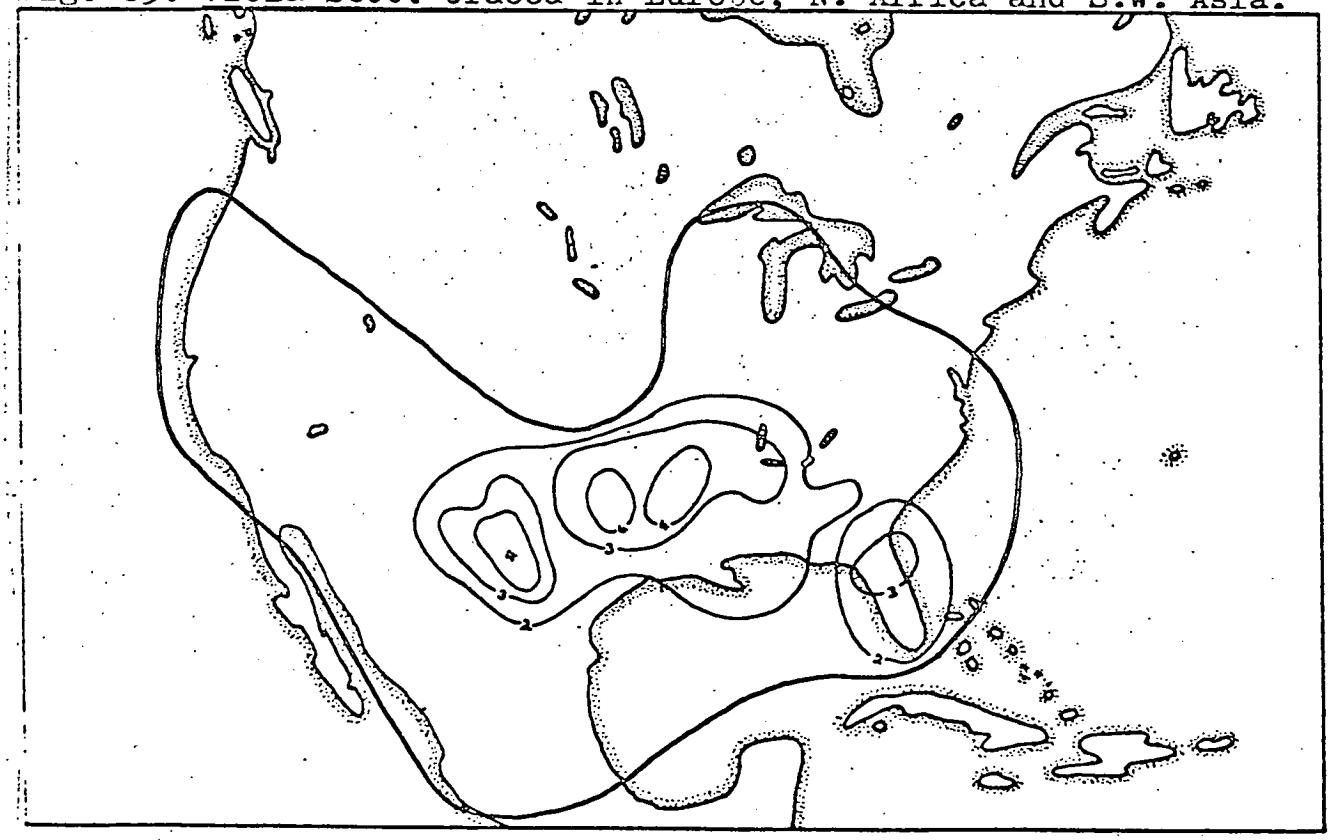


Fig.64. Vicia Sect. Cracca in N. America.

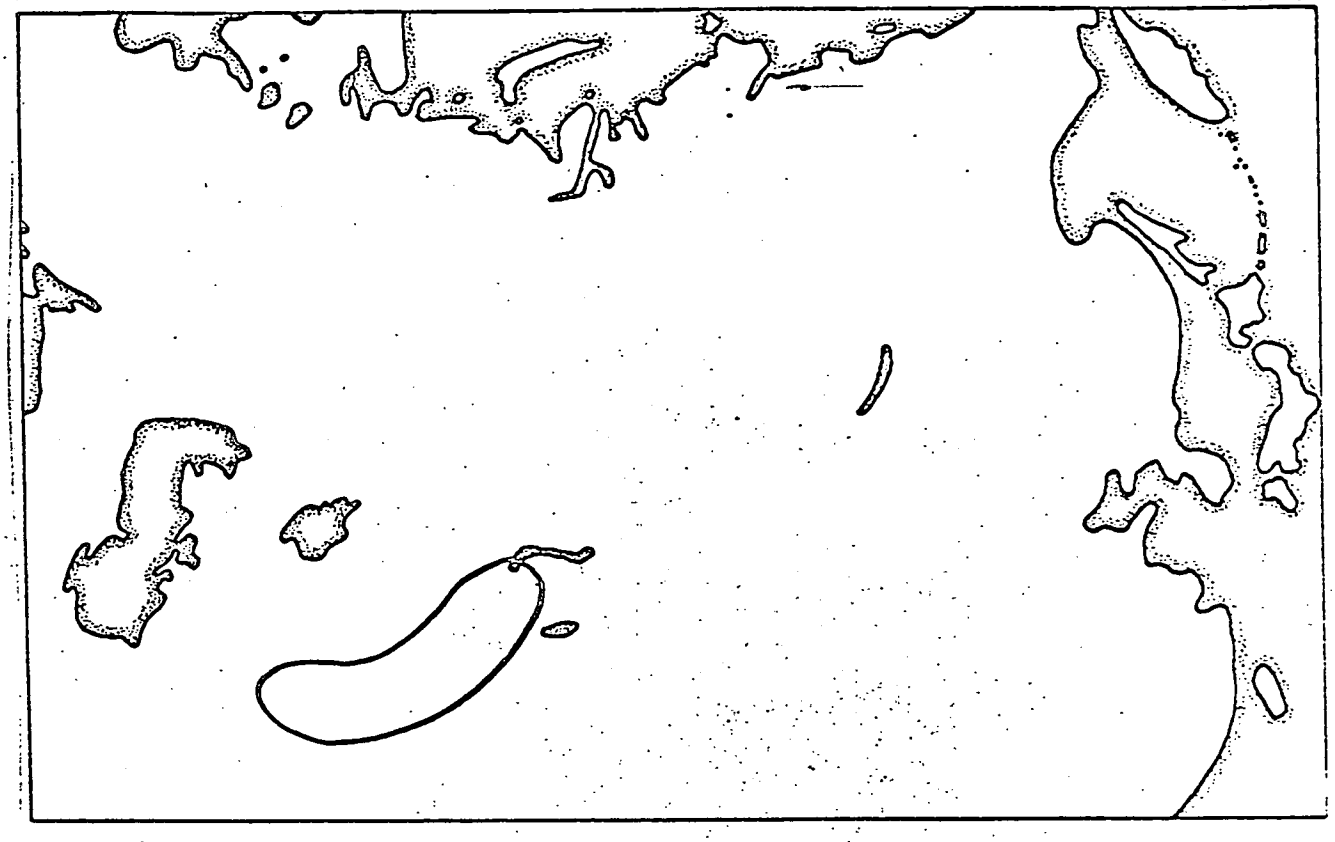


Fig. 65. Vicia Sect. Subvillosae.

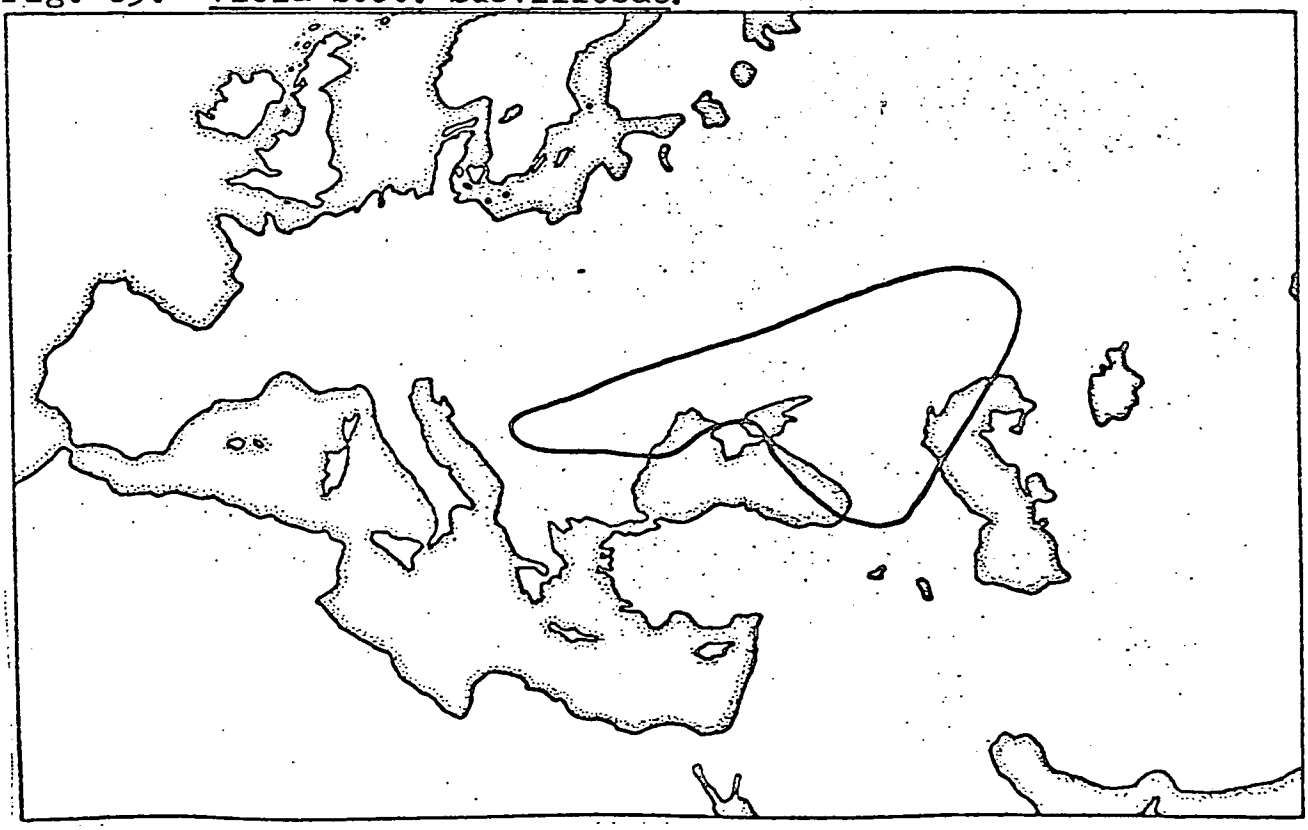


Fig. 66. Vicia Sect. Biennes.

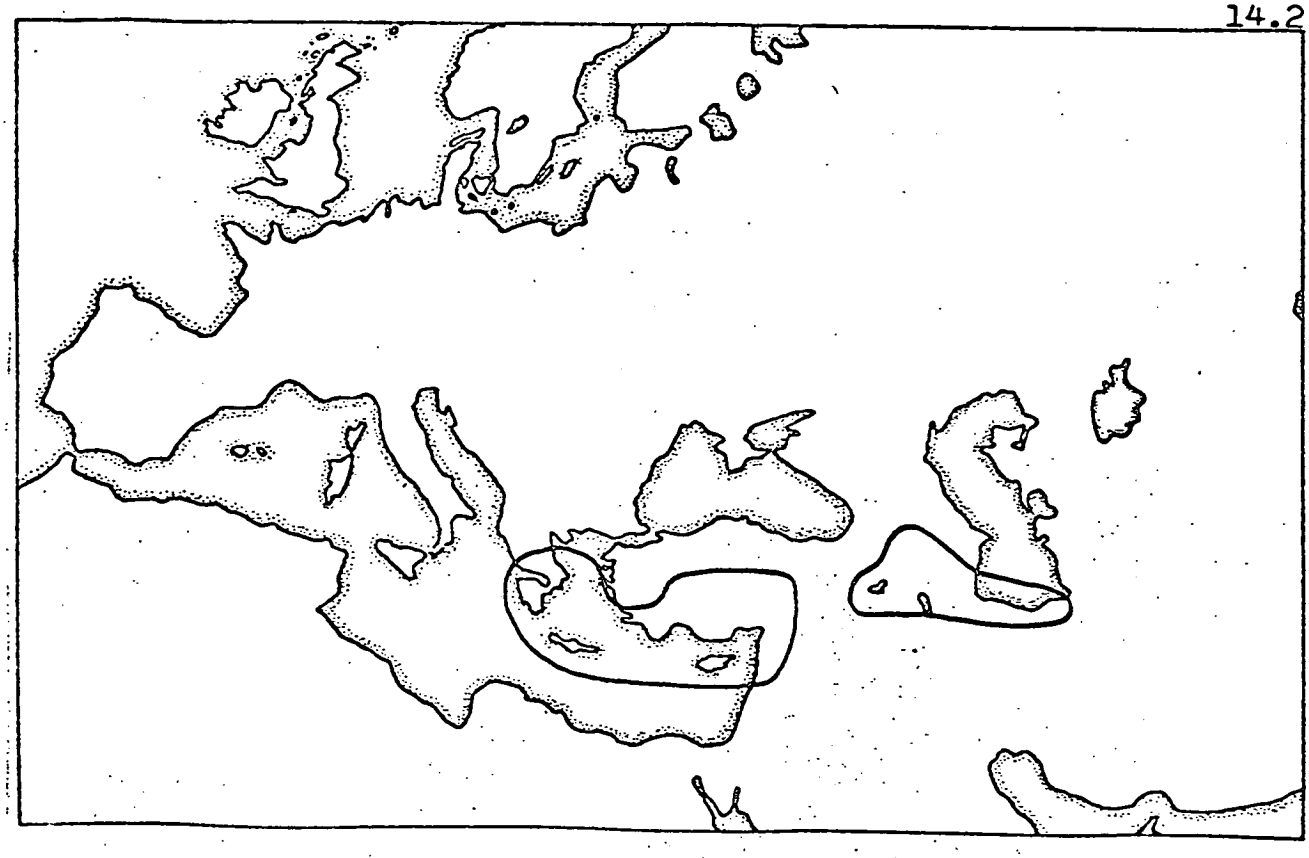


Fig. 67. Vicia Sect. Cappadocicae.

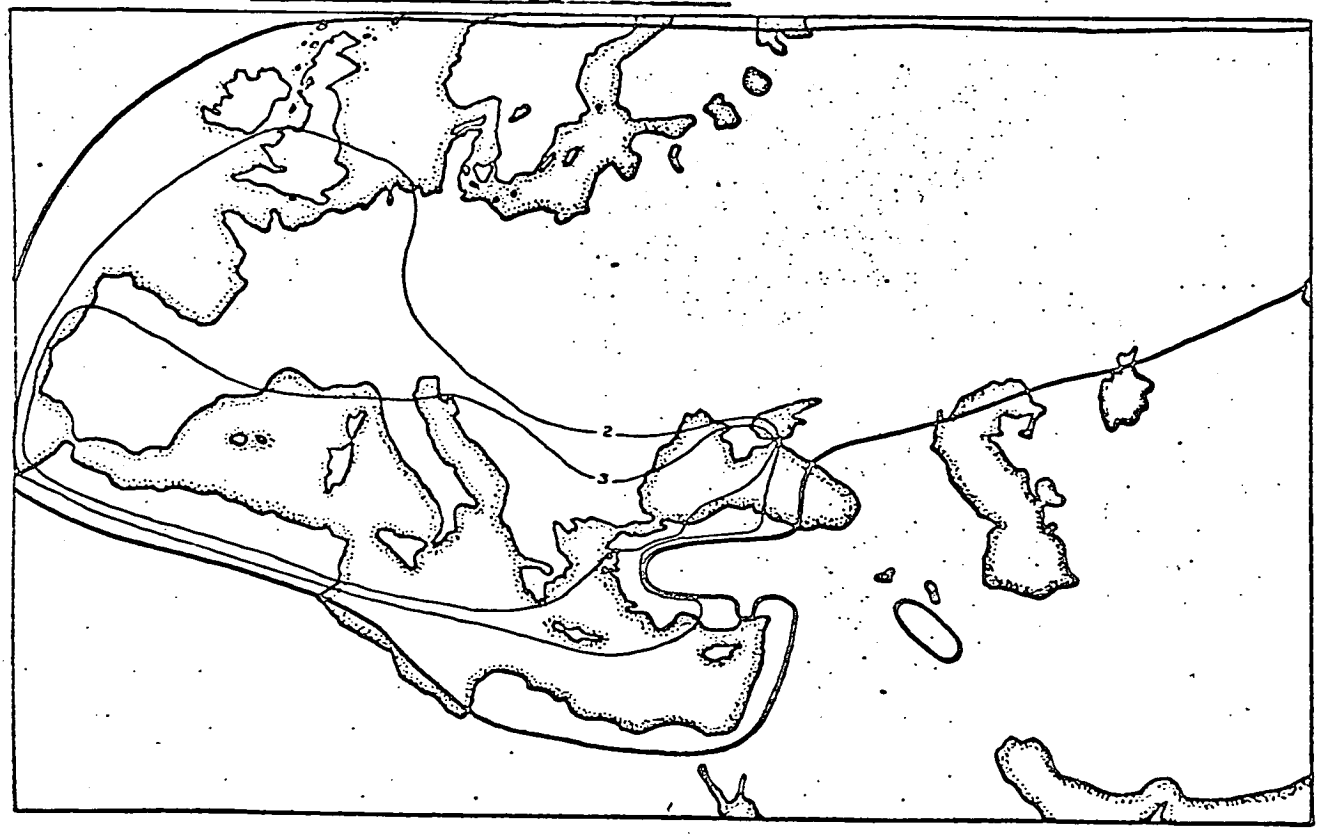


Fig. 68. Vicia Sect. Ervum.

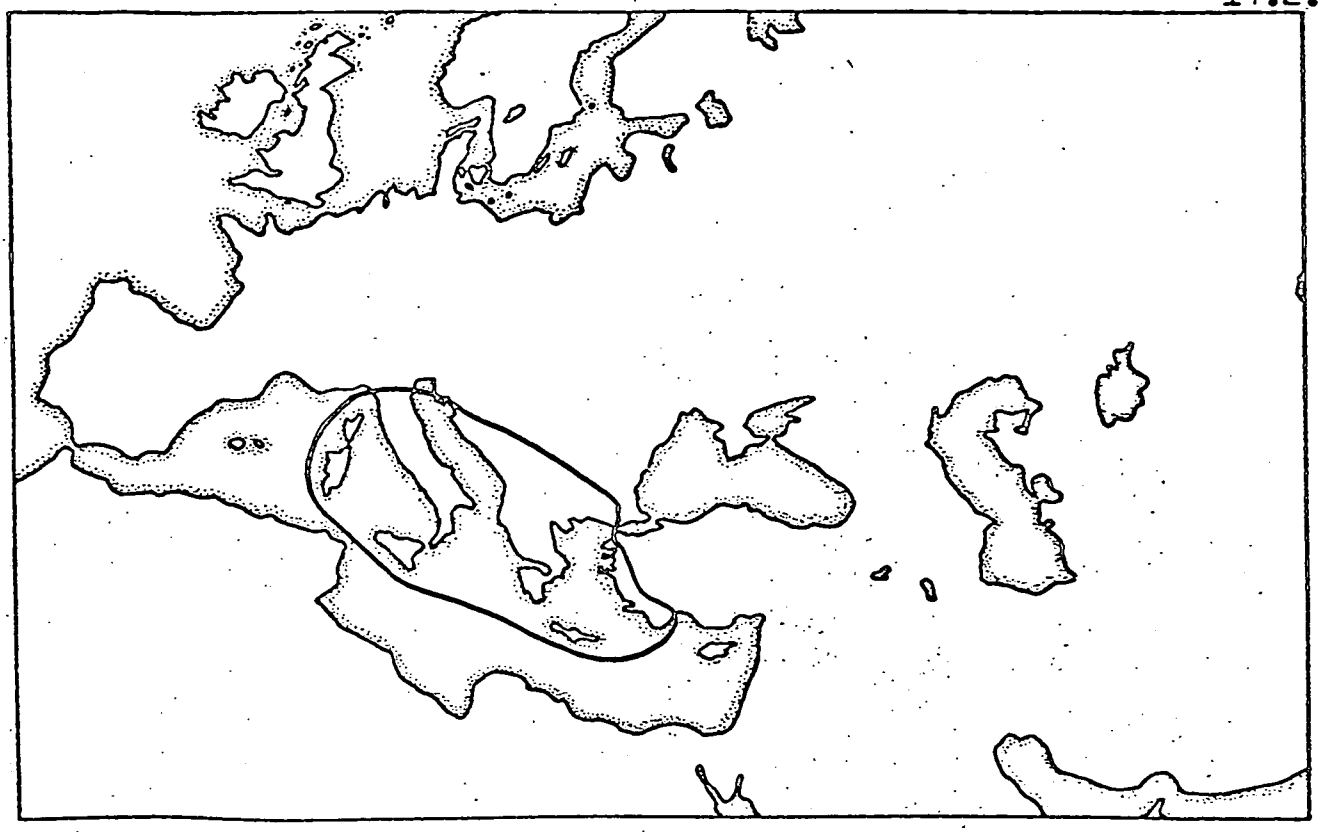


Fig. 69. Vicia Sect. Ervoides.

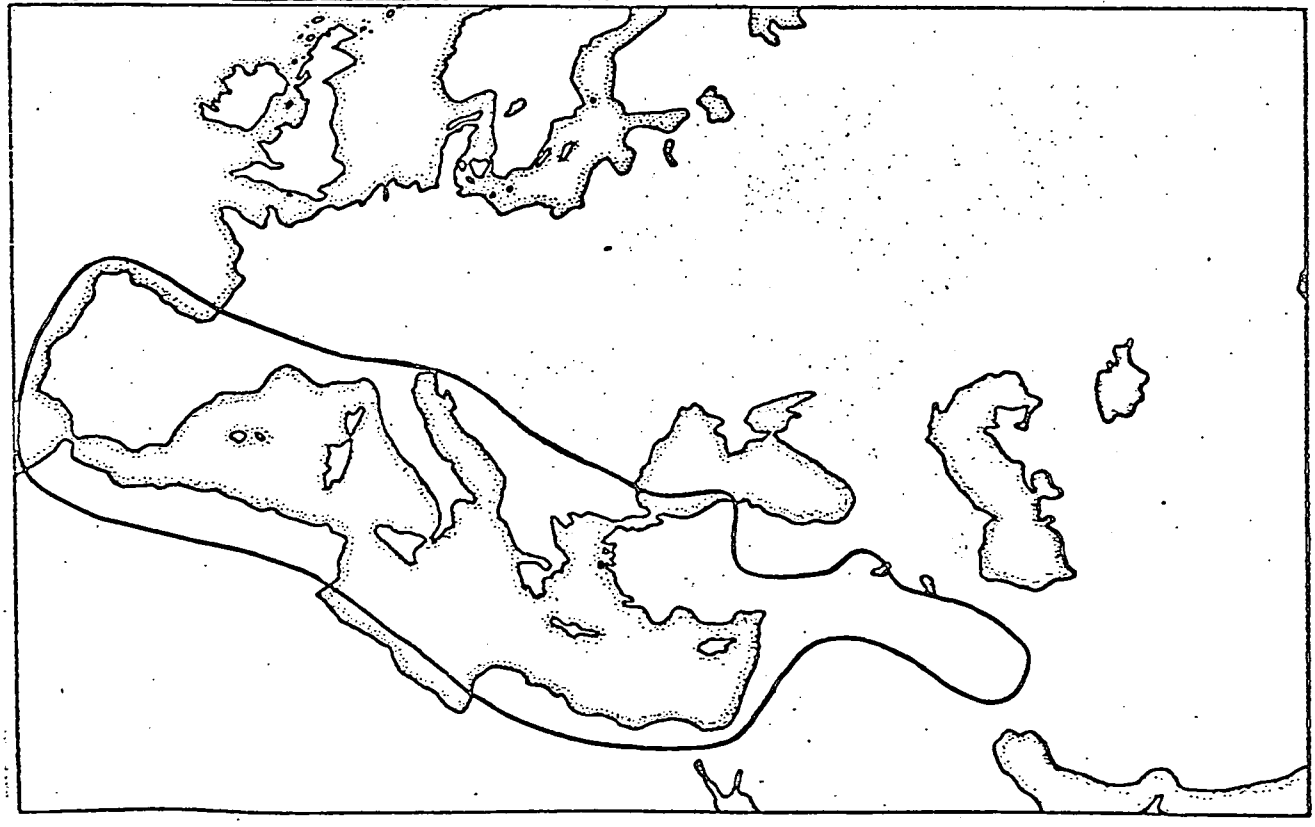


Fig. 70. Vicia Sect. Ervilia.

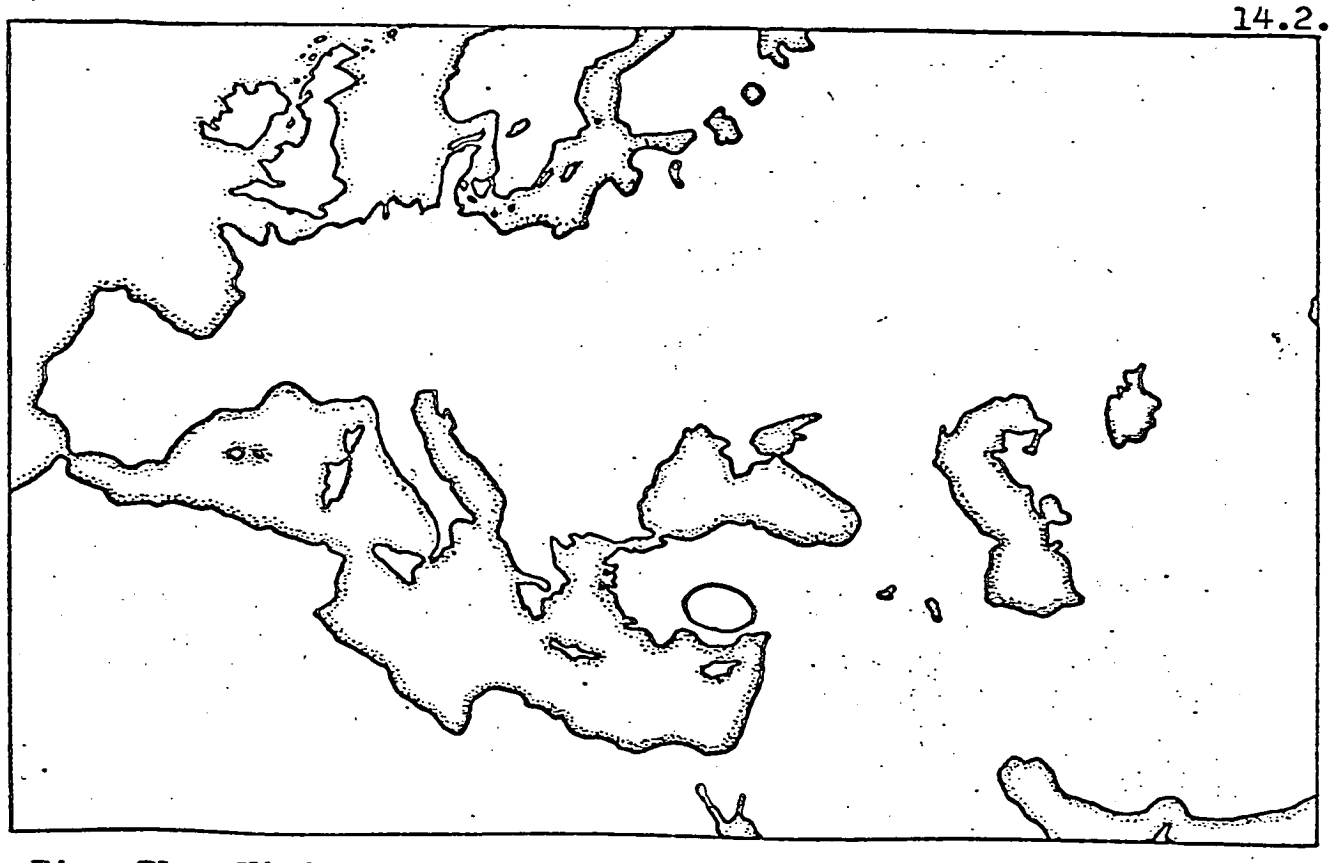


Fig. 71. Vicia Sect. Caesareae.

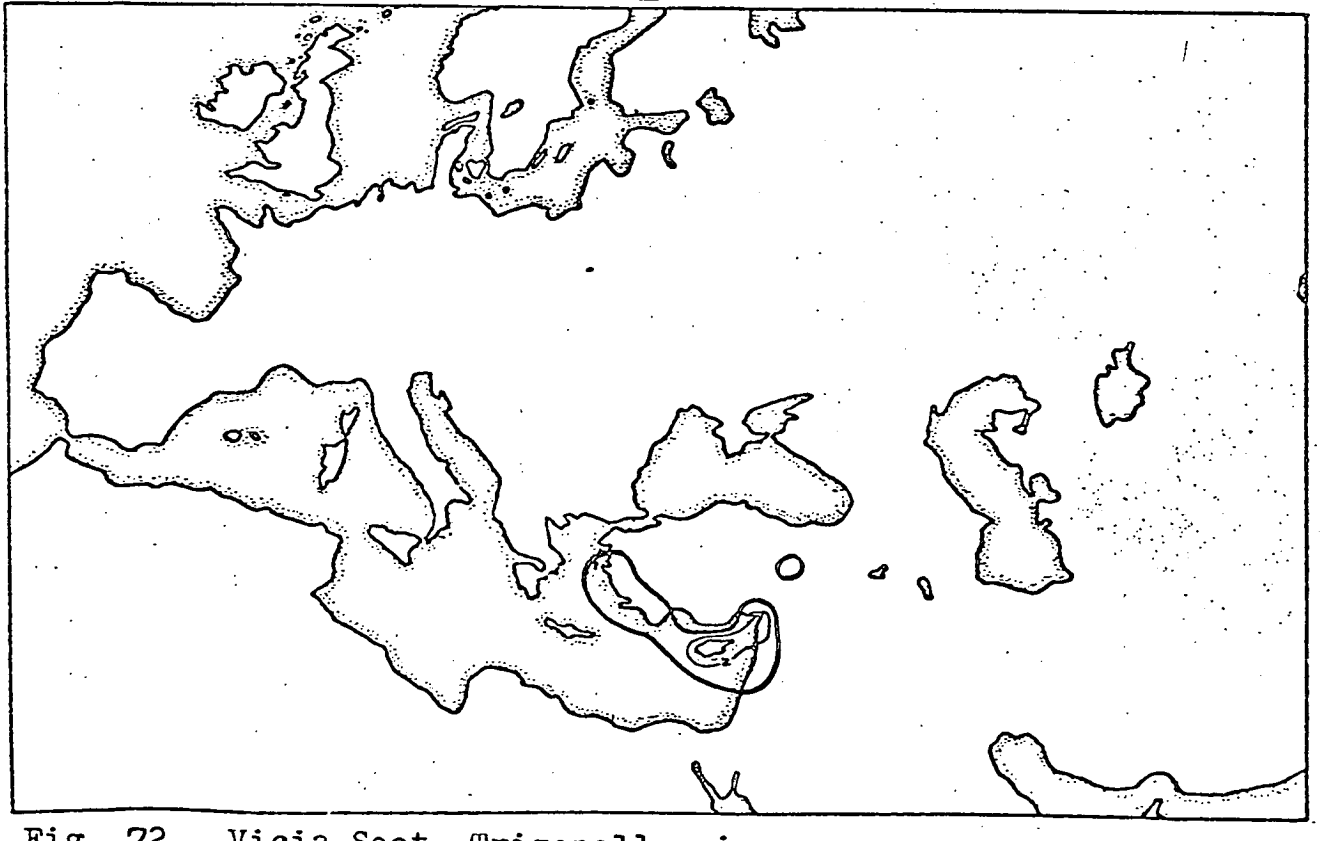


Fig. 72. Vicia Sect. Trigonellopsis.



Fig. 73. Vicia Sects. Leucophaeae(- - -) and Australes (———).

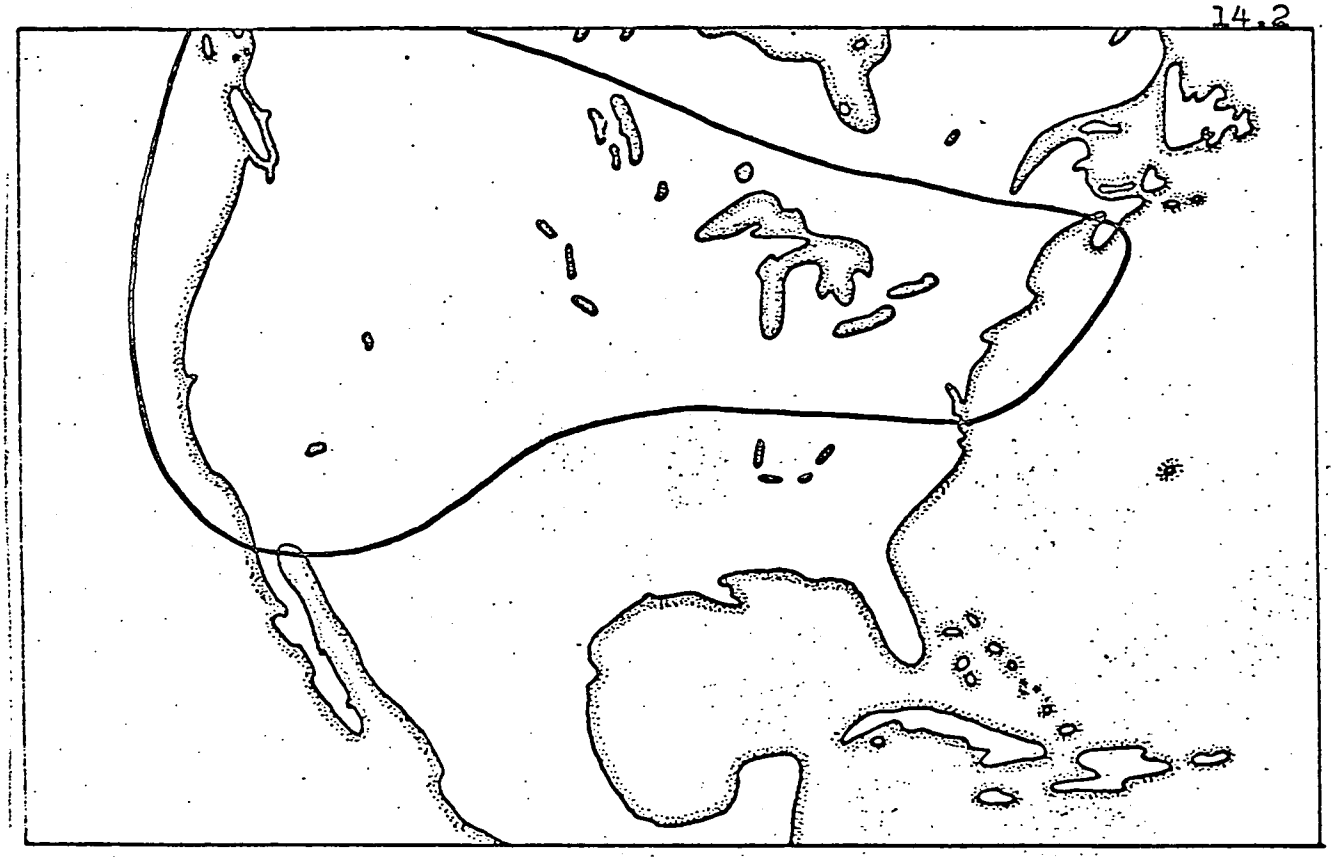


Fig. 74. Vicia Sect. Americanae.

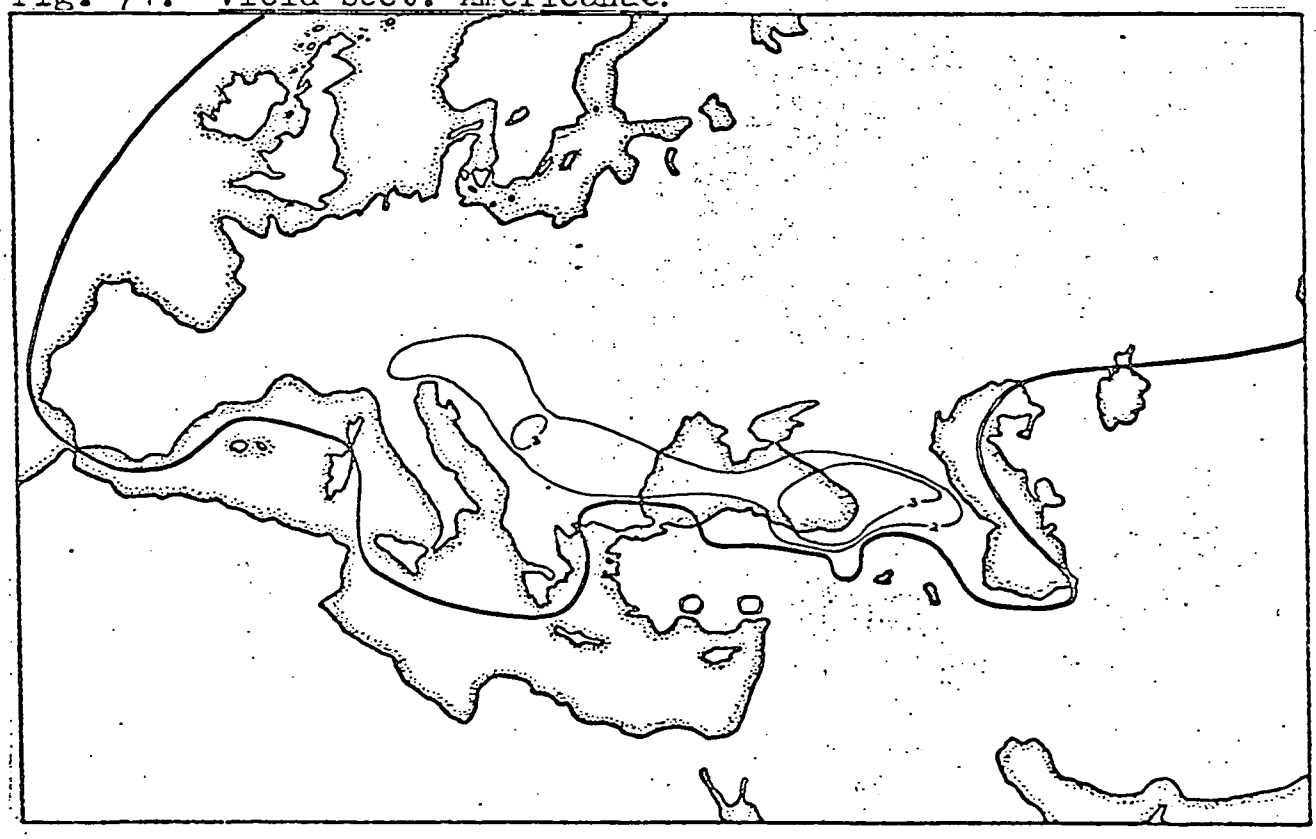


Fig. 75. Vicia Sect. Atossa.

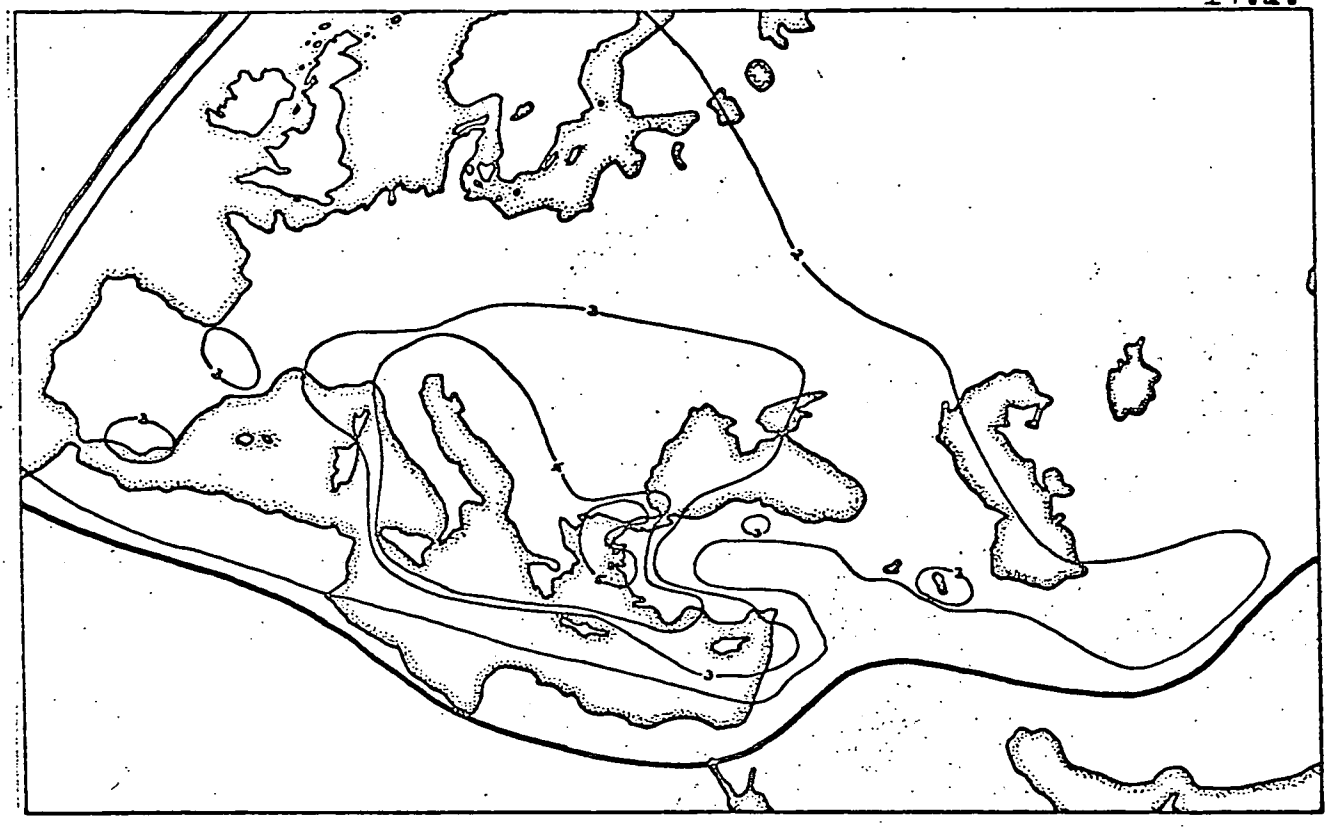


Fig. 76. Vicia Sect. Vicia.

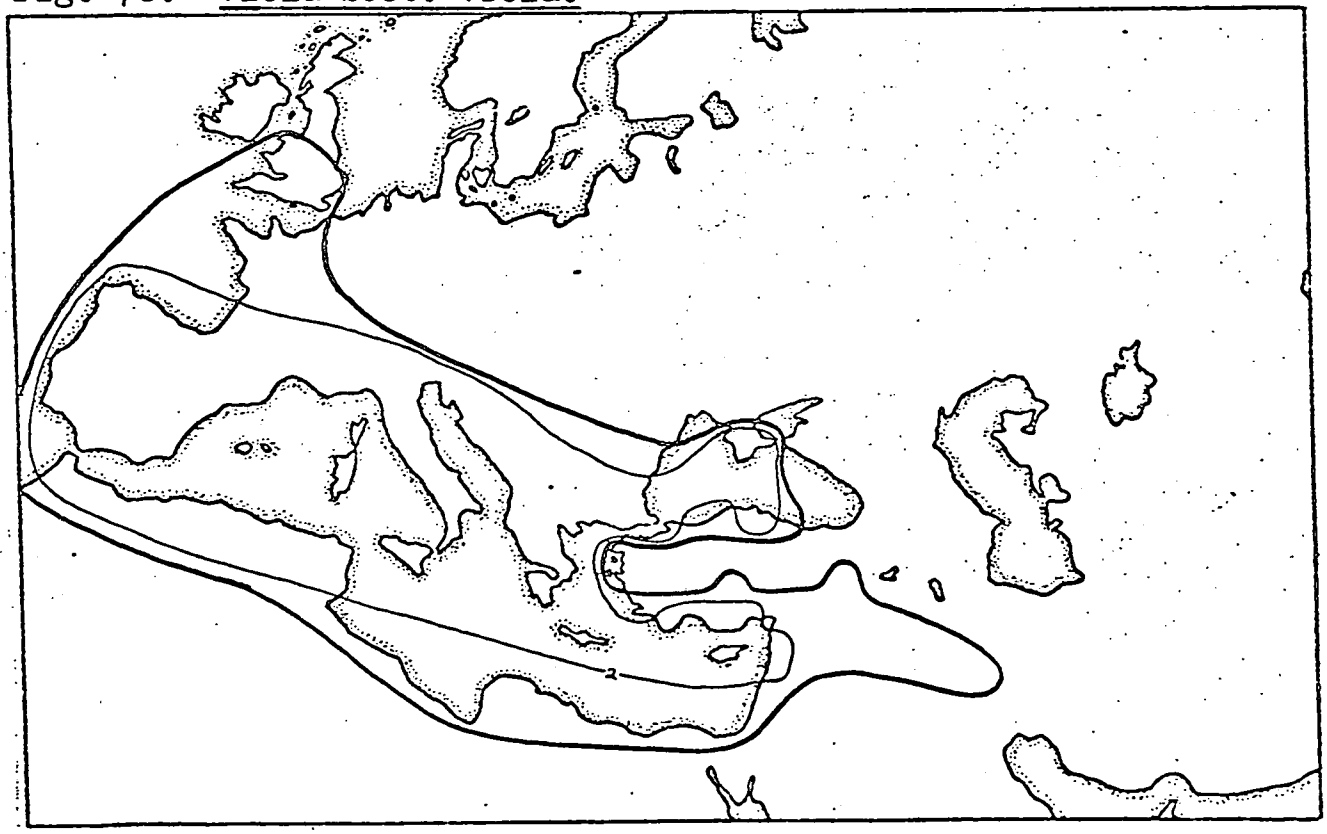


Fig. 77. Vicia Sect. Faba.

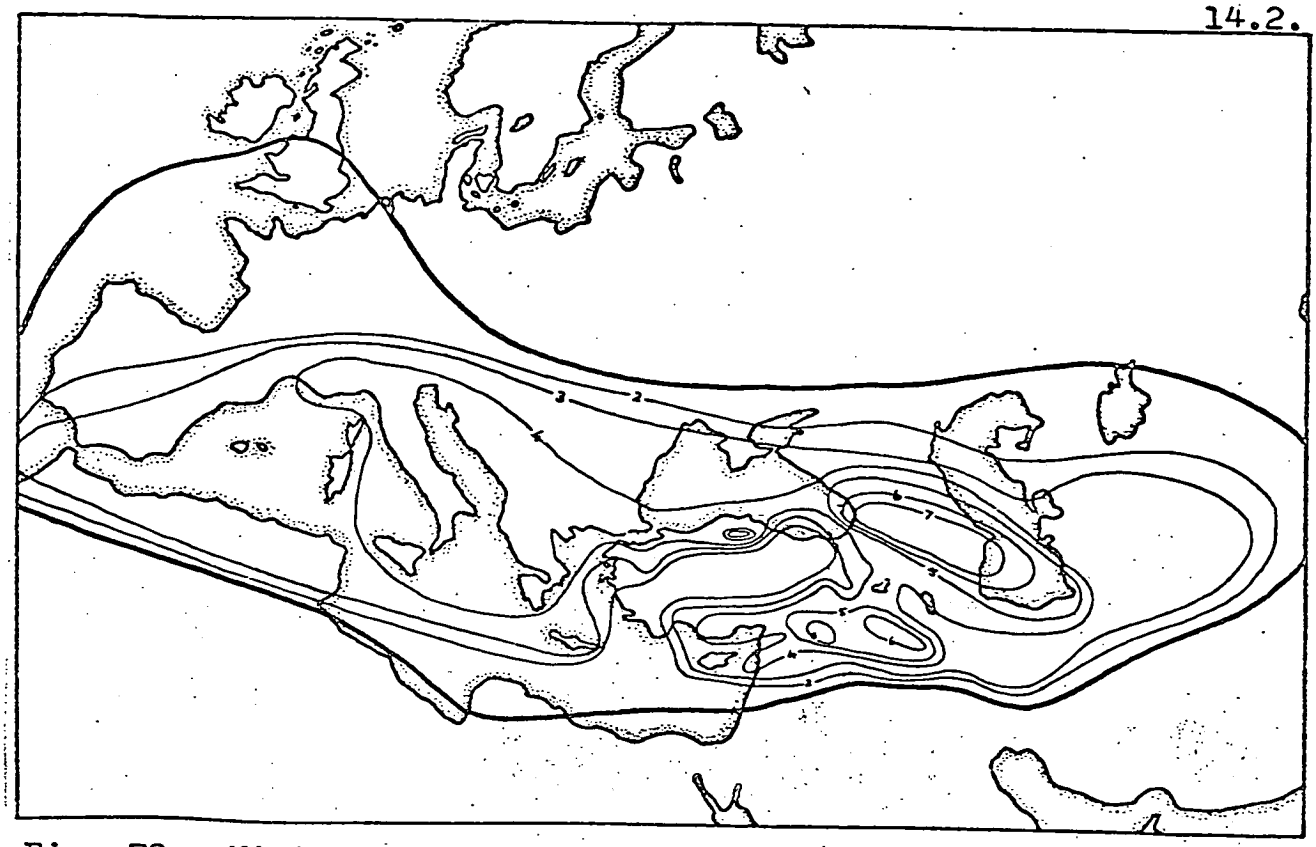


Fig. 78. Vicia Sect. Hypechusa.

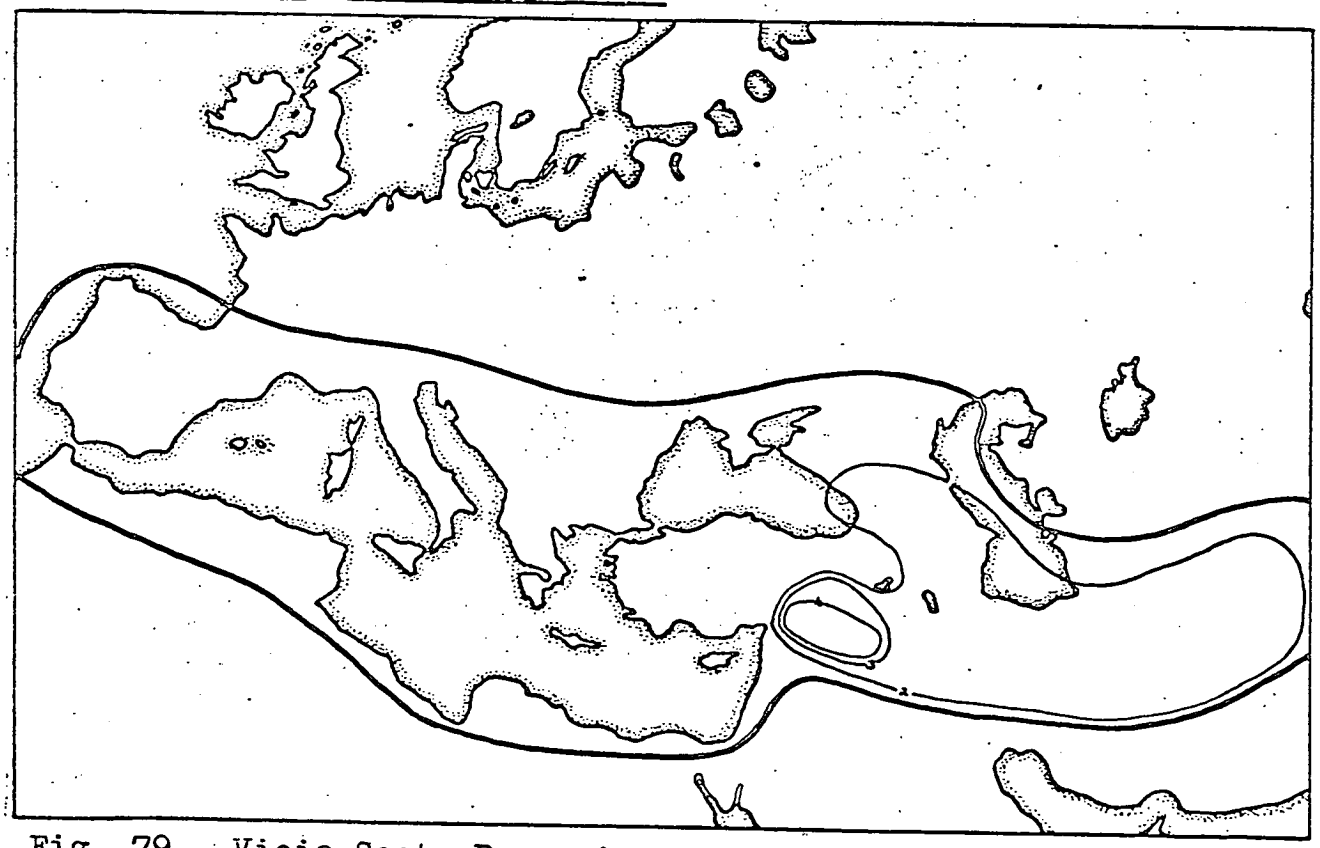


Fig. 79. Vicia Sect. Peregrinae.

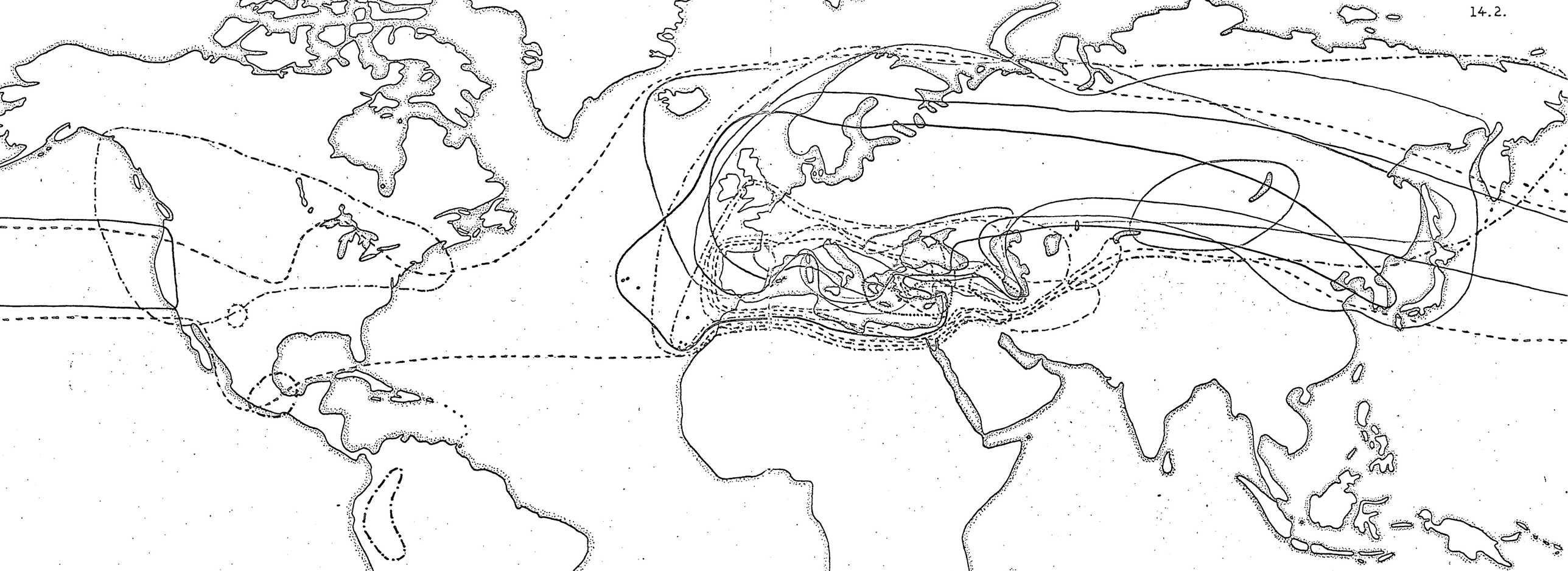


Fig. 80. Map showing distribution of sections of Vicia.

KEY:- sections

Vicilla
Cassubicae
Cracca
Variegatae
Pedunculatae
Americanae
Subvillosae
Biennes
Cappadocicae
Ervum
Ervoides
Ervilia
Caesareae
Trigonellopsis
Australes
Leucophaeae
Atossa
Vicia
Faba
Hypechusa
Peregrinae

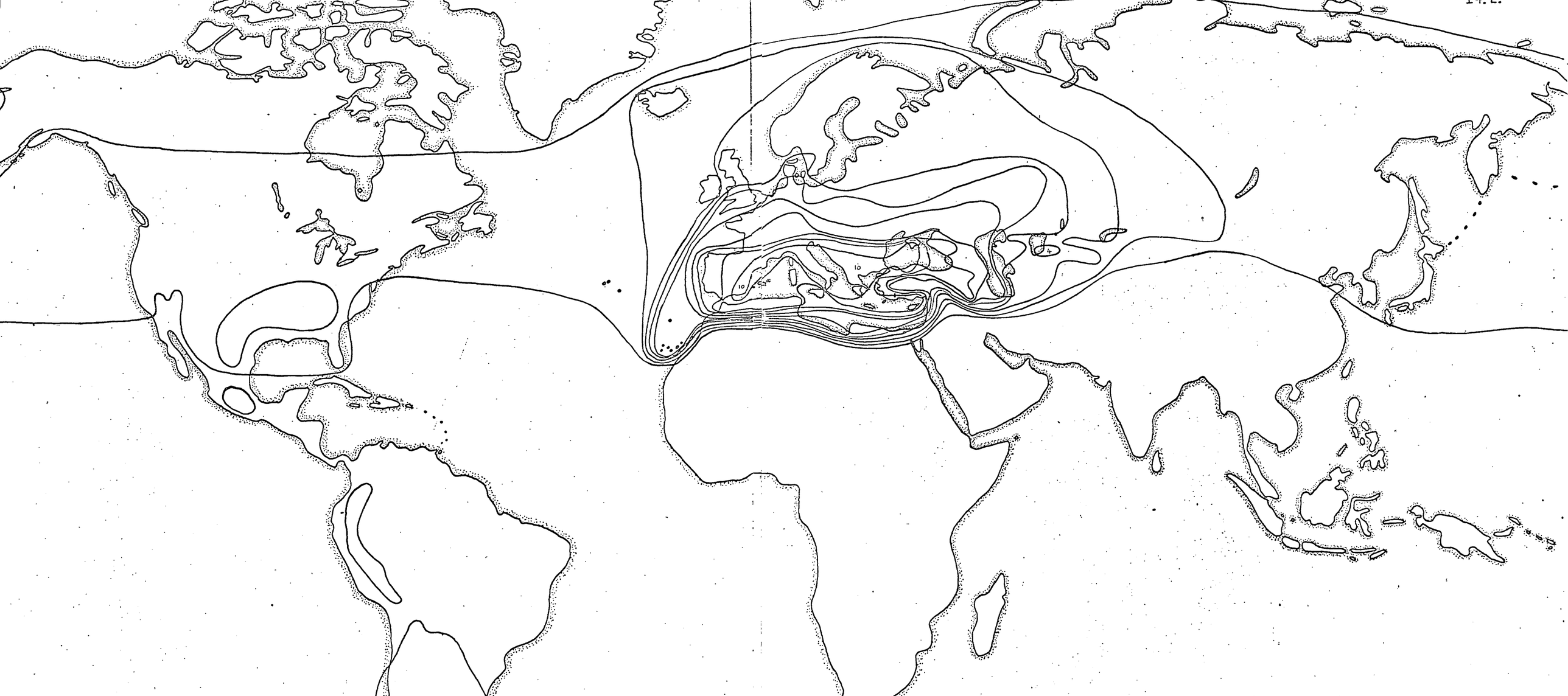


Fig. 81. Iso-section map of Lathyrus.

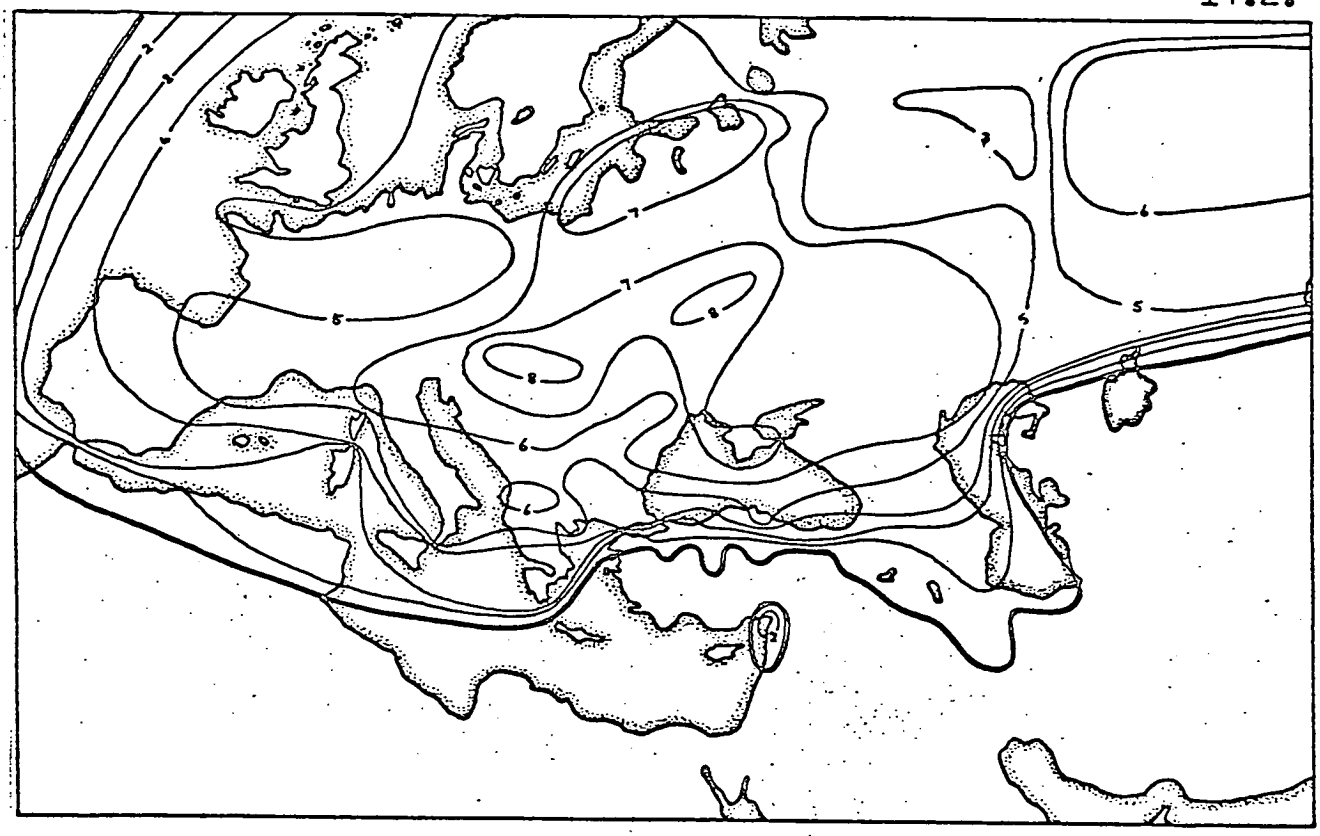


Fig. 82. Lathyrus Sect. Crobus in Europe, N.W. Africa and S.W.Asia.

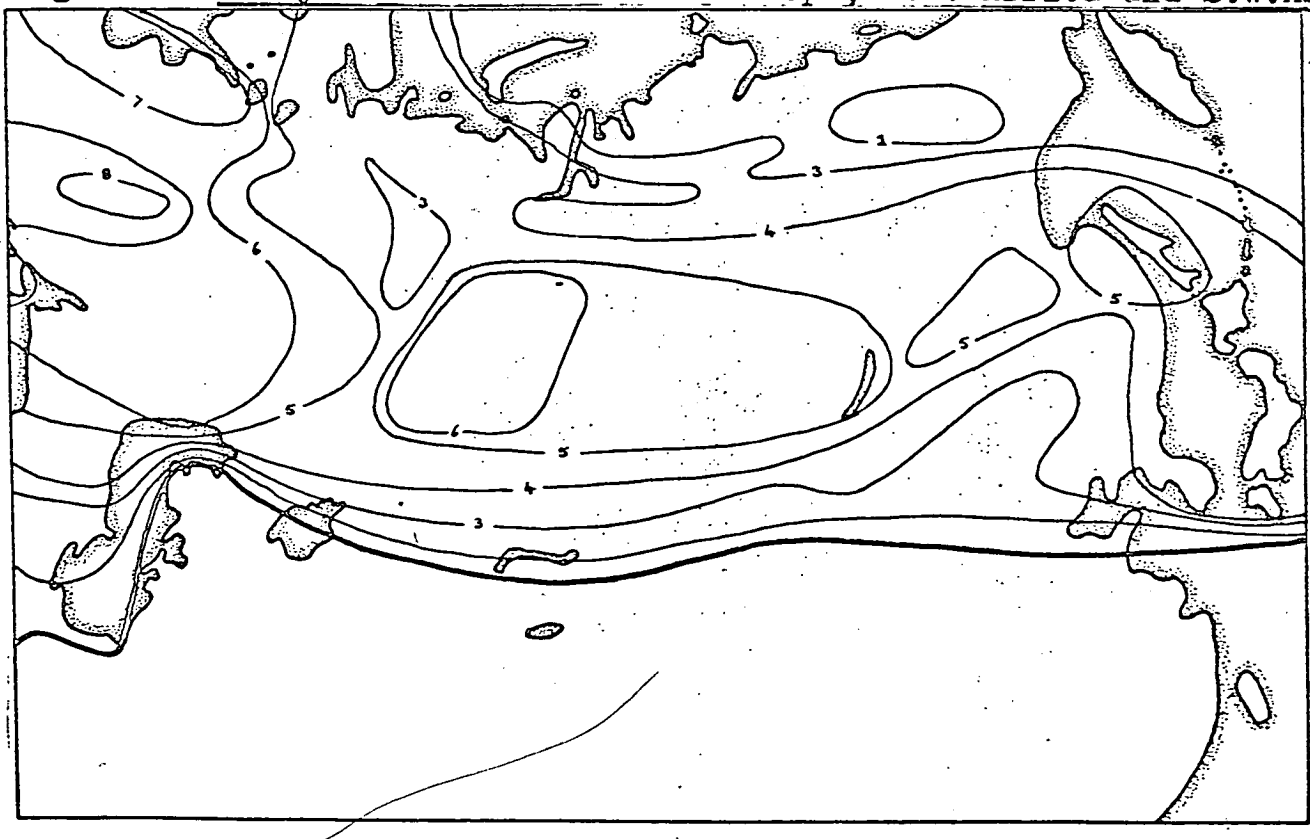


Fig. 83. Lathyrus Sect. Crobus in E. Asia.

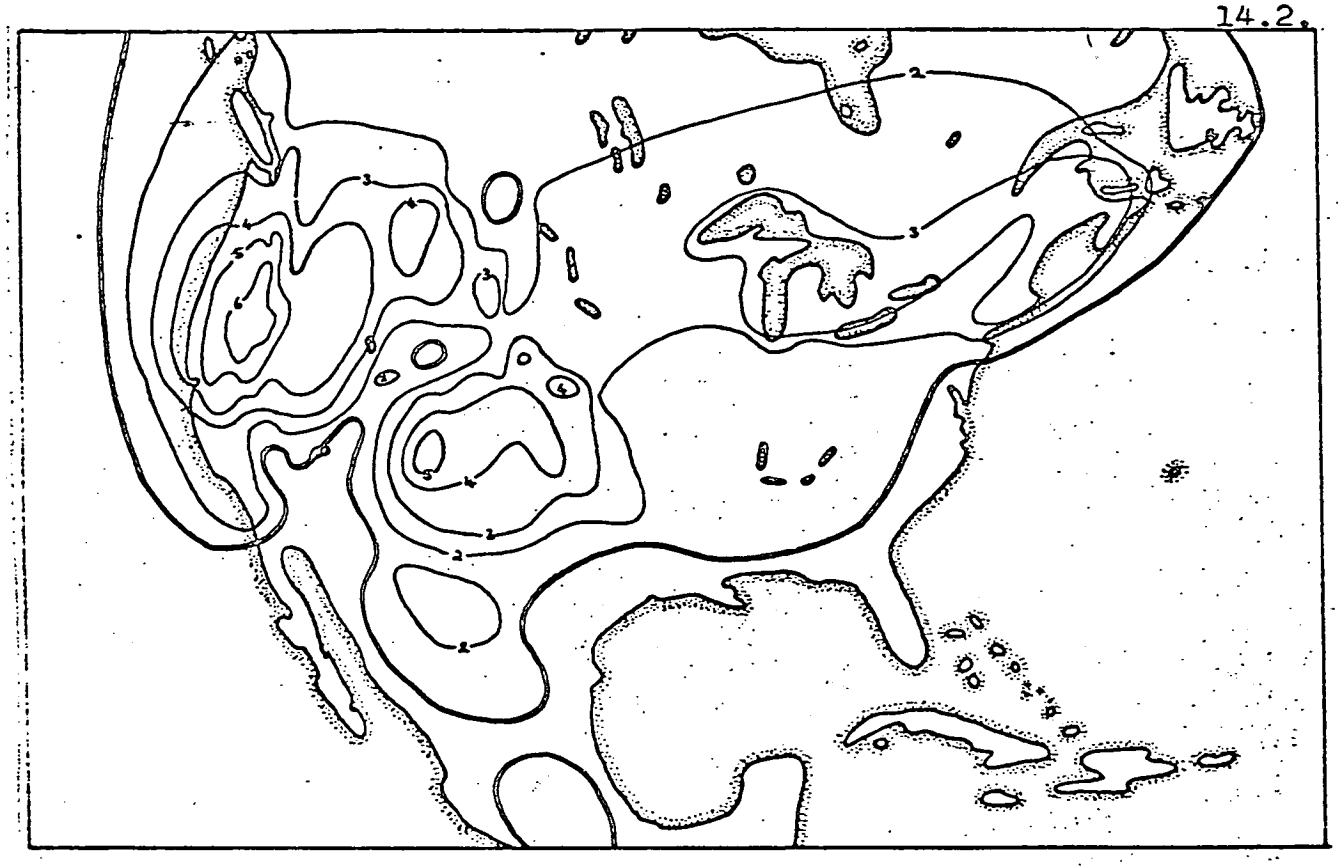


Fig. 84. Lathyrus Sect. Orobus in N. America.

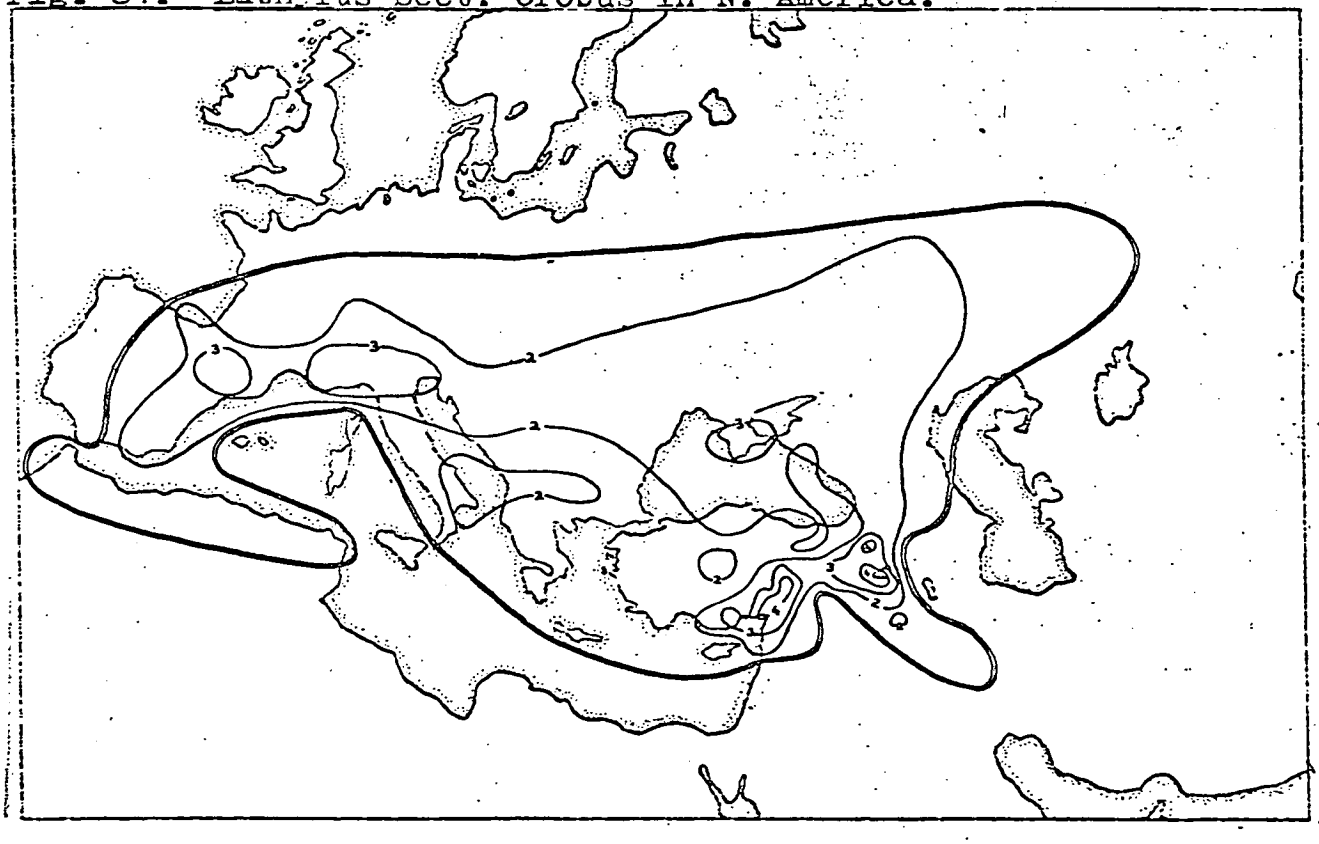


Fig. 85. Lathyrus Sect. Lathyrostylis.

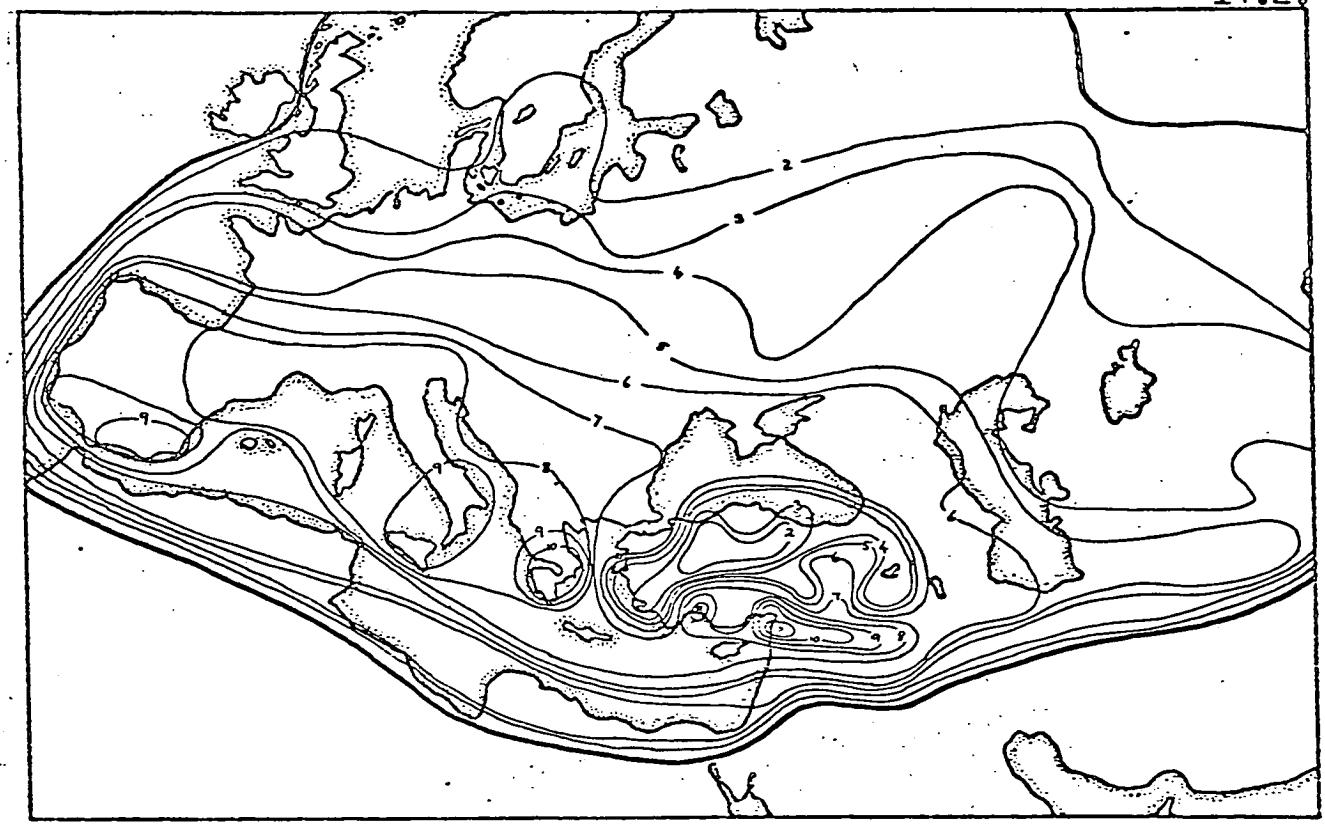


Fig. 86. Lathyrus Sect. Lathyrus.

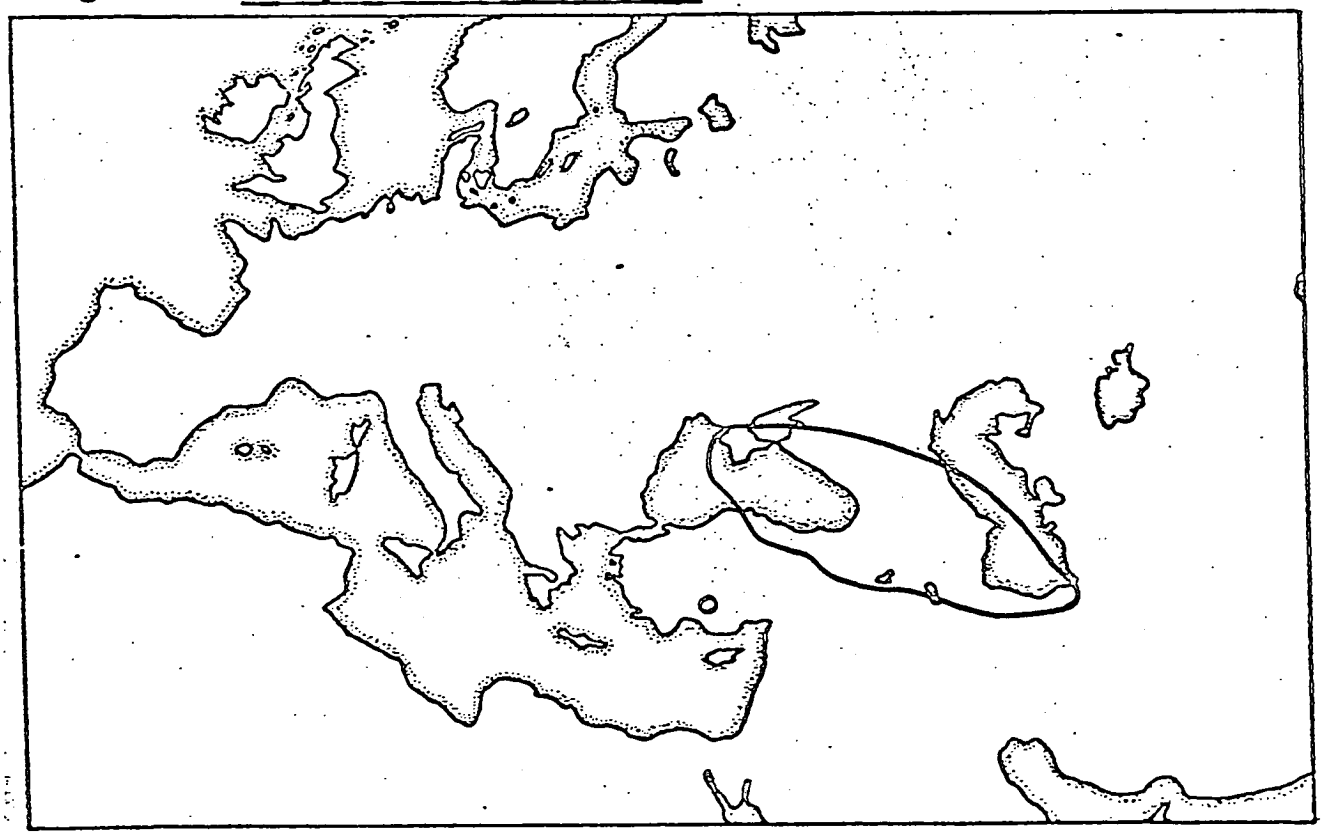


Fig. 87. Lathyrus Sect. Crobon.

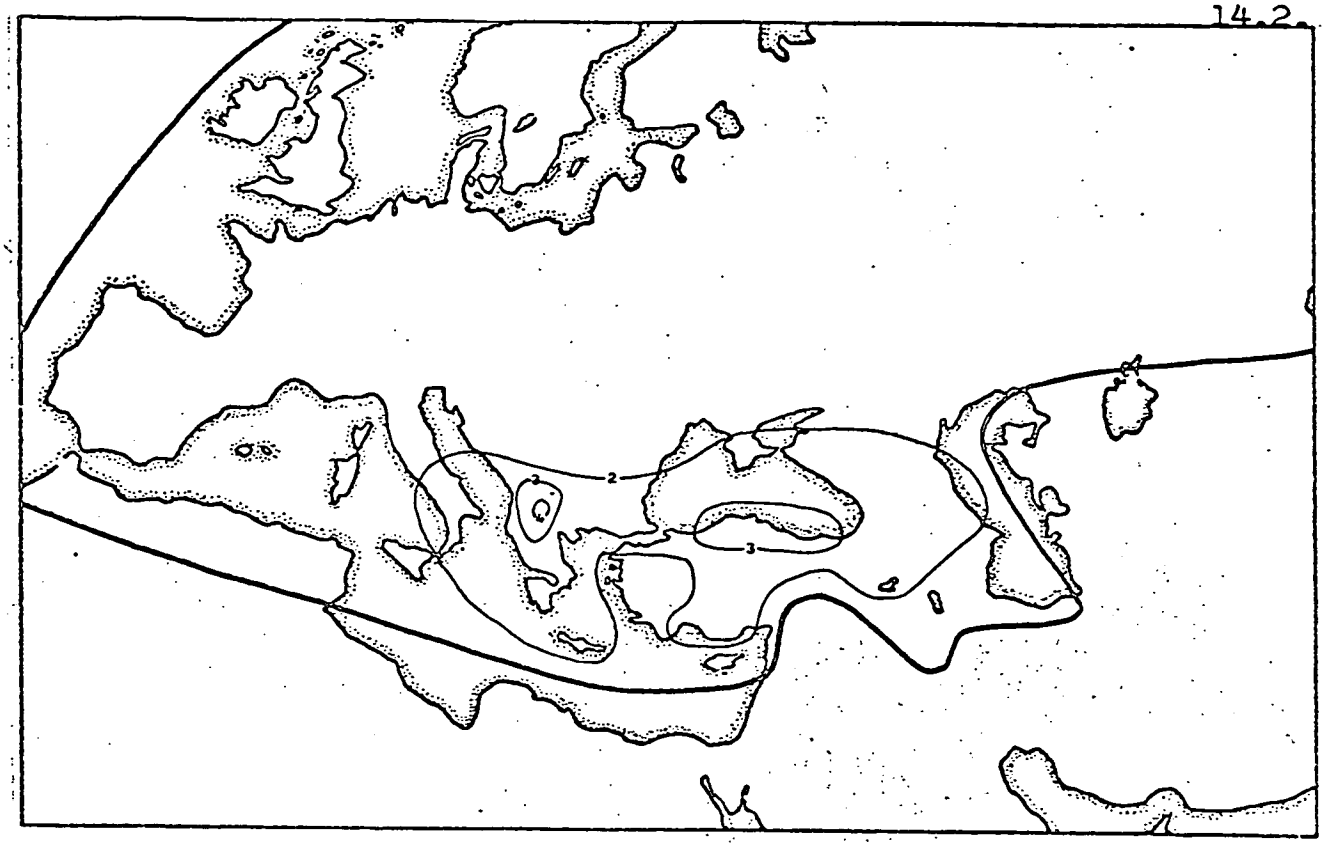


Fig. 88. Lathyrus Sect. Pratensis.

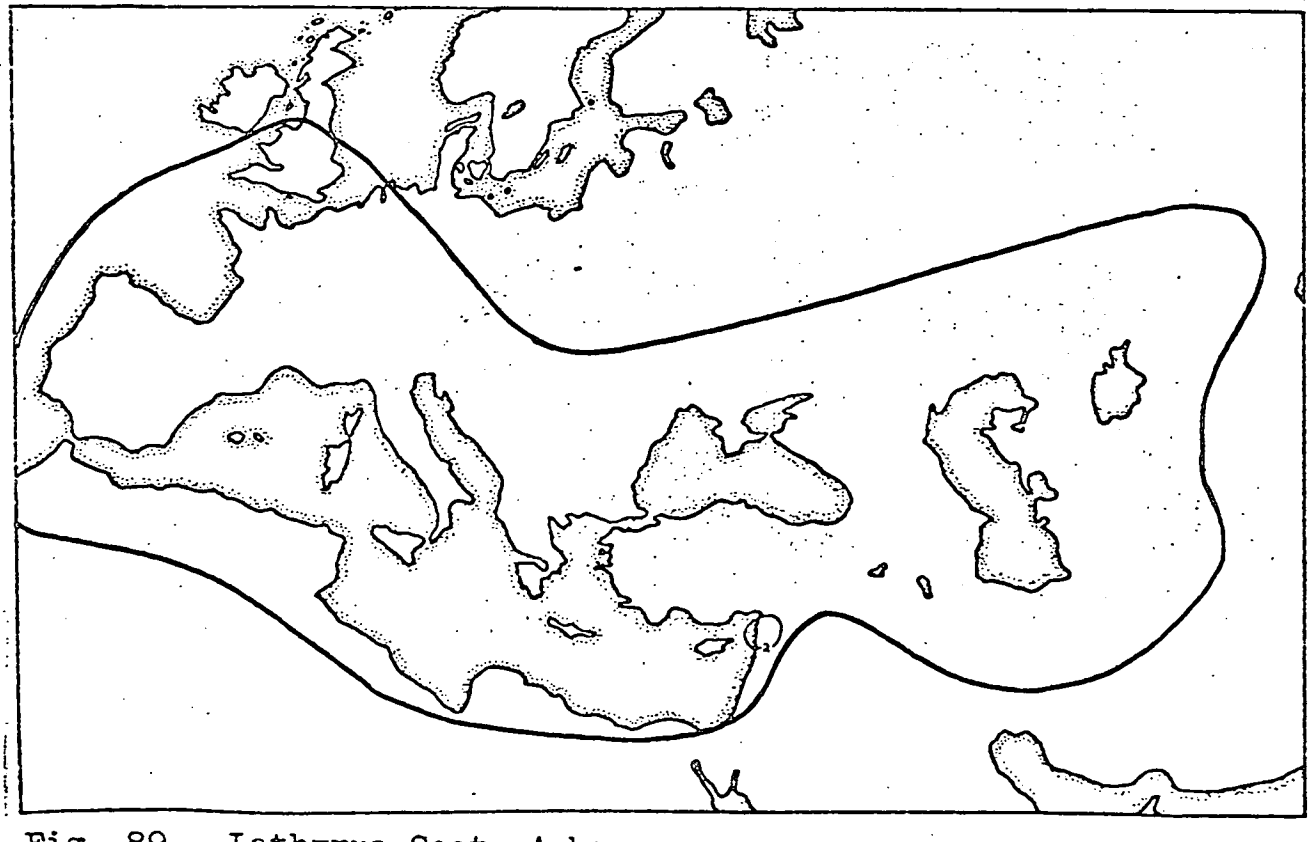


Fig. 89. Lathyrus Sect. Aphaca.

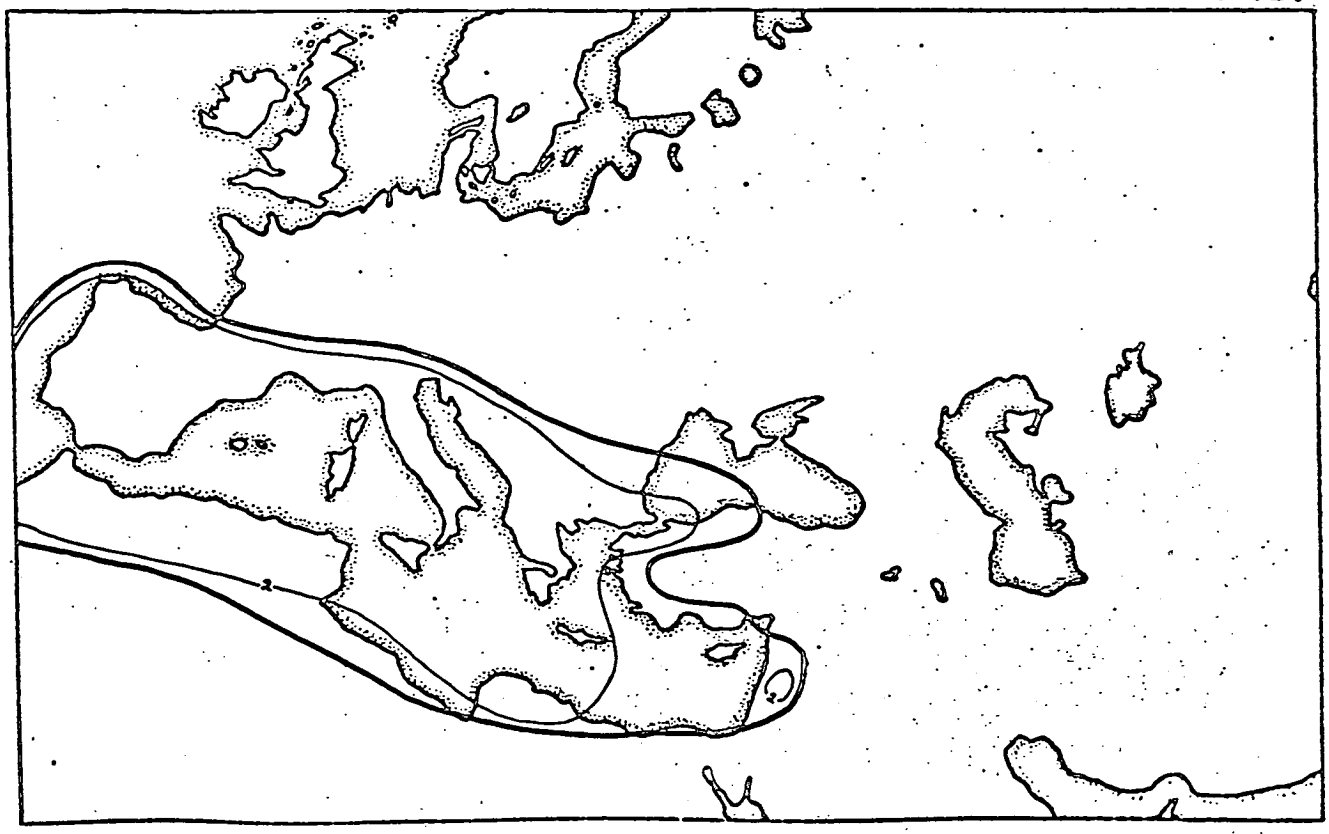


Fig. 90. Lathyrus Sect. Clymenum.

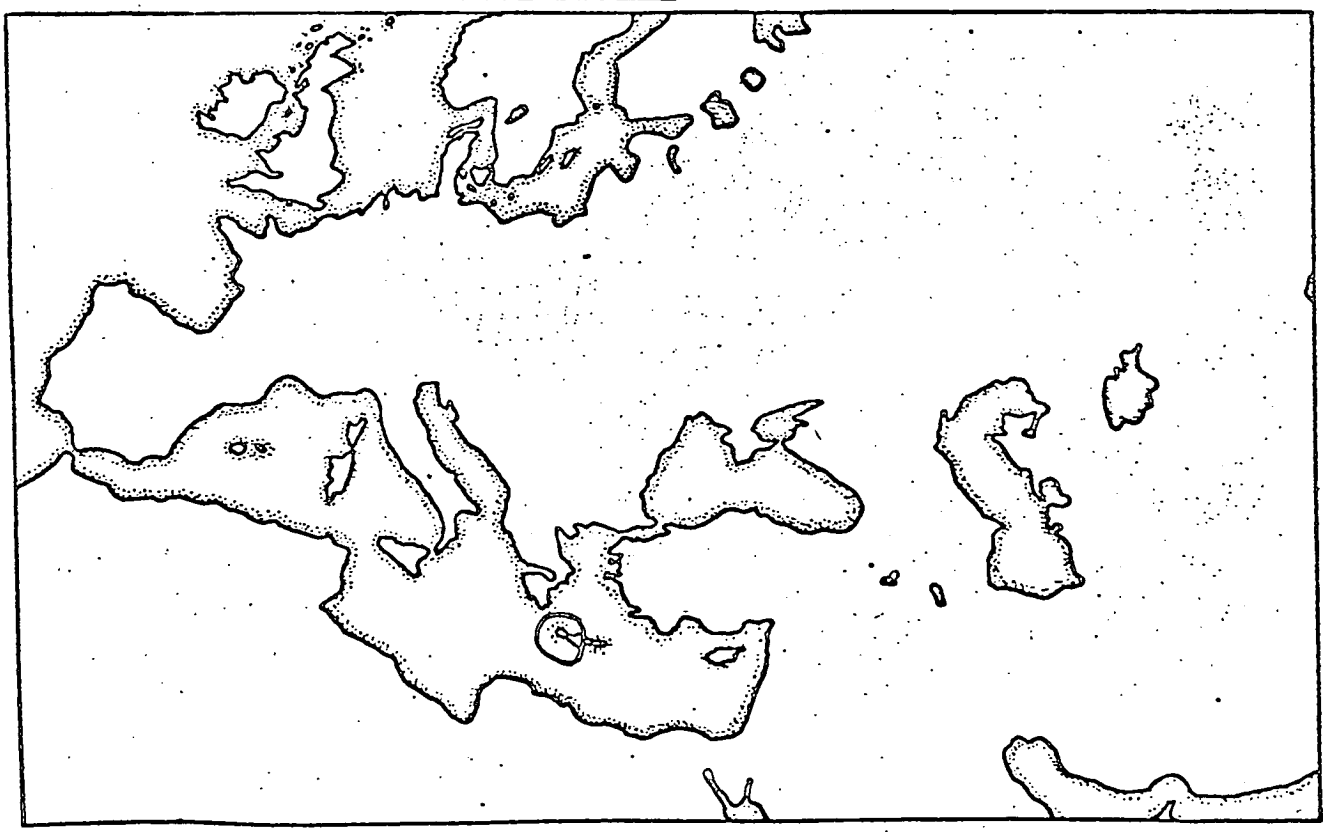


Fig. 91. Lathyrus Sect. Neurolobus.

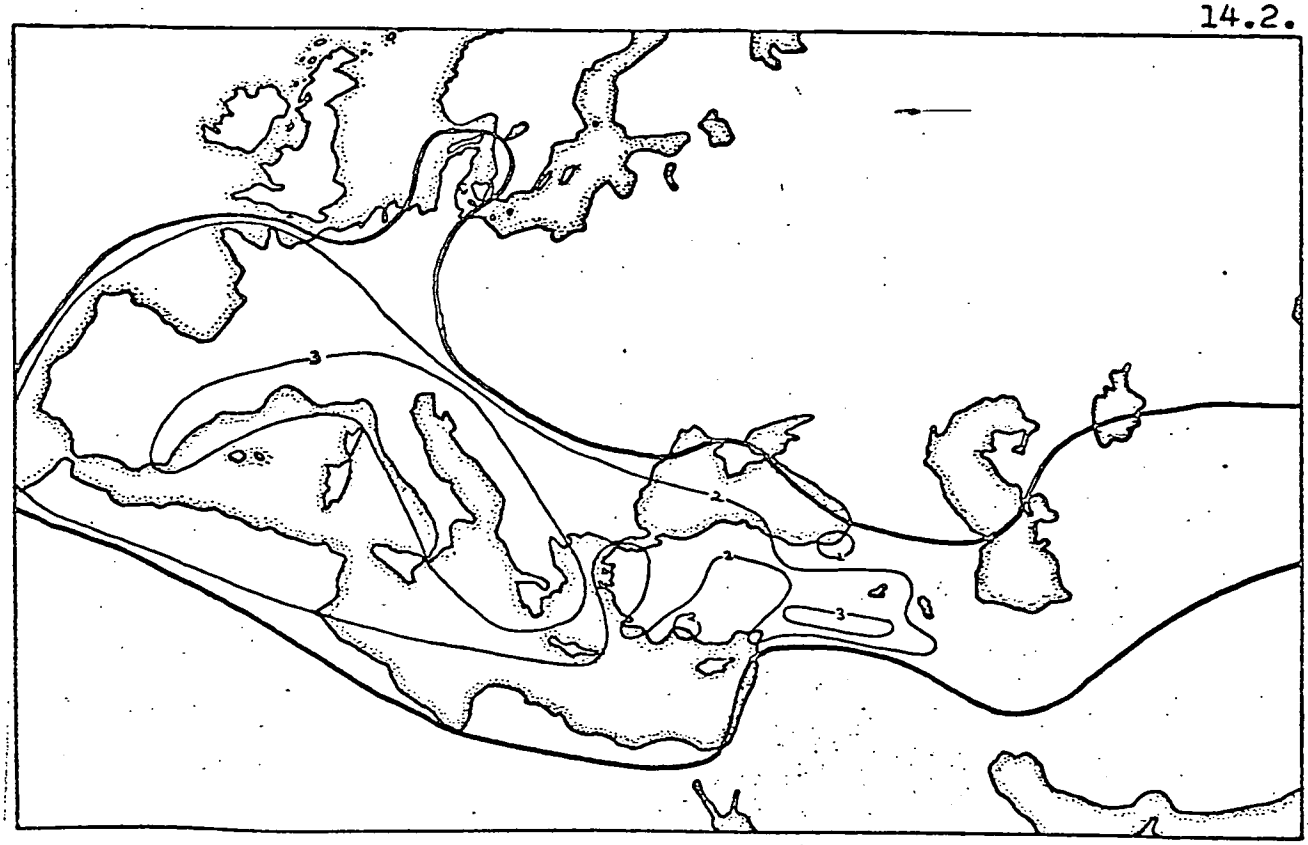


Fig. 92. Lathyrus Sect. Linearicarpus.

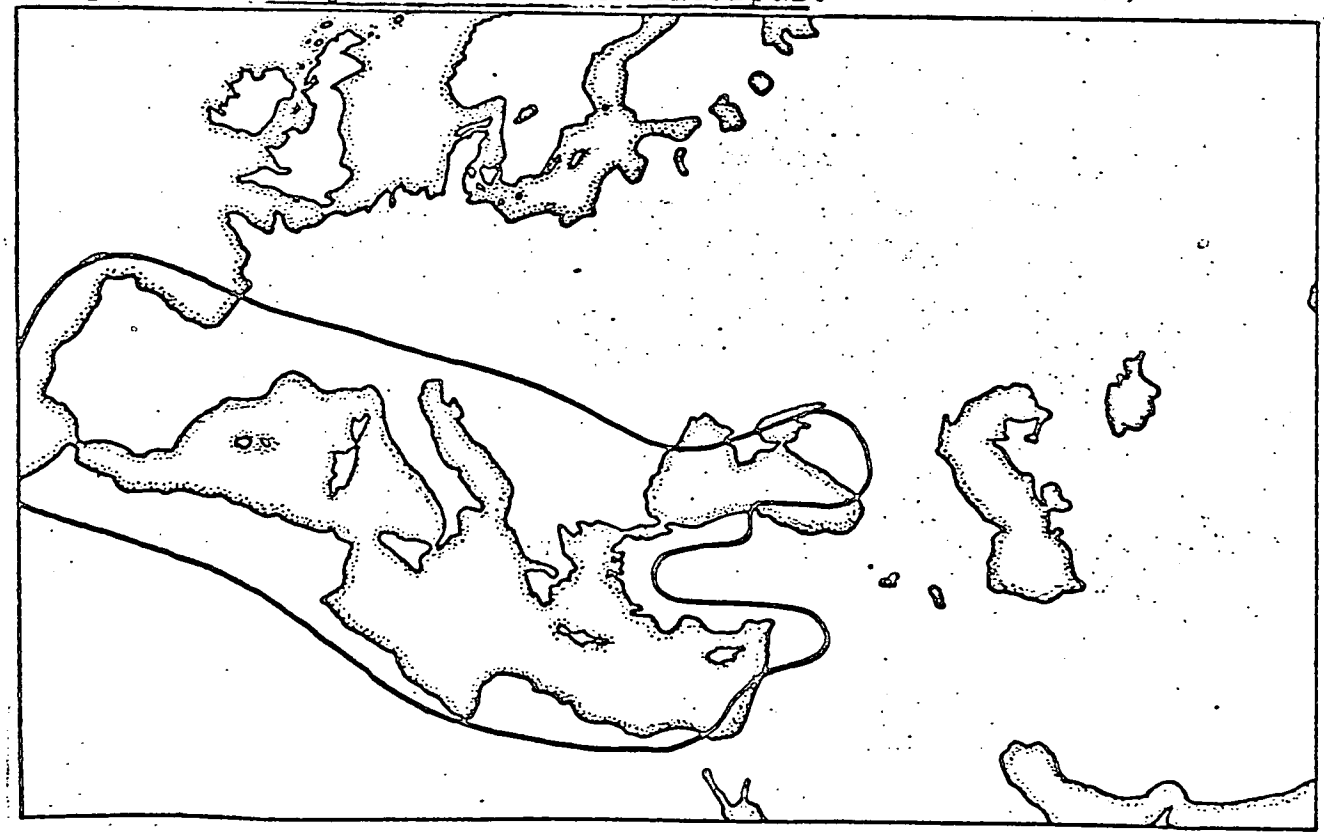


Fig. 93. Lathyrus Sect. Orobastrum.

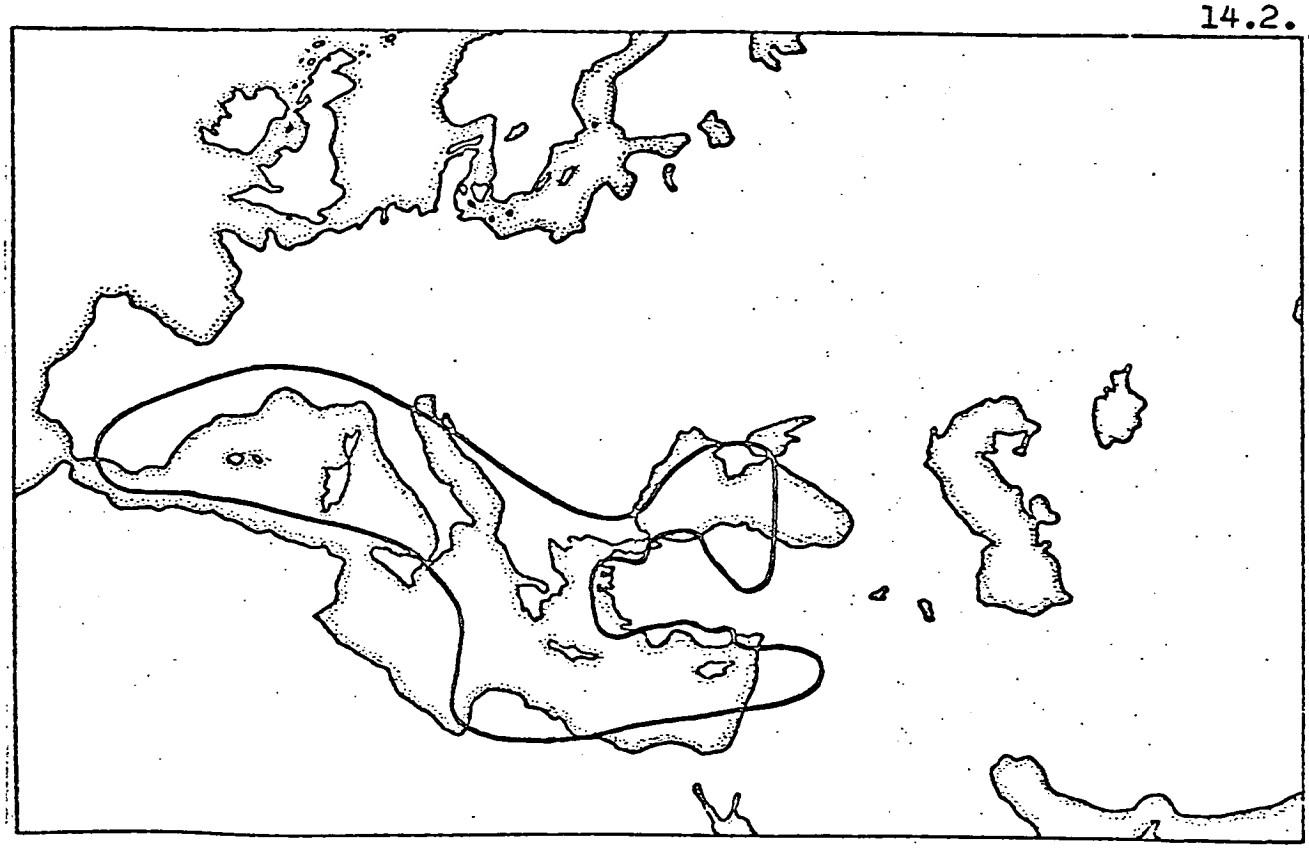


Fig. 94. Lathyrus Sect. Viciopsis.

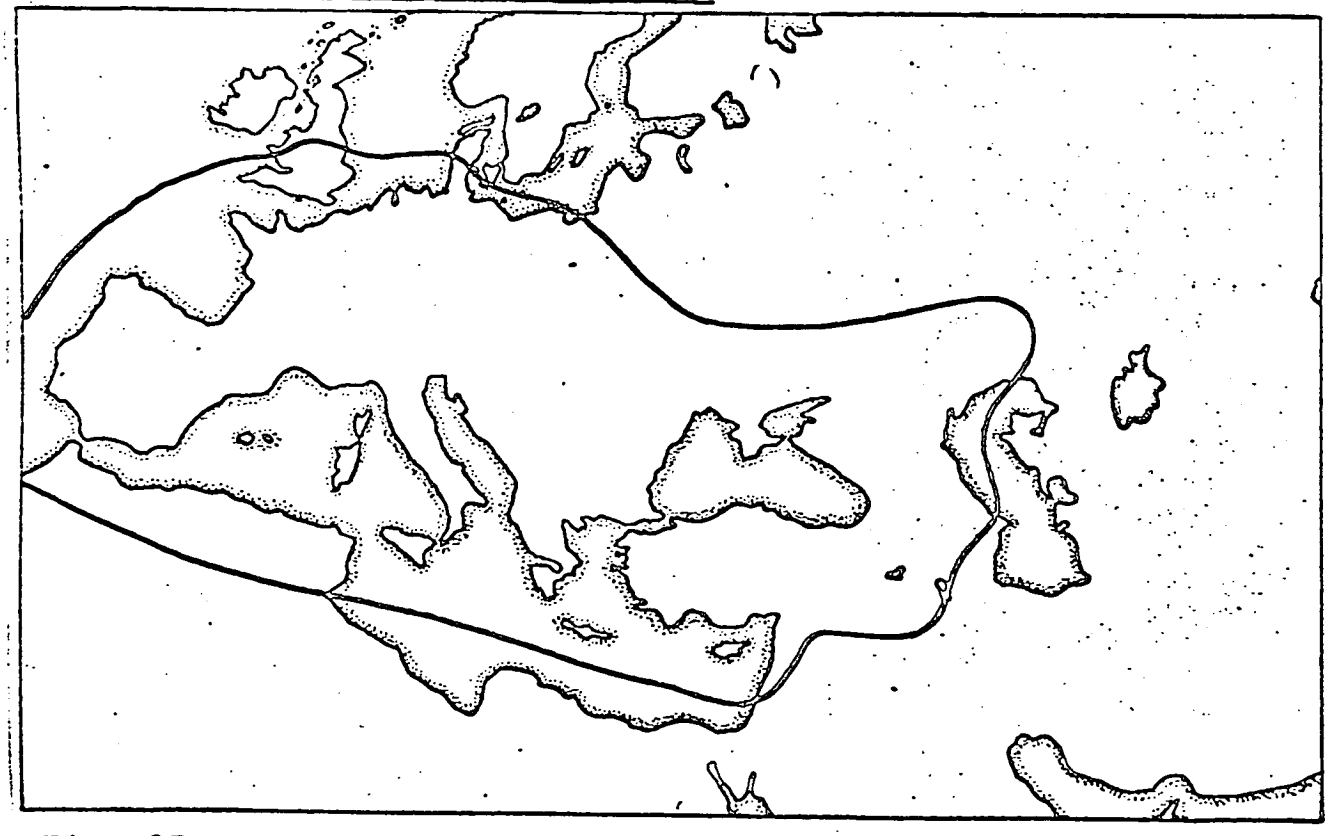


Fig. 95. Lathyrus Sect. Nissolia.

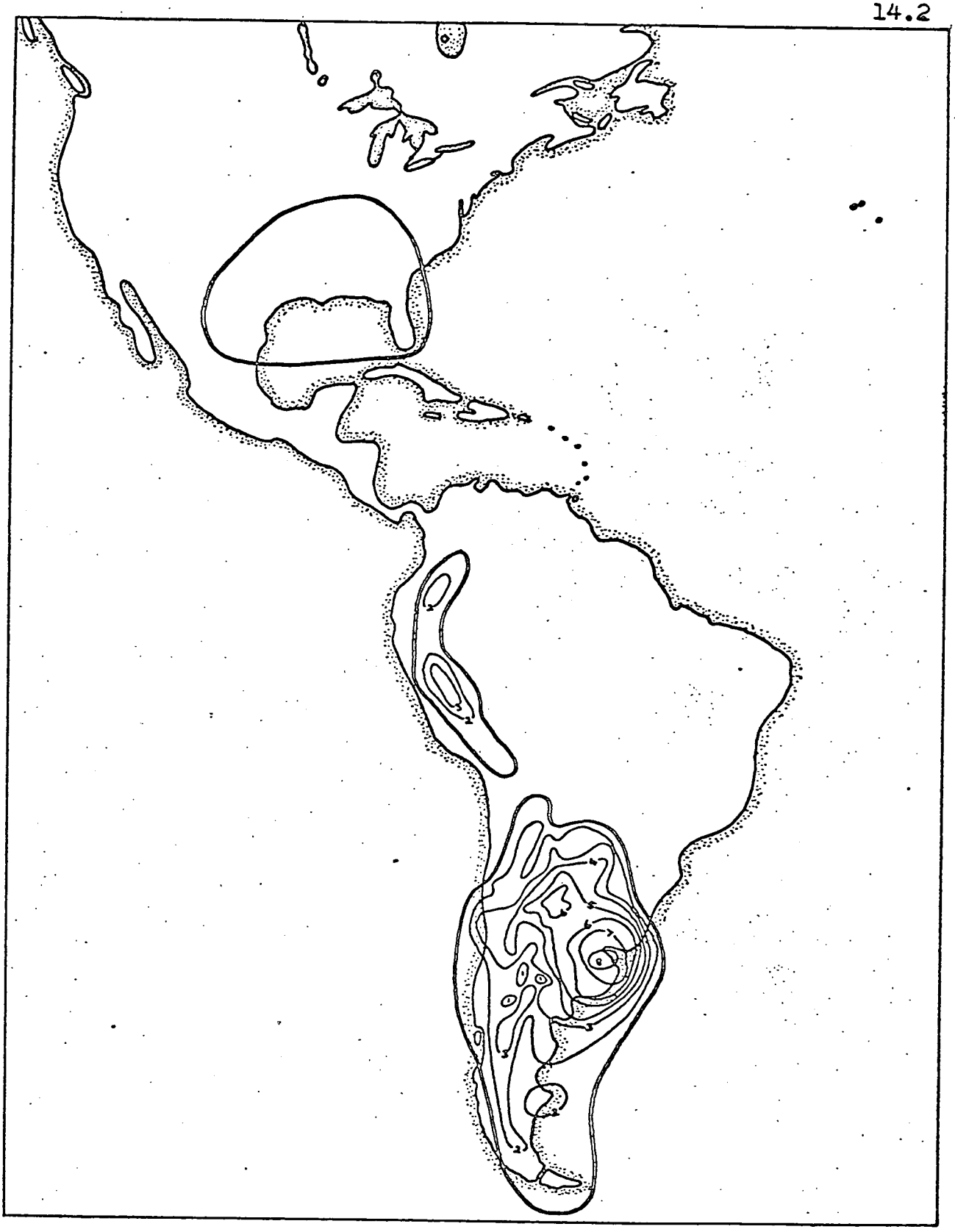


Fig. 96. Lathyrus Sect. Notolathyrus.

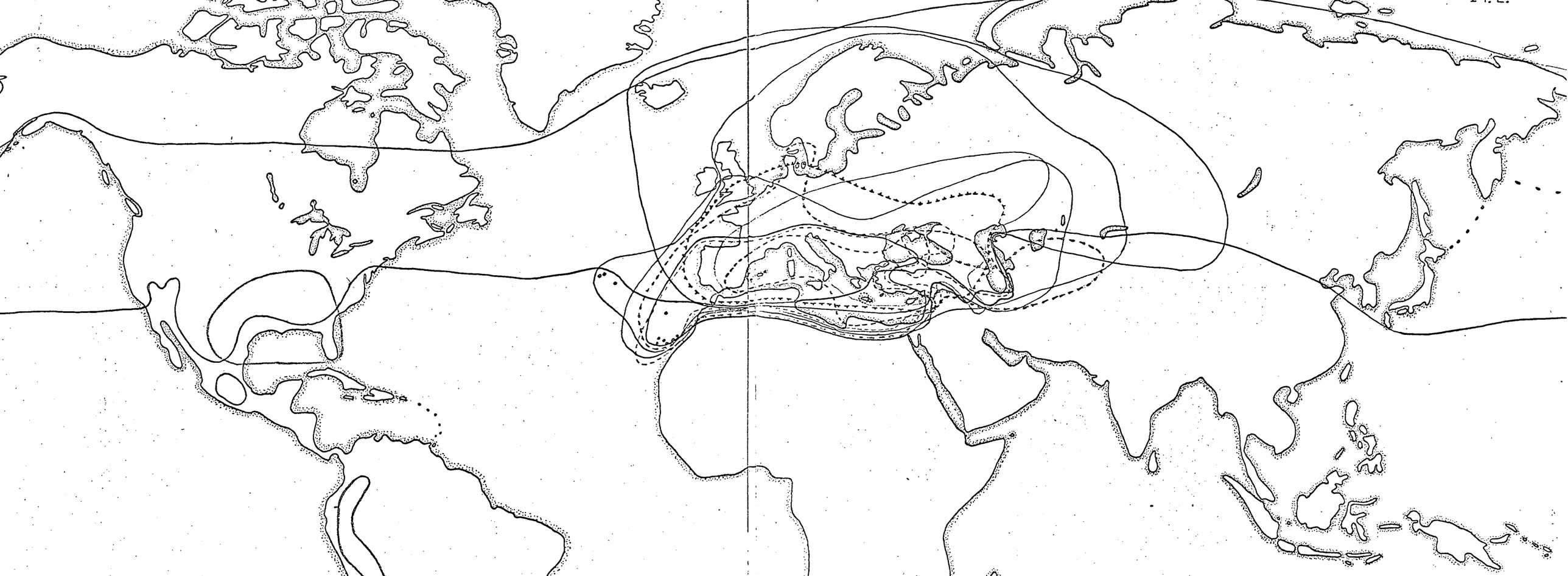


Fig. 97. Map showing distribution of sections of Lathyrus.

KEY: - sections

Orobus	Clymenum
Lathyrostylis	Neurolobus
Lathyrus	Linearicarpus
Orobon	Orobastrum
Pratensis	Viciopsis
Aphaca	Nissolia
	Notolathyrus

the different historical background of each phytochorion. This is discussed further in the next paragraphs.

14.3. THE INTERPRETATION OF PATTERNS OF GEOGRAPHICAL DISTRIBUTION

In 1922 Willis proposed his 'Age and Area' theory to explain patterns of plant distribution. This said that, assuming that the evolution and the dispersal of plants both proceed at a constant rate, the oldest and most primitive members of a group are the most widespread and are found on the periphery of its distribution range, while the more recent and specialised members occur more locally, near the centre of origin of the group. While this theory no doubt has an element of truth and describes one of the general principles of evolution, it is too simple to be relied upon for the interpretation of patterns of distribution, especially outside the tropics. This is because the two factors which the theory assumes to be constant are variable, and because the environment of the area concerned, during the period when evolution and dispersal are taking place, is itself subject to change. These three variables are interdependent: for example, rates of evolution will often increase during a time of enhanced environmental change; also, since one of the results of evolution is frequently the achievement of more effective means of dispersal, specialised members of a group may spread more quickly and widely than their primitive relatives. These factors have a profound influence on patterns of plant distribution.

An isoflor map shows the area where a group is represented by the highest concentration of species; this is the groups' centre of diversity. According to the 'Age and Area' theory, it is also the centre of origin of the group. However, under the influence of the variable factors mentioned above, the centre of diversity may in time become separated from the centre of origin. A study of the Cenozoic geological history of the earth allows one to make some generalised statements about the significance of contemporary centres of diversity (see part 13.5). It is evident, first of all, that any plant group whose centre of diversity lies in the Boreal Subkingdom (Fig. 53) is a descendant of species belonging to the Boreal-Tertiary temperate flora. Until the late Eocene this flora was able to migrate between Europe, Asia and N. America, and was in consequence fairly homogeneous, but from then on the Old and New Worlds were isolated and climatic deterioration caused a general southward movement of floras in the northern hemisphere. At the end of the Tertiary period, previously continuous species distributions in Europe became fragmented, the Boreal-Tertiary flora surviving in two main refugia: the Balkans and S.W. Asia (Euxine and Hyrcanian provinces), and S.E. Asia. The Quaternary Ice Age which followed had an even more drastic effect on the remnants of this flora, causing fluctuating patterns of distribution and progressively eliminating a large proportion of the species. This eventful history of climatic change, which has continued up to the present, must be the main factor underlying patterns of distribution of groups belonging to the

Euro-Siberian, E. Asian and N. American regions. Centres of diversity situated in these areas cannot be thought to show the place of origin of their taxa, but are simply a reflection of the refugia of the Boreal-Tertiary flora. The species concerned most probably evolved at much higher latitudes, in the early Tertiary.

Altogether different considerations apply to genera or sections having centres of diversity in the Tethyan Subkingdom (Fig. 53). The Mediterranean flora is a relatively young, autochthonous one, having developed in situ perhaps since the middle Tertiary. It is believed to have originated chiefly from subtropical ancestors (it has, for example, many woody sclerophyll genera), but to have derived elements also from the Boreal-Tertiary flora. A plant group whose centre of diversity is Mediterranean is therefore very likely to be Mediterranean in origin, and the two centres may well be coincidental. The Irano-Turanian flora is also considered to be derived from subtropical elements; it evolved in Central Asia from the late Mesozoic onwards and in the middle Tertiary extended westwards as the Tethys shrank and became divided by the approach of Africa to Asia. In Anatolia the Irano-Turanian flora came closely into contact with Boreal-Tertiary elements in the north and Mediterranean ones in the west, and received new members, especially from the former, older phytochorion. Elements from the Irano-Turanian flora also penetrated into the E. Mediterranean phytochorion. The convergence of these three quite different floras on a new land surface in the late Miocene and Pliocene resulted in a burst of evolution

in the Irano-Turanian region of Inner Anatolia. As Stebbins (1967) has pointed out, a stimulation in evolution can often be recognised at the interface between regions with different environmental/floristic characteristics. Thus a plant group whose centre of diversity occurs in the Irano-Turanian region probably evolved in this area, and its centre of origin may coincide with the greatest concentration of species today. This is particularly applicable to taxa which occur towards the west of the region; here the flora is very recent and autochthonous.

Where a genus or section extends over more than one phytogeographical region, and has centres of diversity in each, one can sometimes deduce in which direction the group has most likely migrated. For example, if a particular section has centres of diversity in the Euro-Siberian and Mediterranean regions, it is probable that its ancestor was a Boreal-Tertiary species some of whose descendants migrated south and entered the Mediterranean flora. The converse is unlikely, because the Mediterranean phytochorion is much younger than the Euro-Siberian; moreover, the Mediterranean area has been the site of active evolution since its flora began to develop, whereas in the same period conditions to the north were probably rather stagnant at first, becoming catastrophic as the Ice Age advanced. The same argument applies to a distribution-pattern which overlaps the Euro-Siberian and Irano-Turanian regions. However, where a section is richly represented in both the Mediterranean and Irano-Turanian floras, one cannot decide <u>a priori</u> on the direction of migration, since each of these phytochoria has

penetrated the other since their elements met in the middle Tertiary. At the present time, xerophytic floras are spreading at the expense of contracting mesophytic floras in most marginal areas in S.W. Asia.

Chapter 15

THE EVOLUTION OF THE VICIEAE

15.1. Introduction.

15.2. Primitive and advanced groups within the tribe.

15.3. Taxonomy and evolution in the Vicieae.

15.4. Geography and evolution in the Vicieae: conclusion.

15.1.

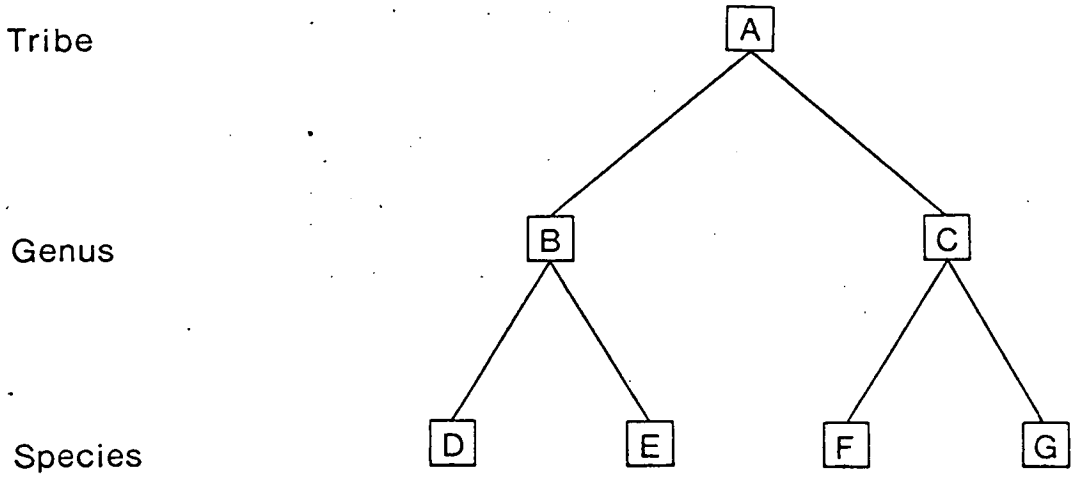
INTRODUCTION

The taxonomic structure of the Vicieae, outlined in Chapters 8 to 12, was based as far as possible on a strict evaluation of phenetic relationships within the tribe, the evidence for which was derived from the characters described in Chapters 3 to 7. The classification attempted to be a 'natural' one, free both from a priori weighting of particular characters and from the influence of evolutionary hypotheses (although the sections in Vicia and Lathyrus were, admittedly, arranged in order of evolutionary advancement). Having achieved this classification, it is legitimate to take a fresh look at the tribe and speculate freely about something which cannot be scientifically verified: the course of evolution in the Vicieae.

The following discussion relies first of all on the assumption that the Vicieae are monophyletic, i.e. that all the extant representatives of the tribe are descendants of one ancestral species, and are more closely related among themselves than to any species outside the tribe. This idea allows the group to be regarded as a unit in evolutionary terms. Evolution at levels above that of the species is predominantly divergent. Due both to divergence among the descendants of the ancestral stock of the tribe, and to extinction of intermediate, linking species, the Vicieae have come to be represented by a number of more-or-less isolated groups of species which are distinguished taxonomically as genera. The category 'genus' cannot

be defined either phenetically or phylogenetically, but within a given taxon of higher rank (in this case, a tribe), genera can be recognised as subordinate units. In my classification of the Vicieae the genera, like the tribe itself, are held to be monophyletic. Examined in closer detail, the genera themselves are found to contain groups of more closely similar species which are called subgenera or sections. They, too, are assumed to be monophyletic and to have evolved by the same divergent process which was responsible for the genera.

There is no fundamental difference, from an evolutionary viewpoint, between super-specific taxa on different levels of the hierarchy; they are all phenetically recognised groups and their rank is chosen by the taxonomist merely in comparison with and in relation to the rest of the hierarchy. Among the descendants of one ancestral species, the rank of a particular taxon does not indicate its relative age, except that it is younger than the next higher taxon to which it belongs. In this diagram, which shows the taxa in a classification



(not an evolutionary tree), B to G are all younger than A; D and E are younger than B; F and G are younger than C; but there is no information about the ages of the BDE group relative to the CFG group. It is, for example, possible that C is younger than D.

These considerations show that even a truly natural classification reflects only part of the evolutionary process which gave rise to its members. The species classification ought to define the ends of the branches of the evolutionary tree, and the hierarchy may partly show which branches are joined to which; but the complete cladistic pattern, and the different levels at which branches diverge from each other and from the trunk of the tree, are beyond the scope of formal taxonomy. The full evolutionary history of the Vicieae can therefore be only a subject of informal discussion.

15.2.
PRIMITIVE AND ADVANCED GROUPS WITHIN THE TRIBE

One of the most useful approaches towards an understanding of its phylogeny is to survey the tribe with a view to tracing character-trends within it. As has been described, both Vicia and Lathyrus possess a wealth of variable characters, and many of these features show that intra-generic specialisation has occurred. Since there is some degree of correlation between trends in different characters, the total variation-pattern creates an impression of developmental structure in each genus. When Vicia and Lathyrus have been

examined in this way, the four smaller genera can be added to the picture and the whole assemblage related to geographical patterns of generic and sectional distributions. This synthesis leads on to a final concept of the main outlines of phylogenesis in the Vicieae.

There are three methods by which one can interpret the evolutionary significance of the different states of a variable character, and thus identify a trend. These are:

1. The character is considered in isolation. When its different states are compared, and their adaptive significance understood, it is found that evolution from one state to another is theoretically possible only in one direction, and they can therefore be arranged in phylogenetic order.

2. When method 1 produces equivocal results, the variation in the character over a much wider taxonomic spectrum is brought into view. Thus, a trait whose intra-generic variation is being considered is placed in the broader context of the tribe or subfamily. This frequently gives a clue to the orientation of its trend. In the case of the Vicieae, since it is evidently a highly evolved tribe within the Papilionoideae, a character-state which is common in the subfamily is likely to be relatively primitive within the Vicieae itself.

3. If approaches 1 and 2 do not lead to a definite conclusion, then an indirect method must be used to interpret the character in an evolutionary sense. This involves comparing and correlating its variation-pattern with those of other characters whose trends have already been firmly established.

The first two methods are as reliable as possible in this field; the third is suspect because it can easily give rise to a circular argument or to wrong assumptions. Thus, for example, a primitive character might persist because it has become correlated with advanced ones.

Vicia. The variable characters which I consider useful in an evolutionary interpretation of Vicia are listed in Table 31:A. The only character whose different states can be definitely classified as primitive and advanced, on its own merits, is 1: perennial/annual. The trend of several other traits can be identified with a fair degree of confidence when Vicia is considered in relationship with the rest of the Vicieae and the Papilionoideae. These are: 2: tendrils present/absent; 3: vernation conduplicate/supervolute; 4: stipules without/with nectaries; 5: stipules monomorphic/dimorphic; 7: peduncle longer/shorter than subtending leaf; 13: lens near/opposite hilum and 14: complete/partial replacement of cortical vascular bundles at nodes. The remaining characters have been interpreted indirectly, as follows. An inflorescence which is paniculate and/or many-flowered is considered to be primitive within Vicia because these features are found almost exclusively in perennials, while few-flowered inflorescences are typical of annuals (character 6). The oblong standard (character 9) is held to be more primitive than the stenonychioid or platynychioid one, because it occurs chiefly in perennials with many-flowered racemes. The laterally

Table 31. Variable characters in Vicia.

A. CHARACTERS SHOWING AN EVOLUTIONARY TREND

		PRIMITIVE STATE	ADVANCED STATE	REFERENCE
HABIT:	1.	perennial	annual	
LEAVES:	2.	tendrils present	tendrils absent	3.2.
	3.	vernation con-duplicate	vernation super-volute	3.3.
	4.	stipules without nectary	stipules with nectary	3.6, 4.1.
	5.	stipules mono-morphic	stipules di-morphic	3.6.
INFLOR-ESCENCE:	6.	paniculate	racemose	4.1.
	7.	peduncle > leaf	peduncle < leaf	4.1.
	8.	many- or several-flowered	1-2-flowered	4.1.
FLOWER:	9.	vexillum oblong	vexillum stenonychi-oid or platynychioid	4.2.3.1.
	10.	style terete or dor-sally compressed	style laterally compressed	4.2.5.
	11.	style uniformly hairy all round	style with uneven hair distribution	4.2.5.
SEED:	12.	hilum long	hilum short (&, perhaps, very long)	4.5.6.
	13.	lens near hilum	lens opposite hilum	4.5.5.
ANATOMY:	14.	complete replace-ment of cortical vascular bundles at nodes	partial replacement of cortical vascu-lar bundles at nodes	5.3.2.

B. CHARACTERS WHOSE VARIATION CANNOT READILY BE CLASSIFIED INTO PRIMITIVE AND ADVANCED STATES

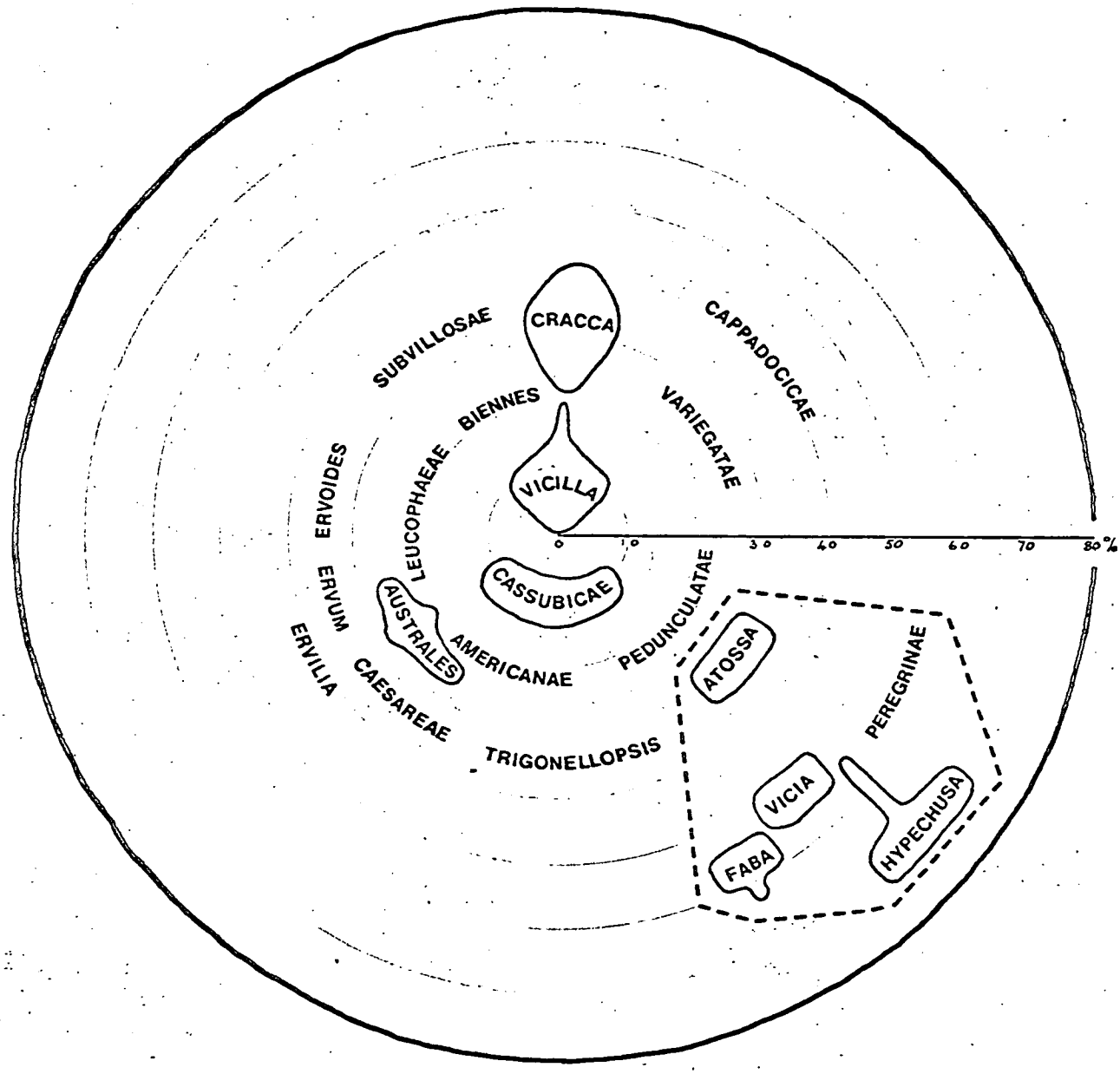
LEAVES:	15.	with many or few leaflets	3.5.
	16.	hypostomatic, amphistomatic or epistomatic	3.8.

			15.2.
FLOWER:	17.	the different patterns of stylar pubescence, when this is uneven	4.2.5.
FRUIT:	18.	shape of legume	4.4.

compressed style (10) is taken to be more specialised than the other two types because it is rare within Vicia and, except for V. dennesiana, is found only in species with a platynychioid vexillum. In contrast, the dorsally flattened style is common in Vicia and is present in all the other genera of the tribe. A uniformly hairy style (11) is considered the primitive condition in Vicia because it is correlated with an oblong standard and the perennial habit. The evolutionary significance of variation in hilum length (12) was discussed in part 4.5.6; although a long hilum is probably a specialisation within the Papilionoideae, its correlation with the perennial habit in the Vicieae suggests that it is primitive within the tribe and that a very short hilum is relatively advanced. Characters 15-18 in Table 31:B cannot be interpreted satisfactorily by these methods. To summarise: of the fourteen characters in Table 31:A, eight (1-5, 7, 13 & 14) have been judged independently within the context of the Papilionoideae; four (6, 8, 9 & 11) by comparing their variation with that of previously-orientated characters; and two (10 & 12) by a mixture of these approaches.

Fig. 98 is a target-diagram showing the relative evolutionary advancement of sections of Vicia, according to possession by their species of the characters listed in Table 31:A. This simple method of presentation, which was devised by Sporne (1956), is discussed by Davis & Heywood (1963). The 'evolutionary values' of the sections were estimated as follows. The primitive aspect of each character was assigned the score 0,

Figure 98. Target-diagram of sections of Vicia.



and the advanced aspect, 1; so the most primitive total score possible is 0, and the most advanced, 14. This range is converted into a percentage scale in the diagram, where the values increase towards the perimeter. In some sections the presence of species of varying specialisation produces a range of values for the group. In these cases (e.g. Sects. Vicilla, Cracca, etc.) the extent of the variation is shown by a line enclosing the section; the position of its name, and the width of the outline, roughly indicate the predominant value of the section. The radial positions of the sections have significance in that, as far as possible, these groups are placed near to one another according to phenetic resemblance. Members of Subgen. Vicia are grouped together and delimited by a broken line.

The diagram shows clearly that Subgen. Vicia is more highly evolved than Subgen. Vicilla. Within the latter, the most primitive sections are Vicilla and Cassubicae, and the most advanced, Ervilia and Cappadocicae. Sect. Subvillosae is the most specialised perennial group and Sect. Biennes the most primitive annual (to biennial) one. Sect. Cracca contains the widest range of values, in line with the fact that it is much the largest section. Subgen. Vicia parallels Subgen. Vicilla in that the perennial species occur in relatively primitive sections, (Atossa and Vicia); the most advanced group within Vicia is the entirely annual Sect. Hypechusa.

Lathyrus. Table 32:A lists the characters in Lathyrus whose variation gives evidence of evolutionary development within

Table 32. Variable characters in Lathyrus.

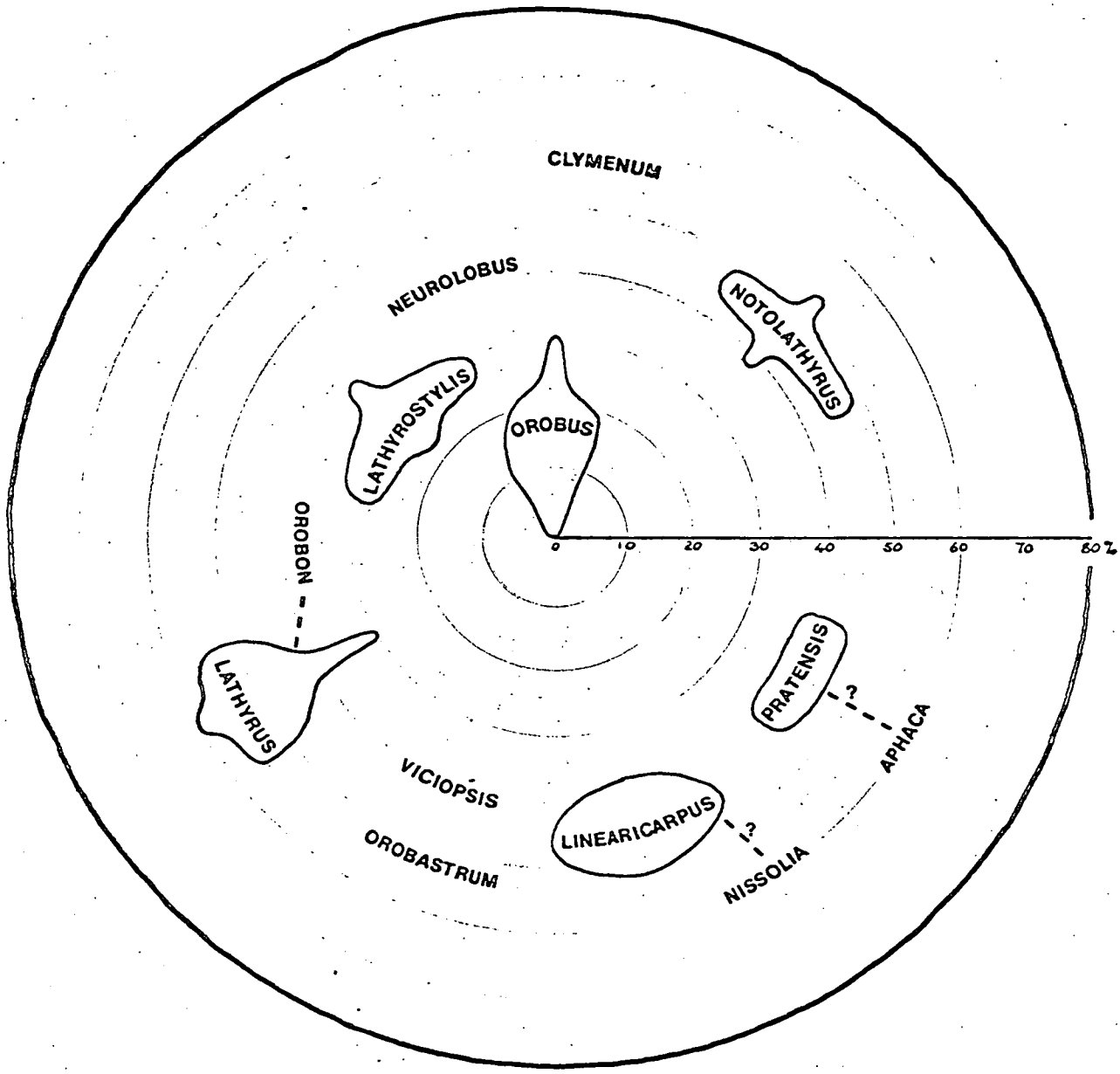
A. CHARACTERS SHOWING AN EVOLUTIONARY TREND

		PRIMITIVE STATE	ADVANCED STATE	REFERENCE
HABIT:	1.	perennial	annual	
STEM:	2.	not winged	winged	3.9.
LEAVES:	3.	tendrils present	tendrils absent	3.2.
	4.	leaflets several-paired	leaflets 1-paired or absent	3.5.
	5.	all leaves with leaflets	at least some leaves phyllodic, or with leaflets absent	3.5, 3.9.
	6.	venation pinnate-brochidodromous	venation parallel-brochidodromous	3.4.
	7.	stipules semi-sagittate	stipules hastate	3.6.
INFLOR-ESCENCE:	8.	many- or several-flowered	1-2-flowered	4.1.
FLOWER:	9.	vexillum oblong	vexillum stenonychioid	4.2.3.1.
	10.	style not contorted	style contorted	4.2.5.
	11.	style linear	style spathulate	4.2.5.
	12.	stigma simple	stigma double	4.2.5.
SEED:	13.	hilum long	hilum short	4.5.6.

B. CHARACTERS WHOSE VARIATION CANNOT READILY BE CLASSIFIED INTO PRIMITIVE AND ADVANCED STATES

LEAVES:	14.	hypostomatic, amphistomatic or epistomatic	3.8.

Figure 99. Target-diagram of sections of Lathyrus.



the genus, and Fig. 99 is a target-diagram of the sections of Lathyrus, based on these traits. The evolutionary trends in Lathyrus were identified and interpreted as follows. Characters 1, 3, 8, 9 and 13 were judged by the same methods as in Vicia. In the case of all the other characters, each one's variation was orientated by comparing its different states with those occurring in the rest of the Vicieae and the Papilionoideae. Thus, phyllodic and unijugate leaves, parallel-brochidodromous venation, hastate stipules, contorted or spathulate styles and double stigmas are all considered to be specialised features within the context of this tribe and subfamily.

Fig. 99 shows that the most primitive section of Lathyrus, as has been asserted by Simola (1968a), Bässler (1966) and others, is Sect. Orobus, while the most advanced are Sects. Nissolia and Aphaca. Sects. Orobus and Lathyrus, the largest groups in the genus, contain the widest value-ranges. The most specialised perennials belong to Sects. Lathyrus, Pratensis, Notolathyrus and Neurolobus, and the most primitive annual group is Sect. Viciopsis.

Lens, Anatropostylia, Pisum and Vavilovia. The four small genera cannot be analysed in the same way as Vicia and Lathyrus because their internal diversity is too limited to show evolutionary trends and their external (inter-generic) relationships are uncertain. Each of them shows considerable specialisation when its characters are compared with those of Vicia

Sect. Vicilla and Lathyrus Sect. Orobus, the most primitive parts of the tribe, but at the other extreme it is meaningless to scale these isolated genera with respect to advanced members of Vicia and Lathyrus; their evolutionary advancement can only be measured in terms of their own ancestors. This concept can be illustrated by comparing Vicia and Lathyrus; for example, Vicia Sect. Cappadocicae would be considered primitive in the context of Lathyrus, because it has multijugate, pinnate-veined leaves, although it is relatively specialised within Vicia.

15.3.

TAXONOMY AND EVOLUTION IN THE VICIEAE

The interpretation of Figs. 98 and 99 leads to some interesting conclusions about the evolutionary structure of the Vicieae. The historical development of systematics in the tribe shows that the most specialised groups are the easiest to recognise, while it is the most primitive groups which have caused the greatest difficulty. This is illustrated by the following examples. (Each group is called by its name in my classification, rather than that used by the authority mentioned, if these names are different.) In Vicia, the first major infra-generic division came with the recognition of Subgen. Vicia by Godron (1849) and Visiani (1852); see Table 4. This is the most highly evolved part of the genus. In Lathyrus, the earliest fragmentation was by Miller (1754), who split off the genera (now sections) Aphaca and Nissolia.

Sect. Clymenum was the next subgroup to be defined (Seringe, 1825: Table 6), and Sect. Lathyrus sensu Kupicha the next (Döll, 1843). As Fig. 99 shows, these four sections are the most specialised in Lathyrus. At the other extreme, the relatively primitive parts of these genera have long been areas of taxonomic confusion. Vicia Subgen. Vicilla contained the large, heterogeneous groups 'Cracca' and 'Ervum' whose complicated history was outlined in parts 2.3.1 and 2.3.3; Sects. Orobus and Lathyrostylis were the last parts of Lathyrus to be circumscribed, and have been subjects of controversy up to the present (see part 2.4.1). With these facts in mind, it seems very significant that the most primitive groups in Vicia and Lathyrus are not only problematical within their own genera, but together form a phenetically striking assemblage in which the two genera have themselves been confused; several species of Vicia Sect. Vicilla, as well as some of Lathyrus Sect. Orobus, were originally described as members of Orobus L. The oroboid members of Vicia and Lathyrus can be separated by up to five pairs of contrasting characters, as shown in Table 23, but these features are inconspicuous and were largely overlooked by early taxonomists.

The target-diagrams of Vicia and Lathyrus differ in several respects. Lathyrus has relatively few sections, and of these only one, Orobus, is very primitive while all the rest show considerable specialisation. There are several equally advanced sections in Lathyrus. Vicia, although comprising about the same number of species as Lathyrus, is divided into many

more sections. These are grouped into two subgenera of which Subgen. Vicia is much the more specialised. Subgen. Vicilla contains the two very primitive sections Vicilla and Cassubicae, and none of its members reaches a really high evolutionary value. The average value of the sections of Vicia is lower than that of sections of Lathyrus. Many of the taxonomic characteristics of the two genera can be related to these differences. Thus, the fact that Vicia is split into more sections than Lathyrus is not evidence of greater diversity; it is a reflection of the taxonomic difficulty of dealing with a large group of plants which shows a paucity of striking, correlated differences. Lathyrus has fewer discontinuities than Vicia, but they are larger.

The different evolutionary/taxonomic structures of Vicia and Lathyrus might be explained by supposing that Lathyrus is significantly older than Vicia and has evolved over a longer period. Since the primitive parts of these genera are most similar, presumably they are their most closely related areas. If Lathyrus is the older group, it can be postulated that Vicia evolved from a relatively unspecialised branch of Lathyrus when the latter had already given rise to the ancestors of some of its more advanced members. If this was the case, one would expect to find evidence of the earlier diversification of Lathyrus in its contemporary geographical distribution-pattern, compared with that of Vicia. Both genera were distinct by the early Tertiary, since each is well represented in Eurasia and America. At this period their members were prob-

ably inhabitants of the cool-temperate Boreal-Tertiary flora. The most similar descendants of these early Tertiary species are thought to belong to sections centred in the Boreal Subkingdom (see part 14.3 and Fig. 53). Tables 33 and 34 show, respectively, that Vicia now contains six such sections while Lathyrus has three; this represents nearly one-third of sections of Vicia, but only one-quarter of sections of Lathyrus. These geographical patterns suggest that Lathyrus was no more diverse than Vicia in the early stages of their development, and therefore, even if Lathyrus is older than Vicia, their disparate structures could not be attributed to this factor. Evidence from the comparative morphology of the two genera suggests that Lathyrus is unlikely to be ancestral to Vicia. Thus, Lathyrus is characterised by having leaflets with supervolute vernation, while Vicia, in common with the rest of the Vicieae (except Vavilovia, in which this character is unknown) and probably the majority of the Papilionoideae, has conduplicate vernation. Since the ancestral stock of the tribe almost certainly had folded leaflets, it is simplest to hypothesise that Vicia is a relatively direct descendant of this ancestor while Lathyrus represents a more specialised branch. The situation is complicated by the isolated occurrence of curled leaflets in Vicia biennis. Although I think it most probable that this trait has arisen as an independent mutation, it might be a highly significant relict character, derived from a lathyroid ancestor!

An alternative explanation for the different structures

of Vicia and Lathyrus is that they are approximately equal in age but have evolved in a different manner. I assume that evolution is the result of natural selection of random mutations (Darwin, 1859). If this is true, then a significant difference in the evolutionary patterns of two isochronous groups, as seen in Vicia and Lathyrus, must be due to a dissimilar operation of selection pressures. This could be due to a number of different causes, arising both from the environment and from the internal constitutions of the plants themselves. It is possible that Lathyrus by chance became adapted to a variety of habitats at an earlier stage than Vicia, and thus developed in a more divergent way. On the other hand, the ancestral stocks of these two genera may have possessed genotypes in which different tendencies were inherent. In this case, one would suggest that Lathyrus had a relatively 'flexible' genotype which favoured the production of variable offspring and provided selective agencies with a rich choice of alternative phenotypes; Vicia had a more conservative genotype which curbed the variability of offspring and rendered them fit only for the same environment as their parents (Mather, 1943). This kind of contrasting emphasis in the breeding systems of Vicia and Lathyrus would be difficult to prove, but it could theoretically have had a profound influence on their development.

The most convincing demonstration of the different evolutionary modes of Vicia and Lathyrus lies in a comparison of their New World representatives. Vicia has five sections in

America: Cassubicae, Cracca, Americanae, Leucophaeae and Australes. Lathyrus has two: Orobus and Notolathyrus. According to current understanding of geological history, the N. American continent separated from Eurasia in Eocene times and was not joined to S. America until the Pliocene epoch (part 13.2). New World natives of the Vicieae must therefore have been isolated from their Old World relatives since the early Tertiary, and those members which are endemic to S. America must have evolved since the Pliocene. Fig. 98 shows that Sects. Australes and Cassubicae, which include all the S. American representatives of Vicia, are relatively primitive, even though Sect. Australes is endemic to S. America and therefore very recently evolved. In contrast, Sect. Notolathyrus is a highly specialised group within Lathyrus (Fig. 99). Although it presumably evolved directly from the stock of the much more primitive Sect. Orobus in N. America, its members reproduce many of the most interesting features of Old World groups, including double stigmas, fruits with internal septa, unijugate leaves, winged stems and hastate stipules. Thus, different sections of Lathyrus, evolving independently, have given rise to parallel adaptations, in accordance with Vavilov's Law of Homologous Series in Variation (1922).

This survey suggests that the more highly evolved, divergent structure of Lathyrus, as compared with that of Vicia, has resulted from some attribute of Lathyrus which has been operative up to the latest stages of its evolution and which is manifest equally in parts of the genus which have long been

separated. I think it unlikely that this situation is due entirely to external factors (e.g. that Lathyrus by chance entered new environments more frequently than Vicia); rather, it seems probable that Lathyrus is intrinsically a more progressive group. The basis of this 'internal' property of Lathyrus may be the presence of a relatively flexible genotype.

There appear to be two factors in the evolutionary process which allow groups to become increasingly distinct and hence more easily recognised by the taxonomist. Firstly, distinctness is achieved 'actively' by a group when it possesses well-marked, relatively specialised traits; secondly, it comes about 'passively' when the neighbours of the group become extinct, and the isolation serves to emphasise the assemblage of characters preserved in the extant plants. As far as I can judge, the first is the more important factor in the delimitation of sections within Vicia and Lathyrus, while the second is the primary reason for the distinctness of these genera and of Pisum, Vavilovia, Lens and Anatropostylia.

It has been demonstrated that within Vicia and Lathyrus not only are the annual groups in general more advanced than the perennial; they are frequently more easily delimited, and the annual species of these genera tend to be classified in a large number of small sections. This phenomenon may be related to a difference in breeding-system between annuals and perennials which is a reflection of the different types of environment inhabited by each. The habitats of perennials are often mixed or deciduous forest communities, hedgerows or

damp meadows. These are closed, secondary systems where the selection pressures are buffered and maintained at a fairly constant level. Moreover, the relatively long generation period in these species checks the evolutionary influence of a varying environment. Annuals, in contrast, usually grow in primary habitats where the system is open and ephemeral and yearly fluctuations in environmental factors may have a profound effect on all the populations of a species. Although annuals tend to have a breeding system which promotes 'fitness' rather then 'flexibility' (Stebbins, 1958), they are more susceptible to selection pressures than perennials. Genetic drift is probably a major factor among populations living in conditions of catastrophic selection such as those which are thought to have prevailed in the Mediterranean basin at the end of the Tertiary. It may be that the small annual sections in Vicia Subgen. Vicilla are products of this kind of evolution. It is noticeable that perennials which inhabit less stable natural environments (screes, steppe, etc.) often belong to better-defined sections than the mesophytic perennials. Examples of these are Vicia Sects. Subvillosae, Variegatae and Leucophaeae, and Lathyrus Sect. Lathyrostylis. This category may perhaps be regarded as intermediate, in an evolutionary sense, between the more extreme xerophytic annuals and mesophytic perennials. These considerations seem to me very relevant and helpful towards an understanding of the taxonomic structure of Vicia and Lathyrus.

Lens and Anatropostylia have both been associated by

taxonomists with the ervoid members of Vicia (ie. with Sects. Ervoides, Ervum, Ervilia and Caesareae). In parts 10.3 and 10.4 it was concluded on morphological and chemical grounds that this connection is probably invalid, and Fig. 98 appears to support this decision. Subgen. Vicilla is distinguished by its narrow spectrum of evolutionary values, and if Lens and Anatropostylia were added to this group their distinctive features would place them far outside this range. In the context of the existing evolutionary pattern of Vicia, it seems very unlikely that two highly individual groups (especially Lens, which includes six species) have arisen recently from Subgen. Vicilla. It is somewhat more conceivable that Lathyrus could have produced genera in this way. However, although Anatropostylia, Lens, Pisum and Vavilovia all possess certain Lathyrus-like characteristics, they each have features which would make them primitive within Lathyrus and which suggest that they are not recent segregants of this large genus.

15.4.

GEOGRAPHY AND EVOLUTION IN THE VICIEAE: CONCLUSION

In part 14.3 it was shown that the contemporary centres of diversity of a plant group are significant in the interpretation of its evolutionary history. Tables 33 and 34 have been compiled from previous maps and tables, to form a basis for an evolutionary discussion of Vicia and Lathyrus; their construction is as follows; The sections of each genus are listed vertically. The geographical location of the centre of diversity

of each section is indicated by an entry, opposite its name, in one of the columns to the right; each column represents a phytogeographical region. The positions of centres of diversity (i.e. areas of greatest species-concentration) are taken from the isoflor maps in Chapter 14, and their classification into different regions is achieved by reference to Takhtadjan's map (Fig. 53 in Chapter 13). The entries in these regional columns consist of numbers which are the relative evolutionary values of the sections, taken from the target-diagrams of Vicia and Lathyrus (Figs. 98 & 99). Some sections have two centres of diversity, or the position of the 'centre' is doubtful, and entries are then made in more than one column. In every case, however, the value of the section is given as constant, no allowance being made for geographical variation in evolutionary value within a section. Due to their small scale, the isoflor maps of sections do not always give a correct indication of the phytogeographical region to which these groups should be assigned. Around the Mediterranean and in S.W. Asia the Euro-Siberian, Irano-Turanian and Mediterranean phytochoria meet and interdigitate, and enclaves of one element are found within the territory of another. Thus Vicia Sect. Cappadocicae appears in Fig. 67 to enter the Hyrcano-Euxine province, but V. cappadocica, the species concerned, in fact belongs to the Irano-Turanian rather than the Euro-Siberian element. Similarly, Fig. 78 suggests that Sect. Hypechusa is centred in the Euro-Siberian region in S.W. Asia; but here again its members are predominantly Irano-Turanian.

Table 33. Evolutionary values and centres of diversity in Vicia.

ISOFLOR MAPS: Figures ↓	Kingdoms → / Regions → / Sections ↓	EURASIA			NORTH AMERICA		SOUTH AMERICA
		Boreal	Tethyan		Boreal	Madrean	
		Euro-Sib.	Medit.	Ir.-Tur.			
57 & 58	Vicilla	0-21					
59 & 60	Cassubicae	7-14			7-14	7-14	7-14
61	Variegatae			21-28			
62	Pedunculatae		21				
63 & 64	Cracca		21-42		21-42		
65	Subvillosae			35			
66	Biennes	21					
67	Cappadocicae		42	42			
68	Ervum		35				
69	Ervoides		35				
70	Ervilia		(42)	42			
71	Caesareae			35			
72	Trigonellopsis		35				
73	Leucophaeae					21	
73	Australes						21-28
74	Americanae				21		
75	Atossa	28-35					
76	Vicia		49-56				
77	Faba		56-63				
79	Peregrinae			56			
78	Hypechusa			56-70			

See comment on following page.

Table 34. Evolutionary values and centres of diversity in Lathyrus.

ISOFLOR MAPS: Figures ↓	Kingdoms →	EURASIA			N.AMERICA	SOUTH AMERICA
		Boreal	Tethyan		Boreal	
	Regions →	Euro-	Medit.	Ir.-		
	Sections ↓	Sib.		Tur.		
82-84	Orobus	0-30			0-30	
85	Lathyrostylis		23-38	23-38		
86	Lathyrus		30-60	30-60		
87	Orobon	38				
88	Pratensis	38-46				
89	Aphaca		60			
90	Clymenum		57			
91	Neurolobus		42			
92	Linearicarpus		38-53	38-53		
93	Orobastrum		53			
94	Viciopsis		38-46			
95	Nissolia		60			
96	Notolathyrus					38-53

The construction of Tables 33 & 34 is described at the beginning of part 15.4. The phytogeographical regions are taken from Fig. 53, and the figures opposite the sections are their relative evolutionary values, taken from Figs. 98 (Vicia) and 99 (Lathyrus).

The correlation between distribution of centres of diversity and evolutionary values follows the same pattern in both genera. The Mediterranean region contains most centres of diversity, while there are relatively few centres in the Euro-Siberian or even Irano-Turanian regions, or in the New World. Sections which have centres of diversity in the Boreal Subkingdom (in both Eurasia and N. America) tend to be more primitive than those centred in the Mediterranean or Irano-Turanian regions or in S. America. This fact strongly suggests that both genera originated in the Boreal-Tertiary flora; the phenetic similarity between Vicia Sect. Vicilla and Lathyrus Sect. Orobus supports this hypothesis and leads to the idea that the tribe itself evolved from ancestors which were part of a northern deciduous forest association. The large number of sections in both genera centred in the Tethyan Subkingdom is evidence that Vicia and Lathyrus were strongly influenced by the geological and climatic changes of the middle and late Tertiary, and that they participated actively in the development of the new Mediterranean flora, and in the westward penetration of Irano-Turanian elements. The Irano-Turanian phytochorion appears to have played a comparatively minor role in stimulating the expansion of the Vicieae, except in that part of S.W. Asia where three phytochoria converge and their elements intermingle. The evidence suggests that this southward shift of emphasis in the evolution of Vicia and Lathyrus was accompanied by trends towards more xerophytic characteristics, giving rise to a predominance

of annuals, and to species adapted to live at high altitudes. It appears that in many groups annuals were evolved which possessed the ability to colonise disturbed habitats. These weedy species, though probably originating in the Tethyan area, are now among the most widespread in each genus; they may have penetrated northwards following the catastrophic glacial events of the Pleistocene, but their distributions have certainly been strongly influenced by man. Examples are Vicia sativa s.l., V. villosa s.l., V. hirsuta, Lathyrus aphaca, etc. This recolonisation of the Euro-Siberian region by species from the Mediterranean flora has had a marked influence on the distribution-patterns of sections; however, since it is unlikely that there has been a significant amount of recent evolution in the Vicieae in the Euro-Siberian area (cf. part 14.3), the spread of weeds has not affected the positioning of centres of diversity.

It seems very probable that Vicia and Lathyrus began their development at high latitudes in the Old World, perhaps in the late Mesozoic or early Tertiary periods. At this stage, representatives of both genera migrated to the N. American continent, either via Greenland or from E. Asia to Alaska. In the case of Lathyrus, the migrants appear to have been of the Sect. Orobus type. The absence of 'oroboid' species of Vicia in N. America seems to conflict with my hypothesis that Sect. Vicilla is the most primitive part of the genus; it is possible, however, that the group was once represented in N. America but has become extinct there. Conversely, the

amphi-Atlantic distribution of Sect. Cracca is surprising, as it suggests a high degree of differentiation in Vicia before the late Eocene (when Eurasia and N. America finally parted). V. americana bears a strong resemblance to members of Sect. Pedunculatae, and in the light of the distribution of Sect. Cracca, it is possible that these groups have a common ancestor which was in existence by that time. The distribution of Sect. Cassubicae is particularly interesting as it provides the closest parallel with that of Lathyrus Sect. Orobus (see Figs. 59, 60, 82-84). Though comprising relatively few species, it has a wide distribution in Eurasia and two very disjunct localities in America. The extinct V. dennesiana, which was endemic to the Azores and is now represented by a few herbarium sheets at Kew, provides an extra clue to the development of Vicia. It is a great pity that this species is lost; it was obviously a very beautiful plant, and might have yielded more information in the form of chemical or cytogenetical data. In morphology V. dennesiana agrees completely with Sect. Cassubicae, except that its style is laterally compressed. It is thus intermediate between Sects. Cassubicae and Cracca, a remarkable fact considering that these are the two groups which occur on both sides of the Atlantic!

I agree with Burkart (1966) that the S. American members of Vicia and Lathyrus are descendants of N. American species, and that they probably migrated south via the Andean chain. The S. American continent separated from Africa at the beginning of the Jurassic period, when the Atlantic began to open.

It was isolated until the end of the Tertiary (Pliocene), when the Panama area was formed (see part 13.2). Since there is strong evidence that the Vicieae originated in high latitudes, it is inconceivable that Vicia or Lathyrus could have spread to the S. American landmass before it broke away from Africa. The means by which temperate plant species have been able to cross the tropical belt in the New World is not fully explained (Moore, 1972). As was described in part 15.3, Lathyrus Sect. Notolathyrus shows many advanced characteristics which are remarkable in being so similar to the adaptations of Old World groups. In contrast, Vicia Sect. Australes is only moderately specialised. Its floral morphology suggests that it may be related to Sect. Americanae.

The distribution of the four small genera of the Vicieae - Lens, Pisum, Vavilovia and Anatropostylia - is shown in Fig. 55. Anatropostylia koeieana is an Irano-Turanian species; Lens and Pisum are centred in the Mediterranean region; Vavilovia is almost confined to the Irano-Turanian region and E. Mediterranean mountains, although V. formosa also grows in the Central Caucasus (Euxine province of the Euro-Siberian region). Since none of their extant species is truly Euro-Siberian, these genera must either have evolved relatively recently in the Tethyan Subkingdom or be descendants of Boreal-Tertiary species which are now extinct. Vicia and Lathyrus have been in separate existence since the early Tertiary, so if any of the small genera are recent, autochthonous derivatives of either Vicia or Lathyrus, they must be very much more closely

related to one than the other. The scree habitat of Vavilovia suggests that it may have evolved in response to the Alpine orogeny. There is no doubt that Vavilovia and the weedy, annual genus Pisum are closely related, and it is conceivable that both are descendants of a tendrillous, perennial 'proto-Pisum-Vavilovia' which belonged to the Boreal-Tertiary flora. If this is true, these two genera have been separate from both Vicia and Lathyrus since at least the middle Tertiary. Lens and Anatropostylia, on the other hand, are each completely isolated, and there is no evidence available from which to build a sound hypothesis of their origins. In these cases it is perhaps wisest to leave them without further comment, except the suggestion that during the last geological period there has probably been a far greater extinction of species than taxonomists usually realise.

ADDENDUM

An important paper by Bässler (1973) has just appeared as my thesis is almost complete. This article is a sequel to his 1966 publication, and sets out in detail the infra-sectional classification of Sect. Orobus (L.) Godron; a synopsis of the series and species recognised by Bässler is given in Table 35. Bässler now accepts O. tuberosus as the correct lectotype of Orobus L, following Green (1929), Gunn (1969) and Czefranova (1971). The name of this species is L. linifolius (Reichard) Bässler (synonymous with L. montanus Bernh.: see Bässler, (1971). He does not touch on the affinities of the N. American species of Lathyrus, which I include in Sect. Orobus.

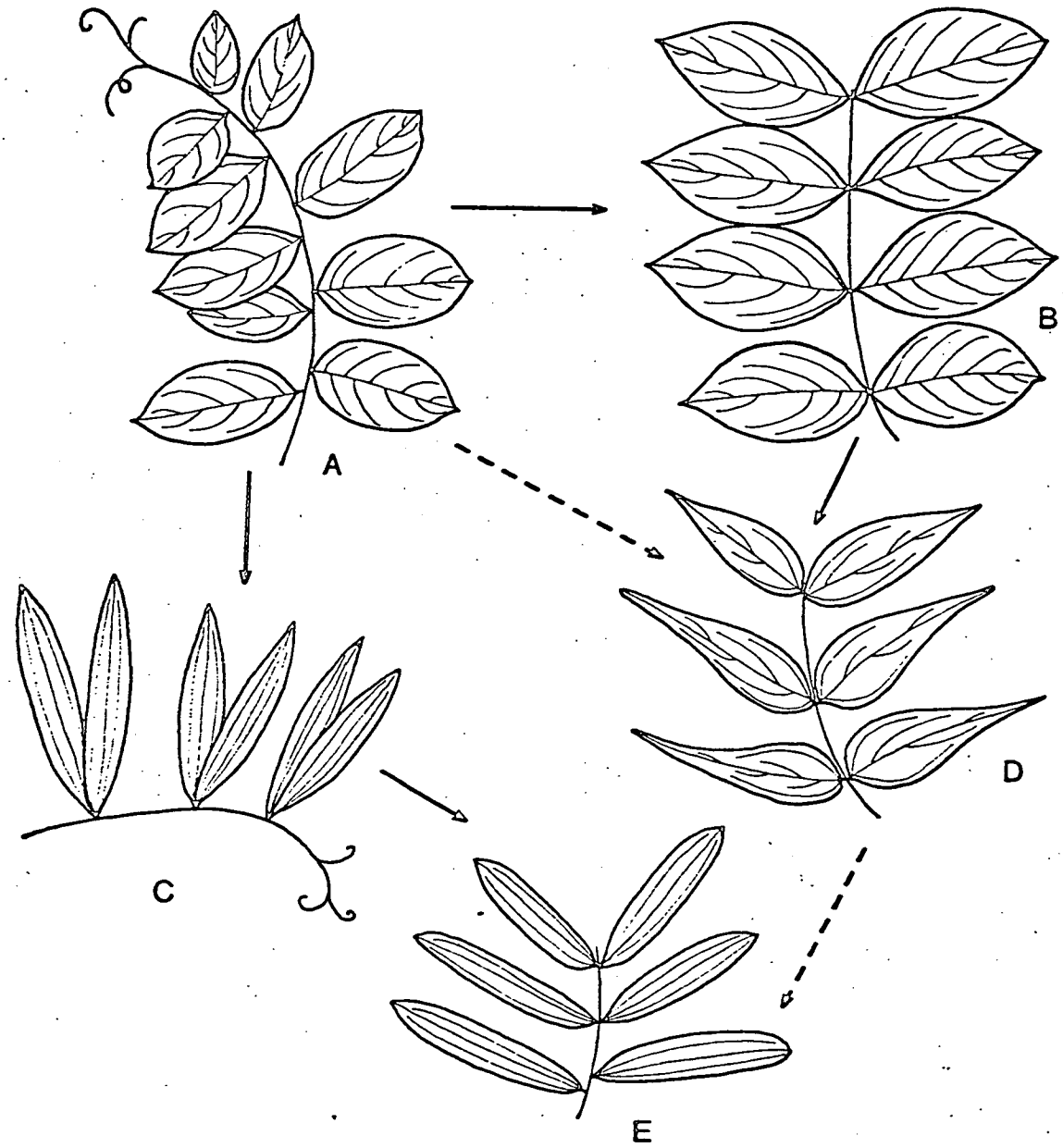
In discussing the leaves of members of Sect. Orobus, Bässler argues that the absence of tendrils is a more advanced state than their presence, and that parallel venation is derived from pinnate; as was shown in parts 3.2 and 3.4, I concur with both conclusions. Fig. 100 is a reproduction of Bässler's diagram which shows these trends in leaf evolution.

With regard to the 'oroboid' species of the Vicieae, Bässler says "The question of whether this group of species of Lathyrus (i.e. Eurasian members of Sect. Orobus) is closely related to some species of Vicia which are similar in habit (V. crocea, V. oroboides, etc.) needs further study. The most probable explanation of this similarity is that certain morphological characters have arisen in each group by parallel evolution as a result of adaptation to similar environments." (freely translated). I discuss this particular problem in part 10.2.

Table 35. Conspectus of taxa in Lathyrus Sect. Orobus, according to Bässler (1973).

Series:	Species:	
1. Davidii Bässler	1. L. davidii	
2. Lutei Fritsch ex Czefranova	2. L. gmelinii	7. L. aureus
	3. L. krylovii	8. L. occidentalis
	4. L. emodi	9. L. laevigatus
	5. L. vaniotii	10. L. transsilvanicus
	6. L. libani	
3. Humiles Bässler	11. L. humilis	
4. Verni Fritsch	12. L. vernus	15. L. venetus
	13. L. frolovii	16. L. alpestris
	14. L. komarovii	
5. Incurvi Bässler	17. L. incurvus	
6. Nigri Fritsch	18. L. niger	
7. Maritimi Bässler	19. L. japonicus	
8. Pisiformes Bässler	20. L. pisiformis	
9. Palustres Bässler	21. L. palustris	23. L. wilsoni
	22. L. dielsianus	24. L. quinquenervius
10. Tuberosi Fritsch	25. L. linifolius	
11. Dominiani Bässler	26. L. dominianus	

Fig. 100. Diagram showing evolutionary leaf-trends in Lathyrus Sect. Orobus (after Bässler, 1973).



The most primitive type of leaf is tendrillous, with several pairs of pinnate-veined leaflets (A). Absence of tendrils (B, D, E), a reduced number of leaflets (C, D, E) and parallel venation (C, E) are all regarded as relatively specialised features.

APPENDIX 1. LIST OF SPECIES GROWN FROM SEED.

The following species were grown at Edinburgh during 1970-72, providing living material for the morphological, anatomical and serological investigations which were reported in Chapters 3-6. Most of the seed samples were obtained from Gatersleben Botanic Garden, Berlin; each of these is indicated by an asterisk and the code number which appeared on the seed packet. The remaining samples, which came from a variety of sources, are identified by their collector's name and the place of origin. Voucher specimens of these species are lodged in the herbarium of the Royal Botanic Garden, Edinburgh.

Anatropostylia

A. koeieana Davis 44753 from Hakkari, Turkey.

Cicer

C. anatolicum Davis 47623 from Erzurum, Turkey.

C. arietinum *CIC 33/68

C. pinnatifidum *CIC 35/68

Lathyrus

L. annuus *LAT ?

L. aphaca Alava 6644 from Silifke, Turkey.

L. aureus Davis 36647 from Bursa, Turkey.

L. blepharicarpus Plitmann 6208 from Judaean Mts near Zora.

L. cicera *LAT 210/67

L. clymenum var. clymenum *LAT 121/66

L. clymenum var. articulatus *LAT 119/66

L. gloeospermus Plitmann 5 v 62 from Arbel Mt., Upper Jordan

Valley.

L. gorgoni Plitmann 7311 from Upper Galilee, Miron to Saza.

L. hirsutus *LAT 133/65

L. incurvus Davis 23863 from Hakkari, Turkey.

L. japonicus Davis 16 ix 1960 from Russia.

L. lentiformis Plitmann 7801 from Upper Galilee (type).

L. nissolia *LAT 136/65

L. ochrus *LAT 315/67

L. pratensis *LAT 544/66

L. rotundifolius *LAT 436/68

L. sativus *LAT 447/65

L. sphaericus *LAT 134/65

L. sylvestris *LAT 235/68

L. tingitanus *LAT 106/67

L. tuberosus *LAT 1/69

L. vernus *LAT 238/66

Lens

L. culinaris *'Lazysa'

L. nigricans *LENS 164/69

L. orientalis *LENS 166/69

Vicia

V. amurensis *LAT 402/66

V. anatolica *VIC 652/68

V. articulata *VIC 298/65

V. benghalensis *VIC 369/67

V. bithynica *VIC 305/65

V. biennis *LAT 579/68

V. cassubica *LAT 240/68

V. cracca *LAT 498/68

V. cuspidata Coode & Jones 838 from Içel, Turkey.

V. disperma *VIC 651/68

V. dumetorum *LAT 94/68

V. ervilia EK/250667/5-3 from Içel, Turkey.

V. faba JS/230667/6-2 from Balikesir, Turkey.

V. filicaulis Bramwell from Bco. Arguineguin, Canary Is.

V. galilaea Plitmann 1804 from Upper Galilee.

V. graminea *VIC 656/68

V. grandiflora *VIC 472/67

V. hybrida *VIC 309/65

V. hyrcanica *VIC 640/68

V. lutea *VIC 642/65

V. melanops *VIC 474/65

V. michauxii *VIC ?

V. monantha *VIC 360/65

V. narbonensis *NAR 1/68

V. neglecta *VIC 645/65

V. palaestina Plitmann 2701-1 from S. Judaean Mts.

V. pannonica *VIC 484/64

V. peregrina *VIC 315/65

V. pisiformis *VIC 88/69

V. pubecens *VIC 646/69

V. sativa subsp. amphicarpa Plitmann, from University campus, Jerusalem.

V. sativa subsp. angustifolia *VIC 597/68

V. sativa subsp. cordata *VIC 454/63

V. semiglabra *LAT 528/69

V. sepium *LAT 400/69

V. sylvatica *LAT 533/68

V. unijuga *LAT 250/68

V. villosa *VIC 650/68

The following species, which are cultivated at the Royal Botanic Garden, Edinburgh, were also used: Lathyrus grandiflorus, L. latifolius, L. roseus, L. venetus and Pisum sativum.

APPENDIX 2. LIST OF NEW TAXA, NEW NAMES AND NEW COMBINATIONS.

The genus Anatropostylia, and its species A. koeieana, have been published (Kupicha, 1973); a reprint of this paper forms part of Appendix 2. The remaining names listed here are at present provisional, but are intended for formal publication.

New taxa

Lathyrus Sect. Linearicarpus Kupicha, sect. nov.

L. Sect. Notolathyrus Kupicha, sect. nov.

L. Sect. Viciopsis Kupicha, sect. nov.

Vicia Sect. Americanae Kupicha, sect. nov.

V. Sect. Australes Kupicha, sect. nov.

V. Sect. Biennes Kupicha, sect. nov.

V. Sect. Caesareae Kupicha, sect. nov.

V. Sect. Cappadocicae Kupicha, sect. nov.

V. Sect. Leucophaeae Kupicha, sect. nov.

V. Sect. Peregrinae Kupicha, sect. nov.

V. Sect. Subvillosae Kupicha, sect. nov.

New combinations

Anatropostylia (Plitm.) Kupicha, stat. nov.

A. koeieana (Rech. fil.) Kupicha, comb. nov.

See reprint of Notes R. B. G. Edinb. 32(2):247-250 (1973), overleaf.

Lathyrus americanus (Miller) Kupicha, comb. nov. Syn: Pisum americanum Miller, Gard. Dict. ed. 8 (1768); Lathyrus nervosus Lam., Encycl. 2:708 (1788); L. armitageanus Westcott ex

STUDIES IN THE VICIEAE I: THE NEW GENUS ANATROPOSTYLIA

F. K. KUPICHA*

ABSTRACT. The new monotypic SW Asian genus *Anatropostylia* is published and its affinity with the rest of the Vicieae is discussed.

INTRODUCTION

The new genus *Anatropostylia* is formally published below, and the reasons for its separation from *Vicia* are discussed.

On the basis of a detailed morphological, anatomical and serological study (to be reported later), the tribe Vicieae is here considered to comprise the genera *Vicia*, *Lathyrus*, *Lens*, *Pisum*, *Vavilovia* and *Anatropostylia*; *Cicer* is excluded.

Anatropostylia (Plitmann) Kupicha, **stat. nov.** Syn.: *Vicia* Sect. *Anatropostylia* Plitmann in Davis, Fl. Turkey 3: 598 (1970).

Annual. Stems angular, branched, ascending. Leaves with 5–9 pairs of leaflets, tendrillous; leaflets lanceolate, aristate, with conduplicate vernation (ptyxis). Stipules finely and palmately laciniate. Inflorescence ± equalling leaf, 3-7-flowered. Calyx subregular, teeth shorter than to equalling tube. Corolla bright lemon-yellow; standard stenonychioid (i.e. with blade distinctly wider than claw), with two small bosses. Staminal tube ending obliquely. Style dorsally compressed, pubescent on adaxial (inner) side below stigma. Legume subterete, the upper suture curved, the lower straight; valves papery, prominently reticulate-veined. Seeds 4, compressed-spherical, scabrid-tuberculate; hilum minute. — Monotypic.

A. koeieana (Rech. fil.) Kupicha, **comb. nov.** Fig. 1.

Syn.: *Vicia koeieana* Rech. fil. in Dansk Bot. Ark. 15, 4: 37, f. 10 (1954-55); *V. singarensis* Boiss. & Hausskn. var. *aristata* Náb. in Publ. Fac. Sci. Univ. Masaryk Brno 35: 100 (1923); *V. aristata* (Náb.) Schischkin in Ber. Tomsker Staats-Univ. 80: 487 (1929), non (Lapeyr.) Dulac (1867); *V. blakelockiana* C. C. Townsend in Kew Bull. 21: 452 (1968).

Type: [W Iran] Kharon (100 km SW of Arak), 1300 m, 31 v 1937, *Köie* 726 (W).

[Iraq] Karoukh Mountain, nr Dargala, 800–1500 m, *Nuri & Kass* 2774. Between Kujar and Kani Grawi, E of Karoukh, 1500–1700 m, *Alkas, Nuri & Sarhank* 27630. [Turkey] B7 Malatya: 62 km from Malatya to Elaziğ, 980 m, *Hub.-Mor.* 9211. B8 Muş: Muş to Chaskei, 1300 m, 31 vii 1916, *Saposhnikov & Schischkin*. C9 Hakkari: Hasitha (Ashuti) between Amadia and Çolemerik, 1450 m, *Nábělek* 2933 (BAV, holotype of *V. singarensis* var. *aristata*, syntype of *V. blakelockiana*); Çukurca in Zap gorge, 1200 m, *D.* 44753!

The species belongs to the Irano-Turanian region.

* This paper embodies part of the work at present being undertaken for the degree of Ph.D. in the University of Edinburgh.

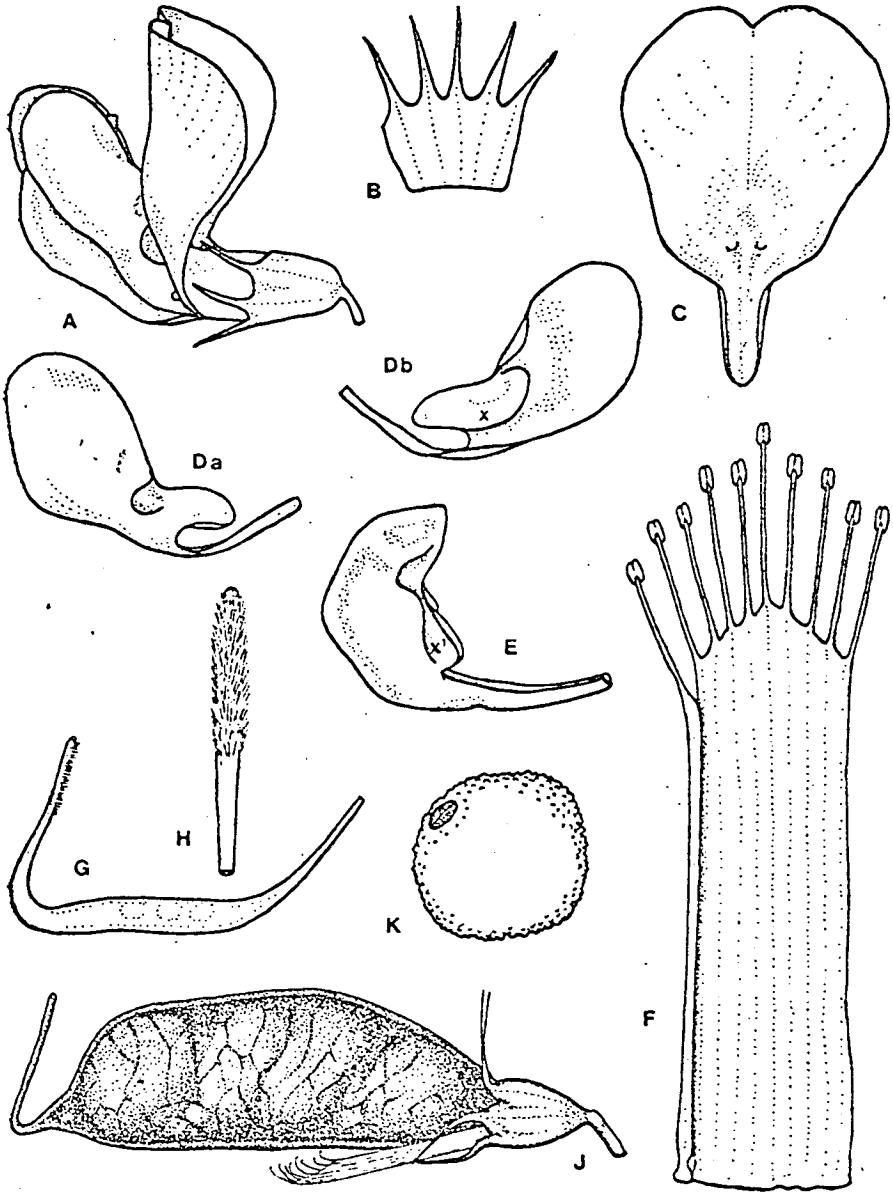


FIG. 1. *Anatropostylia koeieana*. A, flower. B, calyx. C, standard. D, wing: a) from outside, b) from inside. E, keel. (Process 'x' of wing is adnate to hollow 'x¹' of keel.) F, androecium. G, ovary. H, detail of style, adaxial side facing. J, fruit. K, seed. Scale: A-E, J × 4; G × 5; F, K × 8; H × 10. J & K drawn from *D.* 44753; A-H from progeny of this collection.

Discussion

The tribe Vicieae forms a coherent and undoubtedly natural group within which the genera, although each possessing many differential features, are often delimited on the basis of just two or three diagnostic characters. Since these attributes have been found particularly useful as guides for identification, they have traditionally received special taxonomic weighting within the tribe. The three most important traits of this kind are the type of leaflet-vernation (this character has, surprisingly, been overlooked by recent authors); the form of the staminal tube; and the shape of the style and its indumentum-distribution.

Lathyrus is distinguished by having supervolute vernation; the other genera (except *Vavilovia*, whose vernation is unknown) have leaflets folded in bud. In *Vicia* and *Lens* the staminal tube ends obliquely; in *Lathyrus*, *Pisum* and *Vavilovia* it is truncate. Variation in stylar details is very wide and complex, providing characters of both intra- and inter-generic importance. Members of *Lathyrus*, *Lens*, *Pisum* and *Vavilovia* have a dorsally compressed style pubescent on the adaxial face; in the first two genera it is flat, in the last two folded abaxially along the median longitudinal line. The style in *Vicia* species may be terete or compressed dorsally or laterally, with uniformly circumstylar pubescence or with an abaxial tuft of hair, but it is never as in the other genera.

The phenetic relationships between *Anatropostylia* and the rest of the Vicieae are summarised in Table 1. This shows that with respect to the three 'generically important' characters (nos. 2, 8 & 9), *Anatropostylia* agrees completely only with *Lens*; the style is atypical of *Vicia*.

	Characters of Anatropostylia
Vi. Le.	1. Leaves multijugate
Vi. Le. Pi.	2. Leaflet vernation conduplicate
An.	3. Leaflets aristate
An.	4. Both stipules at each node laciniate
Vi. La. Pi. Va.	5. Calyx teeth shorter than to equalling tube
La.	6. Corolla bright lemon-yellow
La. Le. Pi. Va.	7. Vexillum stenonychioid, with 2 bosses
Vi. Le.	8. Staminal tube ending obliquely
La. Le.	9. Style dorsally compressed, pubescent on adaxial side, not folded abaxially
An.	10. Legume subterete, with papery, prominently reticulate-veined valves
An.	11. Style appearing to arise from lower suture of legume
La. Pi.	12. Seeds finely scabrid-tuberculate

Table 1

A comparison between *Anatropostylia* and the other genera of the Vicieae. *Vi.* Character-state typical of *Vicia*, *La.* of *Lathyrus*, *Le.* of *Lens*, *Pi.* of *Pisum*, *Va.* of *Vavilovia* and *An.* character-state peculiar to *Anatropostylia*.

In general facies *A. koeieana* is reminiscent of *Vicia* and *Lens*; this is due to the leaves, which have many pairs of small leaflets (*Lathyrus*, *Pisum* and *Vavilovia* are all characterised by leaves with larger, less numerous

leaflets). The evidence from floral characters provides a different emphasis. A *bright* yellow corolla is unknown within *Vicia* and *Lens* but is quite common in *Lathyrus*. The calyx of *Anatropostylia* distinguishes this genus from *Lens*: in the former the calyx teeth are usually shorter than the tube, in the latter they are several times longer. The vexillum, with its wide blade and narrow claw, and with two bosses at the junction between these areas of the petal, is like a standard of *Lathyrus* or *Lens*, but unlike that of *Vicia*. Seeds with a rough testa are very rare in *Vicia* (occurring only in the closely related *V. cuspidata* Boiss. and *V. lathyroides* L.), but they are quite common in *Lathyrus* and *Pisum*.

The remaining features (the aristate leaflets, the equal pair of laciniate stipules and the details of the fruit) are all anomalous within the Vicieae and each will serve alone to diagnose *Anatropostylia* from other members of the tribe.

Although *Vicia* is the largest genus in the Vicieae, and comprises wide variation in many characters, *Anatropostylia* cannot be included within it without a very significant broadening of its definition. In particular, while *A. koeieana* is retained as a member of *Vicia* there is no character by which *Vicia* can be distinguished from *Lens* apart from the difference in relative lengths of calyx teeth and tube. *Anatropostylia* could be placed in *Lens* on the basis of a few 'key' characters, but the diverse nature of the stipules, calyx, fruit and seeds of these two groups argues against such an arrangement. Thus the isolation of *Anatropostylia* is supported both by its many unique or unusual attributes and by the effect of this separation on the delimitation of *Vicia* and *Lens*.

Loudon, Gard. Mag. 9:525 (1835).

Vavilovia graeca (Quézel & Contandriopoulos) Kupicha, comb. nov. Syn: Pisum graecum Quézel & Contandriopoulos in Nat. Monspeliensia sér. Bot. 16:116 (1965).

New names

Lathyrus whitei Kupicha, nom. nov. Syn: L. longipes White in Bull. Torrey Bot. Club 21:453 (1894), non L. longipes Phil. (1856).

APPENDIX 3. ANATOMICAL INVESTIGATIONS: MATERIALS AND METHODS.

This appendix is supplementary to Chapter 5, and explains in greater detail the methods used to obtain the results described there. The numbered headings correspond to those in the main text.

5.2. Seedling anatomy. I did not investigate the vascular anatomy of the seedling, and the data given here is reported from other authors. Fig. 26 is my own diagrammatic representation of the information assembled by Muller (1937) from his studies and from the observations of earlier workers.

5.3. Cortical bundles in the mature plant, and

5.4. Vascular supply to leaves. These parts are taken together, since they are derived from the same series of investigations. I studied the vegetative vascular anatomy of the 54 species listed in Table 15. In each case, a single specimen was used to represent the species. Plants grown at Edinburgh

provided fresh material of the majority of species (see Appendix 1), while the remaining taxa were represented by herbarium specimens.

All the reconstructions of vasculature were based on hand-cut serial transverse sections of stems and petioles. Sections were easily made from living material of plants with relatively thick stems, using a new razor-blade. Slender stems, or those with wide wings, were sandwiched between pieces of pith to provide a more stable object for cutting. Dried material was softened by soaking for two to three days in 10% KOH and then sectioned in the same way as fresh material, always using pith. The sections were placed in phloroglucinol for a few minutes and then passed briefly through concentrated HCl; this procedure stains lignin bright red, and so enhances the definition of the xylem. After staining, the sections were arranged in order on microscope slides, mounted in dilute glycerine jelly, and covered with cover-slips. It was found that there was no advantage in obtaining extremely thin sections, because, as the parenchymatous tissue is fairly transparent, the path of individual bundles could be traced through the thickness of each section. The sections were observed with a binocular dissecting microscope, and drawings were made of selected sections throughout the internode-node-internode series in each species, to illustrate the sequence of changes in vascular pattern in the stem.

The three-dimensional diagrams (Figs. 28, 29, 31, 33) were assembled from the evidence provided by these drawings; their method of construction is shown in Fig. 101. Vicia pannonica

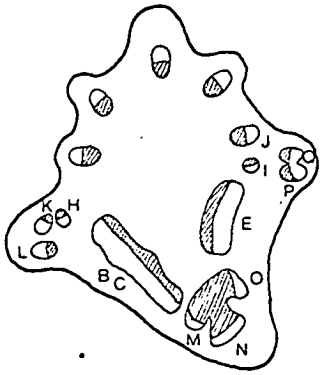
is chosen as the example because it possesses the most complex nodal anatomy. The first two pages of Fig. 101 show a series of transverse sections of the stem, passing through one node, while the third page illustrates how these sections are built up into the final reconstruction. Fig. 31 was based on Fig. 101.

The diagrams in Fig. 32 were obtained in exactly the same way, but since they are concerned only with the leaf-supply the main 'cylinder' of traces in the stem is omitted and only the leaf-traces are drawn.

5.5. Primary cauline vascular systems. The species whose stem vasculature was studied in greater detail are listed in Table 16. I was here interested not only in the behaviour of traces at each node, but in the vascular relationship of successive nodes. The procedure was the same as in the preceding investigations; serial transverse sections of stem were made and drawn as before. In this case, however, the identity of individual bundles in the main stem 'cylinder' had to be carefully monitored through several nodes and internodes. Figs. 34 and 35 illustrate my findings: in these diagrams the 'cylinder' is cut longitudinally and opened out flat.

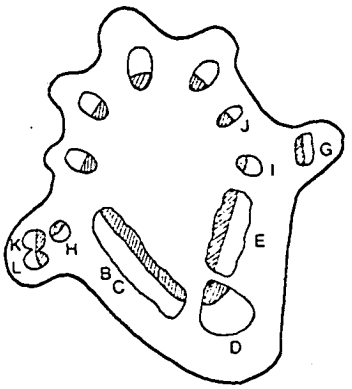
Fig. 101. Construction of three-dimensional diagram of stem vasculature in Vicia pannonica.

G (wing bundle) dichotomises into P & Q. D (median leaf-trace) begins to trifurcate into M, N & O.



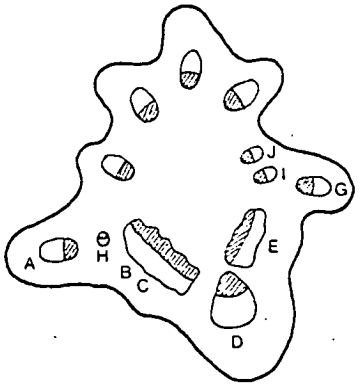
SECTION 4

A (wing bundle) dichotomises into K & L.



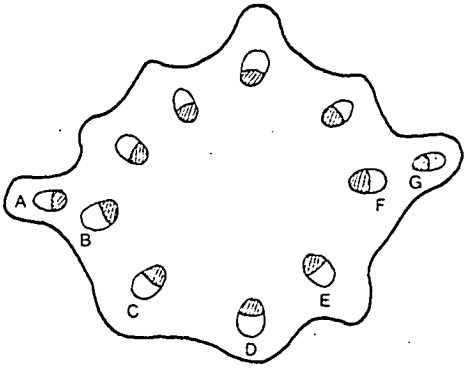
SECTION 3

TOP OF INTERNODE
Bundle H breaks off from B; F divides into I & J; B & C fuse.



SECTION 2

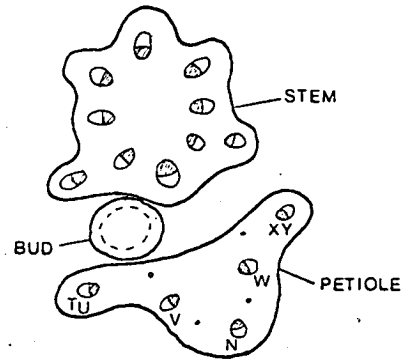
INTERNODE
The stem is vasculated with a ring of bundles (B, C, D, E, F, etc.); the wings of the stem also each contains a single trace (A & G).



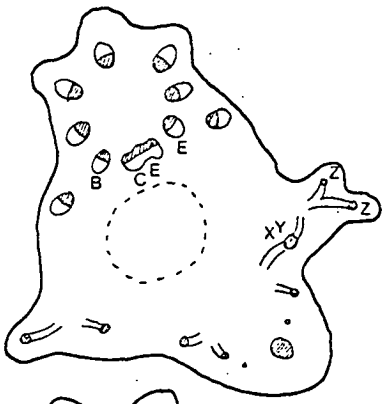
SECTION 1

Fig. 101, continued.

INTERNODE
Stem resumes internode pattern (compare section 1); axillary bud (BUD) and petiole are free. Petiole contains 5 main traces: V, N & W are derived from the median leaf-trace (D); TU and XY are composite.

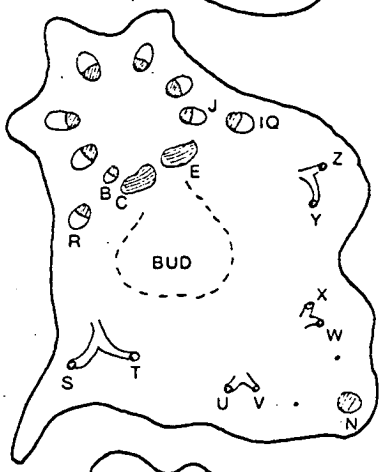


TOP OF NODE
S and Z supply the stipules. X and Y fuse to form XY (one of the pair of upper petiole bundles).



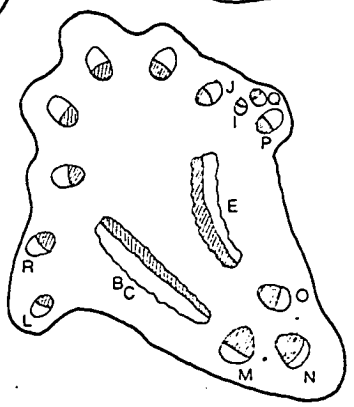
SECTION 7

I and Q fuse to form IQ.
L divides into S & T;
P divides into Y & Z;
M becomes U & V; O becomes W & X. BC and E supply many small traces in a ring for the axillary bud (BUD).



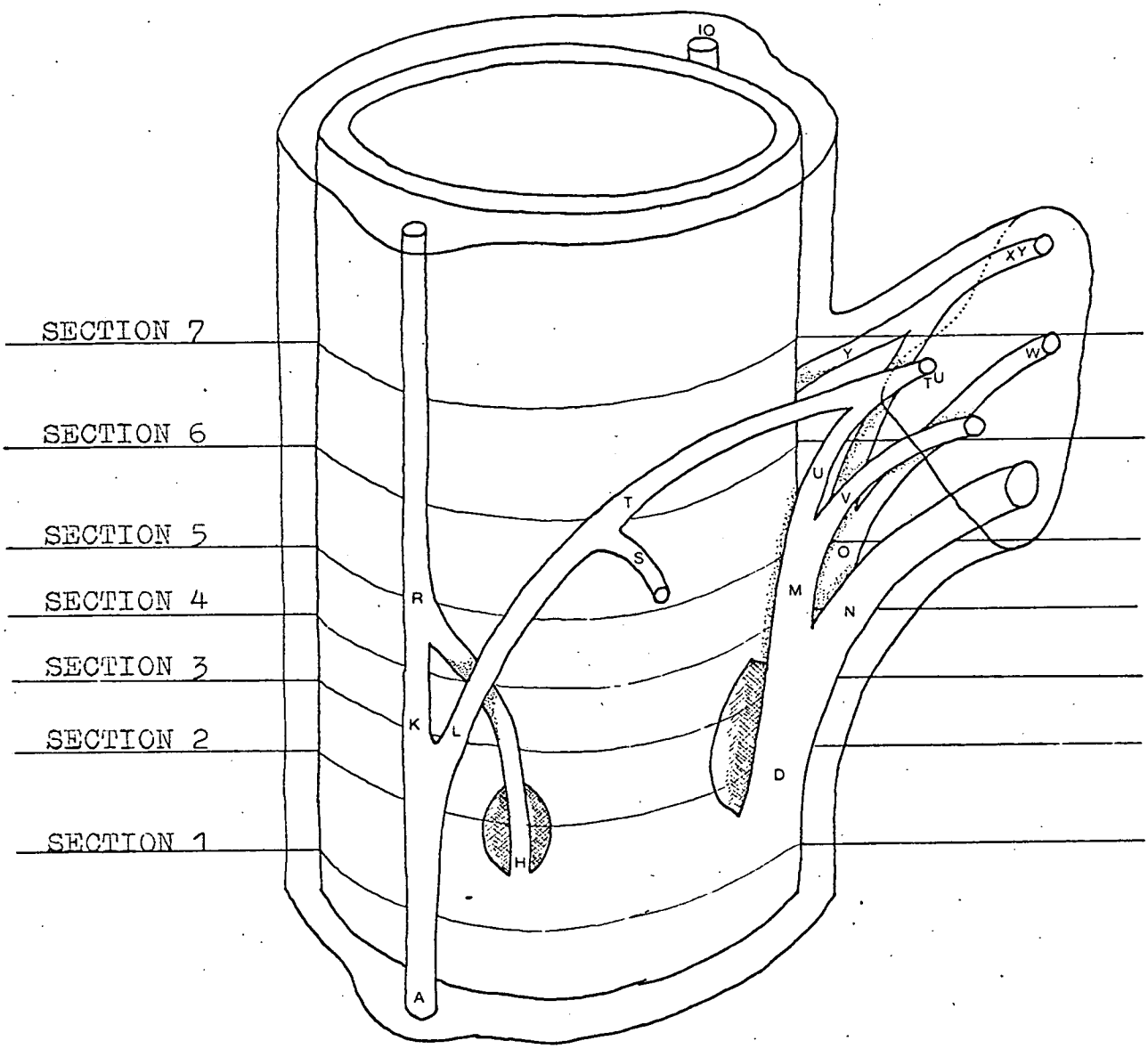
SECTION 6

K & H fuse to form R.
The lateral leaf-traces are L and P.



SECTION 5

Fig. 101, continued.



The behaviour of the leaf-supply traces is being emphasised here, and so the main ring of bundles in the stem (including B, C, E, F in section 1) are represented as a solid cylinder for simplicity; this results in artificial leaf-gaps. The axillary bud supply is not drawn in this diagram, but <u>is</u> shown in Fig. 31. The vertical dimension is exaggerated here, compared with Fig. 31.

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INDEX

The first part of this index deals with members of the Vicieae and Cicereae, while the second lists the other taxa mentioned in the thesis.

1. MEMBERS OF THE VICIEAE AND CICEREAE

The index has four purposes:

a) It lists all the recognised species of the Vicieae and Cicereae (even when their names have not occurred in the text).

b) It gives synonyms, where the name changes involved are considered to be significant indicators of the development of taxonomy in the Vicieae s.l.; the sign '=' means 'a synonym of'.

c) It provides authorities for the species.

d) It is a guide to the text. Thus, page references are given for the most important discussions of the genera Anatropostylia, Cicer, Lens, Pisum and Vavilovia. The two large genera, Vicia and Lathyrus, are treated differently: their members are not given page numbers but are cross-referred to the appropriate conspectus of taxa in parts 11.3 and 12.3.

Abacosa Alefeld = Vicia Sect. Americanae

Anatropostylia (Plitm.) Kupicha 352, 526, 542, 551

A. koeieana (Plitm.) Kupicha

Aphaca Miller = Lathyrus Sect. Aphaca

Arachus Medik. = Vicia Sect. Faba

Atossa Alefeld = Vicia Sect. Atossa

Cicer L. 69, 320, 328

- Subgen. Pseudonónis M. Pop. = C. Subgen. Cicer
- Subgen. Viciastrum M. Pop.
- Sect. Acanthocicer M. Pop. = C. Sect. Tragacanthoides
- Sect. Arietaria Jaub. & Spach = C. Sect. Cicer
- Sect. Cicer
- Sect. Chamaecicer M. Pop.
- Sect. Monocicer M. Pop. = C. Sect. Cicer
- Sect. Polycicer M. Pop. = C. Sect. Vicioides

Sect. Spiroceras Jaub. & Spach
Sect. Tragacanthoides Jaub. & Spach
Sect. Vicioides Jaub. & Spach
C. acanthophyllum Boriss.
C. anatolicum Alefeld
C. arietinum L.
C. atlanticum Coss. ex Maire
C. balcaricum Galushko
C. baldshuanicum (M. Pop.) Lincz.
C. bijugum Rech. fil.
C. chorassanicum (Bunge) M. Pop.
C. cuneatum Hochst. ex Rich.
C. echinospermum P.H. Davis
C. fedtschenkoi Lincz.
C. flexuosum Lipsky
C. floribundum Fenzl
C. garanicum Boriss.
C. graecum Orph.
C. grande (M. Pop.) Korotk.
C. incanum Korotk.
C. incisum (Willd.) K. Malý
C. isauricum P.H. Davis
C. jacquemontii Jaub. & Spach = C. microphyllum
C. judaicum Boiss.
C. kermanense Bornm.
C. korshinskyi Lincz.
C. macracanthum M. Pop.
C. microphyllum Bentham
C. mogoltavicum (M. Pop.) A. Koroleva
C. montbretii Jaub. & Spach
C. multijugum van der Maesen
C. nuristanicum Kitamura
C. oxyodon Boiss. & Hohen.
C. paucijugum Nevski
C. pinnatifidum Jaub. & Spach
C. pungens Boiss.

C. rechingeri Podlech
C. songaricum Steph. ex DC.
C. spiroceras Jaub. & Spach
C. stapfianum Rech. fil.
C. subaphyllum Boiss.
C. tragacanthoides Jaub. & Spach
C. yamashitae Kitamura
Cicercula Medik. = Lathyrus Sect. Lathyrus
Tribus Cicereae Alefeld page 334
Clymenum Miller = Lathyrus Sect. Clymenum
Coppoleria Todaro = Vicia Sect. Ervoides
Cracca Medik. non L. = Vicia Sect. Cracca
Cujunia Alefeld = Vicia Sect. Vicia
Endiusa Alefeld = Vicia Sect. Cracca
Ervilia Link = Vicia Sect. Ervilia
E. sativa Link = Vicia ervilia
Ervum L. = Vicia Sect. Ervum
Sect. Ervilia (Link) Ser. = Vicia Sect. Ervilia
Sect. Lens (Miller) Ser. = Lens
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E. hirsutum L. = Vicia hirsuta
E. lens L. = Lens culinaris
E. monanthos L. = Vicia articulata
E. pubescens DC. = Vicia pubescens
E. tetraspermum L. = Vicia tetrasperma
Faba Miller = Vicia Sect. Faba
Graphiosa Alefeld = Lathyrus Sect. Linearicarpus
Hypechusa Alefeld = Vicia Sect. Hypechusa
Lastila Alefeld = Lathyrus Sect. Lathyrus
Lathyrus L. The conspectus of taxa within Lathyrus is part 12.3, pages 414-417. The sections and species listed below are numbered according to their position in the conspectus.
Subgen. Aphaca (Miller) Czefr. = L. Sect. Aphaca
Subgen. Cicercula (Medik.) Czefr. = L. Sect. Lathyrus
Subgen. Clymenum (Miller) Czefr. = L. Sect. Clymenum

Subgen. Lens (Miller) Godron = Lens
Subgen. Nissolia (Miller) Czefr. = L. Sect. Nissolia
Subgen. Orobus (L.) Petermann = L. Sect. Orobus
Sect. 6. Aphaca (Miller) Reichenb.
Sect. Cicercula (Medik.) Gren. & Godr. = L. Sect. Lathyrus
Sect. 7. Clymenum (Miller) DC. ex Ser.
Sect. Eurytrichon Bässler = L. Sect. Pratensis
Sect. Gloeolathyrus Warburg & Eig = L. Sect. Clymenum
Sect. Lathyrobus (Tamamsch.) Czefr. = L. Sect. Orobus
Sect. 2. Lathyrostylis (Griseb.) Bässler
Sect. 3. Lathyrus
Sect. 10. Linearicarpus Kupicha
Sect. 12. Neurolobus Bässler
Sect. 11. Nissolia (Miller) Reichenb.
Sect. 13. Notolathyrus Kupicha
Sect. 9. Orobastrum Boiss.
Sect. 4. Orobon Tamamsch.
Sect. 1. Orobus (L.) Gren. & Godron
Sect. Platystylis (Sweet) Bässler = L. Sect. Lathyrostylis
Sect. 5. Pratensis Bässler
Sect. 8. Viciopsis Kupicha
Ser. Davidii Bässler see Addendum
Ser. Dominiani Bässler " "
Ser. Humiles Bässler " "
Ser. Incurvi Bässler " "
Ser. Lutei Czefr. " "
Ser. Maritimi Bässler " "
Ser. Nigri Fritsch " "
Ser. Palustres Bässler " "
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L. ervoides (Brign.) Grande
L. montbretii (Fisch. & Meyer) Davis & Plitm.
L. nigricans(Bieb.) Godr.
L. orientalis (Boiss.) Hand.-Mazz.
Navidura Alefeld = Lathyrus Sect. Lathyrus
Nissolia Miller = Lathyrus Sect. Nissolia
Tribus Orobidae Alefeld includes Lathyrus, Lens and Pisum
Subtribus Lathyrosae Alefeld = Lathyrus
Subtribus Orobosae Alefeld = Lathyrus
Subtribus Pisosae Alefeld = Pisum
Orobus L. = Lathyrus Sect. Orobus
Sect. Lathyrostylis Griseb. = Lathyrus Sect. Lathyrostylis
O. croceus Desf. = Vicia crocea
O. formosus Stev. = Vavilovia formosa
O. hirsutus L. = Lathyrus laxiflorus
O. lathyroides L. = Vicia oroboides
O. luteus L. = Lathyrus gmelinii
O. nervosus Boiss. = Lathyrus boissieri
O. niger L. = Lathyrus niger
O. pyrenaicus L. = Lathyrus linifolius
O. saxatilis Vent. = Lathyrus saxatilis
O. trachycarpus Boiss. = Lathyrus trachycarpus
O. tuberosus L. = Lathyrus linifolius
O. variegatus Ten. = Lathyrus venetus
O. vernus L. = Lathyrus vernus

Parallosa Alefeld = Vicia Sect. Ervoides

Pisum L. pages 67, 355, 526, 542

Sect. Alophotropis Jaub. & Spach = Vavilovia

Sect. Lophotropis Jaub. & Spach = Pisum

P. arvense L. = P. sativum s.l.

P. aucheri Jaub. & Spach = Vavilovia formosa

P. graecum Quézel & Contandriopoulos = Vavilovia graeca

P. fulvum Sibth. & Sm.

P. maritimum L. = Lathyrus japonicus

P. ochrus L. = Lathyrus ochrus

P. sativum L.

Platystylis Sweet = Lathyrus Sect. Lathyrostylis

P. cyaneus (Steven) Sweet = Lathyrus cyaneus

Sellunia Alefeld = Vicia Sect. Trigonellopsis

Swantia Alefeld = Vicia Sect. Vicilla

Tuamina Alefeld = Vicia Sect. Peregrinae

Vavilovia Fedorov pages 67, 355, 526, 542

V. graeca (Quézel & Contandriopoulos) Kupicha

V. formosa (Steven) Fedorov

Vicia L. The conspectus of taxa within Vicia is part 11.3, pages 364-368. The subgenera, sections and species listed below are numbered according to their position in the conspectus.

Subgen. Cracca (Vis.) Gams = V. Sect. Cracca

Subgen. Craccoidea Fedtsch. = V. Sect. Cracca

Subgen. Ervilia (Link) Rouy = V. Sect. Ervilia

Subgen. Ervoidea (Gren. & Godron) Rouy = V. Sect. Ervoides

Subgen. Ervum (L.) Rouy = V. Sect. Ervum

Subgen. Faba (Miller) Fedtsch. = V. Sect. Faba

Subgen. Pseudervoidea Rouy = V. Sect. Cracca

Subgen. II. Vicia

Subgen. I. Vicilla (Schur) Rouy

Sect. 6. Americanae Kupicha

Sect. Anatropostylia Plitm. = Anatropostylia

Sect. Arachus (Medik.) Tutin = V. Sect. Faba

Sect. 17. Atossa (Alefeld) Aschers. & Graebner

Sect. 15. Australes Kupicha
Sect. 8. Biennes Kupicha
Sect. 13. Caesareae Kupicha
Sect. 9. Cappadocicae Kupicha
Sect. 2. Cassubicae Radzhi
Sect. 3. Cracca Vis.
Sect. Crocea Radzhi = V. Sect. Vicilla
Sect. 12. Ervilia (Link) W. Koch
Sect. 11. Ervoides Gren. & Godron
Sect. 10. Ervum (L.) Taubert
Sect. 19. Faba (Miller) Ledeb.
Sect. 20. Hypechusa (Alefeld) Aschers. & Graebner
Sect. Lenticula Aschers.& Graebner = V. Sect. Cracca
Sect. 16. Leucophaeae Kupicha
Sect. 5. Pedunculatae Rouy
Sect. 21. Peregrinae Kupicha
Sect. Sepium Radzhi = V. Sect. Atossa
Sect. Subsessiles Rouy = V. Sect. Vicia
Sect. 7. Subvillosae Kupicha
Sect. 14. Trigonellopsis Rech. fil.
Sect. 4. Variegatae Radzhi
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V. amphicarpa Dorth. = V. sativa s.l.
V. amurensis Oett. 11
V. anatolica Turrill 115
V. andicola Phil. 87
V. angustifolia L. = V. sativa s.l.
V. argentea Lapeyr. 67
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V. bithynica(L.) L. 114
V. bombycina Stapf ex Post = Lens montbretii
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V. cretica Boiss. & Heldr. 77
V. crocea (Desf.) B. Fedtsch. 2
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V. cypria Kotschy ex Unger & Kotschy 85
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V. exigua Nuttall 58
V. faba L. 110
V. filicaulis Webb & Berth. 45
V. floridana S. Wats. 59
V. freyniana Bornm. 18
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