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A revision of the species of Trifolium sect. Trifolium (Leguminosae). I. Introduction

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RÉSUMÉ

Dans la partie introductive de sa révision de *Trifolium* sect. *Trifolium* (première étape d'une révision du genre tout entier), l'auteur donne un aperçu de l'histoire de la classification des trèfles, situe la section traitée par rapport aux autres sections reconnues dans le genre et énumère les caractères morphologiques employés au cours de son étude. Il donne des nombres chromosomiques, provenant de ses propres comptages, pour 14 espèces.

SUMMARY

In the introductory part of his revision of *Trifolium* sect. *Trifolium* (a first section of a revision of the whole genus), the author sketches the history of the classification of the clovers, assesses the position of the treated section with respect to the other recognized sections of the genus and enumerates the morphological characters employed during his study. He gives chromosome numbers, based on his own counts, for 14 species.

ZUSAMMENFASSUNG

Im einleitenden Teil seiner Revision von *Trifolium* sect. *Trifolium* (des ersten Abschnittes einer Revision der gesamten Gattung) gibt der Verfasser einen Überblick über die Geschichte der systematischen Einteilung der Kleearten, bespricht das Verhältnis der bahandelten Sektion zu den übrigen Sektionen der Gattung und nennt die im Zuge seiner Untersuchung herangezogenen morphologischen Merkmale. Er bringt auf eigenen Zählungen beruhende Chromosomenzahlen für 14 Arten.

The present paper is part of a revision of the species of *Trifolium* section *Trifolium* (sect. *Lagopus* of some authors), which includes 73 species and many varieties. The species concerned have been studied partly in herbaria and partly in the living state (some have also been grown for constancy tests). For a considerable number, chromosome counts are recorded here for the first time.

A full infraspecific treatment could not be undertaken at the present stage, especially not for some widely cultivated species such as *T. pratense, T. medium* and others which require intimate acquaintance with the cultivars and races. In such cases the author was content to restrict himself to the main subspecific or varietal units. A complete citation of their distribution data could also not be done here for the sake of brevity.

The following herbaria have put their collections at my disposal: Herbarium Aaron Aaronsohn, Zikhron-Ya'aqov, Israel (AAR); Ankara Universitesi, Fen Fakültesi, Botanik Enstitüsü, Ankara, Turkey (ANK); Botanisches Museum, Berlin, Germany (B); British Museum, Natural History, London, Great Britain (BM); Royal Botanic Garden, Edinburgh, Great Britain (E); Istituto Botanico dell'Università, Firenze, Italy (FI); Conservatoire botanique, Genève, Switzerland (G); Department of Botany, Hebrew University, Jerusalem, Israel (HUJ); Royal Botanic Gardens, Kew, Great Britain (K); Linnean Society of London, London, Great Britain (LINN); Institut de botanique de l'Université, Montpellier, France (MPU); Laboratoire de phanérogamie, Muséum national d'histoire naturelle, Paris, France (P); Botanical Department, Naturhistorisk Riksmuseum, Stockholm, Sweden (S); Botanisches Institut der Universität, Wien, Austria (WU). To all the directors and keepers of these herbaria, the author conveys his sincere thanks whether for lending him the material of for rendering him the facilities of carrying out this study in the herbaria and the libraries.

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The author is very obliged to Dr. Irene Gruenberg for her help in nomenclature and to Mr. D. Heller for his collaboration in some sections of the genus *Trifolium.* My thanks are also given to Mrs. Stefa Grizl for her devoted technical help in preparing the manuscript.

A brief history of the taxonomy of the section

Trifolium as a genus was already delineated by Tournefort (1700). Linnaeus (1753) not only recognized a large number of species of this genus, but was first to group them into categories, which, at least part of them, have been later ranked as genera or sections. Linnaeus' groups of *Trifolium* are: *1. Meliloti* with 8 species partly belonging to *Melilotus* and partly to *Trigonella; 2. Lotoidea* with 6 species; *3. Lagopoda* with 17 species, most of them members of *Trifolium* sect. *Trifolium* under review; *4. Vesicaria* with 4 species and *5. Lupulina* with 5 species.

Savi (1808-1810), revising the Italian clovers, tried to divide the genus into two units: "*Trifolia* ebracteata" and "*Trifolia* bracteata". True, the character of the bract is a very essential one in the sectional subdivision of the genus, but by far not the one fit for the subdivision of the whole genus. Savi has published a few species and also clarified some others.

Seringe (1825) has highly advanced the taxonomy of *Trifolium.* His revision embraces about 150 species including several American ones. His division of the genus into 7 sections is more or less well reasoned, although some of the species

of the respective sections have later been transferred to new sections or to other genera. Less successful was his division of *Trifolium* subgen. *Trifoliastrum* (the present sect. *Trifolium*) into 3 sections.

In his "Symbolae botanicae", Presl (1832) attempted to divide the genus *Trifolium* into 9 genera, viz. *Trifolium* (in about the same circumscription as *Trifolium* sect. *Trifolium* under review), *Amoria, Galearia, Mistyllus, Amarenus, Paramesus, Calycomorphum, Lupinaster,* and *Micrantheum.* Although almost nobody has followed Presl in regarding these natural divisions as genera, his delineation of the groups has, with few exceptions, been rightly taken up by the students of the genus, and these groups remain in use up to date.

Koch (1835), who was probably unaware of Presl's work, divided the genus into sections corresponding to Presl's genera. Though his names for the sections were not accepted, he was right in giving the groups sectional rank; this view has been followed by almost all botanists up to the present day.

Bertoloni (1851) included *T. uniflorum* in a separate section, named by him *Lupinaster,* a name already given to another section by Link (1822). Bertoloni's name was later replaced by Čelakovsky (1874) and others by *Cryptosciadium.*

Boissier (1872), presenting 113 species of *Trifolium* in his "Flora orientalis", has described about 15 new species. In his division of the genus he followed Seringe, Presl and others. His ranking and delimitations of the sections are consistent and clear-cut, and correspond almost entirely to our present view.

Čelakovsky (1874) has largely advanced our knowledge of the genus by his critical approach to the delimitation of the sections, and to the taxonomic relations of the eleven sections known at his time. Although retaining most of the sections in their previous limits, he proposed some transfers and tried, rather unsuccessfully, to outline the phyletic relations of the genus and its sections.

Very valuable contributions to the knowledge of the genus were given by Lojacono (1883a, b) in two articles: One of them deals with the American clovers of which 54 species are recorded, while the second is a key to the identification of the 211 species of clovers thus known. Lojacono divided the genus into the subgenera *Trifoliastrum* and *Lagopus,* divisions also accepted by some other botanists. These subgenera are, however, very unnatural and include very remote sections. To mention only the hyatic differences between *Trifolium* sect. *Trifolium* and sect. *Trichocephalum* which were included within his subgenus *Lagopus.* The same is true for the other subgenus which is even more artificial by including such different sections as *Lupinaster* and *Vesicaria.*

Gibelli & Belli (1889, 1890-1893) have, in their monograph of the Italian species of clover, presented a monumental work on *Trifolium* of both Italy and other Mediterranean countries. There are four achievements in their monograph: a critical treatment of the delimitation of the reviewed taxa; a rather comprehensive consideration of the nomenclature referred to; a delimitation of the sections; and a very intelligent establishing of subordinate divisions of the sections, which testifies to their deep knowledge of the species. The dichotomic keys and illustrations are another merit of these authors. The drawbacks in this work are the excessive fusion (lumping) of species, the inadequately reasoned admission of hybrids in convergent species and, of course, the inadequate knowledge of the non-Mediterranean species.

Ascherson & Graebner (1907-1908) followed Gibelli & Belli in most ot the species treated but contributed much to the knowledge of the infraspecific taxa

of many species. However, just this meticulous treatment of the lower units, often based on literature data, encumbers greatly the general view on the species of this genus.

An excellent historical review and a fruitful discussion on the taxonomic treatment of the genus by various authors was given by Bobrov (1947) who has revised the clovers of the USSR. His critical approach to the origin and phyletic position of the various sections is a considerable advance in the study of this genus. However, his retention of Lojacono's subgenera and the establishment of additional sections or subsections to the subgenus *Lagopus* is not only insufficiently reasoned but ignores the factual features that are peculiar to the various groups. Quite recently Bobrov (1967) advanced a theory according to which the genus *Trifolium* should not only be split into several genera (including some new ones), but that some of the latter should also be excluded from the tribe *Trifolieae.* This view, in my opinion, is lacking any substantial basis.

Vicioso (1952, 1953), in his revision of the Spanish clovers, has cleared up some taxonomical problems of this section, especially around *T. squamosum* and *T. gemellum.*

Hossain (1961), for the first time after Boissier (1872), checked the clovers of the Near East and supplied new data on the distribution of many species. He also described some new species and varieties. Despite his critical approach and exactitude in presenting most of the species, there are many omissions and misinterpretations in this revision: his ranking of the sections as subgenera; his inadequate knowledge of many species (e.g. the groups close to *T. alexandrinum* and *T. purpureum*); the omission of about 15 species, among them some already recorded by Boissier in his treatment, etc.

Oppenheimer (1959, 1961), in his enumeration of the Palestine clovers, has, among others, devoted much attention to the elucidation of the species close to *T. alexandrinum (T. berytheum, T. carmeli, T. vavilovii).*

Despite the many investigations, no comprehensive and satisfactory revision has been carried out for the whole genus since Seringe (1825), so that our knowledge of the genus *Trifolium* remained rather fragmentary. Especially important for the taxonomical subdivision of the genus are the American species for which no comprehensive revision has so far been made. What has been done is by far insufficient to supply a clear view of their systematic nature and their relationship with the clovers of other continents. For Africa the work of Gillett (1952) is of great importance.

The present author, in close collaboration with Mr. D. Heller, has carried out an extensive study on the whole genus including the American species, which amount to a hundred or so, and the African species. The first conclusion reached by him is that the genus *Trifolium* is a natural unit which should neither be split into independent genera nor be transferred into a tribe other than the *Trifolieae.* It includes about 240 species (about 1000 binomials), and should be divided into the following sections:

Trifolium sect. *Lotoidea*	America, Africa, Asia, Europe;
Trifolium sect. *Involucrarium*	America;
Trifolium sect. *Paramesus*	Eurasia;
Trifolium sect. *Mistyllus*	Eurasia, N. Africa;

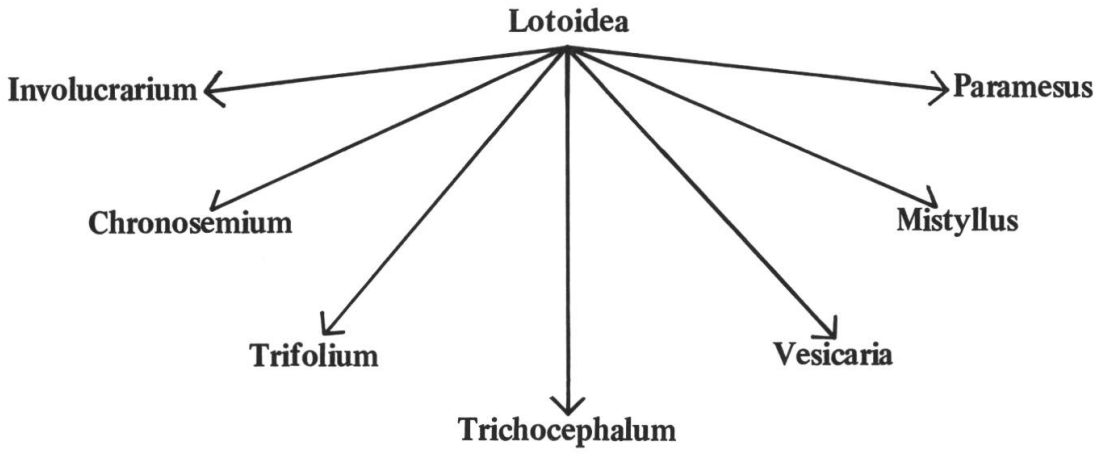
Trifolium sect. *Vesicaria*	Eurasia;
Trifolium sect. *Trifolium*	Eurasia, S. Africa;
Trifolium sect. *Chronosemium*	Eurasia;
Trifolium sect. *Trichocephalum*	Eurasia.

The taxonomic positions of the section and its subdivision

Trifolium sect. *Trifolium,* as conceived in this revision, has been taken by some as genus, by others as a subgenus, but by most as a section. It is one of the two largest sections of the genus and comprises about a score of perennial and over fifty annual species. Although well characterized and clearly delimited from others, some morphological traits are still present in this section that suggest connections with other sections, notably with *Trifolium* sect. *Lotoidea.* Students acquainted with the perennial species of this section will find here "vestiges" of bracts, as in *T. noricum* and *T. longidentatum,* or pedicels at least in the lower flowers of the head, as in *T. pignantii.*

It is a highly derived section and attains within the genus the same level of progression as the sections *Vesicaria, Chronosemium* and *Trichocephalum.* Within the section *Trifolium,* there is a clear evolutionary trend towards elaboration of the dispersal apparatus and dispersal mechanism.

Its systematic position within the genus is not difficult to assess. Looking on the section *Lotoidea* as the most primitive, and there is much evidence to do so, one may consider all the other sections as derivative and specialized. *Trifolium* sect. *Lotoidea,* which has the widest distribution range (America, Africa, Eurasia), is no doubt the only stock from which all other American and Eurasian sections have been directly derived, as outlined in the following scheme, which is based on sufficient morphological and biological evidence.



The above sketch can be reasoned as follows. *Trifolium* sect. *Lotoidea* is the most primitive group of the Eurasian representatives of *Trifolium.* It is the umbellate shape of the inflorescence, the pedicellate and bracteolate flowers and the two- to many-seeded suturally dehiscing pods, that testify to the more primitive structure of the reproductive organs. Carpobiologically, too, there are no special devices developed in this section; the pod-bearing calyces with or without their marcescent corollas are detached from the axis at maturity or after the decay of the plant. Taxonomically, it is the most difficult section; it has been divided by the present author into three subsections: *Lupinaster, Lotoidea* and *Platystylium.* The latter two were subdivided into quite a number of series and subseries, which testify to the complexity of the section.

Trifolium sect. *Involucrarium,* in spite of the advanced feature of the bracts forming an involucre, is still largely "lotoideal" by other features. Its subsection *Physosemium* shows, among others, a highly progressive character by converting the fruiting corolla into a vesicular body which seems to be quite effective in seed dispersal.

In *Trifolium* sect. *Chronosemium,* the pedicellate and bracteolate flowers are preserved. Dispersal is anthobolic, i.e. the dispersal unit is the calyx enclosing the pod, but two carpobiologically progressive characters came into appearance in this section: the persistent corolla serving as an effective anemochorous accessory; and the structure of the calyx with the stipitate ovary and pod which pushes the fruit more to the centre of the diaspore. This section is, no doubt, a terminal link in the anemochorous trend of seed dispersal with the aid of the corolla.

Trifolium sect. *Mistyllus* is a progressive derivative of the *Lotoidea* group. The bracteoles are well developed and a trend is taken in this section towards vesiculation of the calyx as a means of dispersal. While in some members (*T. spumosum, T. setiferum, T. aintabense,* etc.) the dispersal is calycobolic, in *T. argutum,* the terminal link of the line, dispersal is synaptospermic. As against the next section, vesiculation of the calyx is here symmetrical and the calyx lobes are equal in length.

The connection between *Trifolium* sect. *Vesicaria* and sect. *Lotoidea* is well manifested by the pedicellate flowers and the presence of bracteoles in some of the species. There is, however, a carpobiologically marked advance towards a two-lipped calyx, unilateral vesiculation and monospermy. The section starts, no doubt, with the perennial *T. tumens,* where the asymmetry of the calyx is less pronounced than in the annual members of the section. Dispersal is calycobolic but there is a trend in various varieties of *T. tomentosum* to synaptospermy.

Trifolium sect. *Paramesus* is a remote side-branch of sect. *Lotoidea* which reminds in some traits sect. *Trifolium;* it has from the former the minute bracteoles, the dispermy and the mostly regular calyx. From sect. *Trifolium* it has the sessile flowers and the leathery pod apex. The dentate or dentate-glandular stipules and the occurrence of an involucre suggest some connections with sect. *Involucrarium.*

Trifolium sect. *Trichocephalum* is the most derivative group of *Trifolium.* The evolution of the dispersal apparatus is connected here with the extreme reduction and complete sterilization of part of the flowers in the same head. Nature attempted here to transform several flowers of the head into dispersal accessories, whether anemochorous or zoochorous, or into a geocarpous drilling apparatus, that enable

the fruits of the few fertile flowers to penetrate the ground. Accordingly, one can divide this section into three series, the anemochorous one (e.g. *T. eriosphaerum, T. pauciflorum, T. meduseum*), the zoochorous one (e.g. *T. chlorotrichum*) and the geocarpous one (e.g. *T. subterraneum, T. israëliticum*). The phenomenon of transformation of part of the flowers of an inflorescence into a dispersal apparatus for the seeds of the few fertile flowers in the same inflorescence is not rare in some families (e.g. *Umbelliferae, Gramineae*), but not a single similar case is known to me in other sections of *Trifolium.*

Trifolium sect. *Trifolium* is, no doubt, a direct derivative of sect. *Lotoidea* through loss of the bracts, the pedicels, and the elaboration of the fruiting calyx as a dispersal unit. The fact that in some species, especially of the perennial ones, vestiges of bracts and pedicels do occur, is much in support of this suggestion.

The characters differentiating this section from the others are: the flowers are not pedicellate and not bracteolate; all the flowers of the head are well developed; the calyx, although variously shaped, is never vesiculate (as in *Trifolium* sect. *Vesicaria* and sect. *Mistyllus*). While all these characters are already found in the series *Neolagopus* of *Trifolium* sect. *Lotoidea,* the exclusive and characteristic feature of sect. *Trifolium* is the configuration of the calyx throat and calyx teeth. The former ranges from hairy but open to closed by a 2-lipped callosity, with intermediate structures between these extremes (e.g. hairy and callous rings, epidermal protrudings). The calyx teeth vary in size, proportion between the lower tooth and the rest, degree of divergence, etc. The other, less exclusive, character is the structure of the pod, which is usually membranous with a leathery, irregular, cup-like upper part. It contains a single seed, is hidden in the calyx tube and never dehisces suturally. The biology of dispersal is also manifold. In most cases the fruiting calyx separates at maturity from the rhachis of the head; in other cases, the fruiting calyx persists on the rhachis and on the plant; and in still other cases, the fruiting head separates as a whole from the peduncle. On these and some other characters, the species of this section can be grouped in a number of subsections.

The question whether the section as a whole constitutes a phyletically uniform entity or presents an assemblage of groups of different origins, but sharing some common characters through morphological convergence, will be discussed on another occasion. Here we wish only to mention that the divergence of opinion as to whether this group should be classed as a genus, (e.g. Presl 1832), a subgenus (e.g. Hossain 1961), or part of a subgenus (e.g. Čelakovsky 1874, Lojacono 1883b, Bobrov 1947), or a group of sections (e.g. Seringe 1825), or as a section (e.g. Koch 1835, Boissier 1872, Lojacono 1878, 1883a, b, Gibelli & Belli 1889, and others), is not of great importance. The author of the present study joins the "sectionists" for the reason that the characters mentioned are not weighty enough for the rank of a subgenus as conventionally understood.

There is also a divergence of opinions as to the division of the section into subsectional units. The present author approaches in principle the view of Gibelli & Belli (1889) who distinguished within this section a series of groups, classed by them under "stirpes". These represent morphologically, biologically and presumably also phyletically most natural clusters that should be ranked as subsections as will be seen from the following.

The species delimitation within *Trifolium* sect. *Trifolium* (and probably also within other sections of *Trifolium*) is not as problematic as in some other genera,

e.g. *Astragalus, Onobrychis, Vicia,* etc. A thorough examination of this section reveals that there is little overlapping in the main diagnostic characters, and not much grading between the reasonably conceived species; it seems that there are very few (if any) interspecific hybrids. Thus, the main problems are here those of ranking rather than such of delineation of the taxa.

Almost all the species recorded here are conceived as such by most of the authors. However, already at a first reconnaissance of this section, one reveals that it is made up of a whole lot of more or less discrete species-clusters fairly well distinct from one another by sets of reproductive and vegetative characters: to mention the groups of *T. alexandrinum, T. echinatum, T. arvense, T. purpureum, T. scabrum, T. gemellum, T. bocconei, T. pratense.* These groups are separated from one another to an extent as to raise some difficulties in the building up of an evolutionary scheme within the section. They are considered here as subsections and have been further elaborated in accordance with the present more extensive treatment of the section. Part of these subsections has already been accepted by Bobrov (1947) and also implicitly conceived as such by Ascherson & Graebner (1907-1908). Hermann (1936) and others have coined sectional names for them, but these seem superfluous to us. All the above authors, and among them also Gibelli & Belli, have tried to group our subsections into 2-3 higher units, such as: *Prosbatostoma, Intermedia* and *Stenostoma.* But these categories are based mainly on characters which are rather dynamic within the section.

The morphological characteristics of the section and their diagnostic values

Life form

As in most of the other sections, life form varies here from tiny annuals to rhizomatous perennials. The perennial habit is, no doubt, a more primitive character than the annual. This is evidenced by the fact that the annual species are much more derived in regard to their reproductive characters. The fact that polyploidy exclusively occurs in the perennials, while the annuals hitherto examined are all diploid, does not contradict this assumption, since polyploidization could have taken place within the group of perennials themselves.

Noteworthy is the fact that all the perennials of this section form 3 discrete groups which show no obvious phyletic connections with the annuals. Life form is, no doubt, a diagnostic character here as in other sections.

Leaf

There is a whole array of leaf forms in this section, and all are reliably diagnostic. Juvenile (or basal) leaves differ markedly in shape and size from the more adult ones. The former have mostly ovate or obovate or broadly elliptical leaflets, even in species where most of the leaflets are narrowly elliptical or oblong.

The shape of the leaflets varies to a small extent and is generally a reliable character. The nervature patterns of the leaflets are constant for each species. So, for instance, is the arcuate-recurved type of nervature typical of the whole *Scabroidea* subsection.

The configuration of the stipules is also a most reliable character in certain groups: to mention the stipules in the *Stellata* group, and of *T. sylvaticum,* or the leaf-like stipules in *T. medium, T. longidentatum* and *T. wettsteinii.* The extent of adnation of the stipules to the petioles varies from the lower leaves to the upper. An extreme degree of adnation is characteristic of *T. patulum* which reminds by this feature the Tropical African *Ochreata* group of the *Lotoidea* section.

Phyllotaxis

The leaves are usually alternate, but in definite groups of species the uppermost leaves appear constantly opposite. This is generally caused by the approximation of the uppermost buds, which sometimes gives rise to a false dichotomy. Usually, however, one branch of this fork is extremely depressed so that the stem terminates in one pedunculate or sessile head subtended by a pair of opposite leaves.

Ramification

Almost all the species display a diffuse basal branching and there is only little use of this character for taxonomy of the section. However, there are a few species in which the stem character is of diagnostic value, namely where the stem appears to be scapose because of the crowding of the leaves near the base (e.g. in *T. davisii, T. noricum,* etc.).

Indumentum

The hair cover in this section varies from sericeous, hirsute, villous to hispid. The nature of the indumentum is definitely constant, modification may occur in the density of the hair cover, ranging from densely hairy to glabrescent or glabrous, but this refers only to very few species (e.g. *T. pratense, T. medium*). Highly constant is also the direction of the hairs (appressed or patulous, antrorse or retrorse). There are some closely related species which can be distinguished, at a first glance, by this character (e.g. *T. palaestinum, T. purpureum, T. dichroanthum*).

Inflorescence

Heads vary from few-flowered (e.g. *T. congestum*) to such with 100 or more flowers (e.g. *T. trichocephalum*). The shape of the head varies from ovate, cylindrical to spherical, although there is more constancy in the shape of the flowering head and less in that the elongating fruiting head.

Flower and fruit

The most important diagnostic characters are connected with the size, shape and proportion of the flower and flower parts. Flowers range in size from 2 mm *(T. arvense)* to 2.5 cm *(T. trichocephalum)*.

The calyx offers a variety of characters, the most notable of which are: size and shape, proportion between teeth and tube, indumentum, nervature, throat (open, closed, with or without a callosity), proportion between lower tooth and upper ones, nervature of teeth, orientation of teeth, tip of teeth (blunt or sharp-pointed, purple or green), presence or absence of separation tissue at base of fruiting calyx.

Among the characters of the corolla, the following seem to be diagnostic: proportion between corolla and calyx, shape of standard, proportion between standard, wings and keel, colour of corolla, persistence of the latter, etc.

The pod may be stipitate or not, membranous throughout or with cartilaginous leathery operculum at apex.

The dispersal is called abolic where the calyx is not separating from rhachis (e.g. in *T. alexandrinum, T. echinatum, T. latinum*); calycobolic where the dispersal unit is the pod-bearing calyx (in most of the species); and synaptospermic if it consists of the entire fruiting head (e.g. in *T. scutatum, T. plebeium*).

These are the main characteristics upon which the taxonomy of this section is based. They are sufficient to delineate species and subspecific units.

Chromosome numbers

In about 40 out of the 73 species of this section, chromosomes have been counted. Except for 3 species, all are diploids with $2n = 14$ or 16. The following is a list of species examined for chromosome numbers in connection with the present study.

T. alexandrinum L.	$2n = 16$	*T. palaestinum* Boiss.	$2n = 16$
T. berytheum Boiss. & Bl.	$2n = 16$	*T. plebeium* Boiss.	$2n = 16$
T. constantinopolitanum Ser.	$2n = 16$	*T. purpureum* Loisel.	$2n = 16$
T. dasyurum C. Presl	$2n = 16$	*T. scabrum* L.	$2n = 16$
T. echinatum M. B.	$2n = 16$	*T. scutatum* Boiss.	$2n = 16$
T. lappaceum L.	$2n = 16, 14$	*T. stellatum* L.	$2n = 14$
T. meironense Zoh. & Lern.	$2n = 16$	*T. vavilovii* Eig	$2n = 16$

Chromosome countings made by others in other species of this section do not alter much the nature of this section in this regard. The few polyploids are perennials; all the others, both perennials and annuals, are diploids belonging to various

subsections. From the short list recorded here, it is obvious that there is little (if any) application of chromosome numbers for taxonomic purposes. The same is true for other sections and even for many other genera of the *Leguminosae.*

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(To be continued)

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