

Taxonomic Studies on the Tribe Senecioneae of Eastern Asia

I. General Part

by

Hiroshige KOYAMA

Botanical Institute, College of Science, University of Kyoto

Abstract

This is the first part of the taxonomical revision of the Tribe Senecioneae in Eastern Asia. There occur fourteen genera of that tribe. An attempt is made to clarify the relationships among the members from the standpoints of comparative morphology and chromosome study. In the following parts of this paper, the enumeration will be given concerning to respective taxa.

Introduction

The Senecioneae have customarily been considered as a distinct tribe of the Compositae, though there are some genera of doubtful position. Fourteen genera are known in Eastern Asia. All of these genera have correctly been placed in the Tribe Senecioneae, but their definitions are given variously according to the authors concerned. The distribution of most of these genera is not restricted within one botanical region, extending widely to the temperate Eurasia. The number of the species is most abundant in Southwest China, and accordingly, we can find various forms there. We are at present interested in the taxonomical problems to be settled about the relationship within the members of Eastern Asia. Comprehensive contributions have been made on the classification of these genera. No revision has yet been given covering all the members in question. Recently, the materials of the Himalayan regions have been available in Japan, and now we can make further speculation on the affinities and relationships among our genera and species. Particularly, the Himalayan plants now available are excellent materials for the study of morphology and cytology.

All the investigations ever made suggest that our fourteen genera have no common ancestor and are the descendants along various courses of evolution from several ancestors. To know the natural relationships more precisely, we have to prepare the detailed data of phytotaxonomy, and especially those of cytotaxonomy and comparative morphology.

The important problem in taxonomy is to clarify the relationship among the

species. To investigate the interrelationship of our species, I have treated some species groups, because sometimes the genera and sections proposed are, in my opinion, not so homogeneous units.

The investigation on some complex species groups may offer suggestions concerning the speciation and differentiation of the various forms.

For example, *Cacalia hastata* complex is one of the most interesting representatives. This species complex, ranging widely from Europe to Eastern Asia, contains a good deal of confusion in taxonomical treatise, for various authors have treated the group in various ways; also there are many problems in species classification among the taxonomic entities occurring in some widely distributed species, such as *Senecio nemorensis*, *S. scandens*, *S. integrifolius*, *S. aurantiacus*, *Ligularia sibirica* and so on. Such widely distributed species are usually polymorphic, and the extreme forms taken from far distant stations seem to be distinct enough from each other, but numerous intermediate forms, occurring in the intermediate areas between the extremes, make us deny the specific separation for such superficial recognition. Thus, the union into one species is inevitable to give a natural relationship among the various forms of such polymorphic species.

The present study is an attempt to bring together this divergent information so as to clarify the existing problems, as well as to show the relationships among the members defined more easily. To make the classification more clearly, special attention is here paid to the cytological and comparative morphological investigations. It is shown that the information on the chromosomes is very significant to know the systematics of the species under consideration, though much work remains to be done concerning cytology, especially on some Himalayan species of such genera as *Cremanthodium*, *Doronicum*, *Cacalia* and *Senecio*.

In this work, I exclude proper Siberian and Central Asiatic species and include Himalayan species beside proper Eastern Asiatic species.

Acknowledgment

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enumeration of species.

And last but not least, I should like to express my sincere thanks to my father and late grandmother. Without their continuous encouragement, none of my work would have been accomplished.

Historical Account

After the foundation of the Tribe Senecioneae by CASSINI in 1819, no particular amendment has been made for the circumscription of this tribe by any followers. There are about fifty genera widely distributed in the world, fourteen of them occurring in Eastern Asia. Of these genera *Arnica*, *Cacalia*, *Doronicum*, *Senecio* and *Tussilago* are originally circumscribed by LINNAEUS (1754), and *Petasites* by HILL (1756). GAERTNER recognized the genus *Senecillis* in 1791. Around 1820, CASSINI reported various genera: *Ligularia* (1816), *Emilia* (1817), and *Gynura* and *Nardosmia* (1825). These genera were revised by DE CANDOLLE (1836–37) in the worldwide scope, and about 160 species are enumerated in Eastern Asia.

After DE CANDOLLE, a number of species were added by SIEBOLD & ZUCCARINI (1846), MAXIMOWICZ (1850–81), MIQUEL (1866) and so on from our area. In 1850, GRENIER & GODRON reduced *Nardosmia* to a section of *Petasites*. LINDLEY (1857) made the description of *Farfugium* on a cultivated plant from China. Two years later, MAXIMOWICZ described a new genus, *Syneilesis*, based on Chinese *Cacalia aconitifolia* BUNGE, by its peculiar character of having a single cotyledon.

In 1873, BENTHAM delimited the Himalayan genus *Cremanthodium* in HOOKER'S *Icones Plantarum*. In *Genera Plantarum* (1873–76), BENTHAM reduced *Senecillis* and *Farfugium* to *Senecio* Sect. *Ligularia* and *Syneilesis* to *Senecio* Sect. *Cacalia*, and referred two Himalayan species of *Ligularia* to the Andean genus *Werneria*. In his revision of Indian Compositae, C. B. CLARKE (1876) enumerated 68 species of those genera in the sense of BENTHAM. In the *Flora of British India* in 1881, HOOKER f. transferred two species which were placed in *Senecio* Sect. *Cacalia* by C. B. CLARKE to *Senecio* Sect. *Synotis*, and one species of Sect. *Cacalia* to Sect. *Ligularia*. About 10 years later, HOFFMAN (1894) revised the genera of Compositae of the world, and recognized eleven genera in Eastern Asia.

FRANCHET (1875–94), WINKLER (1893–1905), KOMAROV (1900–03) and DUNN (1903) reported many new species from China and Siberia under the system of BENTHAM. In 1879, FRANCHET & SAVATIER described a new genus *Mallatopus* from Japan. From 1920, HANDEL-MAZZETTI made great contributions to our problems. In his revision of the genus *Cremanthodium*, R. GOOD (1928) arrived at a conclusion that "the high alpine Asiatic derivatives of *Ligularia* shall remain grouped together in the phylogenetic and ecological genus *Cremanthodium*".

In 1938, HANDEL-MAZZETTI revised the Chinese species of *Ligularia* and enumerated 82 species.

From the last decade of 19th century, a number of reports have been accu-

mulated by Japanese taxonomists, MATSUMURA, MAKINO, HAYATA, NAKAI and so on, from Taiwan, Korea, Japan and Saghalin. In 1897, MAKINO reduced *Mallatopus* to *Arnica*. In 1915, NAKAI proposed a new section, *Cacalia* Sect. *Dendrocacalia*, based on Bonin *Cacalia crepidifolia*. Later, he (1928) gave generic status to *Dendrocacalia*. In 1915, NAKAI proposed a new genus, *Cyathocephalum*, on the basis of its connated involucre scales and the sterile hermaphrodite florets. The latter character was revised by KITAMURA and he found that the hermaphrodite florets were fertile after long cultivation of the type species, *C. angustum*. As the connate involucre scales are found also in some species of *Cremanthodium*, KITAMURA (1939) reduced *Cyathocephalum* to a section of *Ligularia*. In the same year, KITAMURA revised the genus *Farfugium* emending some important characters. In this paper, KITAMURA noted that *Cremanthodium* as well as *Werneria* should be united with *Ligularia*. In 1942, KITAMURA published *Compositae Japonicae III*, in which he enumerated 11 genera and 71 species in the Subtribe Senecioninae of Tribe Senecioneae, from the areas covering Taiwan, Korea, Japan and Saghalin.

In 1943, B. MAGUIRE revised the genus *Arnica* and enumerated 32 species, excluding the Japanese species, *Arnica mallatopus*, from *Arnica*.

Recently, valuable materials from the Himalayas have become available for Japanese botanists. With the knowledge obtained from those materials, KITAMURA (1955) described several new species of *Cremanthodium* and *Ligularia*, but he did not refer to the classification of the genus *Cremanthodium*.

On the flora of Euro-Siberian region, POJARKOVA reexamined the genus *Cacalia* in *Notulae Systematicae ex Herb. Nom. Kom. XX* (1960), and SCHISCHKIN and others enumerated all the known members of Senecioneae in *Flora URSS XXVI* (1961). In this flora, KUPRIANOVA gave generic status to *Nardosmia*.

Taxonomic Characters

Although comprehensive studies have been made on *Senecio* and the allied genera, we can not find as yet any particular characteristics to indicate the classification of the genera now under consideration, except in the case of single cotyledon in the genus *Syneilesis* and involute blade in *Farfugium*. In fact, among those genera a feature which is characteristic to one group is highly variable in the others. In spite of their distinctness in the genera cited above, our genera seem to be closely related to each other as shown by their morphological features as well as in their geographical distributions. For revising the taxonomic groups proposed by the previous investigators, the following characters will be discussed here in this study.

Morphology

Although the classification in the rank of Section will be modified in the following pages of this paper, the discussions will be given here concerning the morphology and chromosome study by using the current sectional names.

Habit

All the species of our genera are perennial except for some annual species of *Emilia* and of *Senecio*. There are some climbing herbs in *Senecio* Sect. *Synotis* and in *Gynura*, and one example is shrub in *Dendrocacalia*. All the others are erect herbs in their growing habit. The species of *Cremanthodium*, *Farfugium*, *Ligularia*, *Petasites*, *Tussilago*, and some species of *Arnica* have radical leaves, and some species of *Gynura* have subradical leaves. The other species have no radical leaves but have several cauline ones. *Cacalia* Sect. *Taimingasa*, *Miricacalia* and *Syneilesis* have few very large leaves.

Usually our genera have alternate leaves, but *Arnica* has exceptionally opposite leaves. The opposite leaf is suggested by A. CRONQUIST (1955) as being primitive within the Compositae.

Root

No particular feature is found in the roots of the genera. The characteristics of the roots are sometimes useful to diagnose the species. Many genera have the repent rhizomes with fibrous roots, while *Ligularia* and *Cremanthodium* have only the fibrous roots starting from the base of the stems. Some members of *Cacalia* and *Senecio* have long rhizomes. Some species of *Cacalia* and *Miricacalia* have repent thick rhizomes. *Emilia* has a well developed primary root.

In some species of *Gynura*, the subterranean stem develops to form a tuber. The subterranean stems have a tendency to form a tuber in *Syneilesis*, *Farfugium* and *Doronicum*, too.

Leaves

Cotyledon Dicotyledonous plants have generally two cotyledons. It is distinct that *Syneilesis* has only a cotyledon which is orbiculate and convolute. This character is found in all the species of *Syneilesis*. All other genera under consideration have two cotyledons. This feature is peculiar to *Syneilesis* and it is practical to circumscribe this genus by that. However, this peculiar cotyledon may be an apparent cotyledon, for it is observed in the germination of some *Cacalia* species that the first leaf is very similar to the well developed cotyledon of *Syneilesis*. The two cotyledons of *Syneilesis* are considered as being completely reduced in this hypothesis.

Vaginate sheath of petiole This feature is generally considered as an advanced character. *Ligularia* has the vaginate sheath of petiole, but is not restricted in this genus. The vaginate sheath of *Ligularia* is observed in the petiole of cauline leaves as well as in that of radical leaves. The vaginate sheath of some *Cremanthodium* does not differ essentially from that of *Ligularia* except for the size. In the other genera having the radical leaves, the vaginate sheath is found only in the radical leaves. The petiolar base of *Farfugium* does not form the true vaginate sheath but only encircles the stem. The short vaginate sheath but only encircles the stem. The short vaginate sheath is of use to define the section of *Cacalia*, i.e. Sect. *Taimingasa* is distinguished from Sect. *Cacalia*

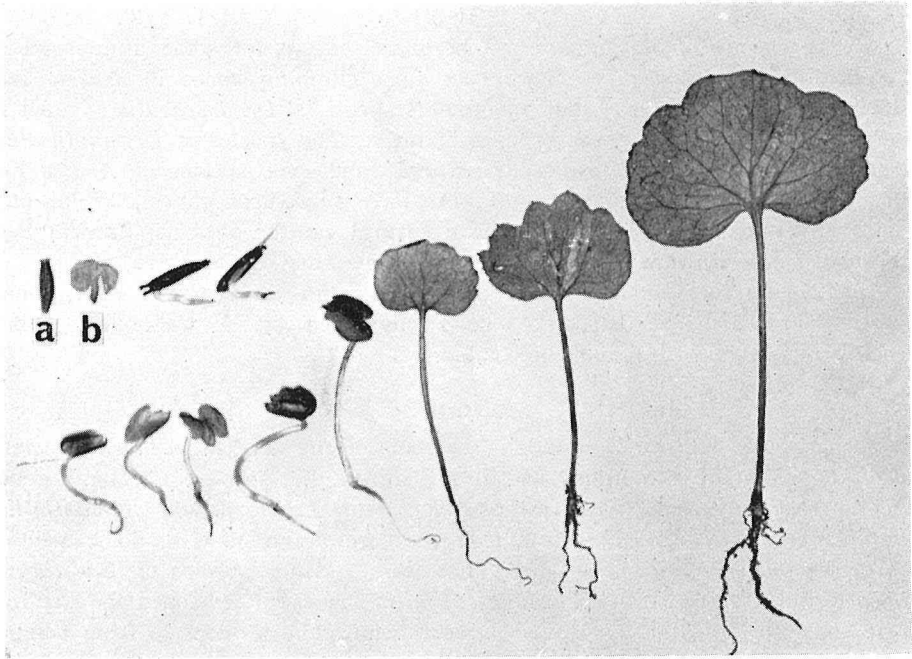


Fig. 1. Germination and seedling of *Syneilesis palmata*.
a. achene. b. embryo in an achene.

by this feature. However, in some species of Sect. *Cacalia*, the petiole base of the lower cauline leaf develops to some extent and takes the appearance of the vaginate sheath. Therefore, this feature may be taken into account as a comparative one.

Vernation The genus *Farfugium* is closely related to *Ligularia*, but easily distinguished from this and the allied genera by the involute vernation of their leaves. This feature is very peculiar to the genus *Farfugium*, as has been pointed out by KITAMURA (1939) in his revision of this genus.

Radical leaves According to the field observation, this character is very obvious and fairly constant to define the natural groups. *Ligularia* Sect. *Ligularia* is distinguished from Sects. *Cyathocephalum* and *Senecillis* by patent radical leaves. The radical leaves of *Senecio* Sect. *Nemosenecio* soon wither, while those of Sects. *Tephroseris* and *Heloserides* persist till the flowering season.

Cauline leaves The cauline leaves of *Cremanthodium*, *Farfugium*, *Ligularia*, *Petasites*, *Tussilago* and *Senecio* Sect. *Tephroseris* do not develop as well as those of *Cacalia* and some other sections of *Senecio*. The cauline leaves of *Ligularia leesicotal* of Himalaya develop well and have thick petioles. But the base of the petiole does not encircle the stem as those of the other species. All the members of *Cacalia* Sect. *Taimingasa*, *Miricacalia* and *Syneilesis* have few (2-3) cauline leaves. While other sections of *Cacalia* have usually 5-9 cauline

leaves, though *C. adenostyloides*, a species of Sect. *Cacalia*, bears only a few (2-4) leaves.

Peltate leaves The peltate leaves are found occasionally in various taxa. The peltate leaves are known, at present, in five or more American species even in the genus *Cacalia*, but none of the Chinese species of *Cacalia* has a peltate leaf.

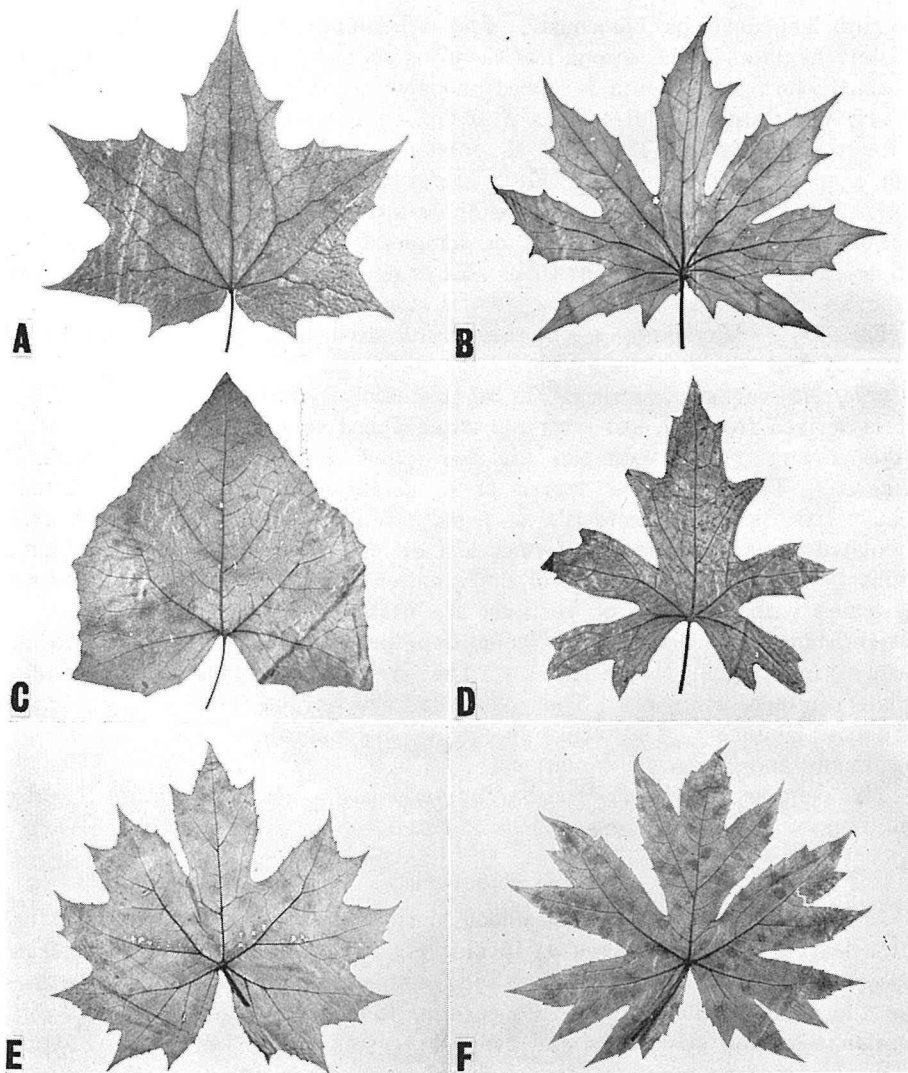


Fig. 2. Leaf shape and venation. Palmate leaves of *Cacalia kiusiana* (A) and *C. delphiniifolia* (B). Triple-ribbed venation of *C. farfaraefolia* (C) and palmate-like leaf of *C. farfaraefolia* var. *acerina* (D). Palmate-like leaves of Sect. *Taimingasa* : *C. pseudotaimingasa* (E) and *C. yatabei* (F).

All the species of *Syneilesis* have the peltate leaves. The peltate construction of leaves seems to be connected with the circular petioles. The petiole of *Miricacalia* is terete except the very base and is attached to the lamina not at the margin but at the inside. I have observed the successive developmental stages of *Cacalia peltifolia* from the germination to adulthood. The first leaf comes out in the form of a closed umbrella, after the cotyledons turn green. The first leaf develops vigorously, and is pentangular in outline, 5-lobed and minutely dentate. The second leaf develops successively, taking the appearance of palmate form, and being 5-7-lobed and roughly dentate. After the cotyledons fall off, the third leaf develops as if springing out from the base of the petiole of the second leaf. This leaf is palmate, 5-7-lobed and roughly dentate. Such a form is found in the adult leaves of *C. delphiniifolia* (H. KOYAMA 1962). The early leaves do not take the peltate construction as seen in the case mentioned above. Taking almost or completely peltate appearance, the fourth leaf develops. The following leaves always develop from the base of the petiole of the preceding leaves, until the stem is stopped by an inflorescence.

Venation MATSUMURA & KOIDZUMI (1910) divided Japanese *Cacalia* into two groups by leaf shape : folia palmatifida and folia indivisa. The leaf of *C. farfaraefolia* var. *acerina* seems to be palmately lobed, but this palmate-like leaf is derived from the leaf with the triple-ribbed venation by adding two teeth of the margin. Such examples are also found in some species of Sect. *Tai-mingasa*. Truly palmate leaves of *C. delphiniifolia*, *C. tebakaensis* and so on have five, seven or more ribs of equal strength, though they have weaker reticulated veins. Thus, the former leaf differs from the latter in its number of ribs. There is a third type of the venation which is fundamentally pinnate. The leaves with this type of venation are hastate or reniform in outline. In *Cremanthodium*, R. GOOD (1928) notes that the radical leaves are of two quite distinct kinds equally represented. The first has long petioles and round or cordate reniform laminae. The second has short or no petioles, and lanceolate or cuneate laminae. The former has principally palmate venation and the latter has pinnate and/or parallel venation.

The venation of the leaf of *Farfugium* is palmate, and that of *Ligularia* is pinnate.

Pubescence

Almost all of the species now under consideration possess multicellular hairs on the leaves, scapes and even on involucre. The achenes of *Emilia*, *Arnica*, *Farfugium*, *Dendrocacalia*, and some species of *Senecio*, *Gynura* and of *Doronicum* have the multi-cellular hairs. Concerning the leaf and achene hairs, corolla venation, pappus structure, and ovarian crystal, D. G. DRURY & L. WATSON (1965) reported the result of their microscopical observations on the forty-five species in Eurasian *Senecio*. Their investigation adds the taxonomical importance to the trichomes of those species. In fact, it seems to be valuable to detect the occurrence of hairs in the herbarium taxonomy.

Leaf hairs D.G. DRURY & L. WATSON distinguish ten types in the cellular construction of leaf hairs and conclude that there can be little doubt that the nine groups (one group includes two hair types, type 9 and type 10) represent true taxonomic relationships among the species. The soundness of Sect. *Tephroseris* which is considered as a natural group by many investigators is confirmed by their observations. Sect. *Tephroseris* has the 5th type of hairs. Sect. *Nemosenecio*, related closely to Sect. *Tephroseris* (H. KOYAMA 1966 a), has also the 5th type of hairs on the leaves beneath. Some species of *Ligularia* have the 5th type of hairs on the leaves beneath. On the scape, however, there are two types of the cellular construction of hairs in *L. fischeri*, *L. sibirica* and *L. hodgsonii*: one consists of a few rows of cells and the other of one row of cells (H. KOYAMA 1966 b).

Achenial hairs As mentioned above, glabrous achene is useful as a key character to the genera concerned. Of such genera as *Cacalia*, *Syneilesis*, *Miricacalia*, *Ligularia*, *Cremanthodium*, *Tussilago* and *Petasites*, the achenes are glabrous. The achenes of all members of *Farfugium*, *Dendrocacalia* and *Doronicum* have hairs. Concerning *Emilia*, *Gynura* and *Senecio*, the glabrous achene is of significance only at the specific level. In some species of *Senecio*, achenial hairs are not constant. For instance, *S. nemorensis* is distinguished from *S. angustum*, vicarious species of *S. nemorensis* in Taiwan, by the glabrous achenes. Many specimens of *S. nemorensis* of Japan, Korea and China have glabrous achenes but occasionally some individuals have hairy achenes.

Inflorescence

The inflorescence consists of a single head in most species of *Cremanthodium*, *Arnica*, *Doronicum*, and in some species of *Ligularia* and *Senecio*, while it consists of a few to many heads in all the other species of our genera. In *Ligularia* there are three types of inflorescence: one consists of a head, the second is corymbose and the third racemose. Three series of Sect. *Ligularia* are distinguished, respectively, by their type of inflorescence. Korean *L. jamesii* is, at present, the sole species known to Series *Monocephalae*. There are plenty of species in both of the other series. Although *L. hodgsonii* and *L. kaialpina* have been referred to Series *Corymbosae*, they have various intermediate forms of inflorescence between corymb and raceme. In the inflorescences of those species, flowering occurs successively from the basal head to the apical one with several exceptions. Such sequence of flowering is also found in Series *Racemosae* and in Sects. *Senecillis* and *Cyathocephalum* of *Ligularia* and even in the genus *Miricacalia*.

On the other hand, in the corymbose inflorescences of *L. dentata* and *L. japonica*, flowering occurs successively from the central head to the marginal one. This sequence of flowering is found generally in Compositae, and is called centrifugal. From these facts, *L. hodgsonii* and *L. kaialpina* may better be transferred to Series *Racemosae*.

As some species of *Cremanthodium* have several heads, the difference between

Ligularia and *Cremanthodium* seems to be obscure. Concerning the racemose *Cremanthodium*, this genus differs from *Ligularia* in the sequence of flowering : the sequence is centrifugal.

The type of inflorescence is also applicable to the specific classification in the genus *Syneilesis*.

Heads

The radiate and discoid heads occur in our genera. *Cacalia*, *Miricacalia*, *Syneilesis*, *Gynura*, *Emilia* and *Dendrocacalia* have discoid heads. In the original description of the genus *Mallatopus*, FRANCHET & SAVATIER (1879) gave importance to discoid heads and compared them with *Eupatorium*, *Mikania* and *Gynura*. In 1897, however, MAKINO reduced this genus to *Arnica*, because the other characters of the genus are not so particular as compared with those of *Arnica*. As for the other genera except for those cited above, the radiate or discoid heads are of use for the classification of infrageneric taxa. In some species of *Senecio* and *Petasites* with discoid heads, the ray florets occasionally appear in some individuals.

Solitary and cernuous This feature is characteristic to the Himalayan *Cremanthodium*. The solitary head is occasionally found in some species of allied genera: *Tussilago farfara*, *Ligularia jamesii*, some species of *Arnica*, *Senecio* and of *Gynura*. These solitary heads are not cernuous. *Cremanthodium* with several heads is very similar to *Ligularia*. However, the branches of the corymb of *Cremanthodium* are divaricate and every head is always cernuous.

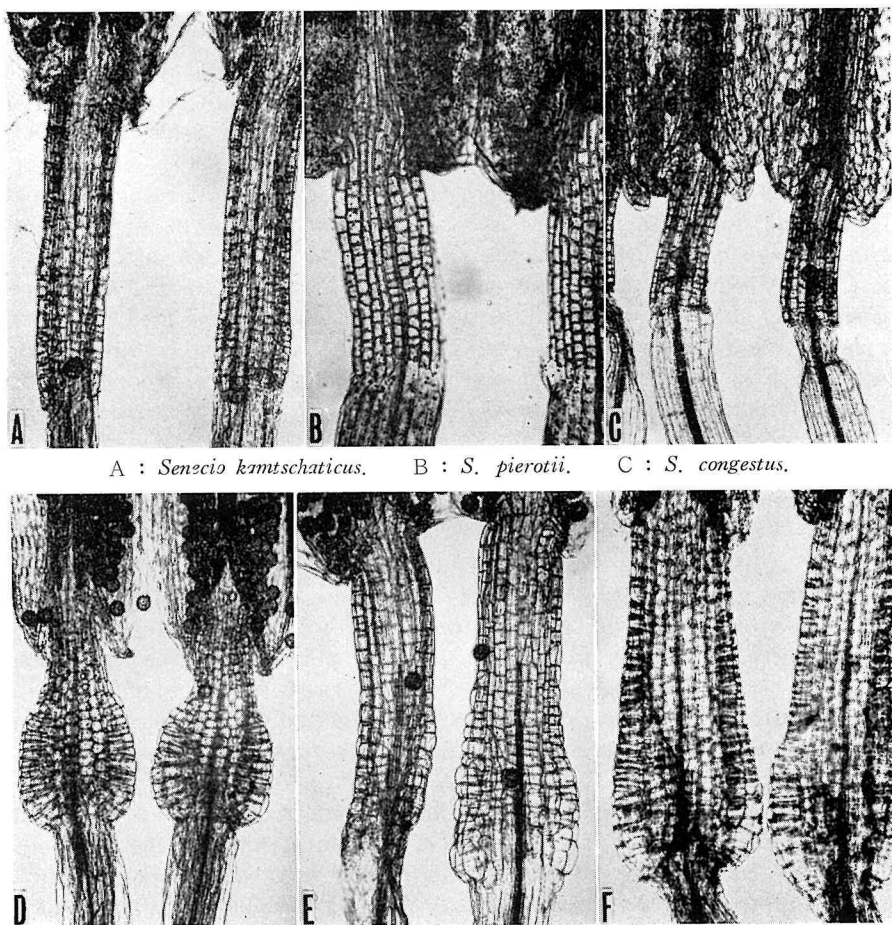
Involucral scales In Senecioneae, generally, the involucral scales are 1-seriate and subequal. This feature well characterizes this tribe. Subtribe Othonninae are distinguished from the others by the fused involucral scales. This feature is also found in some species of *Ligularia*: Sect. *Cyathocephalum* differs from the other sections which have free involucral scales. NAKAI (1915) assigned generic value to this character, but concerning the other respects, Sect. *Cyathocephalum* is not so particular in *Ligularia* as KITAMURA mentioned. The involucral scales of *Ligularia* distinctly imbricate. Therefore, the connate involucre of *Cyathocephalum* may better be interpreted as a feature derived secondarily. Most of the genera have membranous involucral scales, but *Doronicum* and *Arnica* have herbaceous ones.

Size and number The size and number of heads may stand as a useful character at the sectional level in the genus *Senecio*. Sect. *Crociseris* is characterized by the head large in size and small in number, while Sect. *Jacobaea* is characterized by the head small or medium in size and large in number. In some genera, the size and number of heads are fairly constant for all the species. *Arnica* and *Doronicum* have a few large heads, while *Cacalia*, *Dendrocacalia* and *Syneilesis* have many small heads. *Ligularia japonica* and *L. dentata* have fairly large heads as compared with the other members.

Floral parts

Style branches The form of style branch is usually considered as the tribal

character. In the Tribe Senecioneae, generally the style branches are truncate with a ring of hairs at the end. There are, however, slight differences in this character among the members of the genera now under consideration : the style branches taper off and are covered with papillae for their entire length beneath in *Farfugium*, *Ligularia*, *Cremanthodium* and *Gynura*, and they do not taper off in those of the remaining genera. In his revision of the genus *Crassocephalum*, S. M. MOORE (1912) notes that *Crassocephalum* and *Gynura* are quite different from *Senecio* in the form of their style arms. The style arms of the hermaphrodite florets of *Petasites* and *Tussilago* are scarcely branched. As to the genera *Miricacalia*, *Syneilesis*, *Cacalia* and *Arnica*, the forms of style branches are similar to each other. There are slight differences between these genera and *Senecio*, including *Emilia*, in the forms of the style branches and in the places



A : *Senecio kzmshaticus*. B : *S. pierotii*. C : *S. congestus*.

D : *Senecio aquaticus*. E : *S. resedifolius*. F : *S. spathulifolius*.

Fig. 3. The cells of upper part of filaments.

of hairs. The hairs are dense on the whole surface of the apex of the style branches in the former 4 genera, while in *Senecio* and *Emilia* they occur only at the margin of the discoid apex of the style branches.

Filament cells The stamen of disk florets has its anther at the end of the filament. In the genus *Senecio*, the form of the upper part of filament is useful to define the sections. The cell walls of the upper 4–6 mm portion of filament are thicker and are easily distinguished from those of the other part which are not so thick. In his original description of *Senecio* Sect. *Nemosenecio*, KITAMURA notes that the width of the upper part of filament is the same as that of the other part, while in the other sections the width of the former is broader than that of the latter. From a recent microscopical observation, I have found that there are two types in cell form of the upper part of filament: one is composed of the cells of the same size, and the other bears large cells at the base. In the case of the latter type, the part consisting of large cells is wider than the other part of filament. On the other hand, in the case of the former, the width of the upper part of filament is the same as that of the other part. The filament without larger cells at the upper part is found in Sects. *Nemosenecio*, *Tephrosensis* and *Heloserides*. In the remaining sections, the other type is observed. In most of the other genera, the filament is of the former type, but in *Gynura* and *Emilia* the filament shows the latter type. In such genera as *Cacalia*, *Ligularia* and *Syneilesis*, the filament largely develops in thickness just below the so-called upper part, but no thickening occurs in the cell walls there.

The base of anther Generally, in Compositae, the shape of the base of anther is important, and is usually considered as the tribal character. But the shape of anther base in the genera concerned is sometimes variable. HOOKER f. (1881) took up this character to divide *Senecio* into sections. Sect. *Synotis* has anther with long tail. The other sections have anther without tail, except Sect. *Jacobaea* which has a slightly long tail. The long tailed anther is also found in *Farfugium* and in some species of *Cacalia*. In the other genera, the anther has no tail.

Pappus In the Tribe Senecioneae, the achenes have usually pappus. The pappus is not so particularly different among the genera concerned and the pappus hair is usually scabrous. In some species of *Arnica*, the pappus hairs are barbellate. No pappus is found in the ray florets of some species of *Senecio* and *Gynura*. The absence of pappus in ray florets is a special case in the Eastern Asiatic Senecioneae. In Flora of British India, 16 species of *Senecio* are enumerated in a distinct section (Sect. *Madaractis*) characterized by the epappose ray flowers.

Form of floret The disk florets of these genera in question are all hermaphrodite and funnel-shaped. The filament of stamen attaches to the base of the broad part of corolla tube. Usually the narrow part of the corolla tube is easily distinguished from the broad part. The ratio of the narrow part and broad part of corolla is constant in most of the genera concerned. In *Ligularia*, this ratio is specifically constant. In the florets of *Senecio* Sect. *Nemosenecio*,

the narrow part of the corolla tube is 3-4 times as long as the rest, and that of Sect. *Senecio*, *Tephroseris* and *Heloserides* is 2-2.5 times. In the remaining sections in *Senecio*, the narrow part of corolla tube is as long as the rest.

Achene

The genus *Miricacalia* is characterized by the beaked achene. This beak, however, is not so distinct in immature achenes. The juvenile plant in the achene does not fully occupy the inside of the testa. In longitudinal section, the juvenile plant is placed at the broader basal part of the seed. Thus, the beaked achene is not essentially different from the achene of the allied genera, though the mature achene with short beak is clearly distinguished from that without beak.

Chromosome Study

Of the Eastern Asiatic Senecioneae, chromosome accounts of some species have been reported by some investigators previous to my study. *Senecio* is an extremely large genus and is still poorly known cytologically. Most chromosome counts on this genus have been made by K. AFZELIUS (1924, '49). Recently, two-thirds of the currently recognized species of *Senecio* in Washington, Oregon and California have been examined cytologically by R. ORNDUFF et al. (1963) and I. G. PALMBLAD (1965). On the remaining genera, a few of chromosome counts have been reported independently by several students. At the beginning of my study, no previous chromosome data had been reported for Japanese species of *Cacalia*, *Syneilesis* and *Miricacalia*. Chromosome numbers of five species of *Senecio*, a species of *Farfugium* and a species of *Ligularia* had been reported. Recently, M. TAKESHITA reported the chromosome numbers of *Miricacalia* and a species of *Syneilesis* and five species of *Cacalia* (1961). Most of the chromosome counts of our genera in question have been made by myself (1961, '62, '65, '66, '66a, '66b). Karyotype analysis on some species of the Tribe Senecioneae have been made by H. ARANO (1962, '64, '64a).

Because of the apparent variability and wide distribution of the phenotypic characters of these genera, it had been expected at the beginning of this study that the chromosomal information might be considerably helpful to clarify the intricate taxonomic problems. It soon became apparent, however, that there were only three types of chromosome numbers throughout the investigated members of these genera, except some polyploid races and their derivatives.

Material and method A number of individuals which show variations within a species were carried from various localities of Japan and Taiwan to Kyoto, during the course of this study from 1960 to 1966. Most of these plants have been cultivated in pots or in beds at the botanic garden of Kyoto University. Several plants were obtained from seeds.

For cytological study, two or more plants from each source were usually examined. Chromosome counts were made in the root tip cells, after using the 8-oxyquinoline pretreating method in accordance with TJO & LEVAN (1950)

modified by SHIMOTOMAI et al. (1956), that is, growing root tips are pretreated with 0.002 mol/l solution of 8-oxyquinoline for two to six hours at 18° C. At the end of the pretreatment, the materials are fixed in 3 : 1 alcohol acetic fluid for 24 hours at about 5° C., and then stored in 75% alcohol. For examination of meiosis, anthers were dissected out of their florets before fixation, for which 45% acetic acid was used. These procedures were also made in the fields. Aceto-orcein smears have been used throughout the chromosomal study.

All observations were made at the magnification of $\times 1000$ (100×10). Drawings were made with the aid of an ABBÉ'S drawing apparatus at a magnification of about $\times 3000$ ($100 \times 10 \times d.$) on the meiotic chromosomes. For the purpose of karyotype analysis, the somatic chromosomes were photographed through the light microscope at the magnification of about $\times 500$ ($100 \times 10 \times h.$).

Cytotaxonomy

Generic boundaries in Senecioneae have been the subject of much controversy from the standpoints of morphology as well as cytology. By the current definitions of the genera of Tribe Senecioneae, about two-thirds have been examined cytologically. In Table 1, the chromosome numbers of Senecioneae are summarized at the generic level. Most of them are obtained from the summaries of DARLINGTON & WYLIE (1956) and some of them from original papers.

Table 1. Generic summary of chromosome numbers in Senecioneae.

Genus	Gametic chromosome number
<i>Arnica</i>	18, 19, ca. 20, 28, ca. 33-34, ca. 36, 38, ca. 53-54
<i>Bedfordia</i>	30
<i>Brachglottis</i>	30
<i>Cacalia</i>	20, 25, 26, 29, 30, 60
<i>Cineraria</i>	20
<i>Crassocephalum</i>	10, 20
<i>Cremanthodium</i>	29
<i>Crocidium</i> (?)	9
<i>Culcitium</i>	ca. 20, 20, 40
<i>Dimeresia</i> (?)	7
<i>Doronicum</i>	30, 60
<i>Emilia</i>	5, 10
<i>Erechtites</i>	20
<i>Euryops</i> (Othonninae)	ca. 10-11, 10
<i>Farfugium</i>	30
<i>Gamolepis</i>	10
<i>Gynura</i>	10, 11, 20
<i>Haploesthes</i> (?)	18
<i>Honogyne</i>	ca. 67-68, ca. 70
<i>Kleinia</i>	10, ca. 50
<i>Lepidospartum</i>	30
<i>Liabum</i> (Liabinae)	14
<i>Ligularia</i>	24, 29, 30

<i>Luina</i>	30
<i>Miricocalia</i>	26, 27
<i>Neurolaena</i> (Liabinae)	11
<i>Notonia</i>	10
<i>Othonna</i> (Othonninae)	10
<i>Petasites</i>	26, 29 (3n=87), 30
<i>Peucephyllum</i>	20
<i>Psathyrotes</i> (?)	17, 19
<i>Schistocarpha</i> (Liabinae)	8
<i>Senecio</i>	5, 9, 10, 12, 18, 20, 22, 23, 24, 25, 30, 40, 45, 46, ca. 48, 50, ca. 60, ca. 90, ca. 92
<i>Syneilesis</i>	26 (3n=78)
<i>Tetradymia</i>	30, 62
<i>Tussilago</i>	30
<i>Werneria</i> (Othonninae)	ca. 21, 50, ca. 50, ca. 52, ca. 53, ca. 54, ca. 75, ca. 77, ca. 103, ca. 106,

* The genera, of which the subtribal name are not given in parenthesis, belong to the Subtribe Senecioninae.

** The genera marked with (?) are to some extent discordant taxonomically for those of Senecioninae.

Although chromosome numbers are useful as an aid in delimiting some genera of Senecioneae, they are of little use in circumscribing *Senecio* from its satellite genera, because of the cytological heterogeneity of *Senecio*. Unfortunately, the Himalayan species of *Cremanthodium*, *Gynura* and *Doronicum* have scarcely been examined cytologically, but most of the Japanese species of the genera *Senecio*, *Farfugium*, *Ligularia*, *Syneilesis*, *Miricocalia*, *Petasites*, *Arnica*, *Emilia* and *Cacalia* have been studied along this line.

According to the reports by K. AFZELIUS (1924, '49), R. ORNDUFF et al. (1963) and the others, the chromosome numbers are definite to the sections of *Senecio*, except for some polyploids and aneuploid derivatives (Table 2). This information suggests that the chromosome number is useful to classify sections.

Table 2. Chromosome numbers of the sections of *Senecio*.

Section	Gametic chromosome number	Distribution
<i>Senecio</i>	20	cosmopolitan
<i>Nemosenecio</i>	24	Japan & Taiwan
<i>Synotis</i>	10	Southeastern Asia
<i>Tephrosieris</i>	12, 23, 24, 45	Eurasia & N-America
<i>Crociseris</i>	20	NE-Asia & N-America
<i>Jacobaea</i>	20	NE-Asia & N-America
<i>Lobati</i>	23, 24	North America
<i>Amplectentes</i>	20	N. & Central America
<i>Aurei</i>	ca. 20-23, 23, 24	N. & Central America
<i>Bolanderiani</i>	23	N. & Central America
<i>Columbiani</i>	20, 40	N. & Central America

<i>Eremophili</i>	20	N. & Central America
<i>Suffruticosi</i>	20	N. & Central America
<i>Tomentosi</i>	23, ca. 46, ca. 46-48, ca. 48	N. & Central America
<i>Fruticosi</i>	30	Central America
<i>Palmatinervii</i>	30	Central America
<i>Sanguisorboidii</i>	30	Central America
<i>Terminales</i>	30	Central America
<i>Corymbocephalus</i>	20	Chili
<i>Suffructecius</i>	20, 40	Chili
<i>Pericallis</i>	30	Canary isl.
<i>Fruticulosi</i>	20	Northern Africa
<i>Leptophylli</i>	10	Southern Africa
<i>Paucifolii</i>	30	Southern Africa

In the genus *Farfugium*, two species including four varieties and two forms are known from Eastern Asia. Both species were examined cytologically. The somatic number of both species is 60 and the gametic number is 30 and 31. The number 31 was counted only by Y. MIYAJI (1914) on *Ligularia tussilaginea* var. *crispata*, which is now referred to *F. japonicum* f. *crispatum*. He noted that the gametic number 31 was observed on only one PMC at meiosis.

Ligularia is a fairly large genus with nearly 90 species. The center of distribution of this genus is in Asia. The data of chromosome numbers of this genus are too scanty to discuss the sections cytotaxonomically. Thirteen species are examined cytologically and the somatic numbers 48, 58 and 60 and the gametic numbers 29 and 30 are reported. The number 48 has been found by A. SOKOLOVSKAJA & O. STRELKOVA (in DARLINGTON & WYLIE) only in *L. altaica*. This number is very important to elucidate the evolutionary trend in *Ligularia*. The haploid numbers 29 and 30 are reported by K. AFZELIUS (1924) in *L. sibirica*, but he has doubted as follows: ". . . . die Zahl als 29 oder 30 anzugeben, obgleich ich der Überzeugung bin, dass 30 die wahrscheinlichste Zahl ist". Concerning *L. stenocephala* of Japan, the numbers 29 and 60 are reported by myself and H. ARANO (1962), respectively. Recently, 58 chromosomes are counted on the root tip cells of the present species. Among the 10 remaining species examined cytologically, four have 58 chromosomes and six have 60 chromosomes. As has been noted by K. AFZELIUS (1949), the number 29 might be easily derived from 30 by reduction, and both numbers seem to be rather constant for the clone.

In the Himalayan genus *Cremanthodium*, which includes about 50 species, only one species *C. reniforme* was studied and was found to have 58 chromosomes. This datum is not sufficient to discuss the relationship between *Ligularia* and this genus from the chromosome accounts.

In a broad sense, *Senecio* includes over 2000 species, distributed throughout the world. The number $X = 5$ had been considered as the basic number of the present genus, since K. AFZELIUS offered in 1924. Lately, ORNDUFF et al. proposed the basic number of $X = 10$ for *Senecio* and considered $X = 5$ as being derived through aneuploid loss.

About 120 species are known in Eastern Asia. Thirteen species among them are examined cytologically. There are evidently two types of basic numbers (H. KOYAMA 1966 a) : one is $X_c = 12$ and its derivatives by a multiplication and a deficiency, the other is $X_a = 10$ and its derivatives in the same way. In the series of $X_c = 12$, the number 46, which may be derived from 48, is counted in two species. Gametic number 24 and somatic numbers 48 and 90 are also reported in one of them. As I have not seen the original paper by A. SOKOLOVSKAJA & O. STRELKOVA (in DARLINGTON & WYLIE), I am not certain whether number 90 may be approximate or not. The number 23 may be derived from 24 by reduction. As reported by ORNDUFF et al. and others, most of the American species have the gametic number 23. The remaining three species have 24 and 48 somatic number, and 24 gametic number, respectively. These three species are referred to Sect. *Tephroseris*. The number 19 reported by ISHIKAWA (1916) on *S. vulgaris* may be derived from 20. The diploid number 36 counted by SUZUKA & KORIBA on *S. cannabinifolius* is doubtful. The other reports on the remaining seven species show that the gametic chromosome numbers of these species are 10 and its derivatives by multiplication.

Syneilesis, which is similar to *Cacalia* but has a single cotyledon, includes six species and one variety. Four species are examined cytologically. All of them have the somatic number 52, except one triploid race.

Monotypic genus *Miricacalia* is endemic to Japan. Chromosome counts were made by M. TAKESHITA (1961) and by myself (1961, '62). The number 52 was counted by TAKESHITA in the root tip cells, and 54 by myself also in them. As twenty-seven bivalents were observed by me in the PMC, the number 54 may be correct in the present species.

LINNEAN genus *Cacalia* has its wide distribution in Asia and America. Fifteen species are examined cytologically in the Sino-Japanese region and eight in America. The gametic number 20 is reported by AFZELIUS (1924) only on one species of America. The gametic numbers 25 and ca.25 are reported on two species of America. Lately, the number 50 in diploid condition is observed on two species of America. The somatic number 52 is counted for four species of Japanese *Cacalia*. The same number is reported on most species of *Syneilesis* and in West Mediterranean *Petasites fragrans*. As mentioned above, the number 54 of *Miricacalia makineana* may belong to the series having 52 chromosomes. The number 50 of American *Cacalia* may also belong to the 52-series. There are differences in the chromosome morphology between *Cacalia* and *Syneilesis*. The subterminal homologous chromosomes of the former have the satellites on their shorter arms, while those of the latter have no satellite. On the other hand, median chromosomes of *Miricacalia makineana* have satellites in addition to the subterminal chromosomes.

The somatic number 58 is counted in two species of *Cacalia*, but on one of them, 60 chromosomes are also reported by TAKESHITA and ARANO independently. In the same way with the case of *Ligularia*, the number 58 may easily be considered as a derivative from 60. The nine species and nine varieties of

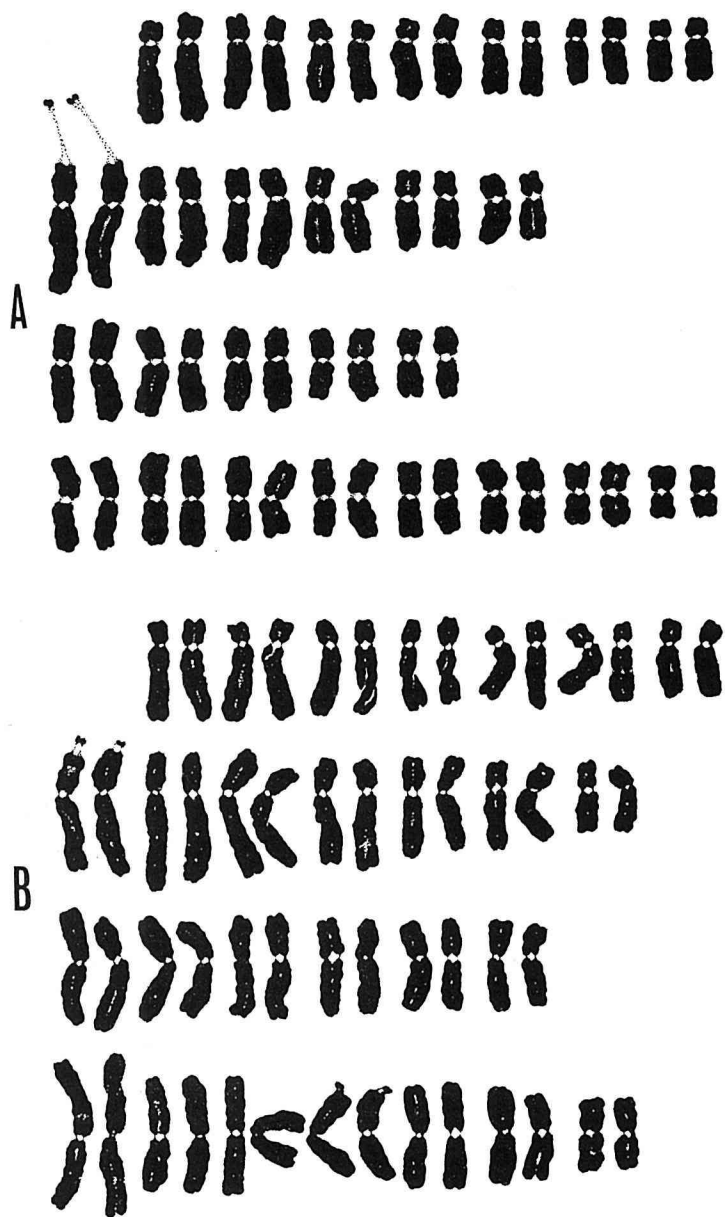


Fig. 4. Serial arrangement of the somatic metaphase chromosomes. $\times 2500$.
 A : *Cacalia delphinifolia* ($2n = 52$, from Mt. Iide in Honshu)
 B : *Miricacalia makineana* ($2n = 54$, from Mt. Akaboshi in Shikoku)

Japanese *Cacalia* have 60 chromosomes in diploid condition. The somatic number sixty is most common among the allied genera, *Ligularia*, *Farfugium*, *Tussilago*, *Bedfordia*, *Tetradymia*, *Doronicum* and also even in *Petasites*. According to the reports by B. L. TURNER et al. (1962), J. H. BEAMAN & B. L. TURNER (1962) and ORNDUFF et al., three species of Mexican and one of American *Cacalia* have also 60 chromosomes in $2n$. This number is also counted in *Senecio* by Mexican, the South African and of the Canary island materials, as shown in Table 2. *Cacalia auriculata* var. *kamtschatica* has diploid race with the somatic number of 60 chromosomes and tetraploid race with that of 120, as observed by myself (1966) on Japanese materials.

Concerning the chromosome morphology of these species with 60 chromosomes, karyological problems have not been investigated in detail, since it is very difficult to figure correctly the size and form of the chromosomes high in number in a cell. Recently, H. ARANO (1964) published his karyological accounts on



Fig. 5. Somatic metaphase chromosomes in the root tip cell of *Cacalia adenostyloides* ($2n = 60$, from Mt. Ohmine in Honshu). $\times 1900$.

Cacalia and its allied genera. It is very regretful that the karyotypes of his report can not be compared with those of mine, since the karyotypes analysed by ARANO are far different from those of mine and also by TAKESHITA on the same species.

Of about 15 species of *Petasites*, ten species are examined cytologically. *Petasites fragrans* with radiate heads has 52 chromosomes in diploid condition and eight species with discoid heads have 60 chromosomes in $2n$. *Petasites japonicus* is subdivided by KITAMURA (1942) into two subspecies : subsp. *japonicus*.

occurs in China, Korea, Ryukyu, Kyushu, Shikoku and Honshu, and subsp. *giganteus* in Northern Honshu, Hokkaido, Kurile and Saghalin. According to the summaries of DARLINGTON & WYLIE, the somatic number of 87 chromosomes is reported by K. YAMAMOTO in this species. In 1962, T. IMAZU & N. FUJISHITA examined the somatic chromosome number of *P. japonicus* collected from 211 localities of Japan.

In *P. japonicus* subsp. *japonicus*, they found a diploid race with $2n = 58$ and a triploid one with $3X = 87$. In *P. japonicus* subsp. *giganteus*, they did not find a triploid race but a diploid one.

The genus *Arnica* has over 40 species. There are only three species in Eastern Asia. Thirteen species were examined cytologically by various investigators. The apomixis in *Arnica* was investigated by AFZELIUS in 1936 and NYGREN in 1954. According to the report by ORNDUFF et al., irregular meiosis has been observed in all species they examined. Thus, the evolutionary trend of chromosomes of *Arnica* seems to be complicated by the apomixis. Two basic numbers of chromosomes are proposed, by BÖCHER & LARSEN (1955) and ORNDUFF et al. (1963) as 19, and by BATTAGLIA (1952) and NYGREN (1954) as 5. The somatic chromosome number 38 of the Japanese species of *Arnica* seems to be derived from the basic number of $X = 19$.

No species of *Doronicum* and *Gynura* occurs in Japan. Six species of *Doronicum* are examined cytologically on the materials of Europe. Four species of them have 60 chromosomes and two species 120 chromosomes in diploid condition. From the observation of secondary association at first and second metaphase, K. LINDQVIST (1950) notes that the basic number of the genus is lower than 30. About fifteen species of *Gynura* occur in Eastern Asia, but only two of them are examined. Both of them have the same somatic number of 20 chromosomes. The somatic chromosome number of two African species are reported to be 20 and 40, respectively.

About twenty species of *Emilia* are known in tropical Africa and Asia. Some of them are widespread in the American tropics as introduced weeds, and only one species occurs in Japan. The gametic number of 5 chromosomes was reported in *Emilia sonchifolia* by AFZELIUS (1924), BALDWIN (1946, '49) and R. M. KING (1964), in *Emilia sagittata* (under *Senecio*) by ISHIKAWA (1916), AFZELIUS (1924) and BALDWIN (1949). 10 chromosomes in haploid condition were counted in *E. coccinea* by BALDWIN (1946, '49) and R. M. KING (1964). *Emilia sagittata* and *E. coccinea* are now referred to *Emilia javanica*. Thus, the chromosome numbers are counted only in two species. Lately, ARANO reported the somatic number of 20 chromosomes in *E. sonchifolia* of Japan. This number is also observed by myself in the same species collected from Taiwan. Accordingly, both species have diploid and tetraploid races.

Evolutionary Trends of the Chromosome Numbers

Circumscribing the genera of Senecioneae in a broader sense, about 40 genera

(more than two-thirds of the genera of our tribe) have been examined cytologically. The basic chromosome numbers are not fixed concerning the several genera investigated, so the cytological heterogeneity is found within a genus. This fact is, to a certain extent, useful to elucidate the phylogeny in this tribe.

The ancestral basic number for the tribe has been postulated by AFZELIUS and most workers as $X = 5$, and by ORNDUFF et al. as $X = 10$. The postulation of $X = 5$ is based principally on the consideration that the taxa with the basic number are few but morphologically primitive. While the postulation of $X = 10$ is based on the fact that the species having that basic number are common among our members. Indeed commonness of a character is not in itself an indication of primitiveness as pointed out by B. L. TURNER & W. H. LEWIS (1965). It seems to be true that the polyploid taxa with odd numbers of $n = 15, 25, 35$, etc. should be relatively common if the basic number were $X = 5$, as suggested by ORNDUFF et al.

For the haploid chromosome numbers, the following is reported on Senecioneae: 5, 7, 9, 10, 11, 12, 14, 17, 18, 19, 20, 22, 23, 24, 25, 26, 27, 28, 29, 30, 38, 40, 45, 46, 50, 60, and 62, excepting some numbers reported as approximate ones. Among them, 7, 14, 17 and 18 occur on the species which have some other unusual characters and may better be separated from our tribe. The numbers 17 and 18 may be derived via 19 (38) from the number 20, but it is necessary to reexamine the number 17 cytologically. The number 19 is considered to be one of the basic numbers of *Arnica*, *Dimeresia*, with the chromosome number of 7, and *Liabum*, with that of 14, may better be excluded from Senecioneae as suggested by ORNDUFF et al.

The haploid numbers may be interpreted to have relationships shown in Fig. 6. The numbers marked with a circle are haploid numbers and those without marks are diploid ones. The numbers marked with parenthesis are those not yet counted actually. The dotted lines *a*, *b*, *c*, *d*, *e* and *f* show the possible evolutionary trends among those numbers.

In the genus *Senecio*, there are evidently three types of chromosome numbers: $X_a = 10$ and its derivatives; $X_b = 30$; and $X_c = 12$ and its derivatives. The number 10 is most frequent, and observed in 11 sections. The number 30 may be derived from several numbers along the course of *a*, *b* and *c*, given in the above figure. The courses of *a* and *b* seem to be less probable than *c*, since the number 30 is never counted in diploid condition.

There is a difficult problem on the relationship between the numbers 10 and 12. Judging from the considerable reports on the evolutionary trends of chromosome numbers of the phanerogam, the number 10 may be derived decreasingly from the number 12, though the number 11 in haploid condition has not yet been counted in *Senecio*. The number 22 in haploid condition may be derived decreasingly from 23 along the course of *d*.

The number 26 may be derived increasingly from either the number 24 or 13 along the courses of *e* and *f*, respectively, though the latter is not yet observed in this tribe.

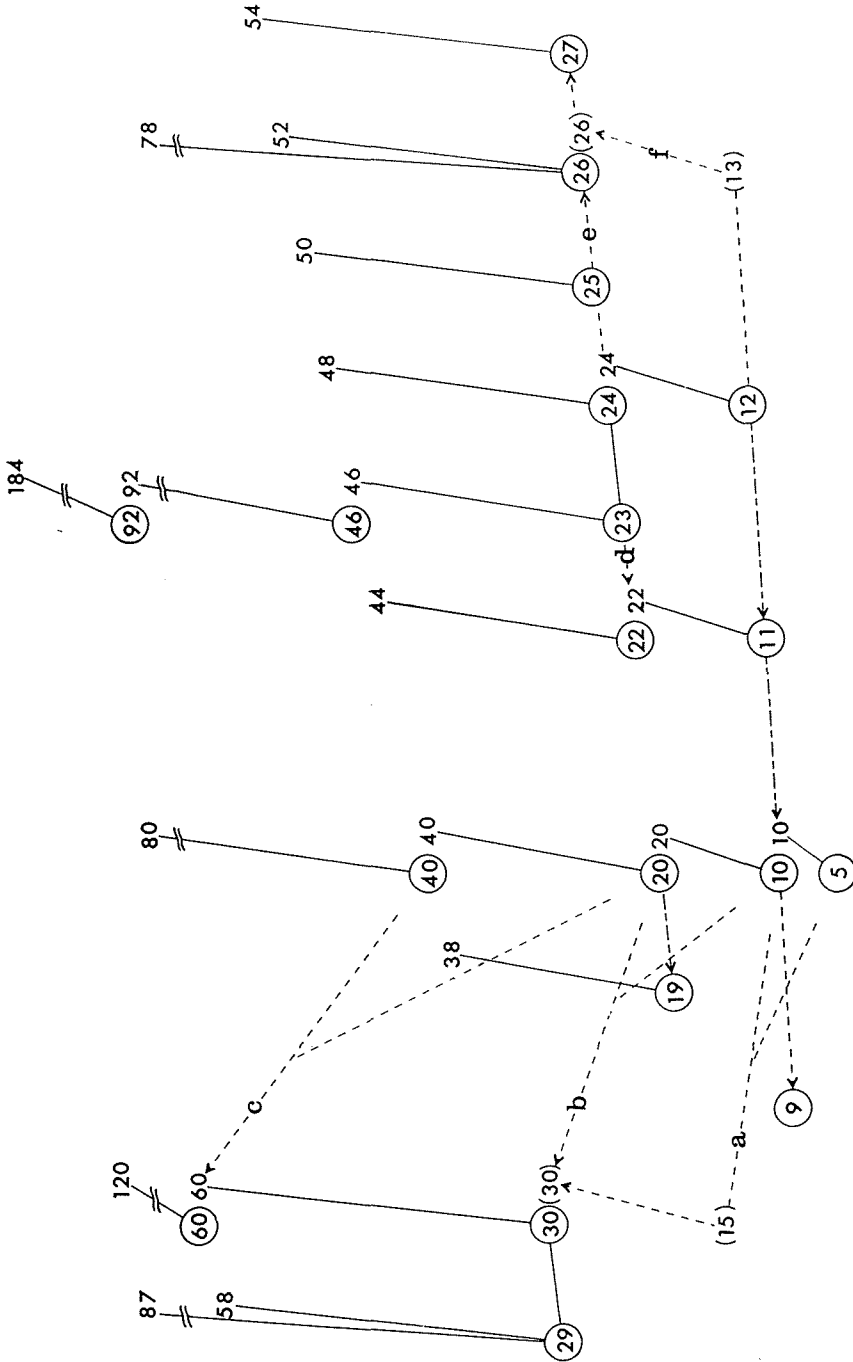


Fig. 6. Possible evolutionary trends of chromosome numbers on the Tribe Senecioneae.

The above interpretation is an attempt to clarify the relationships of chromosome numbers among the genera. Of such genera which have two or more types of chromosome numbers as *Cacalia*, *Ligularia*, *Petasites* and *Senecio*, the basic numbers will be discussed concerning the accounts cited above.

Distribution

Among the genera treated in this study, *Cremanthodium*, *Syneilesis*, *Miricacalia*, *Farfugium* and *Dendrocacalia* are endemic in Asia. Almost all members of *Ligularia* occur in Asia. *Farfugium* is confined to littoral cliffy places of subtropical and warm-temperate zones of Eastern Asia. *Cremanthodium* is found only in high alpine zones of Sino-Himalayan mountains. *Ligularia*, *Syneilesis* and *Miricacalia* are the inhabitants of temperate zones of mountains. *Dendrocacalia* is found only on Hahajima and Mukojima and never on Chichijima in the Bonin Archipelago.

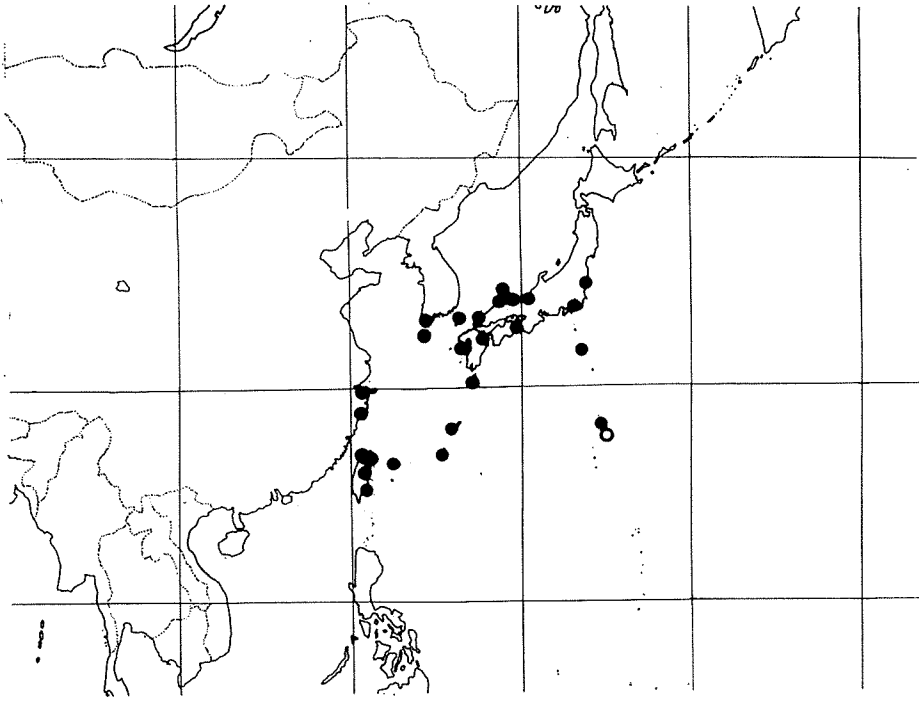


Fig. 7. Distribution of *Farfugium* (disks) and *Dendrocacalia* (circle).
Vertical distribution : subtropical and warm temperate zone

The genus *Cacalia* extends widely in Asia as well as in North and Northern South America. The large genus *Senecio* occurs in almost every part of the temperate regions through the world. The remaining six genera have their centers of distribution outside of Eastern Asia. *Arnica* has its center of distribution in North America, and some species in the circumpolar arctic region (N. POLUNIN 1959), and a few species in the temperate region of the Old World. *Doronicum* and *Tussilago* occur mainly in Eurasia. *Petasites* has a fairly wide area of distribution in the temperate region of the northern hemisphere. *Emilia* and *Gynura* are the members of tropical regions of Asia and Africa. Five genera, *Farfugium*, *Syneilesis*, *Miricacalia*, *Arnica* and *Dendrocacalia*, do not occur in the Himalayan region.

Table 3. Generic and Sectional summaries of chromosome numbers of the genera treated in this study

Genus	Section	Gametic chromosome number	Distribution
<i>Arnica</i>		19	N-America & Asia
<i>Cacalia</i>		26, 30, 60	E-Asia & N-America
	<i>Cacalia</i>		
	<i>Taimingasa</i>	26, 29, 30	Korea & Japan
<i>Cremanthodium</i>		29	Himalayas
<i>Dendrocacalia</i>		-	Bonin
<i>Doronicum</i>		-	Eurasia
<i>Emilia</i>		5, 10	Africa & Eurasia
<i>Farfugium</i>		30	Eastern Asia
<i>Gynura</i>		10	Asia & Africa
<i>Ligularia</i>		29, 30	Asia & Europe
	<i>Ligularia</i>		
	<i>Cyathocephalum</i>	29	Eastern Asia
<i>Miricacalia</i>		26, 27	Japan
<i>Petasites</i>		29(3n=87), 30	N-Hemisphere
<i>Senecio</i>		20	cosmopolitan
	<i>Senecio</i>		
	<i>Crociseris</i>	20	NE-Asia & N-America
	<i>Jacobaea</i>	20	NE-Asia & N-America
	<i>Nemosenecio</i>	24	Japan & Taiwan
	<i>Synotis</i>	10	Southeastern Asia
	<i>Tephrosieris</i>	12, 23, 24, 45	Eurasia & N-America
<i>Syneilesis</i>		26(3n=78)	Eastern Asia
<i>Tussilago</i>		-	Europe & S-Asia

- : No species has been examined for chromosome number in Eastern Asia

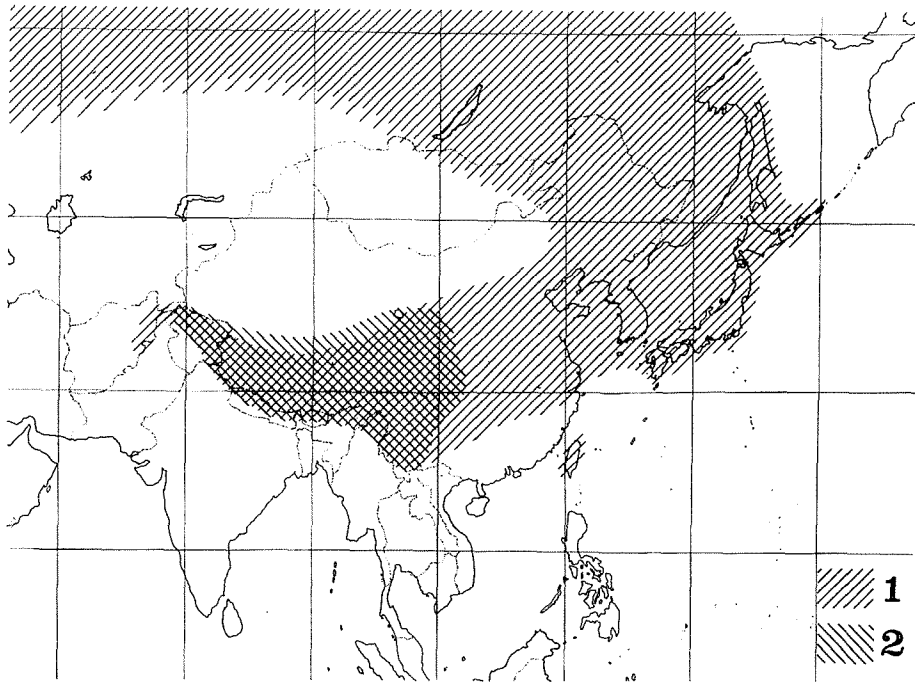


Fig. 8. Distribution of *Ligularia* (1) and *Cremanthodium* (2).
Vertical distribution : temperate and alpine zone

Relationship

The relationships among our genera may be considered as follows. The Sino-Himalayan *Cremanthodium* may be considered as the high alpine derivatives of *Ligularia*, as pointed out by R. Good (1928). As mentioned in the previous pages, *Cremanthodium* differs from *Ligularia* only by its cernuous head. It is difficult to speculate the relationship between *Cremanthodium* and *Ligularia* based on the chromosome number, as there is only one species of *Cremanthodium* examined cytologically. However, we may allude to the relationship between *Cremanthodium reniforme* with 58 chromosomes and the members with 60 (-2) chromosomes of *Ligularia*.

Farfugium has occasionally been considered to be a member of *Ligularia*. Although G. P. DE WOFF & P. D. SELL (1958) and W. J. DRESS (1962) have recognized the involute vernation of *Farfugium* as an interesting character, they do not consider *Farfugium* as a distinct genus. All members of *Farfugium* have densely pilose achenes, while all members of *Ligularia* have glabrous achenes. In *Senecio*, the pubescence of achene is variable. But the pubescence in *Senecio*

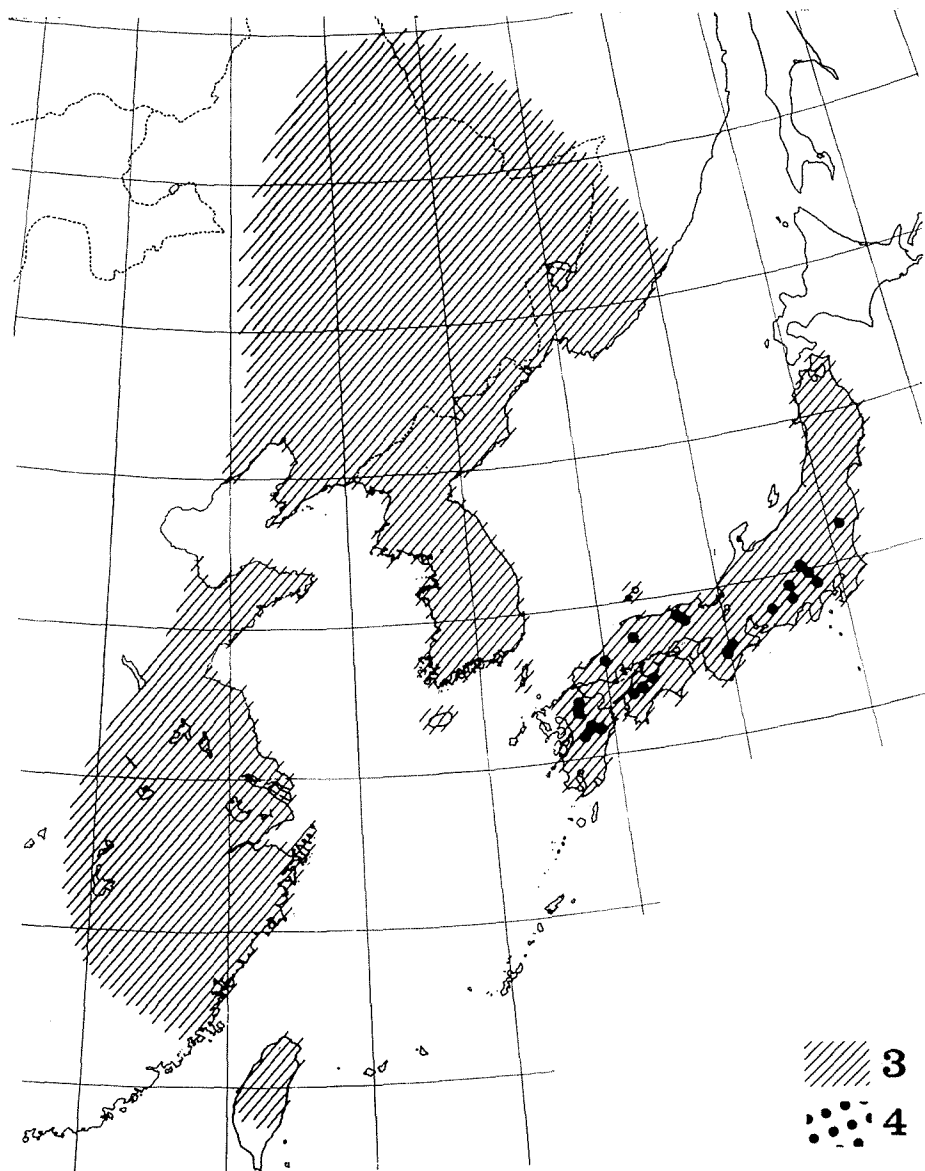


Fig. 9. Distribution of *Synlelesis* (3) and *Miricacalia* (4).
Vertical distribution : temperate zone (As for southern
area, only in mountains)

does not interfere directly in the difference between *Farfugium* and *Ligularia*. The fact that *Farfugium* has the same chromosome number as *Ligularia* may suggest the relationship between the two genera.

As pointed out by SHULTZ-BIPONTIUS (1845) and others, *Cacalia*, *Syneilesis*, *Miricacalia*, *Gynura* and *Emilia* are closely related to *Senecio* and may have a common ancestor with *Senecio*. Although *Syneilesis* and *Miricacalia* are distinctly separated from *Cacalia*, the relationship among them may easily be considered from similar appearances as well as chromosomes.

The Eurasian *Senecio* is divided into two groups by the filament cell form of the upper part. Each group is characterized by the basic chromosome number different from each other. As *Gynura* and *Emilia* have the basic number of 10, they may be allied to the group of *Senecio* with the basic number of $X_n = 10$. It is very interesting that *Gynura*, *Emilia* and one group ($X_n = 10$) of *Senecio* have the same type of filament cell.

Concerning the species of *Cacalia* treated in this study, there are two types of venation and of basic chromosome number as already mentioned. These species may be separated into two natural groups: one has 52 chromosomes and palmate venation and the other 60 and pinnate venation. *Syneilesis* and *Miricacalia* may be related to the former group according to the venation and basic number. *Cacalia suaveolens* of North America has 40 chromosomes in diploid condition and pinnate venation. This species may be related to the latter group. The chromosome number of *C. suaveolens* may suggest that the chromosome number of 60 may be derived from the other basic number of $X_n = 10$ along the line of *c* as attempted in evolutionary trends of chromosomes.

Tussilago, a monotypic genus of Eurasia, is closely related to *Petasites*, but differs from the latter by the solitary and monoecious head.

Arnica is distinct among our genera in having the opposite leaves and the large radiate heads which are considered to be primitive characters in the family Compositae. The basic chromosome number for *Arnica* may be considered as 19, but this number is not certainly primitive if considered from the evolutionary trends of chromosome numbers. It is still difficult to discuss the relationship between *Arnica* and the other genera in question.

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