Taxonomic Implications of Fruit Wall Anatomy and Karyology of *Crepis* sect. *Ixeridopsis* (Compositae; Lactuceae)

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*Crepis*속 *Ixeridopsis*절(국화과 ; 상치족)의 과피의 해부구조, 핵형 및 유연관계

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Abstract

The mature fruit wall structures were investigated in six taxa of *Crepis* sect. *Ixeridopsis*. Mature fruit of all examined taxa have 10 longitudinal costae, which have a similar thickness in transverse section. Based on the histological difference, the fruit wall structures of the examined species are divided into two main types Type I and Type II, and Type II is further subdivded into Type II-A and Type II-B. Type I has thick non-degenerated intercostae (*Crepis lactea*); Type II-A has broader libriform fibers (*C. naniforma, C. nana* subsp. *ramosa*). Type II-B has thinner costae (*C. elegans, C. flexuosa, C. nana* subsp. *nana*). The chromosome morphology of *C. nana* subsp. *nana* was also investigated. Somatic chromosome number was $2n=14$. The type of resting nuclei was prochromosome type. Karyotype composition was 4m+2sm+1st. According to the evidence from chromosomal and fruit wall anatomical data, the interrelationships within *Crepis* sect. *Ixeridopsis* are discussed.

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Introduction

Of 27 sections of *Crepis* (Compositae; Lactuceae) sect. *Ixeridopsis* is defined by its unique basic chromosome number ($x=7$), and comprises nine species and one subspecies (Babcock, 1947; Tzvel, 1964). Recently sect. *Ixeridopsis* was separated by Weber(1984) as a new genus *Askellia*. Despite its rather distinct position, relationships within sect. *Ixeridopsis* as well as with other sections or genera, are still uncertain. Hence histological analysis in fruit wall structure of six taxa in *Crepis* and karyoloy of *Crepis nana* subsp. *nana* was carried out for a better understanding of sectional and species relationships.

Earlier studies in *Ixeris* and its related genera have proved that both anatomical structures of fruits (i.e., achenes) and karyological characters provide significant information in discussing generic and species relationships (Pak and Kawano, 1990a, b, c). However, no information on fruit wall structure is available for the taxa of sect. *Ixeridopsis*. As regards karyology, information is available only from the three species *Crepis elegans*, *C. flexuosa*, and *C. nana*. Emphasizing resemblance in chromosome number ($x=7$) and external morphology, (e.g., leaf and involucre shape and growing habit) with some species of *Ixeris*, Babcock *et al*. (1937) suggested that sect. *Ixeridopsis* may be of hybrid origin between ancestral groups of *Crepis* and *Ixeris*. In order to evaluate this hypothesis, critical comparison in karyology between sect. *Ixeridopsis* and *Ixeris* is needed.

Materials and Methods

Five species and one subspecies of sect. *Ixeridopsis* were investigated with respect to their fruit wall structure (table 1). For anatomical study, mature fruits collected from dry herbarium specimens or fixed in the field, were microtome-sectioned by standard paraffin methods (for details on technical methods and terminology of wall structure see Pak and Kawano, 1990a).

For karyological study of somatic cells, root tips were collected from young plants grown from seeds of *Crepis nana* subsp. *nana* (voucher: *Chinnappa CC3851*, KYO). Methods to prepare specimens of interphase nucleus and metaphase chromosomes are described elsewhere (Pak and Kawano, 1990b).

Observations

Mature fruit wall anatomy

In all the six taxa examined, the achenes have ten costae which are nearly equal in thickness (figs. 8-13). Histologically, all the taxa have a more or less collapsed endocarp and one-cell-layered persistent exocarp (completely collapsed in *Crepis lactea*). A diversity is found in the mesocarp with respect to the presence or absence of a persistent mesocarp

Table 1. Species of *Crepis* sect. *Ixeridopsis* examined and collection sities.

Taxa[1)]	Voucher specimens[2)]
C. elegans Hook.	Canada. Alberta: Jasper, Mccabe 8312.
	Alberta: Calgary, Malte & Watson 1267.
	Wyoming: Banff, Canby 163. Park, Hartman 24422.
	Yukon: Canol Rlod, Rorsild & Breitung 10875.
	U.S.A. Alasaka: Salina, Went 340.
C. flexuosa (DC.)	India. Kashimir: Baltistan, Stewart 20586.
Benth. & Hook. f.	Kashimir: Baltistan, Webster & Nasir, 29 June 1955 s. n.
	Kashimer: Satpura Nullar, Stewart 20298.
	Punjab: Kangra, Koelz 7036.
	U. S. S. R. Turkestan: Nagragal, 2 July 1929, Popov s. n.
C. lactea Lispsch.	U.S.S.R. Turkestan: Pamir, Lipschitz 818
	Canada. Alaska: Paxon, July-Aug, 1934, Went s.n.
C. nana Richards	Canada. Alaska: Yukon, 22 July 1926. Muris s.n.
ssp. *nana*	Baffin: Eglinton Fiorid, 24 Aug. 1950, Rathlishberger s. n.
	Labrador: Ramah, Stecker 324.
	British Columbia: Mt. Marble, 14 July 1938, Thompson & Thompson s. n.
	U.S.A. Alaska: Mt. Hayes Quad. 22 Aug. 1989, Murrary & Paker s. n. (ALA).
ssp. *ramosa* Babc.	U.S.A. Washington: Jefferson, Thompson 9921.
C. naniforma Babc.	India. Kashimir: Ladak, Koelz 2846.
	Punjab: Kangra, koelz 6666.

1) Species classification followed Babcock (1947).

2) All collections deposited at UC uncless otherwise noted.

at the intercostal region, and the position of libriform fibers and the thickness of fiber-sclereids in the costal and intercostal region. Based on the histology of the mesocarp, the fruit wall structures of the taxa examined are found to be divided into two main types: Type I and Type II; the Type II is further subdivided into Type II-A and Type II-B (table 2).

Type I

This type is found only in *Crepis lactea* (figs. 1, 2, 8) and is characterized by having thick, persistent intercostal tissue.

Costae are 3-6 cells thick (70.0-82.5 μm thick) in transverse section. One to three layers of fiber-sclereids with helical thickness to form the upper layers of costae. Below this layer libriform fibers are positioned (fig. 2), forming a bundle composed of 36-42 cells. The intercostae are 1-3 cells thick (35.0-42.5 μm thick) in transverse section. Mesocarp of intercostae are fiber sclereid cells.

Table 2. Comparisons in the structure of fruits among *Crepis* sect. *Ixeridopsis*.

Taxa[1]	Body width (mm)	Total length (mm)	Body length (mm)	Beak length (mm)	Costa Thick-ness (μm)	Costa Number of fiber-sclereid cell layers	Costa Number of libriform fiber cell	Costa Number of broader libriform fiber cell layers	Intercosta Thick ness (μm)	Intercosta Number of fiber-sclereid cell layers	Type[3] of fruit wall structure
C. lactea[2]	0.6-0.8	5.0-6.0	4.5-5.7	0.2-0.5	70.0-82.5	1-3	36-42	2-3	35.0-42.5	2-3	I
C. naniforma[2]	0.5-0.6	5.6-6.5	5.4-6.1	0.2-0.4	62.5-67.5	---	20-42	1-2	---	---	II-A
C. nana ssp. ramosa[2]	0.5-0.7	4.5-7.0	4.3-6.7	0.2-0.4	55.0-77.5	---	33-59	1-2	---	---	II-A
C. elegans	0.5-0.6	5.1-5.3	4.3-4.5	0.7-0.8	37.5-42.5	---	16-28	---	---	---	II-B
C. flexuosa	0.5-0.6	4.6-6.2	4.4-5.6	0.2-0.6	42.5-50.0	---	26-34	---	---	---	II-B
C. nana ssp. nana	0.6-0.7	5.9-6.4	5.6-6.2	0.2-0.4	35.0-50.5	---	16-24	---	---	---	II-B

1) Classification followed Babcock (1947).

2) Measurements were based on 5 fruit sample except in *C. lactea*, *C. naniforma*, *C. nana* subsp. *ramosa* with 2 samples.

3) See text for fruit wall type.

Type II

Type II is distinguished from Type I in lacking the mesocarp at intercostal region, and is observed in the remaining five taxa. The Type II-A refers to achenes from *Crepis naniforma* (figs. 3, 9) and *C. nana* subsp. *ramosa* (figs. 4, 5, 10) is distinguished by having one to two layers of broad libriform fiber cells below the exocarp of the costae; such are lacking in the three other taxa. In this subtype costae are 1-2 cells thick (55.0-77.5 μm thick). The costae are formed by 20 to 59 libriform fiber cells. No fiber-sclereids are present. Libriform fiber cells of the upper layers are 10-12 μm in diameter (fig. 5).

The type II-B is characterized by lacking the broader libriform fibers as found in *Crepis elegans* (fig. 11), *C. flexuosa* (figs. 6, 7, 12), and *C. nana* subsp. *nana* (= *C. nana* subsp. *typica*, fig. 13). In this subtype, costae are only 35.0-50.0 μm in thickness and are formed mainly by 16 to 34 libriform fiber cells. Fiber-sclereids are not present. The libriform fibers (5-8 μm in diameter) below the exocarp are narrower than those (10-12 μm in diameter) in Type II-A.

Karyology

The somatic chromosome number in *Crepis nana* subsp. *nana* was $2n=14$ (figs. 16, 17) as reported already by Babcock and Jenkins (1943). Nuclei at the resting stage have many darkly stained, round shaped condensed blocks (fig. 14). The regions surrounding these blocks are stained evenly, and thus the nuclei are of the prochromosome type (for typification see, Tanaka, 1971). Chromosomes are clearly differentiated into early- and late -condensing parts in prophase. Chromosomal condensation occurrs in the proximal parts

Table 3. Measurements of somatic chromosome of *Crepis nana* subsp. *nana*

Chromosome number	Length of arms (μm)	Total length (μm)	Arm ratio	Type
1	0.5+1.0+1.5	3.0	1.5	m
2	0.4+0.9+1.4	2.7	1.5	m
3	1.7+2.1	3.7	1.2	m
4	1.7+2.0	3.7	1.2	m
5	1.3+1.7	3.0	1.3	m
6	1.0+1.4	2.4	1.4	m
7	1.0+1.7	2.7	1.6	m
8	1.0+1.7	2.7	1.6	m
9	1.2+2.2	3.4	1.8	sm
10	1.1+2.1	3.2	1.8	sm
11	0.8+1.7	2.5	2.1	sm
12	0.8+1.7	2.5	2.1	sm
13	0.0+2.3	2.3	69.0	st
14	0.0+2.1	2.1	63.0	st

of both arms (fig. 15). The total genomic size is about 39.9 μm during metaphase (table 3). The length of chromosomes ranges from 2.1 μm to 3.7 μm. In the somatic chromosome complement, four pairs of chromosomes have centromeres at median position (nos. 1-4; figs. 16, 17), two pairs at submedian position, and one pair in subterminal position. The first chromosome pair has a secondary constriction in the distal portion of their short arms.

Discussion

As presented above, a significant diversity exists i he fruit wall anatomy of *Crepis* sect. *Ixeridopsis*. The Type I (referred to the structure of *Crepis lactea*) is the most distinctive and shows no particular histological coincidences with the Type II-A and II-B as seen in all the remainder. In other words, in terms of fruit wall histology, there is no evidence to support an inclusion of *Crepis lactea* in sect. *Ixeridopsis*. Evidence from fruit wall anatomy may support Tzvelev (1964), who discussed that *Crepis lactea* has a distinct position in the section.

Despite a doubtful assignment of *Crepis lactea* in sect. *Ixeridopsis*, if we look at fruit wall structure of related genera/sections and particularly those of *Ixeris*, which is considered most closely related to *Crepis* sect. *Ixeridopsis* (Babcock, 1947), then the structure referred to as the type II-B is found to be prevalent. Therefore, the Type II-B probably represents an archaic structure of the section, and the Type II-A is drived. Hence, in terms of cladistics, within sect. *Ixeridopsis, Crepis naniforma* and *C. nana* subsp. *nana* are closely related to each other in sharing the derived fruit wall structure (Type II-A). A common evolutionary line leading to *Crepis naniforma* and *C. nana* subsp. *nana* seems to have been derived

from an ancestral group comprising *C. elegans*, *C. flexuosa*, and *C. nana* subsp. *nana* (all with Type II-B). It is uncertain how *Crepis lactea* (with Type I) joins this pattern of evolutionay relationships.

Relationships within sect. *Ixeridopsis* suggested by evidence from fruit wall anatomy do not agree with ones suggested by Babcock (1947, p 528) at all. He suggested, on the basis of comparison in shape of leaves and inner involucral members as well as in geographic distribution, that *Crepis flexuosa* is the most primitive, *C. elegans* and *C. nana* subsp. *nana* the most advanced, and *C. lactea* and *C. naniforma* intemediate.

As regards the hypothesis for an intergeneric hybrid origin of sect. *Ixeridopsis* between *Crepis* and *Ixeris* (Babcock *et al.*, 1937, p.202), I can only say that the karyotype of *Crepis nana* subsp. *nana* is clearly dictinct from that of *Ixeris alpicola*. In fact, despite coincidence in chromosome number ($2n=14$), the karyotype of *Crepis nana* subsp. *nana* (4m+2sm+1st) is completely different from that of *Ixeris alpicola* (5m+2sm) (Pak and Kawano, 1990b). In addition, *Crepis nana* subsp. *nana* has interphase nuclei of prochromosome type, rather than of diffuse type as in *Ixeris alpicola* (Pak and Kawano, 1990b).

In summary, the present study clarified (1) a doubtful assignment of *Crepis lactea* in sect. *Ixeridopsis*, (2) a derived position of *Crepis naniforma* and *Crepis nana* subsp. *ramosa* in contrast to a primitive position of the other species, and (3) a karyomorphology of *Crepis nana* subsp. *nana* distinct from that of *Ixeris alpicola*. Species relationships suggested in the present study do not agree with ones suggested ealier by Babcock (1947), and whether sect. *Ixeridopsis* is of hybrid origin between *Crepis* and *Ixeris* or not is still unsolved. These problems, together with a question on the appropriate position of *Crepis lactea*, must be resolved in more comprehensive cladistic or macromolecular studies.

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摘 要

*Crepis*屬 *Ixeridopsis*節의 *C. elegans*, *C. flexuosa*, *C. lactae*, *C. nana* subsp. *nana*, *C. nana* subsp. *ramosa*, *C. naniforma*의 과피의 解剖學的 구조 및 *C. nana* subsp. *nana*의 核型學的 形質을 조사하였다. 조사한 5 종 1 아종의 수과의 해부학적 구조는 거의 같은 크기의 10 개의 costa를 가지고 있으나, 중과피를 이루는 libriform 섬유세포와 sclereid 섬유세포가

costa 및 intercosta 에서의 위치, 분포양상, 세포층의 수, 두께에 있어서 다양성을 나타내었다. 이러한 중과피에서 나타나는 조직학적 차이점을 토대로 하여 이절에서 나타나는 과피를 크게 2 가지로 유형화 (Type I, II) 하였다. 즉 Type I은 *C. lactea*에서 보여지는데, libriform 섬유세포는 costa의 아래 부분에 위치하고, 그 위에 sclereid 섬유세포가 1-3 세포층이 놓여 있으며, 바깥쪽에는 외과피가 접해 있다. 또한 intercosta의 두께가 35.0-42.5 μm 이고, sclereid 섬유세포만으로 구성되어 있는 독특한 유형이다. Type II는 costa를 구성하는 libriform 섬유세포의 종류에 따라 다시 두개의 subtype (Type II-A, B)으로 나뉘었다. Type II-A는 libriform 섬유세포가 중앙 대부분에 위치하고, 바로 아래쪽과 그 위에 폭이 넓은 libriform 섬유세포가 차지하며, 가장 바깥에 한층의 외과피가 접해 있다. 이 유형은 *Crepis naniforma*와 *Crepis nana* subsp. *ramosa* 에서 보여진다. 가장 낮은 costa를 갖는 Type II-B는 costa의 전체를 폭이 좁은 섬유세포 만으로 구성되어 있으며, 이 type은 *Crepis elegans*, *C. flexuosa*, *C. nana* subsp. *nana*에서 보여진다.

Crepis nana subsp. *nana*의 핵형학적 형질은 체세포 염색체의 수가 $2n=14$ 이고, 휴지핵의 형태는 prochromosome 유형이다. 전 게놈의 길이는 39.9μm이고, 염색체의 길이는 2.1 μm 에서 3.7μm 이다. 핵형은 중부염색체 4 쌍, 차중부 염색체 2 쌍, 차단부 염색체 1 쌍으로 구성된다. 이들 결과를 근거로 하여 이 분류군의 종간 혹은 근연군 간의 유연관계를 추론하였다.

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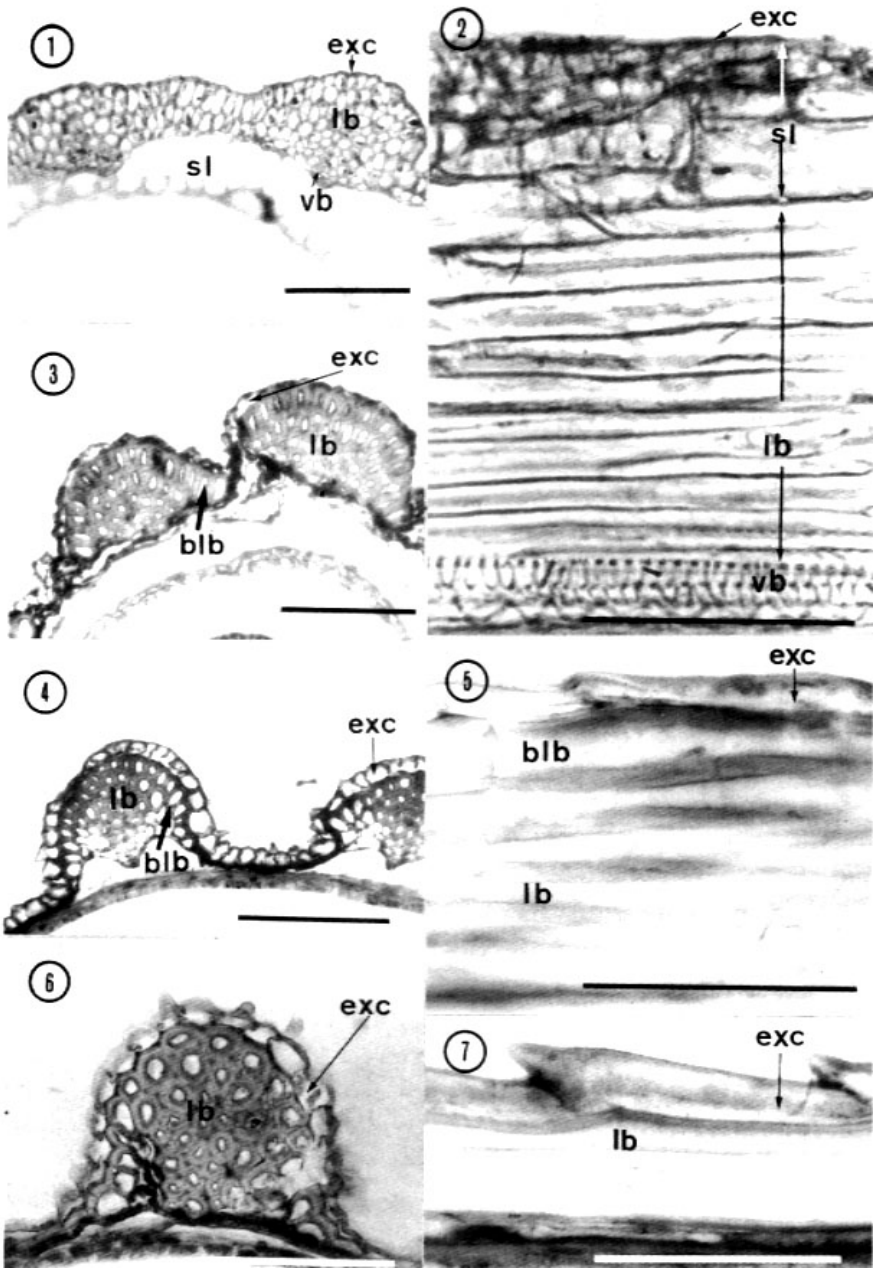

Fig. 1-7. Structure of the fruit wall in *Crepis* sect. *Ixeridopsis*. 1, 3, 4, 6: Transverse sections of fruit showing structure of costae and intercostae; 2,5,7. Longitudinal sections of costae. 1,2. *C. lactea* (Type I). 3, 5. *C. naniforma*. 4. *C. nana* subsp. *ramosa*(Type II-A). 6,7. *C. flexuosa*(Type II-B). exc, exocarp; lb, libriform fiber cell; blb, broader libriform fiber cell; sl, fiber-sclereid cell; vb, vascular bundle. Scales equal 100 μm in figs. 1, 3, 5, 6 and 50 in figs. 2, 5, 7.

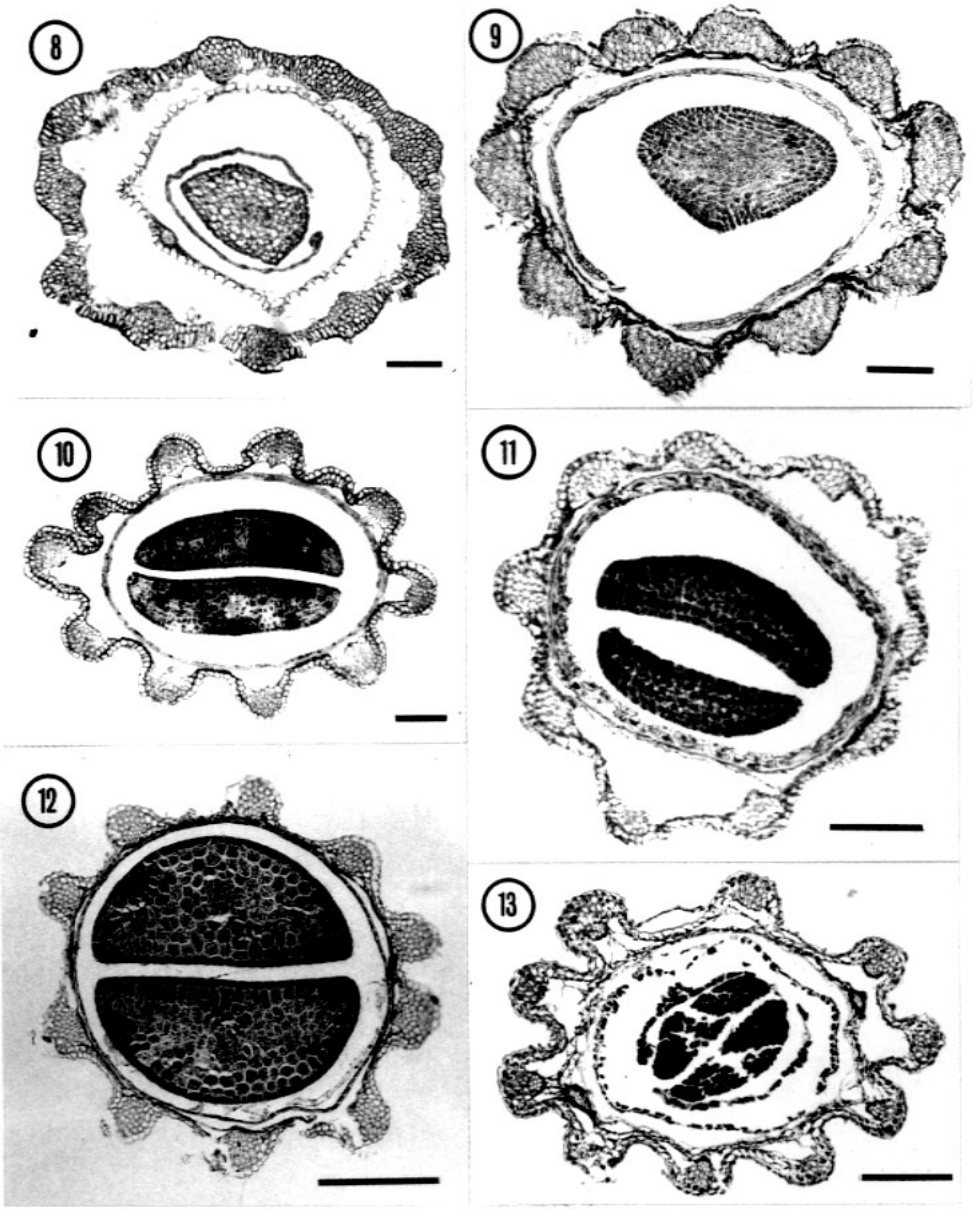

Fig. 8–13. Transverse section of fruits of *Crepis* sect. *Ixeridopsis*. 8, *C. lactea*; 9, *C. naniforma*; 10, *C. nana* subsp. *ramosa*; 11, *C. elegans*; 12, *C. flexuosa*; 13, *C. nana* subsp. *nana*. All scales equal 100 μm.

Fig. 14-17. Karyomorphology of *Crepis nana* subsp. *nana*. 14, Photomicrographs of resting nuclei; 15, Prometaphase chromosomes; 16, Mitotic metaphase chromosomes; 17, Karyotype at mitotic metaphase. Arrows indicate secondary constricton. Scale equals 3 μm.