BIOSYSTEMATIC STUDY OF ONOBRCHIS VICIIFOLIA SCOP. AND ONOBRCHIS ALTISSIMA GROSSH. (FABACEAE) IN IRAN

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Morphologic characters, meiotic chromosome number and behavior were analyzed in different wild populations of *Onobrchis viciifolia* Scop. and *Onobrychis altissima* Grossh. belonging to *O.* sect. *Onobrychis* in Iran. All Iranian populations of *O. viciifolia* and *O. altissima* studied here were tetraploid and showed $2n = 4x = 28$ chromosome number. The basic chromosome numbers ($x = 7$) is consistent with the proposed base number of $x = 7$ for *O. viciifolia* and *O. altissima*. For *O. altissima*, two ploidy levels ($2n = 2x = 14$ and $2n = 4x = 28$) have been reported from Caucasus. Results support the hypothesis that *Onobrchis viciifolia* and *O. altissima* are related as a progenitor-derivative pair of species. The fact that no diploid populations of *O. altissima* were found in Iran, would suggest a relatively recent origin of the species, most probably in Caucasus. Almost these taxa displayed regular bivalent pairing and chromosome segregation at meiosis. Meiotic abnormalities observed included varied degree of sticky chromosomes with laggards and bridges in anaphase to telophase, asynchronous nuclei in metaphase II and desynapsis in metaphase I. Also *O. viciifolia* Scop. is considered as a new record from this section for Iran. These taxa of the genus are cultivated as fodder in Iran.

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Key words. chromosome number, *Fabaceae*, meiotic behavior, *Onobrychis* sect.*Onobrychis.*

بررسی‌های بیوسیستماتیک دو گونه اسپرس (Onobrychis viciifolia, O. altissima) در ایران

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ویژگیهای ریخت‌شناسی، تعداد و رفتار کروموزومی در مرحله میوز در جمعیتهایی از گونه‌های *Onobrychis viciifolia* و *O. altissima* متعلق به بخش *Onobrychis* مورد تجزیه و تحلیل قرارمی‌گیرد. تمام جمعیتهای متعلق به مناطق مختلف ایران تتراپلویید بوده و تعداد کروموزومهای آنها $2n = 4x = 28$ می‌باشد. شمارش کروموزومی پایه $x = 7$ ثابت می‌ماند. برای گونه *O. altissima* شمارشهای قبلی، $2n = 2x = 14$ و $2n = 4x = 28$ از منطقه قفقاز بوده است. نتایج، این نظریه را تأیید می‌نماید که زوج گونه *Onobrychis viciifolia* و *O. altissima* گونه‌های خویشاوندی هستند که از نسل مشترکی مشتق شده‌اند. عدم وجود پایه‌های دیپلویید *O. altissima* در ایران نشان می دهد که احتمالا ظهور جدید این گونه در قفقاز است. اگرچه جفت شدن کروموزومها و جدا شدن آنها در مرحله میوز منظم بود، لیکن بی‌نظمی‌های میوز شامل چسبندگی کروموزوم‌ها و تأخیر و تشکیل پل در آنافاز و تلوفاز، ناهم‌زمانی هستکها در متافاز II و دسیناپیس در متافاز I مشاهده گردید. گونه *O. viciiflia* برای اولین بار از ایران گزارش می‌شود و هر دو گونه مذکور جزو گونه‌های کاشته شده می‌باشند.

Introduction

The genus *Onobrychis* with nearly 130 species is distributed mainly in the north temperate regions, but centers of diversity are in the eastern Mediterranean area and western Asia. *Onobrychis* includes annual or perennial, mostly caulescent herbs (rarely spiny shrubs), which have an indumentum of simple hairs or rarely they are glabrous. A few taxa of the genus such

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Table 1. *Onobrychis* taxa studied and acronyms.

Taxa	Locality	Altitude	Voucher specimen	Abbreviations
O. altissima	Firuz kuh	2280 m	14192 (BASU)	alt
O. altissima	Saein	1770 m	14201 (BASU)	alt
O. altissima	Ardebil	1540 m	14202 (BASU)	alt
O. altissima	Kaleibar	1650 m	14204 (BASU)	alt
O. altissima	Varzaghan	1930 m	14209 (BASU)	at
O. viciifolia	Taham	2000 m	14198 (BASU)	vic
O. viciifolia	Bostan abad	1525 m	14199 (BASU)	vic

as *O. viciifolia* are cultivated as fodder or for ornamental value (Lock & Simpson 1991; Yakovlev et al. 1996; Mabberley 1997). The taxonomy of the genus continues to be subject of much confusion, mainly because of the different approaches to species delimitation, resulting in varying numbers of recognized species (Boissier 1872; Sirjaev 1925; Hedge 1970; Ball 1978; Duman & Vural 1990; Aktoklu 2001). Recently some new taxa of the genus have been described from Iran (Ranjbar et al. 2004 & 2007; Ranjbar 2008). Most of the cytological studies in the genus have concentrated on the chromosome count (Baltisberger 1991; Karshibaev 1992; Slavivk et. al. 1993), with little work focused on detailed karyological criteria for taxonomic purposes (Khatoon et al. 1991; Mesicek & Sojak 1992). From these reports, it is evident that the chromosome count is known for just over a quarter of the species. Two basic chromosome numbers (x = 7 and x = 8) and tetraploidy levels (2n = 2x = 14, 2n = 4x = 28, 2n = 8x =56 and 2n = 2x = 16, 2n = 4x = 32) are present in the genus (Abou-el-Enain 2002). The elucidation of the origins of species has between greatly aided in recent years by the ability to make comparisons between putative progenitor species and their derivatives at the molecular level (Crawford 1990; Avise 1994). We describe here meiotic behavior of different populations of two species, *O. viciifolia* and *O. altissima*, and its significance in their taxonomic relationships.

Materials and methods

Phenetic analysis

This study is mainly based on herbarium material. Several sheets have been examined for each species, received on loan from the following herbaria: W, WU, TARI, FMUH, Herbarium of Research Center of Natural Resources and Animal Affaris of Mashhad, Isfahan, Shiraz, Tabriz, Kerman and Zahedan. Moreover, during several excursions in Iran, some of the species were studied in the field by the authors. The species analyzed in this study are listed in Table 1. A total of 37 quantitative/qualitative characters related to vegetative and reproductive organs were studied in 40 plants from 5 populations of *O. altissima* and 2 populations of *O. viciifolia* (Table 2). The data was transferred as an Excel file to the statistical package Unistat 4 and cluster analysis (UPGMA) and principal coordinates analysis (PCO) were performed using MVSP Version 3.2 (Kovach 1985-2002). The hierarchical cluster analysis was used to determine inherent or natural groupings in the data and the output obtained is shown in the dendrogram.

Cytogenetics

In this study we describe the meiotic chromosome number and behavior of two *Onobrychis* species: *O. altissima* (5 populations) and *O. viciifolia* (2 populations). Voucher specimens are deposited in the herbarium of Bu-Ali Sina University (BASU), Hamedan, Iran. 15 flower buds from at least 5 randomly selected plants in the ideal stage for meiotic studies were collected and fixed in 96% ethanol, chloroform and propionic acid (6:3:2) for 24 h at room temperature, and then washed and preserved in 70% ethanol at 4°C until used. Microsporocytes were prepared by squashing and stained with 2% acetocarmine. Chromosome number was determined in 5 plants per population during diakinesis. The meiotic chromosome association was evaluated in at least 20 cells in diakinesis and the meiotic behavior up to this phase was evaluated in more than 250 microsporocytes. For grouping the species and populations showing similar meiotic behavior, UPGMA as well as ordination based on principal coordinates analysis (PCO) using MVSP Version 3.2 was performed on standardized data (Kovach 1985-2002).

Results and discussion

Phenetic analysis

Onobrychis altissima occurring in Armenia, Azerbaijan, Georgia, Iran and Turkey. It is a tall-growing, usually erect species with oblong or elliptic leaflets and small, almost unarmed fruits. *O. altissima* is very closely related to the cultivated sainfoin, *O.*

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Table 2. Morphological comparison between different populations of *Onobrychis viciifolia* and *O. altissima*.

Characters	14192-alt	14201-alt	14204-alt	14209-alt	14202-alt	14198-vic	14199-vic
Stem [length cm]	62	53	47.5	63	45	27	25
Stem indumentum (glabrous = 0, loose = 1, dense = 2)	2	0	1	0	1	1	0
Stem indumentum [length mm]	0.4	0	0.65	0	0.25	1	0.5
Leaf [length cm]	10	10	7	10	10	12.5	5
Leaflet number	6	8	5	7.5	6	6.5	5
Leaflet [length mm]	19.5	18	26.5	17	19.5	12.5	16
Leaflet [width mm]	5	4.25	7.5	4	4	5	3.75
Leaflet indumentum on lower surface (glabrous = 0, hairy = 1)	0	1	1	0	1	1	1
Leaflet indumentum on lower surface [length mm]	0.85	0.7	0.65	0.8	0.7	1	0.7
Stipule [length mm]	12	7	6.75	6	6.5	10.5	7
Stipule [width mm]	4.5	4	4.5	4	3.75	3.25	4.5
Stipule indumentum (glabrous = 0, loose = 1, ciliate = 2)	1	0	1	0	0	2	2
Stipule indumentum [length mm]	0.7	0.3	0.25	0	0.2	0.2	0.3
Petiole [length mm]	16	11	12	7.5	12	12.5	11.5
Petiole indumentum (glabrous = 0, loose = 1, dense = 2)	0	0	2	0	0	1	2
Petiole indumentum [length mm]	0.5	0.7	1	0.8	0.65	0.2	0.45
Flower number	29	47	31	36.5	31	32	23
Calyx [length mm]	9	8.5	8	7	7.1	6.7	5.5
Calyx tooth [length mm]	5	5	4.5	3.5	4.1	4	3
Calyx tube [length mm]	3.2	3	3.1	3	3	3	2.5
Calyx tube [width mm]	5	6.2	5	4	5.1	5	4
Calyx indumentum [length mm]	0.8	0.8	0.65	0.7	0.3	0.9	0.5
Standard [length mm]	12	11.2	11.25	11.1	11.75	9.7	11.75
Standard [width mm]	9	8	8.2	8	8.5	7	7.1
Keel [length mm]	11	12.5	11.1	11.1	12.25	9.5	11
Keel [width mm]	5	5	5	4.3	4.6	4	4.1
Keel claw [length mm]	3	4.1	3.3	3	3.3	2.8	3
Wing [length mm]	4.75	3.1	4.6	3	4.1	3	4
Wing [width mm]	2	1.9	1.9	1.5	1.9	1.5	1.5
Wing claw [length mm]	1.55	1	1.5	1	1.3	1	1.2
Wing auricle [length mm]	1.2	0.8	1	0.8	1	0.7	0.7
Pod [length mm]	?	6	6	6.5	6	5.5	6.8
Pod [width mm]	?	5	5.1	5	5	4.8	5.5
Pod indumentum [length mm]	?	0.3	0.3	0.2	0.2	0.3	0.35
Seed [length mm]	?	3.2	3.2	3	3	3	3.8
Seed [width mm]	?	2.5	2.3	2.5	2.5	2.5	3
Bracteole [length mm]	1.5	1	0.9	1	1	1	0.8

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sativa, and may be a progenitor of it (Hedge 1970). The wild distribution of *O. viciifolia* is uncertain, but for long it has been widely cultivated as a fodder plant throughout Europe and parts of Asia and is now naturalized in many places (Hedge 1970). All of the specimens cited in this study are apparently wild gatherings. Although *O. viciifolia* is generally recognized by having small teeth on crest of pod and wings shorter than 3 mm, it is extremely closely related to *O. altissima* in Iran, and it is doubtful whether they can be clearly distinguished from each other. Results from cluster and PCO analyses based on morphologic characters showed two major clusters/groups. Two populations (Taham and Bostan abad) of *O. viciifolia* are placed in the first cluster/group and all populations of *O. altissima* are placed in the second cluster (Figs. 1 & 2).

Cytogenetics

Chromosome number and ploidy level

Two basic chromosome numbers (x = 7 and x = 8) and ploidy levels ($2n = 2x = 14$, $2n = 4x = 28$, $2n = 8x = 56$ and $2n = 2x = 16$, $2n = 4x = 32$) are present in the genus *Onobrychis* (Abou-el-Enain 2002). For *O. viciifolia*, one ploidy level ($2n = 4x = 28$) and for *O. altissima*, two ploidy levels ($2n = 2x = 14$, $2n = 4x = 28$) have been previously reported (Takhtajan 1990). All wild populations of *O. viciifolia* and *O. altissima* studied here showed $2n = 4x = 28$ chromosome number and formed only bivalents in metaphase I (Table 3). *O. viciifolia* and *O. altissima* are similar in life history, breeding system, ecology, and geographical distribution in Iran (Map. 1). Also all Iranian populations of these species are tetraploid ($2n = 4x = 28$) and strongly resemble each other in leaf shape, stem indumentum, number of leaflets and flowers and length of standard, keel and pod. The strong morphological similarity between the two species was commented upon by Hedge (1970), and a close relationship between the two was postulated by Hedge (1970). They behave as a monocarpic perennial in its natural habitat. On the comparative biology of *O. viciifolia* and *O. altissima* has led to the hypothesis that these two species have a progenitor-derivative relationship with the former species having differentiated from the later.

Meiotic behavior

The meiotic irregularities observed in different *Onobrychis* species studied showed variation and included the occurrence of varied degree of sticky chromosomes, laggards and bridge formation in anaphase I & II, telophase I & II, desynapsis in metaphase I and asynchronous nuclei in metaphase II (Table 3 & Figs. 3-20).

Meiotic abnormalities

Anaphase and telophase laggard chromosomes

Data with regard to laggard chromosomes are provided in Table 3. Only Kaleibar population (14204) of *O. altissima* and two populations of *O. viciifolia* showed formation of laggard chromosomes from anaphase I to telophase II, while other populations studied did not form any laggard chromosomes (Figs 6, 9 & 15). The highest percentage of AI/TI cells with laggard chromosomes occurred in Taham population (14198) of *O. viciifolia*. AII/TII cells with laggard chromosomes were observed only in Kaleibar population (14204) of *O. altissima*. Laggards and non-oriented chromosomes may produce micronuclei, if they fail to reach the poles in time to be included in the main telophase nucleus (Koduru & Rao 1981; Utsunomiya et al. 2002), leading to the formation of micro-pollen and, probably, to gametes with unbalanced chromosome numbers (Mansuelli et al. 1995). Non-oriented bivalents may be related to impaired attachment of kinetochores to the spindle fibers (Nicklas & Ward 1994). It has been suggested that infertility in polyploids is not solely due to the production of aneuploid gametes formed by improper segregation of chromosomes during anaphase/telophase stages, the genetic factors may also bring about pollen sterility as evidenced in different tetraploid species (Hazarika & Rees 1967; Pagliarini 1990 & 2000; Baptista-Giacomelli et al. 2000).

Chromosome stickiness

Sticky chromosomes were observed from early stages of prophase till the final stages of meiosis in some of populations studied. Chromosome bridges resulting from stickiness were observed in anaphase I and II as well as telophase I and II stages (Figs. 4 & 8). The thickness of bridges observed and the number of chromosomes involved in their formation varied among different meiocytes and the species studied. Chromosome stickiness may be caused by genetic and environmental factors, and several agents have been reported to cause chromosome stickiness (Pagliarini 2000).

Desynapsis

Desynapsis is considered as the precocious separation of bivalents in metaphase of meiosis I leading to the formation of varying degree of univalents. A complete desynapsis was observed only in Taham population (14198) of *O. viciifolia* (Fig. 5). Desynapsis occurs either due to the action of recessive ds genes in a

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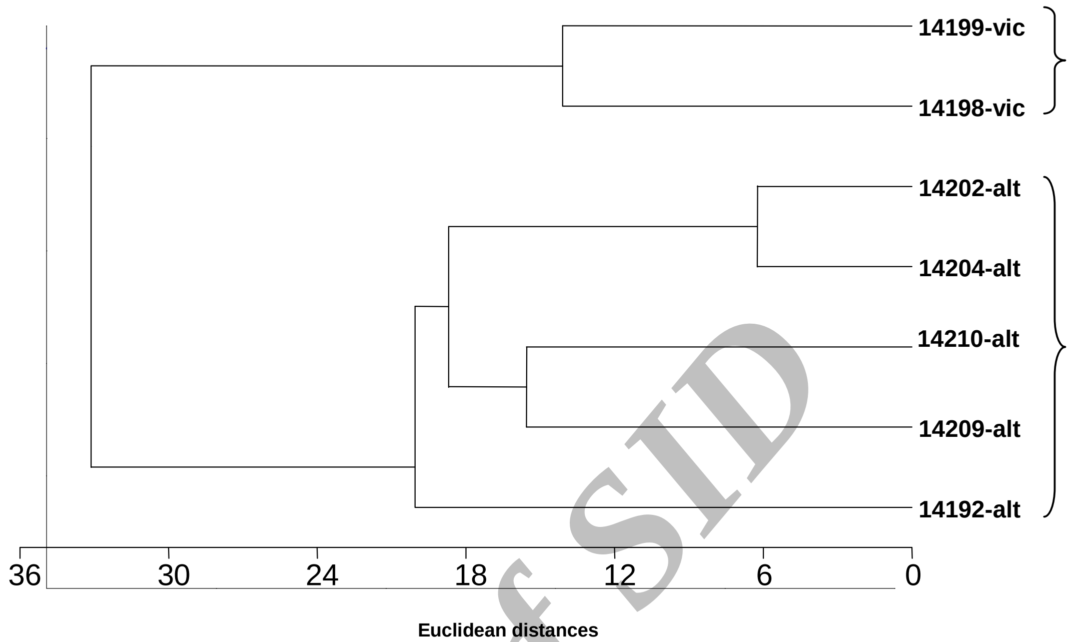

Fig. 1. UPGMA clustering of *Onobrychis* populations based on morphologic characters (abbreviations are as listed in Table 1).

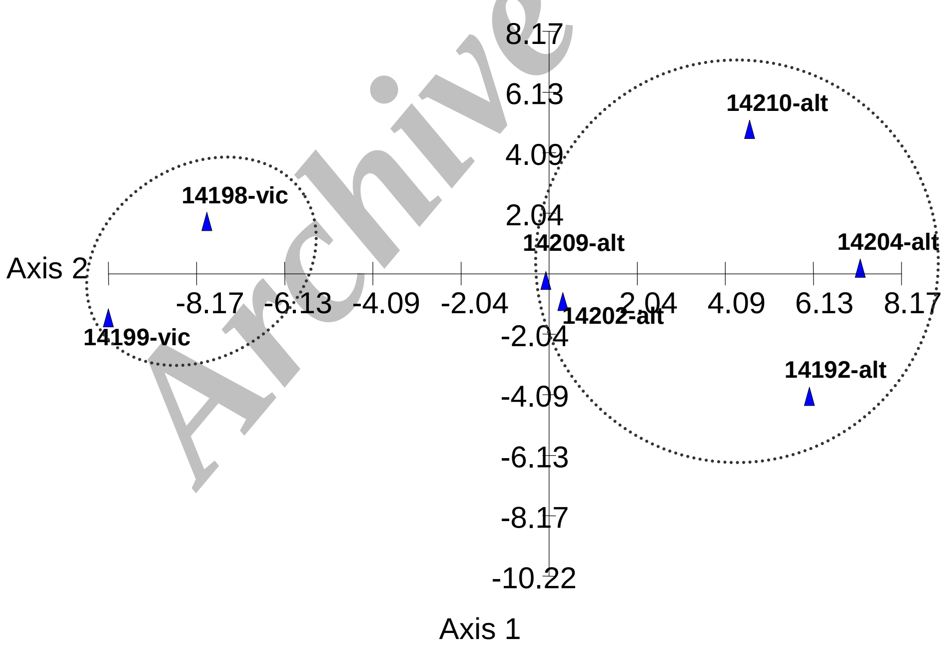

Fig. 2. PCO ordination of *Onobrychis* populations based on morphologic characters (abbreviations are as listed in Table 1).

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Table 3. Meiotic beheavior in different populations of *Onobrychis viciifolia* and *O. altissima*.

Taxa	14192-alt	14202-alt	14201-alt	14204-alt	14209-alt	14199-vic	14198-vic
Cell number	285	1336	933	2673	2288	782	2106
Z/P	144	132	161	886	1252	71	1409
D/MI	82	347	263	356	30	35	272
% B-chromosomes	0.00	10.64	0.00	0.00	0.00	0.00	0.00
AI/TI	2	123	206	78	190	55	177
% Laggard/Bridge	0.00	0.00	0.00	7.69	0.00	5.45	17.51
% Desynapsis	0.00	0.00	0.00	0.00	0.00	0.00	1.12
PII	16	239	12	173	249	115	38
MII	5	35	41	72	121	29	10
% Asynchronous nucleus	0.00	26.80	17.14	20	9.09	65.38	60
AII/TII	36	460	250	1108	446	480	200
% Laggard/Bridge	0.00	0.00	0.00	0.09	0.00	0.00	0.00
n	7	7	7	7	7	7	7
Ploidy level	4	4	4	4	4	4	4

Abbrevaitions used in table 3: Z/P = Zygotene/ Pachytene; D/MI = Diakinesis/Metaphase I; n = Chromosome number; AI/TI = Anaphase I/Telophase I; PII = Prophase II; MII = Metaphase II; AII/TII = Anaphase II/Telophase II.

homozygous situation or early chiasma terminalisation which may lead to the formation of meiocytes with double normal chromosome number. In several cases such univalents may have difficulty during anaphase I movement and become lagged therefore producing aneuploid gametes causing reduction in pollen fertility of plants. However they may skip the first anaphase and form restitution nucleus resulting in the formation of unreduced gametes as reported in some other species (Veilleux 1985; Sheidai et al. 2006 & 2007).

B-chromosomes

B-chromosomes or accessory chromosomes that occur in addition to the standard or A-chromosomes in some of the plants, are smaller than other chromosomes and do not form any association with them, although they could arrange themselves along with the A-chromosomes on the equatorial plane of the spindle and move to the poles during anaphase. In some cases they occurred as laggard chromosomes. The significance of B-chromosomes is to be found in their widespread occurrence in hundreds of flowering plants, and also in gymnosperms and in some lower forms such as ferns, bryophytes and fungi (Jones & Rees 1982; Camacho et al. 2000). This abnormality only was observed (10.64%) in Ardebil population (14202) of *O. altissima* (Fig. 11).

Cluster analysis and ordination based on cytoenetic characters showed two major clusters/groups. Two populations (Taham and Bostan abad) of *O. viciifolia* are placed in the first cluster/group and all populations of *O. altissima* are placed in the second cluster, supporting results from phenetic analysis. The second major cluster comprises two sub-clusters; Firuzkuh and Varzaghan populations are placed in the first sub-cluster/group and the other populations placed in the second one (Figs. 21 & 22).

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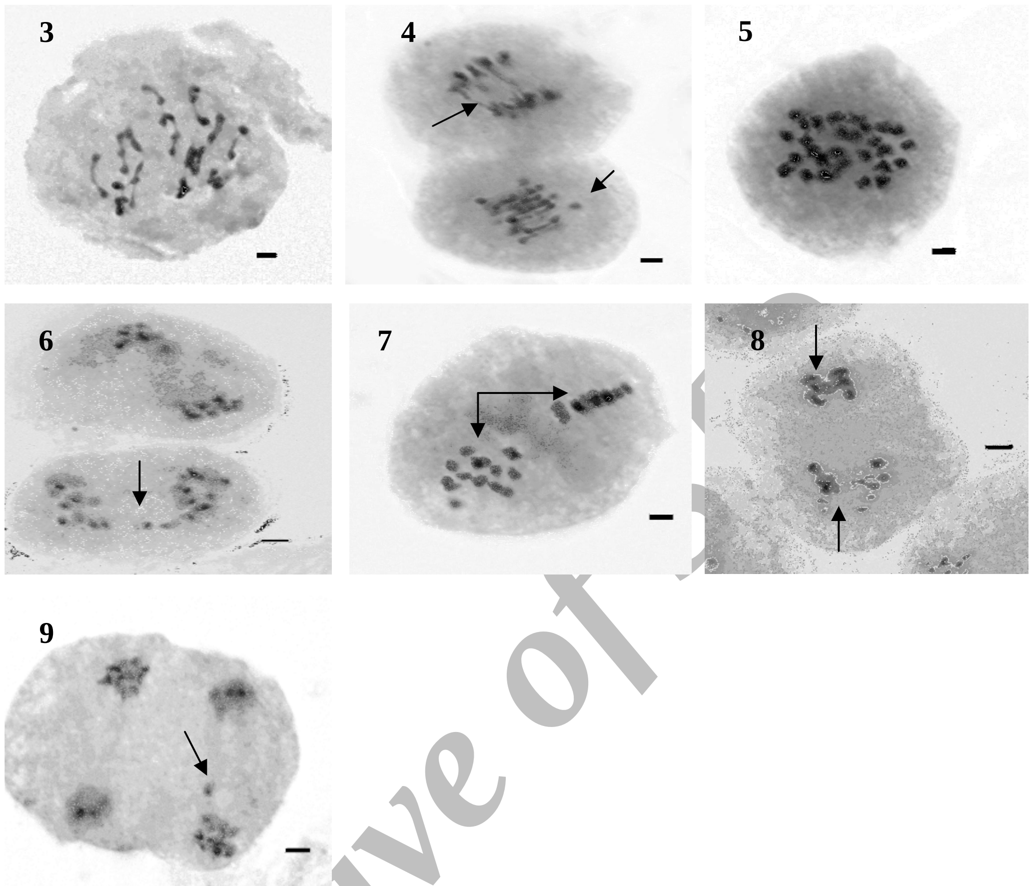

Figs. 3-9. Representative meiotic cells in *Onobrychis viciifolia*. 3) Early metaphase I; 4) Anaphase I with bridge (arrows); 5) Perfect desynapsis with 28 univalents; 6) Telophase I with laggard chromosomes; 7) Asynchronous nucleus in metaphase II; 8) Anaphase II with bridge; 9) Telophase II with laggard chromosome. Scale bars = 3 µm.

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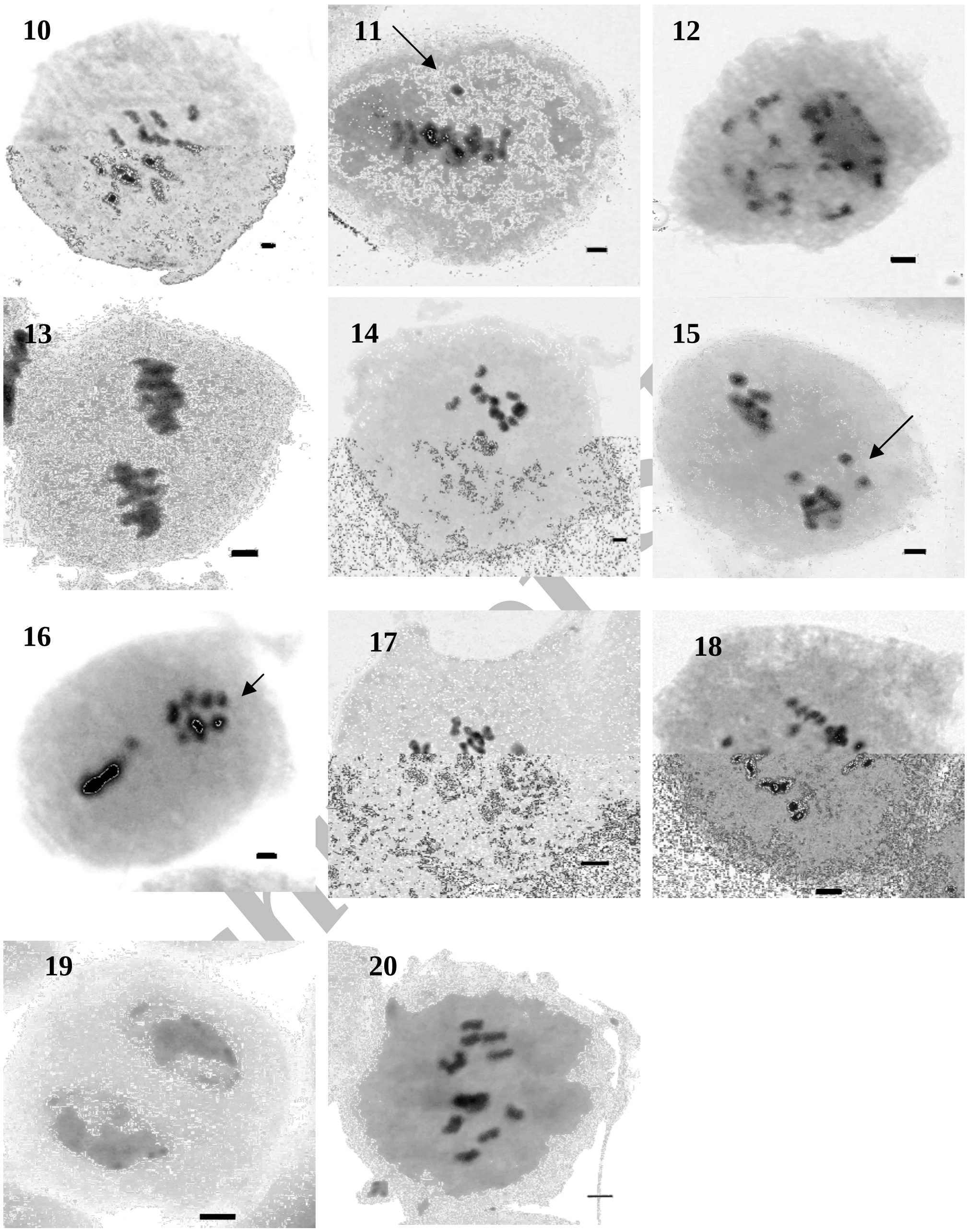

Figs. 10-20. Representative meiotic cells in different populations of *Onobrychis altissima*. [10 & 11: Ardebil population (14202)], 10) Early metaphase I; 11) Metaphase I showing 14 bivalents and 1 B-chromosome. [12 & 13: Varzaghan population (14209)], 12) Pachytene; 13) Metaphase II. [14-16: Kaleibar population (14204)], 14) Early metaphase I; 15) Telophase I with laggard chromosomes; 16) Asynchronous nucleus in metaphase II. [17-19: Firuz kuh population (14192)], 17) Early metaphase I; 18) Anaphase I; 19) Telophase I. [20: Saien population (14201)], 20) Early metaphase I. Scale bars = 3 µm.

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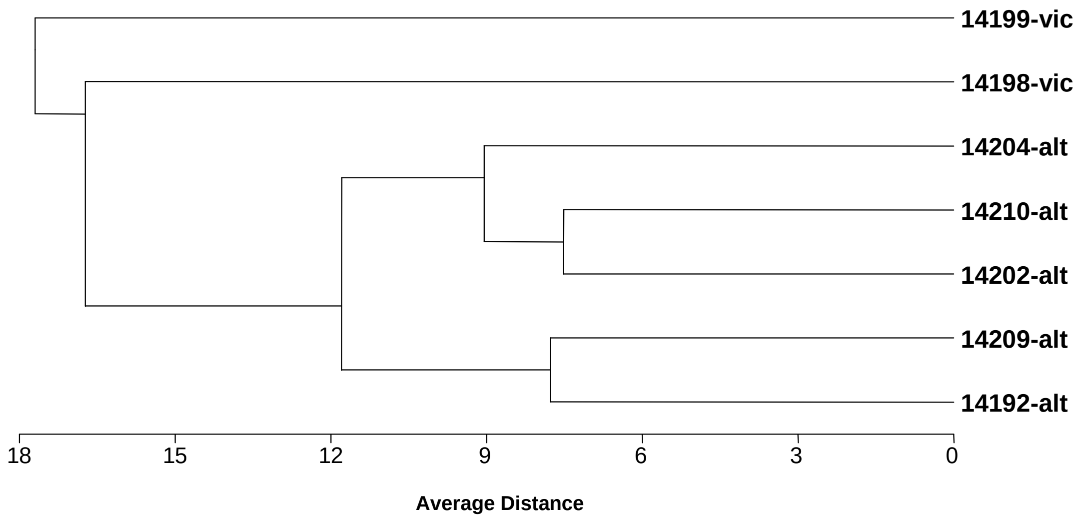

Fig. 21. UPGMA clustering of *Onobrychis* populations based on cytogenetic characters (abbreviations are as listed in Table 1).

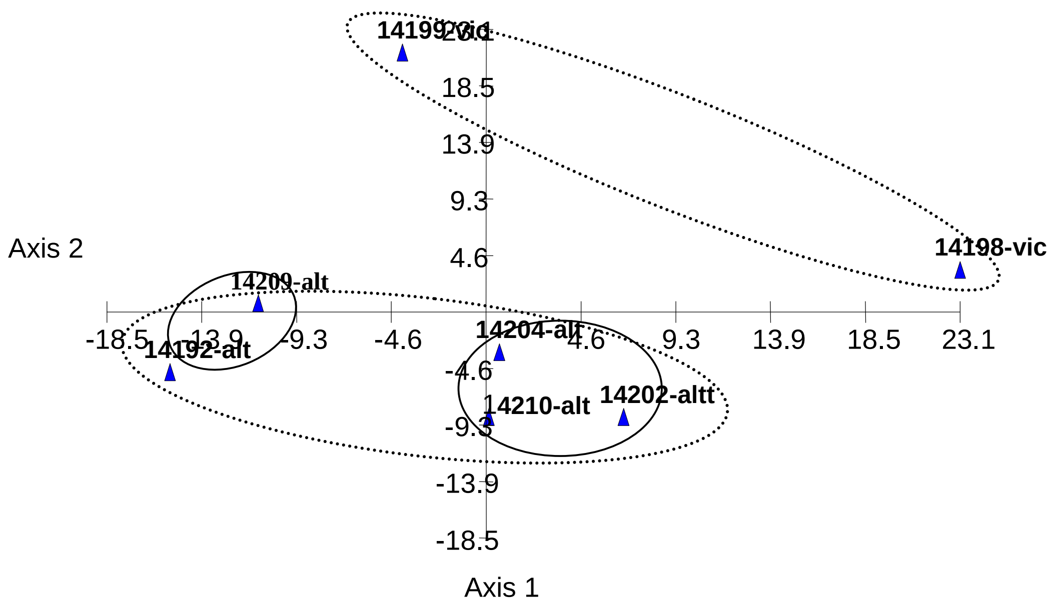

Fig. 22. PCO ordination of *Onobrychis* populations based on cytogenetic characters (abbreviations are as listed in Table 1).

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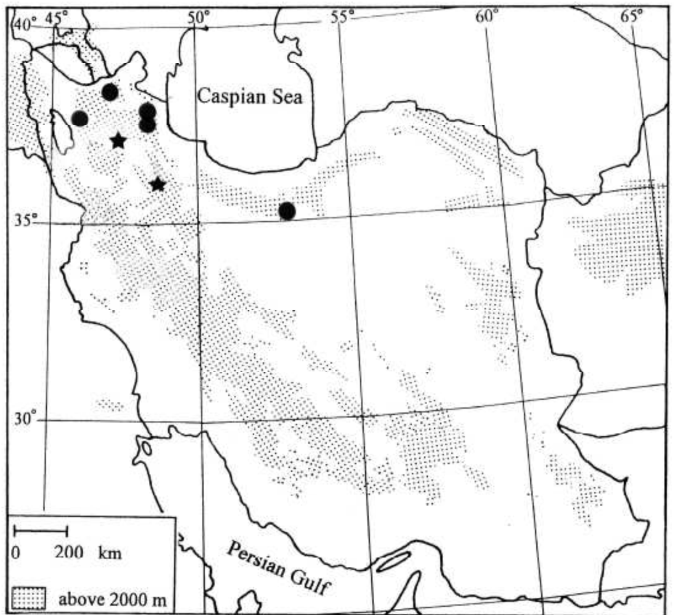

Map 1. Distribution map of *Onobrychis viciifolia* (★) and *O. altissima* (●) in Iran based on fresh material in this study.

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