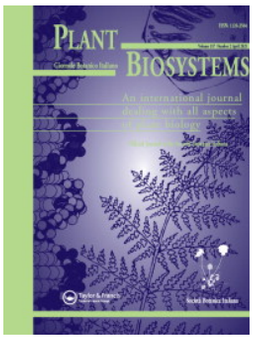

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Karyological studies of Iranian *Allium* (Amaryllidaceae) species with a focus on sect. *Acanthoprason*. 2. Meiotic chromosomes

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ABSTRACT

Meiosis in pollen mother cells (PMCs) was studied of 23 Iranian *Allium* species (33 accessions, 105 individuals) that belong to two subgenera and six sections. Materials of 13 species were sampled from (near) type locations. Gametic chromosome numbers, chromosome configurations at metaphase I, chiasma frequency, as well as type and percentages of abnormalities were recognized. The basic chromosome number for all taxa investigated was $x=8$. Most taxa were diploid and showed eight bivalents or in rare cases two or four pairs of univalents, but in *A. subakaka*, *A. ubipetrense* and *A. zagricum* tetravalents also occurred. Meiosis in less than 10% of PMCs of diploid accessions was disturbed displaying lagging chromosomes, chromatid bridges, micronuclei, or unbalanced chromosome segregations, but very rarely more than one kind of irregularities were found within one dividing cell. One to three B chromosomes were found in 11 accessions, and were recognized for the first time in *A. alamutense*, *A. elburzense* and *A. iranshahrii*. Our data showed no correlation between the occurrence of B chromosomes and the chiasma frequency, and also no noticeable effect of habitat factors on meiotic chromosome behavior. The studied accessions of *A. atroviolaceum* and *A. sabalense* were tetraploid ($n=16$) showing irregular meiosis in 20–69% of the PMCs which is regarded as sign of autopolyploidy. Since only two out of 31 investigated accessions belonging to subg. *Melanocrommyum* were tetraploid, we may suggest a trivial role of polyploidy in the evolution of this subgenus.

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Allium; chiasma frequency; chromosome behavior; diakinesis; Iran; male meiosis; pollen mother cells (PMCs)

Introduction

Meiosis is the common feature of eukaryotic sexual reproduction and plays a key role in life cycles of all sexually reproducing organisms (Mirzaghaderi and Hörandl 2016). In spite of obvious high costs of sex, the sexual reproduction in eukaryotes prevails, i.e. less than 1% of seed plants and 10% of ferns asexually reproduce (Hörandl 2013; Speijer et al. 2015), and asexual cases are perceived as a curiosity of nature (Cnudde and Gerats 2005). In meiosis one replication of DNA is followed by two nuclear divisions, meiosis I and meiosis II (Petronczki et al. 2003). Meiosis I is unique and involves the segregation of homologues chromosomes whereas like in mitosis, in meiosis II sister chromatids are segregated (Ma 2005). The three unique features of meiosis are synapsis, homologous recombination and reduction division. Before meiotic anaphase I, reciprocal recombination between homologs (cross overs) are temporarily hold together by the cytologically visible associations called chiasmata. Crossing over between homologues chromosomes is essential for correct segregation at anaphase I. Independent assortment of homologous chromosomes and crossing over which occur during meiosis, and also random fertilization, all help generating genetic diversity upon which natural selection can act and therefore speciation takes place (Rice and Chippindale 2001).

In angiosperms, meiosis is organized quite differently in male and female organs and the fate of meiotic products are also divergent. In anthers, pollen mother cells (PMCs) enter more or less synchronous meiotic division to produce microspores (Hamant et al. 2006). Upon completion of meiosis, each microspore undergoes one or two rounds of mitosis and develops into a pollen grain (Ma 2005). Since fast access is given and rather stereotyped cellular processes govern male meiosis in plants, many studies and many data on meiosis originated from studies of pollen mother cells (Hamant et al. 2006) and started already in the first years of twentieth century. Haploid chromosome number, metaphase I chromosome configurations, chiasma frequency per bivalent, the kind and percentage of abnormalities at meiosis I and II, behavior of B chromosomes etc. are just some microscopic cytological features to be observed during meiotic analyses. Distinct advantages of pollen mitosis also contributed valuable cytological information in angiosperms and gymnosperms (Khoshoo 1966).

During the last two decades *Allium* species occurring in Iran were a main target of taxonomic research activities resulting

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in a large number of anatomical (Khorasani et al. 2018a), morphological (Khorasani et al. 2018b), molecular (Veiskarami et al. 2019), and karyological (Dolatyari et al. 2018) contributions (only a few most recent publications were cited). Also, more than 50 species and subspecies were newly described or reported from Iranian territory (Govaerts et al. 2022).

Alliums possess many advantages to be considered as a good model for male meiotic cytological examinations. First, the size of chromosomes is large enough to be easily visualized by light microscopes just after a simple method of squashing anthers in traditional stains like aceto-orcein. Second, developing cymose umbel-like *Allium* inflorescences present many flowers at different developmental stages. Third, every flower includes six anthers each of which follows its own developmental steps, but all meiocytes of one anther pass the meiotic stages simultaneously. Finally, inflorescences are initially hidden in a closed spathe, and with a higher likelihood in this un-split stage flower buds with white anthers containing dividing meiocytes can be found.

In addition to the review of previous chromosome reports on Allium taxa occurring in Iran by Dolatyari et al. (2018), recently published chromosome data are also available (Hosseini 2018; Maragheh et al. 2019; Abdali and Miri 2020; Bagheri et al. 2020; Sayadi et al. 2021) We excluded the contributions of Mastali et al. (2018) and Oroji Salmasi et al. (2019) because the published data of materials studied nursed doubt about the correct *Allium* identifications and also because of uncertain mitotic plates they presented. Most of all new chromosome counts were based on mitotic division.

Allium L. is the largest genus of petaloid monocots in Iran. By and large, around 153 species belonging to eight subgenera and 32 sections occur (Dolatyari et al. 2018; Bagheri et al. 2020; Dolatyari et al. 2020; Memariani et al. 2022). Based on our bibliographic searches, chromosome counts for 68% (104 species) have already been reported. Hitherto, in 75 species solely the diploid level of $x = 7$, 8, 9 and 10, and also in 22 species simultaneously diploid and polyploid levels (tri- to hexa-ploidy) were reported. The dominant basic chromosome number in the Iranian species is $x = 8$ (Dolatyari et al. 2018; Fritsch 2018; Hosseini 2018; Sayadi et al. 2021). In 23 species a broad range of 1, 2, 3, 4, 9, 10 and 18 B chromosomes were reported. The extreme B chromosome frequencies of 0–9 and 0–18 were earlier counted in *A. schoenoprasum* L. (Bougourd and Parker 1979; Mehra and Pandita 1979; Zhukova 1980; Tardif and Morisset 1992). Only for 23 *Allium* species occurring in Iran, we could find previous gametic chromosome reports mainly based on analyses of first pollen mitosis or meiosis in pollen mother cells (see the online supplementary 1). Worth to note that only for *A. rubellum* M. Bieb., *A. iranicum* (Wendelbo) Wendelbo, *A. asarense* R.M. Fritsch & Matin and *A. schisticola* R.M. Fritsch, Moazzeni & Dolatyari the meiotic data were described on materials from Iran (Ghaffari 2006a, 2006b; Dolatyari and Saeidi Mehrvarz 2017; Dolatyari et al. 2020). Thus, the current knowledge about meiotic characters of Allium species occurring in Iran is in need of a broad and detailed supplementation. The present work continues detailed karyological studies on the genus in Iran and presents precise meiotic data by studying PMCs of 23 species.

Material and methods

Material collection

The herbarium vouchers, immature inflorescences and bulbs of the 33 examined accessions (23 species plus one subspecies) were collected from 15 Iranian provinces. Materials of 13 species were sampled from (near) type locations (Table 1). These taxa belong to two subgenera and six sections (Table 2). The herbarium vouchers were deposited in the Iranian biological resource center (IBRC). Collected bulbs were planted at the living collection of this center. These plants were also used to verify taxonomic determinations. We tried to fix inflorescences from wild populations (16 accessions) whenever possible, otherwise we sampled these materials from cultivated plants (17 accessions, see Table 1). As in our previous karyological work on the Iranian alliums (Dolatyari et al. 2018), the main focus was set on the subgenus *Melanocrommyum* and the section *Acanthoprason* (25 accessions).

Fixation of meiotic materials

Inflorescences enclosed in un-split spathes were fixed in freshly prepared Carnoy I solution (1:3 v/v of glacial acetic acid and absolute ethanol), after having opened the spathes for better penetration of the fixative, for 12–16 h and then again were kept in fresh fixative for 24 h, both steps at room temperature. For long-term preservation before laboratory analyses, we substituted fixative with 70% alcohol and kept materials in the refrigerator at 4 °C.

Meiotic spreads preparation and microscopic observations

White-colored anthers still much shorter than in early anthesis were prepared and squashed in a drop of 2% aceto-orcein on microscope slides applying the commonly used technique. They were analyzed under a BX51 Olympus light microscope furnished with a DP25 digital camera. Nearly from each dividing cell images were taken in bright field and phase contrast modes at ×600 and ×1200 magnifications. On the whole, around 10,000 digital images were taken from the examined materials. For each accession at least 100 PMCs at prophase I – metaphase I were examined to report well-based gametic chromosome numbers and chromosome configurations.

Estimating irregularities

As in the nature mostly one inflorescence represents one individual grown from one seed, the opportunity was provided to estimate chromosomal behavior and meiotic abnormalities at intra-population level. Normally and abnormally dividing meiocytes were separately counted for each individual and then average percentages were calculated for all studied individuals of each accession (Table 2). The frequency of chiasmata per bivalent was scored at least from ten cells at late diakinesis or metaphase I (sub)stages. Abnormal meiocytes showed chromatid bridges, micronuclei, lagged chromosomes and unbalanced chromosome segregations at anaphase-telophase I and/or II. Very rarely more than one kind of irregularities were found within one dividing cell.

Table 1. Characterization of the investigated taxa and accessions (in alphabetical order).

Taxon	Accession No.	Collection site	Herbarium No.
Subgenus *Allium* section *Allium*			
Allium atroviolaceum Boiss.	P1008926‡	Razavi Khorassan: between Mareshk and Bolghur villages. N 36 49 28.5, E 59 35 0.5, 2247 m	1326
Subg. *Allium* sect. *Avulsa* F.O. Khass.			
Allium umbilicatum Boiss.	P1009439	Alborz: Karaj to Chalus, Kondur junction. N 35 50 32.3, E 51 03 26.1, 1340 m	1649
Subg. *Melanocrommyum* (Webb & Berthel.) Rouy sect. *Acanthoprason* Wendelbo			
Allium akaka S.G. Gmel. ex Schult. & Schult.f. subsp. *akaka*	P1009775†‡	Ardebil: E of Khalkhal, Aznav spring. N 37 34 43.8, E 48 34 25.2, 1900 m	1610
Allium akaka subsp. *bozgushense* R.M. Fritsch	P1011312†	E Azerbaijan: Mianeh, Ishligh, Charan, Bozghush mountain range. N 37 42 5.2, E 47 32 34.8, 2704 m	1823
Allium alamutense Razyfard, Zarre & R.M. Fritsch	P1009698†‡	Qazvin: Alamut, 50 km before Moalem Kelayeh. N 36 23 33.1, E 50 12 52.3, 2412 m	1838
Allium austroiranicum R.M. Fritsch	P1009622‡	Esfahan: 13 km before Semirom from Shahreza. N 31 29 53.1, E 51 34 54.6, 2815 m	1441
	P1009650‡	Fars: 8 km from Eghlid towards Yasuj. N 30 51 41.9, E 52 34 58.5, 2854 m	1814
	P1009666‡	Kohgiloyeh & Boyerahmad: Sisakht, Bizhan pass, ca. 20 km a Sisakht to Yasuj. N 30 54 58.4, E 51 34 6.1, 2598 m	1837
Allium chlorotepalum R.M. Fritsch & M. Jaeger	P1011002	Esfahan: Damaneh, slopes SW of Damaneh. N 32 59 40.7, E 52 30 31.4, 2741 m	1907
	P1010994†	Esfahan: Daran, slopes E of Analujeh village. N 32 55 13.5, E 50 33 50, 2724 m	1908
	P1011026	Markazi: Arak, hills E of Hoseinabad village. N 34 01 37.1, E 49 47 0.4, 2011 m	1815
Allium derderianum Regel	P1009475†‡	Alborz: Chalus road, 25 km before Gachsar from Karaj. N 36 02 6.6, E 51 12 1.2, 1909 m	1619
Allium graveolens (R.M. Fritsch) R.M. Fritsch	P1011018†	Markazi: W of Arak, hills and mountains S of Marzijeran village. N 34 06 45.6, E 49 38 22.2, 2018 m	1658
Allium haemanthoides Boiss. & Reut. ex Regel	P1011119†	Kermanshah: Paveh, Khanghah, Atashgah mt. N 35 00 56.9, E 46 19 21, 1893 m	1659
Allium iranshahrii R.M. Fritsch	P1011289	W Azerbaijan: Oshnavieh, Razhan, Khalilkuh. N 37 23 4.4, E 44 47 37.4, 3017 m	1915
	P1011271†	W Azerbaijan: Piranshahr, Silveh, Mashkan, Chighidarreh mt. N 36 45 42.1, E 44 59 17.4, 2835 m	1824
Allium mahneshanense Razyfard, Zarre & R.M. Fritsch	P1010506†‡	Zanjan: Dandi towards Takht-e Soleiman, mountains NW of Anguran lead and zinc mine. N 36 38 13.9, E 47 23 50, 2854 m	1656
Allium materculae Bordz.	P1009920‡	E Azerbaijan: NE of Marand, 3 km before Dogijan a Zarghan. N 38 30 4.8, E 46 02 1.8, 2192 m	1839
	P1009955‡	E Azerbaijan: Marand, 4 km before Zonoz a Marand. N 38 36 16.2, E 45 47 45.4, 1543 m	1818
Allium minutiflorum Regel	P1010973	Esfahan: ca. 95 km before Esfahan a Naein. N 32 44 42.2, E 52 44 30, 2232 m	1916
	P1009582‡	Markazi: 25 km before Meimeh a Delijan. N 33 38 11.3, E 50 59 8.5, 2087 m	2247
Allium sabalense R.M. Fritsch	P1009858‡	E Azerbaijan: S of Ahar, Ghosh-e Dagh mountain. N 38 20 4.2, E 47 03 12.5, 2461 m	1848
	P1009764‡	Ardebil: Asalem towards Khalkhal, 1 km a Mojereh village in old road. N 37 35 1.5, E 48 37 19.8, 1986 m	1850
Allium stipitatum Regel	P1009633‡	Esfahan: 25 km a Semirom towards Vanak. N 31 31 41.8, E 51 25 11.4, 2727 m	1440
Allium subakaka Razyfard & Zarre	P1009965‡	W Azerbaijan: 30 km before Qotur. N 38 26 45.9, E 44 40 58.6, 1524 m	1618
Allium ubipetrense R.M. Fritsch	P1011070	Lorestan: Doroud towards Khorramabad, Razhan pass, Razhan red crescent, gravel road towards the limestone mountains W of the pass. N 33 34 15.6, E 48 49 5.7, 2536 m	2245
	P1011039	Markazi: Shahzand, Suraneh, Mts. SW of Emamzadeh Abdollah. N 33 52 3.3, E 49 26 20.7, 2577 m	1820
Allium zagricum R.M. Fritsch	P1011079†	Lorestan: N Khorramabad, Qalemorghi, Rimeleh, Poshtmeleh, Mt. Taf. N 33 38 59.9, E 48 27 24.9, 2285 m	1673
Subg. *Melanocrommyum* sect. *Asteroprason* R.M. Fritsch			
Allium elburzense Wendelbo	P1009503†‡	Tehran: 19 km before Polur, Mobarak Abad village. N 35 47 14, E 51 58 3.7, 1894 m	1506
Subg. *Melanocrommyum* sect. *Melanocrommyum* Webb & Berthel.			
Allium cardiostemon Fischer & C.A. Mey.	P1009998‡	W Azerbaijan: 61 km before Orumieh a Salmas. N 38 01 2.4, E 44 57 51.4, 1842 m	1641
Allium keusgenii R.M. Fritsch	P1011091	Kermanshah: Ravansar towards Paveh, Mts. opposite of the Bencheleh village. N 34 48 57.6, E 46 36 28.1, 2176 m	1803
Subg. *Melanocrommyum* sect. *Procerallium* R.M. Fritsch			
Allium jesdianum Boiss. & Buhse subsp. *jesdianum*	P1010963†	Yazd: Taft, Deh Bala, Sheikhalishah, Shirkuh mt. N 31 37 29.1, E 54 05 59.5, 2856 m	1911
Allium remediorum (R.M. Fritsch) R.M. Fritsch	P1011118†	Kermanshah: Paveh, Khanghah, Atashgah mt. N 35 00 56.9, E 46 19 21, 1893 m	1660

†:Material collected in the wild from (near) type location, ‡:meiotic materials sampled from plants collected in the nature and grown in experimental farm.

Table 2. Meiotic data for the 33 studied accessions.

Taxon	Access. No.	N.I.I.	*n*	Refer. Ims.	Ch.Co. MI.	Ch. F./B	Typ. I.	Exam. PMCs	% I. AI – TI	% I. AII – TII
Subgenus *Allium* sect. *Allium*										
Allium atroviolaceum	P1008926	2	16	Figure 1a–d	varied numbers of univalents to multivalents		L. Ch., Ch. B.	566	191 out of 316 cells (60%)	86 out of 150 cells (60%)
Subgenus *Allium* sect. *Avulsa*										
Allium umbilicatum	P1009439	5	8	Figure 1e–h	8II	1.9	L. Ch., Ch. B., M.	733	5 out of 281 cells (1.74%)	6 out of 352 cells (1.7%)
Subgenus *Melanocrommyum* sect. *Acanthoprason*										
Allium akaka subsp. *akaka*	P1009775	2	8	Figure 1i–l	8II	2.12	L. Ch., Ch. B.	642	21 out of 245 cells (8.57%)	7 out of 297 cells (2.35%)
Allium akaka subsp. *bozgushense*	P1011312	1	8	Figure 1m–p	8II	2.1	L. Ch., Ch. B.	422	7 out of 230 cells (3.04%)	0 out of 92 cells (0%)
Allium alamutense	P1009698	3	8	Figure 2a–d	8II, 7II + 2I	1.93	L. Ch., Ch. B., M.	630	23 out of 530 cells (4.33%)	–
		1	8+1B		8II, 7II + 2I, 6II + 4I	1.27		288	129 out of 188 cells (68.6%)	
Allium austroiranicum	P1009666	2	8	Figure 2e–h	8II, 7II + 2I	1.78	L. Ch., Ch. B., M.	1516	31 out of 694 cells (4.33%)	22 out of 722 cells (3.04 %)
	P1009622	4		Figure 2i–l		1.92	L. Ch., M.	1535	46 out of 1185 cells (3.88 %)	4 out of 250 cells (4%)
	P1009650	1		Figure 2m–p		1.76	L. Ch., Ch. B.	350		14 out of 250 cells (5.6%)
Allium chlorotepalum	P1011002	1	8	Figure 3a–c	8II	2.06				
		1	8+1B			2				
	P1010994	6	8	Figure 3d–g	8II, 7II + 2I	1.91				
		2	8+1B		8II + 1B, 7II + 2I + 1B, 6II + 4I + 1B	2.18, 1.51				
	P1011026	1	8	Figure 3h–l	8II	1.95	Ch. B.	200	1 out of 100 cells (1%)	
		5	8+1B			2				
		1	8+2, 3B			2.21				
Allium derderianum	P1009475	3	8	Figure 3m–p	8II	1.95	Ch. B., M.	420		9 out of 320 cells (2.81%)
		1	8+1B			2.18	L. Ch., Ch. B.	300		15 out of 200 cells (7.5%)
Allium graveolens	P1011018	2	8	Figure 4a–d	8II, 7II + 2I	2.07				
		1	8+2B			1.96				
Allium haemanthoides	P1011119	3	8	Figure 4e–h	8II, 7II + 2I	2.07				
Allium iranshahrii	P1011289	2	8	Figure 4i,j	8II	2.39				
		1	8+1B			2.25				
	P1011271	5	8	Figure 4k,l	8II, 7II + 2I	2.75				
		1	8+1B		8II	2.37				
Allium mahneshanense	P1010506	2	8	Figure 4m–p	8II	2.07	L. Ch., Ch. B.	768	43 out of 668 cells (6.4%)	
		1	8+2B		8II, 7II + 2I	2.1				
Allium materculae	P1009920	6	8	Figure 5a–d	8II, 7II + 2I	2.25	L. Ch., Ch. B., M.	764	10 out of 260 cells (3.84%)	8 out of 404 cells (1.98%)
	P1009955	3		Figure 5e–h		2.03		1701	37 out of 1020 cells (3.6%)	6 out of 581 cells (1.03%)
Allium minutiflorum	P1010973	2	8	Figure 5i,j	8II	1.96				
	P1009582	7		Figure 5k,l		2.33	L. Ch., M.	590	8 out of 340 cells (2.35%)	7 out of 150 cells (4.6%)
Allium sabalense	P1009858	1	16	Figure 5m,n	12II + 2IV, 10II + 3IV, 8II + 3IV+ 1VI	ca. 1.93	L. Ch., Ch. B.	222	54 ou of 122 cells (44.26%)	
	P1009764	2	16, 16+1B	Figure 5o,p; Figure 6a,b	16II, 13II +1IV + 2I, 13II + 6I, 12II + 2IV , 11II + 2IV + 2II	ca. 1.43	L. Ch., Ch. B., M.	803	10 out of 49 cells (20.4%)	137 out of 654 cells (20.9%)
Allium subakaka	P1009965	2	8	Figure 6c–f	8II, 6II + 1IV	2.05	L. Ch., Ch. B., M.	428	4 out of 328 cells (4.26%)	
Allium ubipetrense	P1011070	3	8	Figure 6g,h	8II, 6II + 1IV, 4II + 2IV	2.4				
	P1011039	4		Figure 6i–k	8II, 7II + 2I, 6II + 1IV	2.03				
Allium zagricum	P1011079	4	8	Figure 6l–n	8II, 7II + 2I, 6II + 1IV, 5II + 2I + 1IV, 2II + 3IV	2.28				
Subgenus *Melanocrommyum* sect. *Asteroprason*										
Allium elburzense	P1009503	1	8, 8+1B, 8+2B	Figure 6o,p	8II	2.37, 2.42, 2.33	L. Ch., Ch. B., M.	720	17 out of 320 cells (5.31%)	14 out of 300 cells (4.66%)
Subgenus *Melanocrommyum* sect. *Melanocrommyum*										
Allium cardiostemon	P1009998	2	8	Figure 7a–c	8II	1.75	L. Ch., Ch. B., M.	1554	44 out of 1022 cells (4.3%)	10 out of 432 cells (2.31%)
Allium keusgenii	P1011091	2	8	Figure 7d,e	8II	2.31	L. Ch., Ch. B., M.	444	4 out of 114 cells (3.5%)	4 out of 230 cells (1.73%)
Subgenus *Melanocrommyum* sect. *Procerallium*										
Allium jesdianum subsp. *jesdianum*	P1010963	1	8	Figure 7f–h	8II	2.13	L. Ch., Ch. B.	701	7 out of 227 cells (3.08%)	22 out of 374 cells (5.88%)
Allium remediorum	P1011118	3	8	Figure 7i,j	8II	2.2	L. Ch., Ch. B., M.	1231	15 out of 355 cells (4.22%)	17 out of 776 cells (2.19%)
Allium stipitatum	P1009633	2	8	Figure 7k,l	8II	2.3	L. Ch., Ch. B.	456		7 out of 356 cells (1.96%)

Access. No.: Accession number, **N. I. I.:** Number of investigated individuals, **n:** Gametic chromosome number, **Refer. Ims.:** Reference images, **Ch. Co. MI:** Chromosome configurations at metaphase I, **Ch. F./B:** chiasmata frequency per bivalent, **Typ. I:** types of irregularities (lagged chromosomes: L. Ch., chromatid bridge: Ch.B, micronuclei: M., unequal segregation: U.S.), Exam. PMCs: examined pollen mother cells, **% I. AI – TI:** Percent irregularities at anaphase I – telophase I, **% I. AII – TII:** Percent irregularities at anaphase II – telophase II.

Results and discussion

We report here the gametic chromosome number, chromosome configurations at metaphase I, chiasma frequency per bivalent, amount of irregularities at anaphase I – telophase I, as well as at anaphase II – telophase II (Table 2). Meiotic spreads of the studied accessions showing regular meiosis as well as variations and abnormalities were arranged in Figures 1–7. Altogether we could study meiosis in 105 individuals.

The basic chromosome number for all taxa investigated is $x = 8$. The studied accession of *A. atroviolaceum* and the two examined accessions of *A. sabalense* were tetraploid, the other investigated materials were diploid. The tetraploid taxa showed varied chromosome configurations at metaphase I (Figures 1a and 5m,o).

Normally (in 16 diploid accessions) just eight bivalents were spotted, and in other 11 diploid accessions besides eight bivalents, in very low frequencies seven bivalents and two

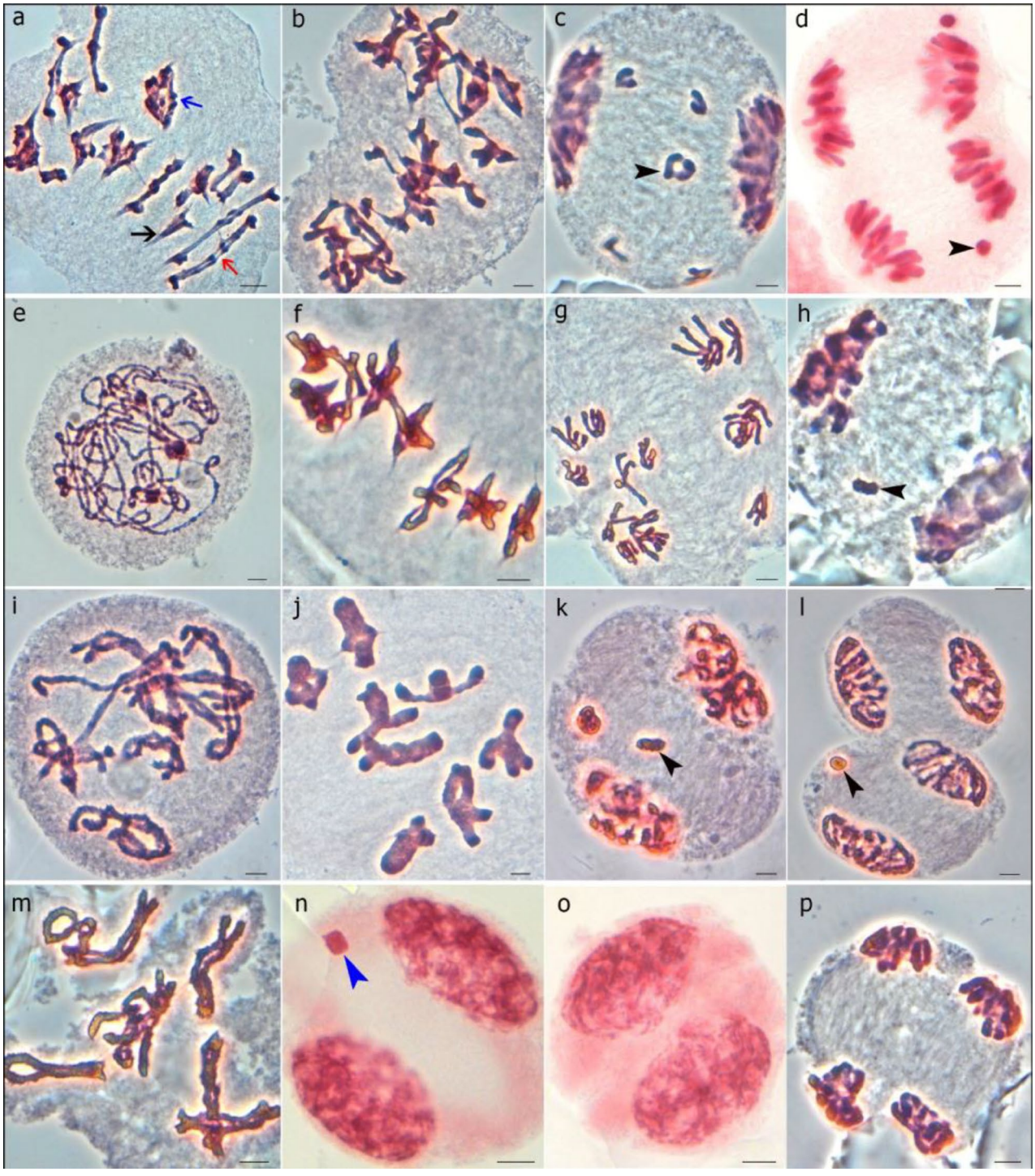

Figure 1. Male meiotic plates of the investigated taxa of sections *Allium*, *Avulsea* & *Acanthoprason*. (a, b) metaphase I, (c) late anaphase I, (d) late anaphase II in *A. atroviolaceum*; (e) pachytene, (f) metaphase I, (g) anaphase I (9–7 segregation), (h) telophase I in *A. umbilicatum*; (i) diplotene, (j) metaphase I, (k) telophase I, (l) telophase II in *A. akaka* subsp. *akaka*; (m) late diplotene, (n, o) telophase I, (p) telophase II in *A. akaka* subsp. *bozgushense*. All scale bars = 5 µm. Black, red and blue arrows indicate uni-, bi-, and tetravalents; black and blue arrowheads indicate lagged chromosomes and micronuclei, respectively.

univalents were observed (Figures 2f,j,n, 3e, and 4f). Diploid accessions of *A. subakaka*, *A. ubipetrense* and *A. zagricum* constitute a group in which tetravalents were found as a shared common meiotic chromosome behavior (Figure 6g,m; Table 2).

The simultaneous occurrence of eight bivalents, seven bivalents and two univalents, and six bivalents and four univalents only were observed in an individual with one B chromosome from *A. alamutense* (Figure 2c, accession P1009698). Worth to note that the highest percentage of abnormalities at anaphase-telophase I (68.6%) was also counted for this individual, a confirmation for the role of chiasmata in correct chromosome segregations.

One or two B chromosomes were found in nine accessions of *A. alamutense*, *A. chlorotepalum*, *A. derderianum*, *A. graveolens*, *A. iranshahrii*, *A. mahneshanense*, and *A. sabalense* (Figures 2b,c, 3b,d,e,k,n,o, and 4b,c,d,j,n,p). In *A. chlorotepalum* (accession P1011026) 0–3 B chromosomes and in *A. elburzense* 0–2 B chromosomes were observed (Figures 3i,j and 6o; Table 2).

Comparison of ours with previous reports

Chromosome numbers and ploidy levels of the investigated species do not differ from previous counts, except differences mentioned above for B chromosomes (for detailed comparison see the online supplementary 2). Since the material of the doubtful count of Oroji Salmasi et al. (2019) for *A. elburzense* cannot be verified, we present here the first diploid chromosome count for this species. In the previous meiotic data for Iranian species 0, 1 and 2 B chromosomes were detected only in *A. paniculatum* L. (see the online supplementary 1).

In this contribution we present meiotic data for Iranian materials of 23 species and 1 subspecies of the genus *Allium*. We could not find earlier meiotic data for these taxa except for *A. stipitatum* (Ved Brat 1965).

Chiasmata frequency and abnormalities percentages

On the whole, each bivalent was held together at least by one chiasma and at most by three chiasmata. The lowest chiasmata frequency (1.27) is reported for one individual of *A. alamutense* and the highest (2.75) for the studied individual of *A. iranshahrii* without B chromosomes. Ved Brat (1965) reported a range of 1.53 to 2.76 chiasmata per bivalent in the eighteen diploid species and 1.89–3.02 in the three polyploids of the genus *Allium* he investigated. The only shared species of his list with ours is *A. stipitatum* for which he reported a slightly higher index than our estimation, 2.47 versus 2.3, respectively. We found distal to proximal distribution of chiasmata along chromosome arms (see Figures 1–7), a rather identical pattern among the examined *Melanocrommyum* accessions. According to the chiasma position, the configurations at metaphase I were rings, rods and chains (Figures 6g,i,c). In metaphase I of the investigated taxa of subg. *Melanocrommyum*, one bivalent, likely the counterpart of the shortest chromosome of the idiograms reported by Dolatyari et al. (2018), was held together just by one distal chiasma. Only behaviors of A chromosomes were considered in calculations, i.e. the behaviors of B chromosome were excluded. Our data showed no correlation between the occurrence of B chromosomes and the chiasmata frequencies.

Lagged chromosomes (Figures 1c,d,h,k,l, 2d,k,p, 3p, 4l, 5d,g,h, 6b,p, and 7c), chromatid bridges (Figures 2d, 3c, 4h, and 7j,l), micronuclei (Figures 1n and 2l), unbalanced chromosome segregations (Figures 1g and 5p) were meiotic irregularities found in the studied materials. Very rarely two or more types were detected in one cell (Figure 5g). Percentages of these abnormalities in meiosis I and II were counted. Blanks in Table 2 (columns 8 & 9) refer to accessions with uncertain calculations.

In tetraploid taxa, the percentages of irregularities at anaphase-telophase I were between 20.4 (*A. sabalense* P1009764) and 60 (*A. atroviolaceum*). Most irregularities (68.6) were counted for one individual with 1B chromosome of diploid *A. alamutense*. This high number of lagged chromosomes and micronuclei is correlated with a low chiasma frequency (1.27), simply confirming the necessity of chiasmata for formation of bivalents and correct segregation at anaphase I as stated by Hirose et al. (2011). In other words, the common meiotic behavior of the above-mentioned accessions is the presence of univalents at metaphase I (Figures 1a, 2c, and 5o). Less than 10% of anomalies were estimated in the other investigated diploid taxa, and only 1% in one individual of *A. chlorotepalum* (P1011026) without B chromosome.

The tetraploid accession of *A. atroviolaceum* presented most abnormalities at anaphase-telophase I and II (Figures 1c and d). In all other accessions, but not in accession P1009582 of *A. minutiflorum*, we found lower numbers of abnormalities for meiosis II than for meiosis I with the lowest number (1.06%) for accession P1009955 of *A. minutiflorum* (Table 2).

B chromosomes behavior

One or two B chromosomes are reported here for the first time in *A. alamutense*, *A. elburzense* and *A. iranshahrii* (Figures 2b,c, 4j, and 6o). Also taking into consideration the data of Dolatyari et al. (2018), we can conclude that the frequency of B chromosomes can vary even among different individuals of one distinct accession (e.g. accession P1011289 of *A. iranshahrii*). Pairing between B chromosomes (Figures 4c,k, and 6o) or pairing between B and A chromosomes of one complement were microscopically observed at prophase I, but at metaphase I no connection between B and A chromosomes was detected. In some cells of *A. graveolens* and *A. elburzense*, two B chromosomes seem associated by chiasmata at metaphase I (Figures 4c,k and 6o). In general, at anaphase I, Bs are not obeying the Mendelian law of equal segregation. For example, in the investigated accession of *A. elburzense* two B chromosomes moved in some cells to one pole and in other cells segregated equally to both poles (Figures 4d,p). The accessions meiotically studied here from *A. graveolens* (P1011018), *A. mahneshanense* (P1010506) and *A. chlorotepalum* (P1011002, P1011026) were earlier studied mitotically by Dolatyari et al. (2018), and the number of B chromosomes was identical in root meristem cells and in PMCs, probably an evidence for missing pre-meiotic and/or meiotic genetic drive mechanism of Bs (Chen et al. 2022) in these species.

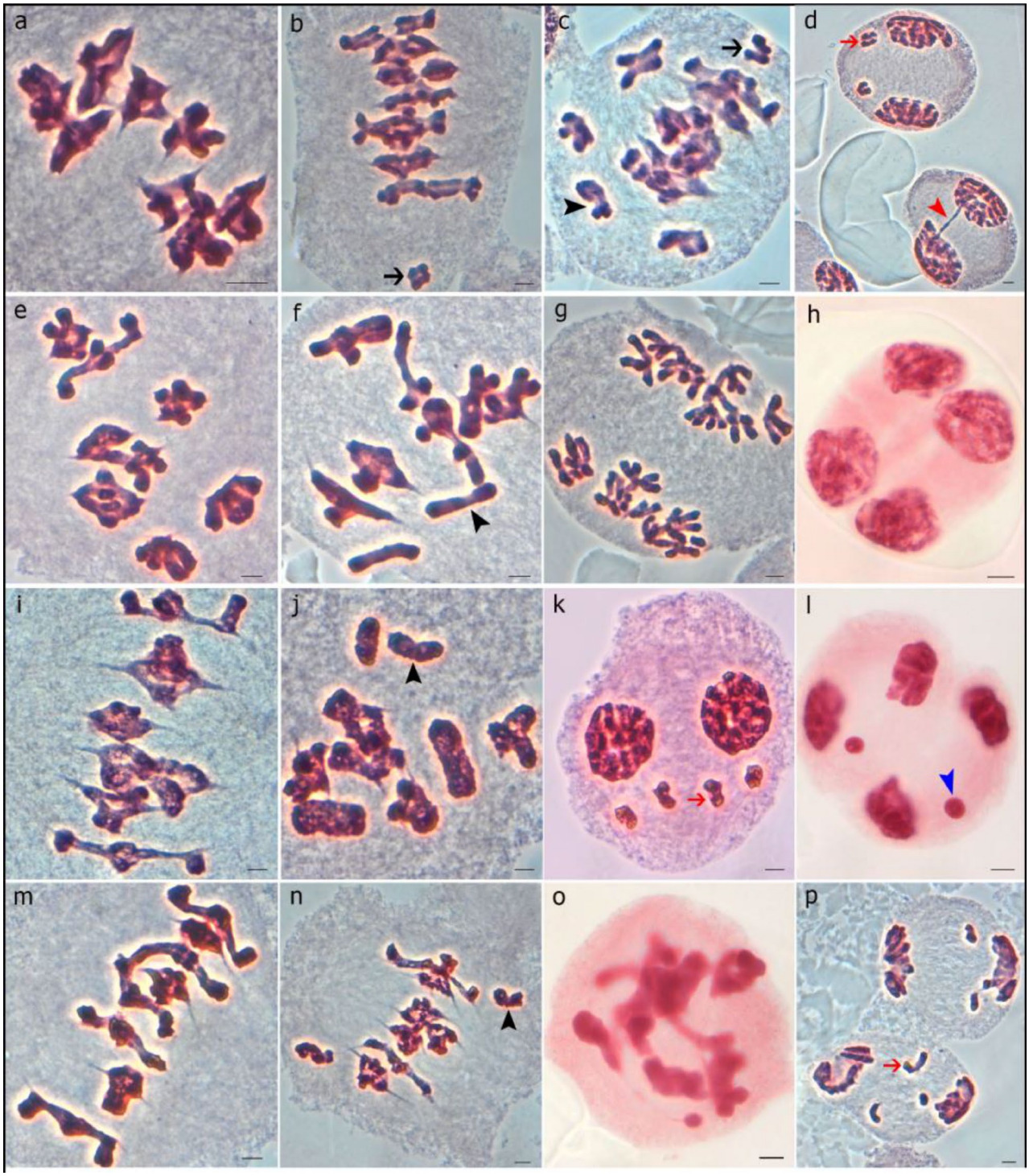

Figure 2. Male meiotic plates of the investigated taxa of sect. *Acanthoprason* (cont. 1). (a, b, c) metaphase I, (d) telophase I in *A. alamutense*; (e, f) metaphase I, (g) anaphase I, (h) telophase II in *A. austroiranicum* (P1009666); (i) metaphase I, (j) late diakinesis, (k) telophase I, (l) telophase II in *A. austroiranicum* (P1009622); (m, n) metaphase I, (o) diplotene, (p) late anaphase I in *A. austroiranicum* (P1009650). All scale bars = 5 µm. Black and red arrows indicate Bs and lagged chromosomes, black, blue and red arrowheads indicate univalents, a micronucleus and a chromatid bridge, respectively.

Plowman and Bougourd (1994) reported that under drought conditions the germination rate and survival of *A. schoenoprasum* individuals with B chromosomes were higher than that of individuals without B chromosomes. Such advantages likely counteract the dispensable nature of Bs in the genus *Allium*.

We did not see any meaningful effect of the presence of B chromosome on the behavior pattern of standard (A) chromosomes. Ved Brat (1965), though with uncertainty, linked abnormal meiosis in a clone of *A. paniculatum* with the presence of B chromosome.

Polyploidy

Hitherto polyploidy was reported in 28 (18%) Iranian Allium species, i.e. 18 species of the subg. *Allium*, five of subg. *Melanocrommyum*, three of subg. *Reticulatobulbosa* (Kamelin) N.

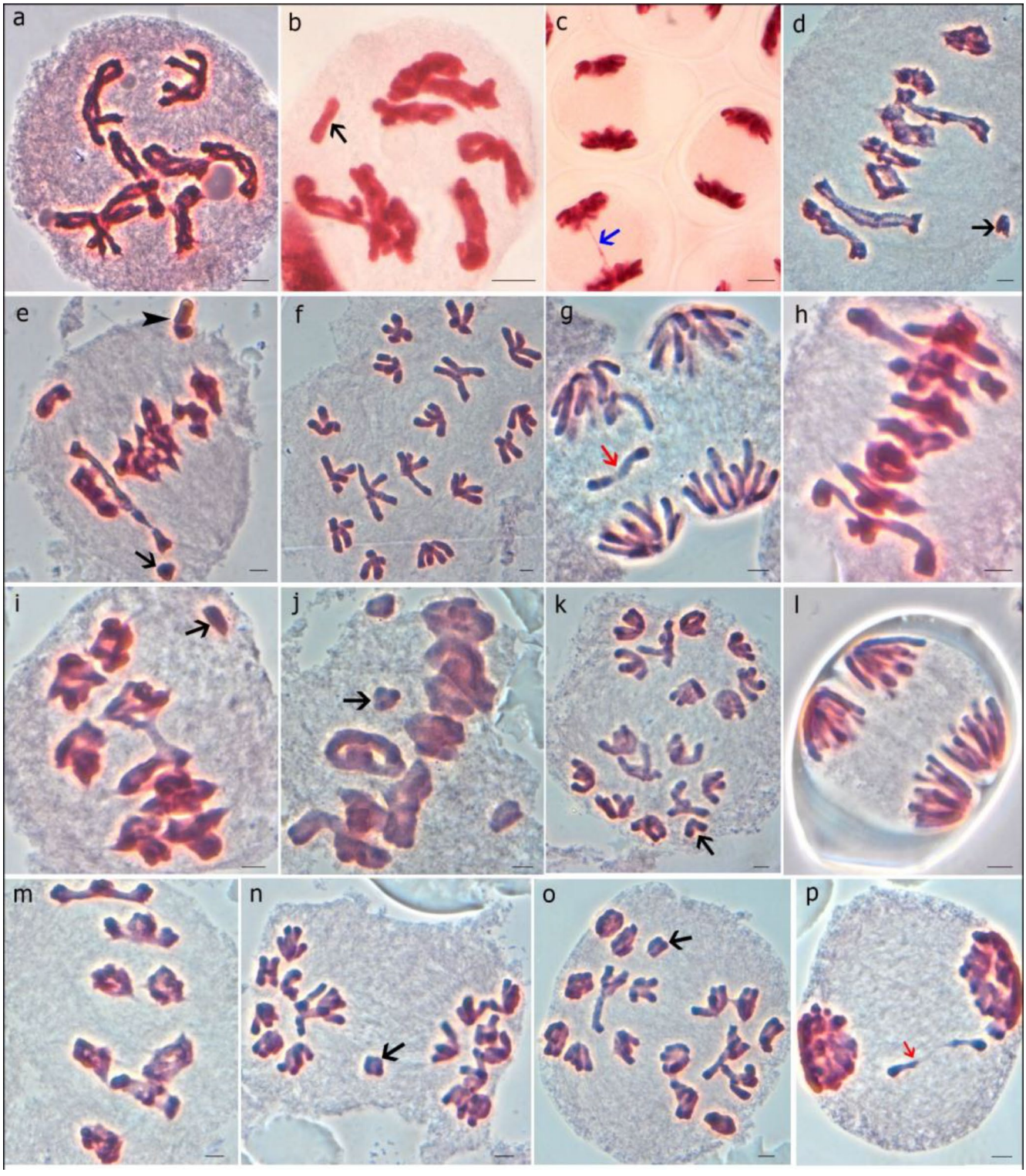

Figure 3. Male meiotic plates of the investigated taxa of sect. *Acanthoprason* (cont. 2). (a, b) early diakinesis, (c) late anaphase I in *A. chlorotepalum* (P1011002); (d) metaphase I, (e) metaphase I, (f) metaphase II, (g) anaphase II in *A. chlorotepalum* (P1010994); (h) metaphase I, (i) late diakinesis, (j) metaphase I, (k) metaphase II, (l) anaphase II in *A. chlorotepalum* (P1011026); (m) metaphase I, (n) anaphase I, (o) metaphase II, (p) telophase I in *A. derderianum*. All scale bars = 5 µm. Black, blue and red arrows indicate Bs, a chromatid bridge and lagged chromosomes; black arrowhead indicates univalents, respectively.

Friesen, and one species of the subgenera *Cepa* (Mill.) Radic and *Polyprason* Radic, resp. (Dolatyari, unpublished data). Interestingly, for 22 species both diploid and polyploid levels were reported. If we ignore the odd chromosome reports of $2n=21$ and 28 for *A. qaradaghense* Feinbr. and *A. subvineale* Wendelbo by Miryeganeh and Movafeghi (2011), so far only in *A. capitellatum* Boiss. ($2n=32$, (Vosa 1977)) solely the polyploid level was reported. The count of $2n=64$ for *A. monophyllum* Vved. (Kurita 1956) is an obvious mistake as proved by a different karyotype and $2n=16$ in Iranian plants (Fritsch 2018). Nine percent of our investigated accessions are polyploid confirming tetraploidy in *A. atroviolaceum* (Vosa 1977; Pogosian 1983; Ghaffari 1987; Abdali and Miri 2020) and in

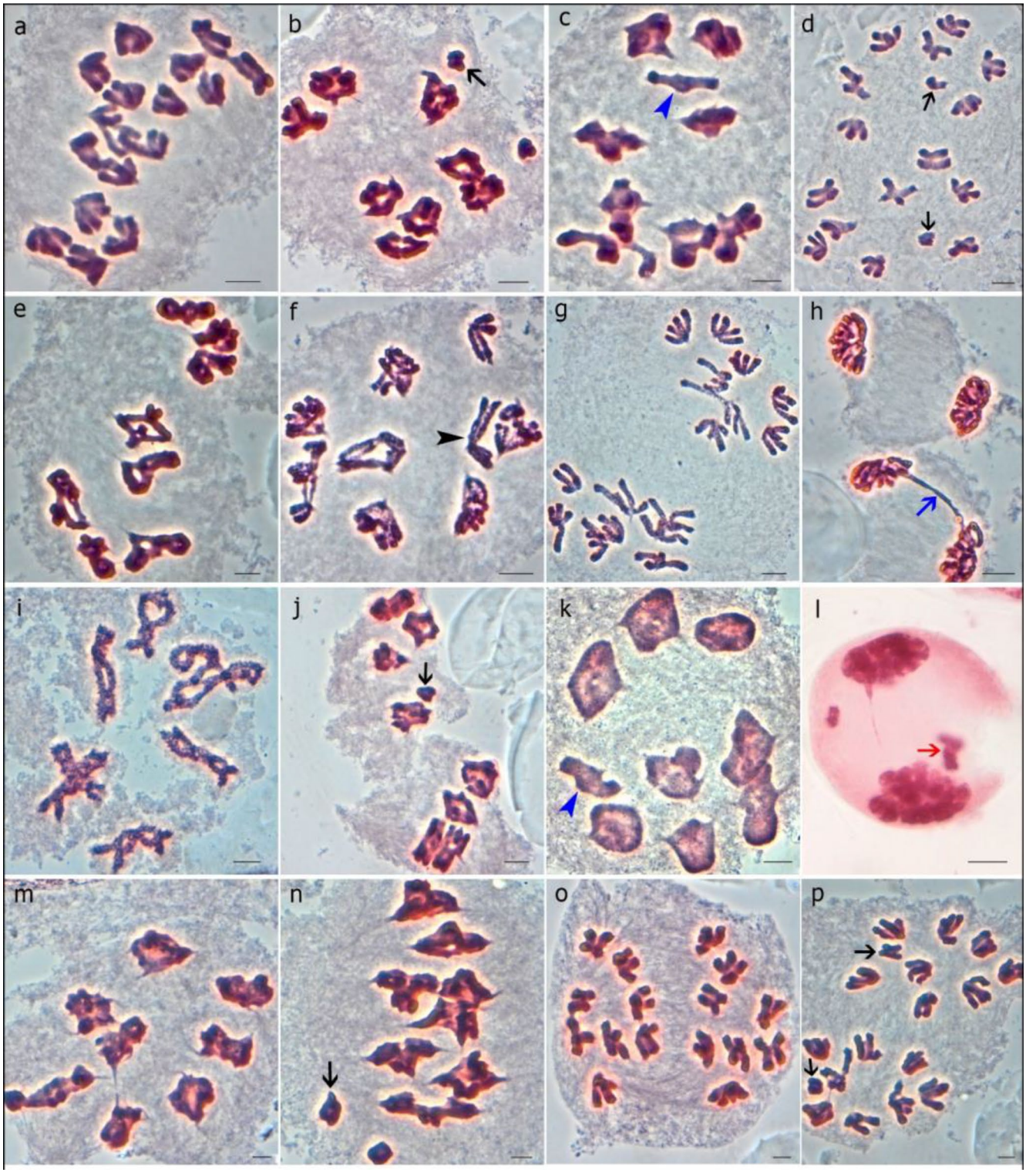

Figure 4. Male meiotic plates of the investigated taxa of sect. *Acanthoprason* (cont. 3). (a) early anaphase I, (b, c) metaphase I, (d) metaphase II in *A. graveolens*; (e, f) metaphase I, (g) metaphase II, (h) telophase I in *A. haemanthoides*; (i) late diplotene, (j) metaphase I in *A. iranshahrii* (P1011289); (k) metaphase I, (l) telophase I in *A. iranshahrii* (P1011271); (m) late diakinesis, (n) metaphase I, (o, p) metaphase II in *A. mahneshanense*. All scale bars = 5 µm. Black, blue and red arrows indicate Bs, a chromatid bridge and lagged chromosomes; black and blue arrowheads indicate a univalent and paired Bs, respectively.

accession P1009858 of *A. sabalense* as reported by Dolatyari et al. (2018). We found a second tetraploid accession of *A. sabalense* but no diploid one as reported by Dolatyari et al. (2018).

Since only two out of 31 investigated accessions belonging to subg. *Melanocrommyum* were tetraploid, we may suggest a trivial role of polyploidy in the evolution of this subgenus.

Considering exceptions like segmental allopolyploids (Stebbins 1971) and autopolyploids with regular bivalent formation (Weiss and Maluszynska 2000), autopolyploids are usually characterized by polysomic inheritance and multivalent formation in meiosis, whereas allopolyploids usually show disomic inheritance and bivalents (Zielinski and

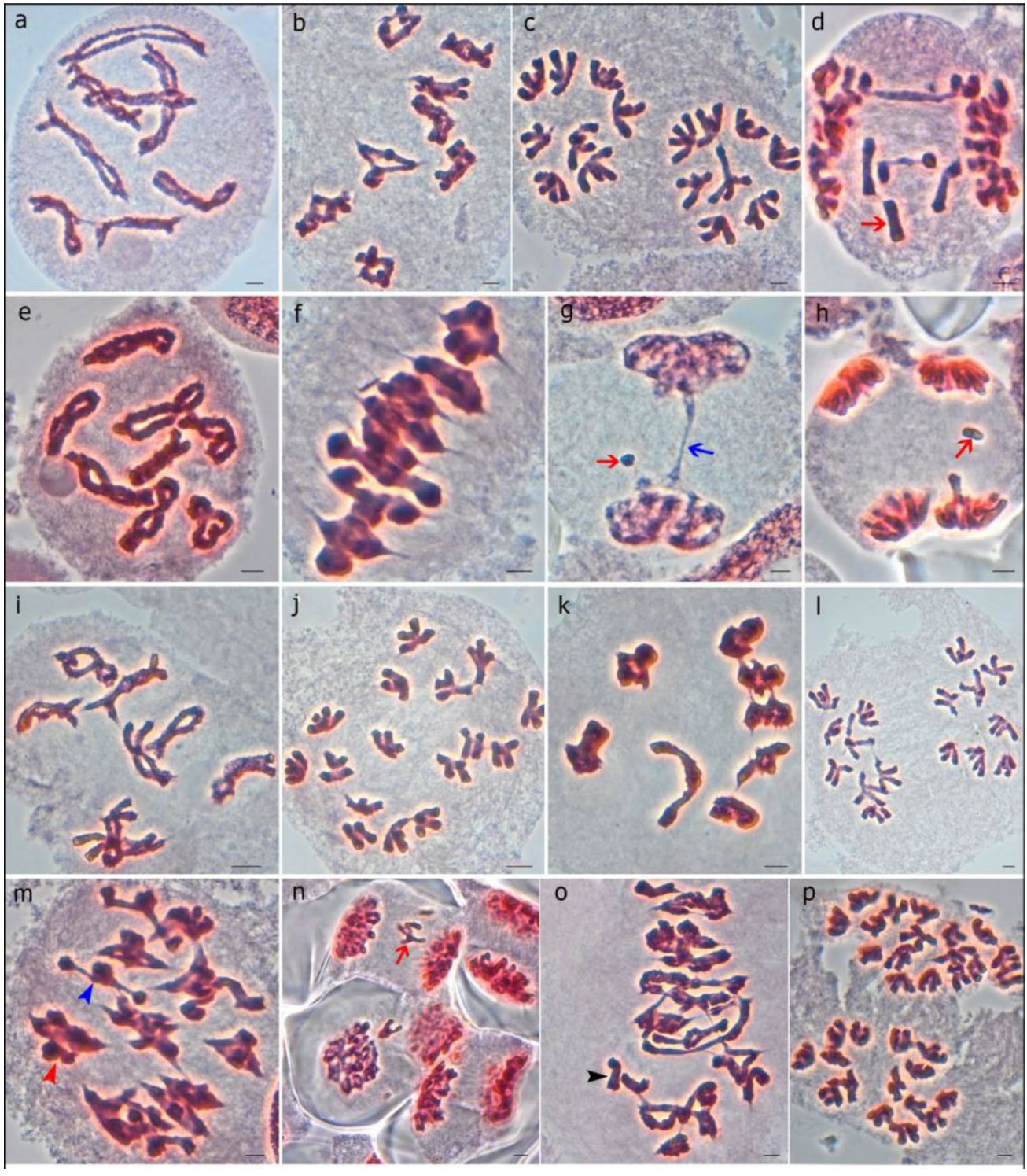

Figure 5. Male meiotic plates of the investigated taxa of sect. *Acanthoprason* (cont. 4). (a) late diplotene, (b) late diakinesis, (c) metaphase II, (d) late anaphase I in *A. materculae* (P1009920); (e) diakinesis, (f) metaphase I, (g) telophase I, (h) telophase II in *A. materculae* (P1009955); (i) diakinesis, (j) metaphase II in *A. minutiflorum* (P1010973); (k) metaphase I, (l) metaphase II in *A. minutiflorum* (P1009582); (m) metaphase I, (n) late anaphase I in *A. sabalense* (P1009858); (o) metaphase I, (p) metaphase II (15–17) in *A. sabalense* (P1009764). All scale bars = 5 µm. Black, blue and red arrowheads indicate uni-, bi- and tetravalents; blue and red arrows indicate a chromatid bridge and lagged chromosomes, respectively.

Mittelsten Scheid 2012). The varied numbers of multivalents (especially quadrivalent) configurations at -metaphase I and the high percentages of irregularities at meiosis I and II we found in *A. atroviolaceum* and *A. sabalense* favor the auto-tetraploid offspring of these taxa. Dolatyari et al. (2018) presented the karyotype formula $2n = 32 = 7m + 21$ msm + 4 sm^{satP} and four satellited chromosomes of type P for the tetraploid accession (P1009858) of *A. sabalense*, probably another evidence for its autopolyploid origin.

Environmental effects on meiosis

Since the studied samples were obtained both from natural habitats and also from the experimental farm, this

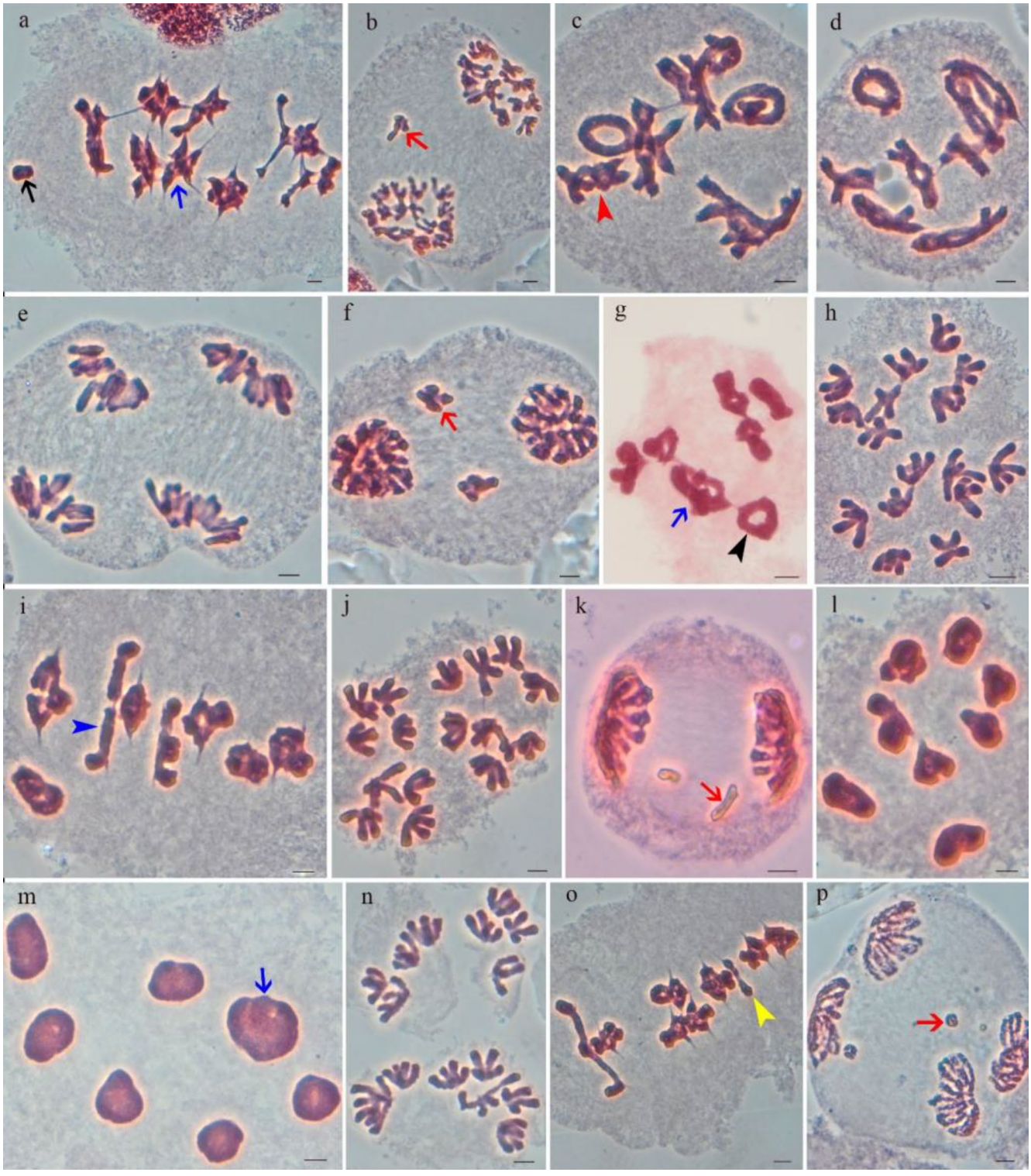

Figure 6. Male meiotic plates of the investigated taxa of sect. *Acanthoprason* (cont. 5), *Asteroprason*, (a) late diakinesis, (b) metaphase II in *A. sabalense* (P1009764); (c) and (d) diakinesis, (e) anaphase II, (f) metaphase II in *A. subakaka*; (g) metaphase I, (h) metaphase II in *A. ubipetrense* (P1011070); (i) metaphase I, (j) metaphase II, (k) telophase I in *A. ubipetrense* (P1011039); (l) and (m) metaphase I, (n) metaphase II in *A. zagricum*; (o) metaphase I, (p) telophase II in *A. elburzense*. All scale bars = 5 µm. Black, blue, and red arrows indicate uni-, tetravalents, and lagged chromosomes; black, blue, red and yellow arrowheads indicate ring, rod and chain configurations, and paired Bs, respectively.

opportunity was provided to detect even small differences in chromosomal behaviors. Regardless of impacts of ploidy levels on chromosomal configurations and percentages of abnormalities, in all examined diploid taxa a nearly identical meiotic trend was observed, though about half of investigated material was fixed from cultivated plants. Also, in *A. subakaka*, *A. ubipetrense* and *A. zagricum* besides uni- and bi-valents also tetravalents were observed. Only material of *A. subakaka* was obtained from the experimental farm. These species belong to different taxonomic subgroups of sect. *Acanthoprason* but share identical ecological requirements (montane steppe slopes) (Fritsch and Abbasi 2013).

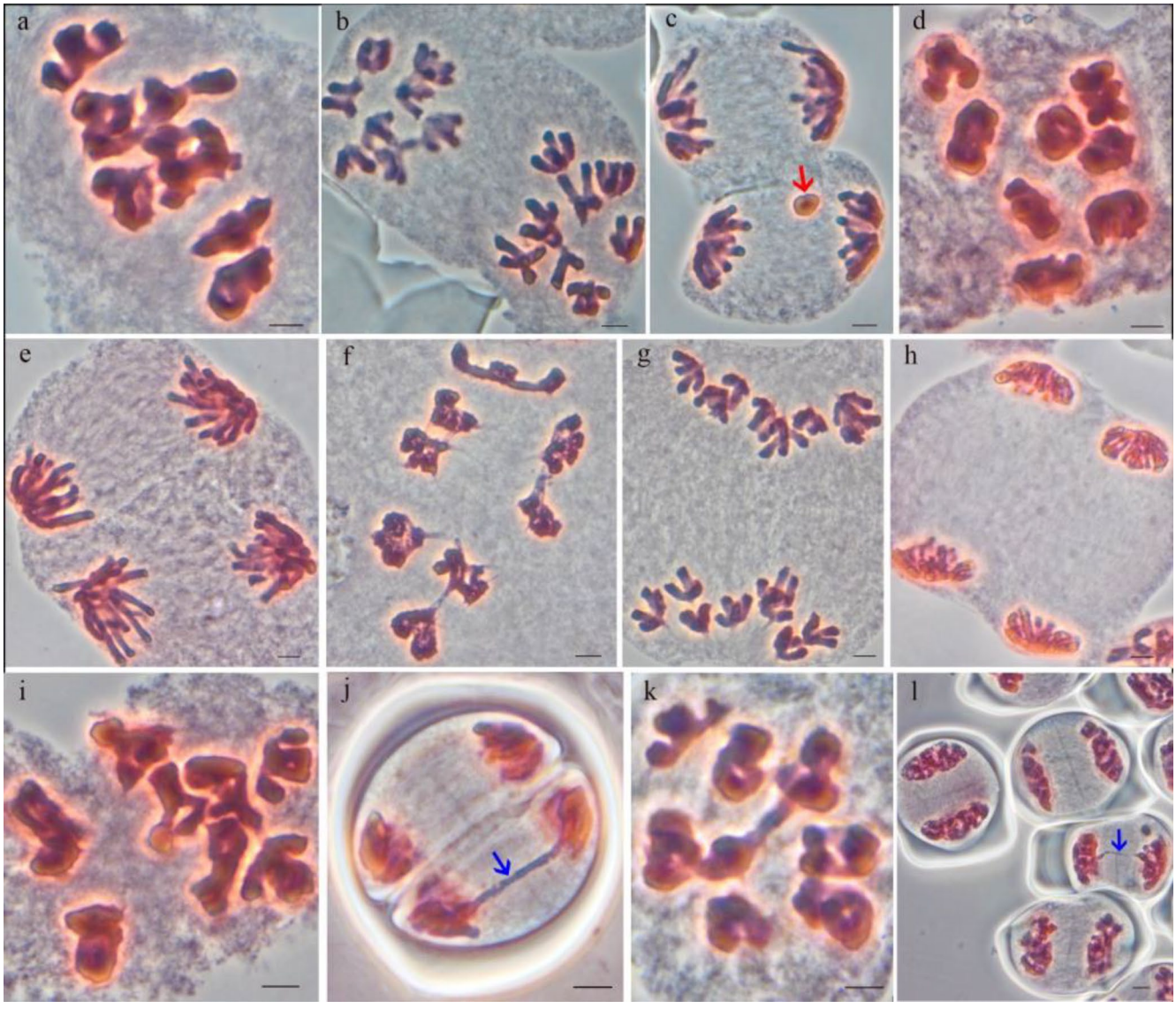

Figure 7. Male meiotic plates of the investigated taxa of sections *Melanocrommyum* & *Procerallium*. (a) metaphase I, (b) metaphase II, (c) late anaphase II in *A. cardiostemon*; (d) late diakinesis, (e) late anaphase II in *A. keusgenii*; (f) diakinesis, (g) anaphase I, (h) telophase II in *A. jesdianum*; (i) diakinesis, (j) telophase II in *A. remediorum*; (k) diakinesis, (l) telophase I in *A. stipitatum*. All scale bars = 5 µm. Blue and red arrows indicate chromatid bridges and a lagged chromosome, respectively.

Accepting the fact that genetic as well as environmental factors influence meiotic chromosome behaviors (Sheidai et al. 2003), only under controlled environmental conditions it will be possible to document, for example, the influence of abiotic factors on meiotic indices. Also, the variable response to an environmental stress factor, even within the same species, indicates a plasticity in factors and mechanisms governing and impacting meiosis. Moreover, relying only on gross karyological information may not lead to detection of subtle changes (Fuchs et al. 2018). Altogether, based on our data we could not find noticeable differences among accessions sampled from natural habitats or the farm. Probably the collection of bulbs during field work and culture condition were not stressful for the bulbs and had no detectable impact on later meiotic division. However, any interpretations on the impact of environmental factors must be made with caution and after considering all points mentioned above.

Meiotic abnormalities and their impact on bulbil development

Levan (2010) inferred that in the *A. paniculatum* group (subg. *Allium* sect. *Codonoprasum* (Rchb.) Endl.) formation of inflorescence bulbils is directly correlated with polyploidy and the hybrid nature of the complex though bulbils have also been reported as key character for all, also diploid, variants of *A. carinatum* L. (Rothmaler 1976; Stearn 1980). Our polyploid accession of *A. atroviolaceum* developed both seeds and inflorescence bulbils, but no bulbils were seen for the tetraploid studied accessions of *A. sabalense*. The meiotic spreads showed a chaotic meiotic division in both species.

Inflorescence bulbils are known from quite many species in sect. *Allium*. Mathew (1996) keys out eight species having sometimes only bulbils and no flowers in the inflorescence which comprise polyploids as well as diploids like garlic (*A. sativum* L.).

Polyploidy was hitherto only sporadically reported in members of subg. *Melanocrommyum*, mostly for plants of garden origin (Fritsch, unpublished data). We found chromosome data for 54 out of 78 species from this subgenus in Iran (Dolatyari, unpublished data), and only for five species (9%) both diploid and polyploid levels were reported. Solely *A. cyrilli* Ten. is a predominantly tetraploid species (invariably mitotic counts), but inflorescence bulbils were never seen in living or herbarium specimens (Fritsch, own observations). On the other hand, Wendelbo (1971) mentioned the presence of inflorescence bulbils in the diploid species *A. grande* Lipsky (as *A. chelotum* Wendelbo) and *A. koelzii* (Wendelbo) K. Perss. & Wendelbo (as *Nectaroscordum koelzii* Wendelbo). Thus, the question remains open as to whether a chaotic male meiosis and vegetative reproduction are correlated, not only in the mentioned tetraploid species but in subg. *Melanocrommyum* generally. Perhaps future detailed information on female meiosis, floral biology and reproductive processes in these and other species can contribute to solve this question.

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No potential conflict of interest was reported by the authors.

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