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Karyomorphological studies of *Lachenalia* (Asparagaceae): six species containing *L. barkeriana**

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ラケナリア属（キジカクシ科）の核形態学的観察（*L. barkeriana* 等6種）

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Summary

Karyomorphological studies were conducted on the six species of *Lachenalia*. The chromosome numbers of *L. calcicola* (2n = 52), *L. callista* (2n = 14), *L. canaliculata* (2n = 18), and *L. ensifolia* var. *maughanii* (2n = 26) were reported for the first time, and those of *L. barkeriana* (2n = 16) and *L. haarlemensis* (2n = 18) were consistent with previous reports.

Keywords: Karyotype, Chromosome number, *Lachenalia calcicola*, *Lachenalia callista*, *Lachenalia canaliculata*, *Lachenalia ensifolia* var. *maughanii*

Introduction

Lachenalia (Asparagaceae) is a large and morphologically diverse genus comprising more than 140 bulbous species endemic to southern Africa (Duncan et al. 2022).

The sectional classification of *Lachenalia* is based on a multilocus DNA phylogeny (Duncan et al. 2022). In addition, chromosome studies have been performed on 95 species (Duncan 2012; Hamatani and Tagashira 2019), demonstrating their chromosome numbers of 2n = 10, 12, 14, 15, 16, 17, 18, 20, 21, 22, 23, 24, 26, 27, 28, 29, 30, 32, 36, 40, 42, 44, 49, and 56 (e.g., Crosby 1986; De Wet 1957; Fernandes and Neves 1962; Hamatani 2011; Hamatani et al. 1998, 2004, 2007; Johnson and Brandham 1997, Mofett 1936, Spies 2004 and Spies et al. 2000, 2002, 2008, 2009). Based on previous information on their chromosome numbers, the basic chromosome number of this genus has been reported (Spies et al. 2011), and detailed karyomorphological studies have been conducted (e.g., Hamatani 2011; Hamatani et al. 1998, 2004, 2007, 2009, 2010; Mofett 1936 and Spies 2004). However, previous studies on *Lachenalia* species have encountered limitations in determining chromosomal numbers. Therefore, to investigate the cytogenetic relationships among *Lachenalia* species, we examined the chromosomal characteristics of *Lachenalia* species in detail.

This study conducted cytogenetic analysis on six previously unreported *Lachenalia* species and published their basic chromosomal information.

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Table 1. Chromosome numbers of six species of *Lachenalia* studied.

Species	Section*	Chromosome number (2n)		References
		Present count	Previous count	
Lachenalia barkeriana U.Müll.-Doblies, B.Nord. & D.Müll.-Doblies	Lachenalia subsect. Inflatae	16	16	Nordenstam 1982
			14, 16	Müller-Doblies et al. 1987
Lachenalia calcicola (U.Müll.-Doblies, B.Nord. & D.Müll.-Doblies) G.D.Duncan	Polyxena	52	—	(New Count)
Lachenalia callista G.D.Duncan & T.J.Edwards	Lachenalia subsect. Lachenalia	14	—	(New Count)
Lachenalia canaliculata G.D.Duncan	Lachenalia subsect. Coriaceae	18	—	(New Count)
Lachenalia ensifolia (Thunb.) J.C.Manning & Goldblatt var. *maughanii* (W.F.Barker) G.D.Duncan	Polyxena	26	—	(New Count)
Lachenalia haarlemensis Fourc.	Lachenalia subsect. Coriaceae	18	18	Johnson & Brandham 1997

* Referred from Duncan et al. 2022

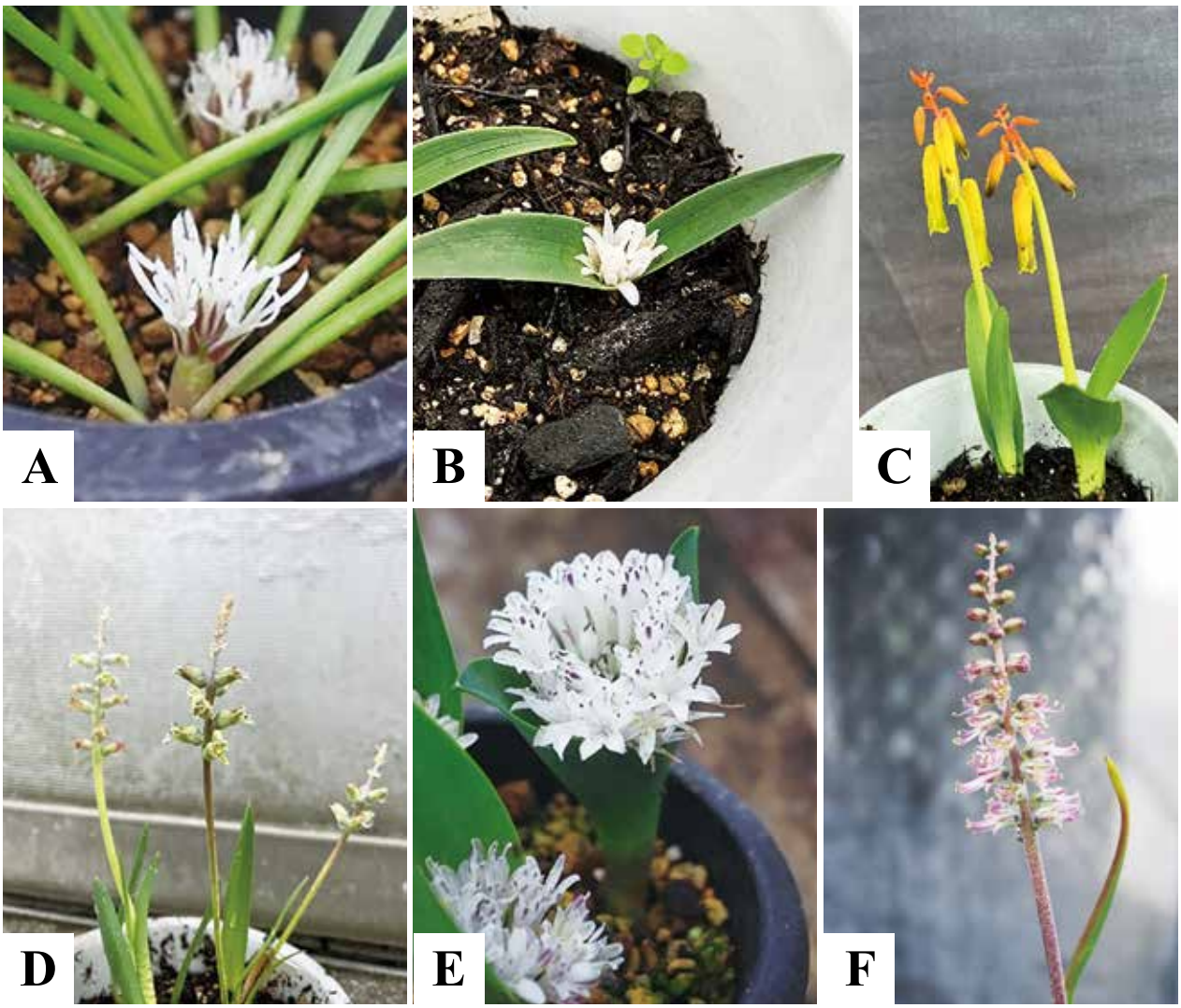

Figure 1. Flowers of *Lachenalia* studied.
A: *L. barkeriana*, B: *L. calcicola*, C: *L. callista*, D: *L. canaliculata*, E: *L. ensifolia* var. *maughanii*, F: *L. haarlemensis*.

Material and Methods

The plant species used in this study are listed in Table 1, and their flowers are shown in Fig.1. Seeds were introduced from a nursery and cultivated in the Hiroshima Botanical Garden.

For the cytogenetic research, root tips were harvested and pre-treated in 2 mM 8-hydroxyquinoline at 20 ℃ for 2 to 4 h before being preserved and stored in a 3:1 ethanol and acetic acid solution below freezing temperature for a few days. Then, they were macerated in the 1:1 mixture of 45 % acetic acid and 1 N hydrochloric acid at 60 ℃ for 1.5 min and squashed with 2 % aceto-orcein solution. After observing the meristematic tissues, the resting nuclei and mitotic metaphase chromosomes were classified according to Tanaka (1980), and the metaphase chromosomes were characterised by their centromeric positions, following Lavan et al. (1964).

Results and Discussion

The sections were prepared according to Duncan et al. (2022), and the chromosome numbers (2n) observed in this study and previous counts are described in Table 1. The chromosome numbers of the six species were 2n = 14, 16, 18, 26, and 52. The chromosome numbers of *L. calcicola* (2n = 52), *L. callista* (2n = 14), *L. canaliculata* (2n = 18), and *L. ensifolia* var. *maughanii* (2n = 26) were reported here for the first time. The number of *L. barkeriana* (2n = 16) was consistent with the data described by Nordenstam (1982) and Müller-Doblies et al. (1987), and for *L. haarlememsis* (2n = 18), which confirmed the previous data described by Johnson and Brandham (1997).

The mitotic metaphase and karyotypes are shown in Fig. 2 and 3, respectively. The bar graphs for the lengths of the short and long arms of each chromosome for each taxon are shown in Fig. 4, and the karyomorphological analyses are described in Table 2.

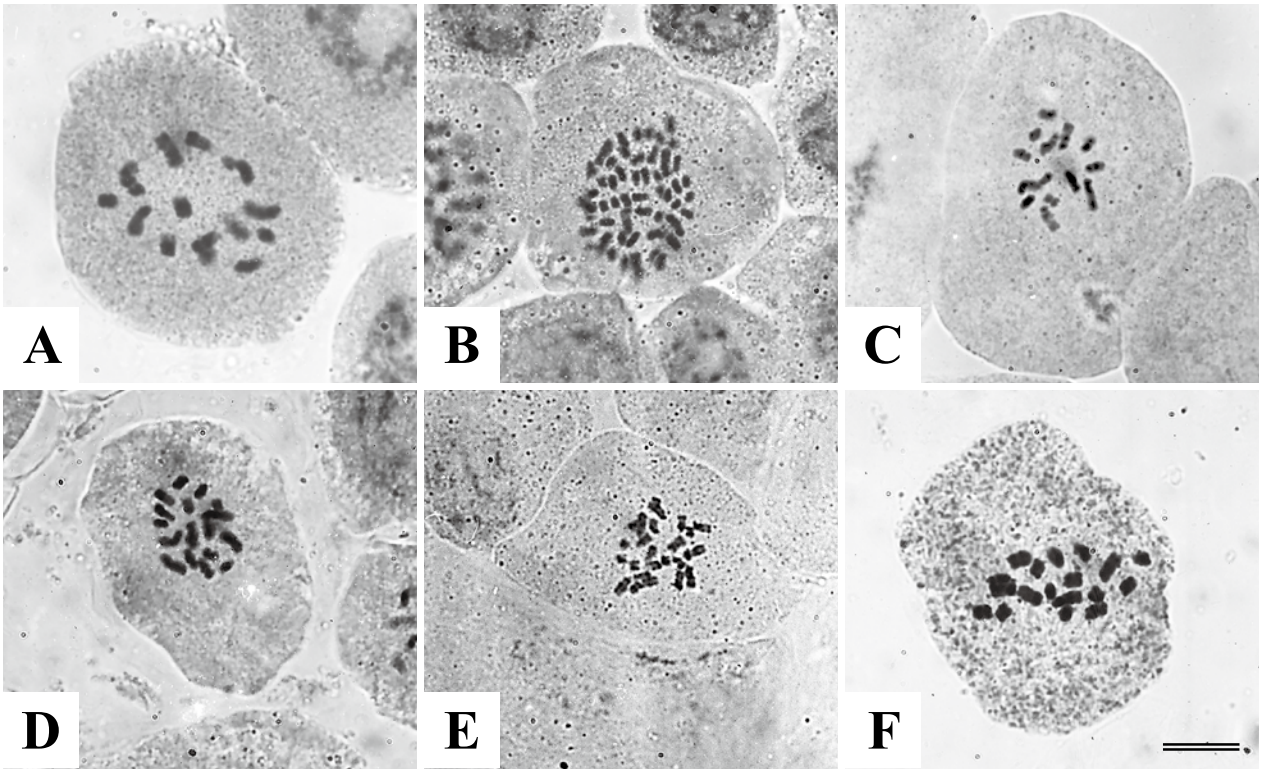

Figure 2. Somatic chromosomes at mitotic metaphase in *Lachenalia* studied.
A: *L. barkeriana*, B: *L. calcicola*, C: *L. callista*, D: *L. canaliculata*, E: *L. ensifolia* var. *maughanii*, F: *L. haarlemensis*. Bar = 10 μm.

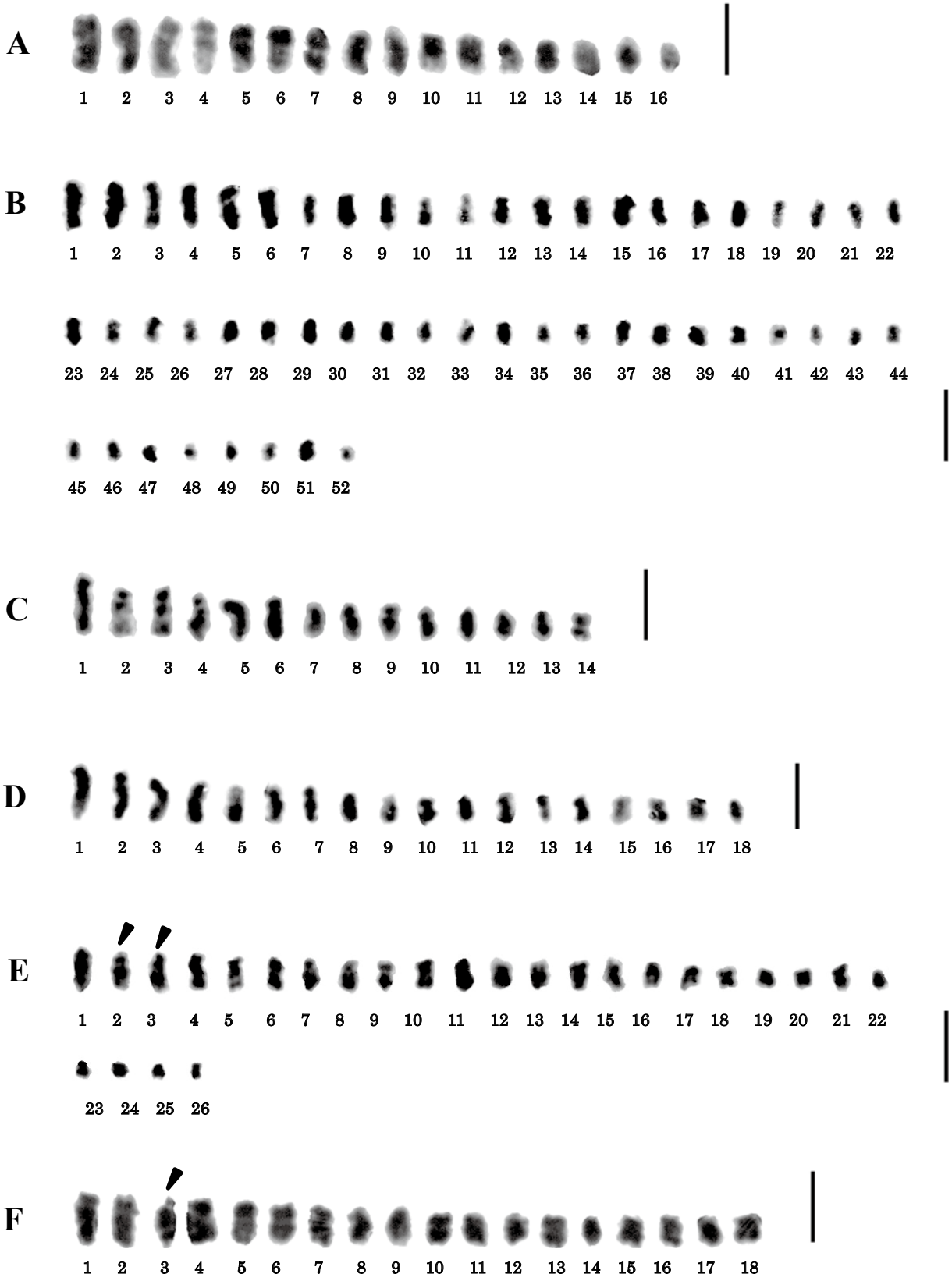

Figure 3. Karyotypes in the six species of *Lachenalia* studied.

A: *L. barkeriana*, B: *L. calcicola*, C: *L. callista*, D: *L. canaliculata*, E: *L. ensifolia* var. *maughanii*, F: *L. haarlemensis*. Arrows show satellites. Bars indicate 5 μm.

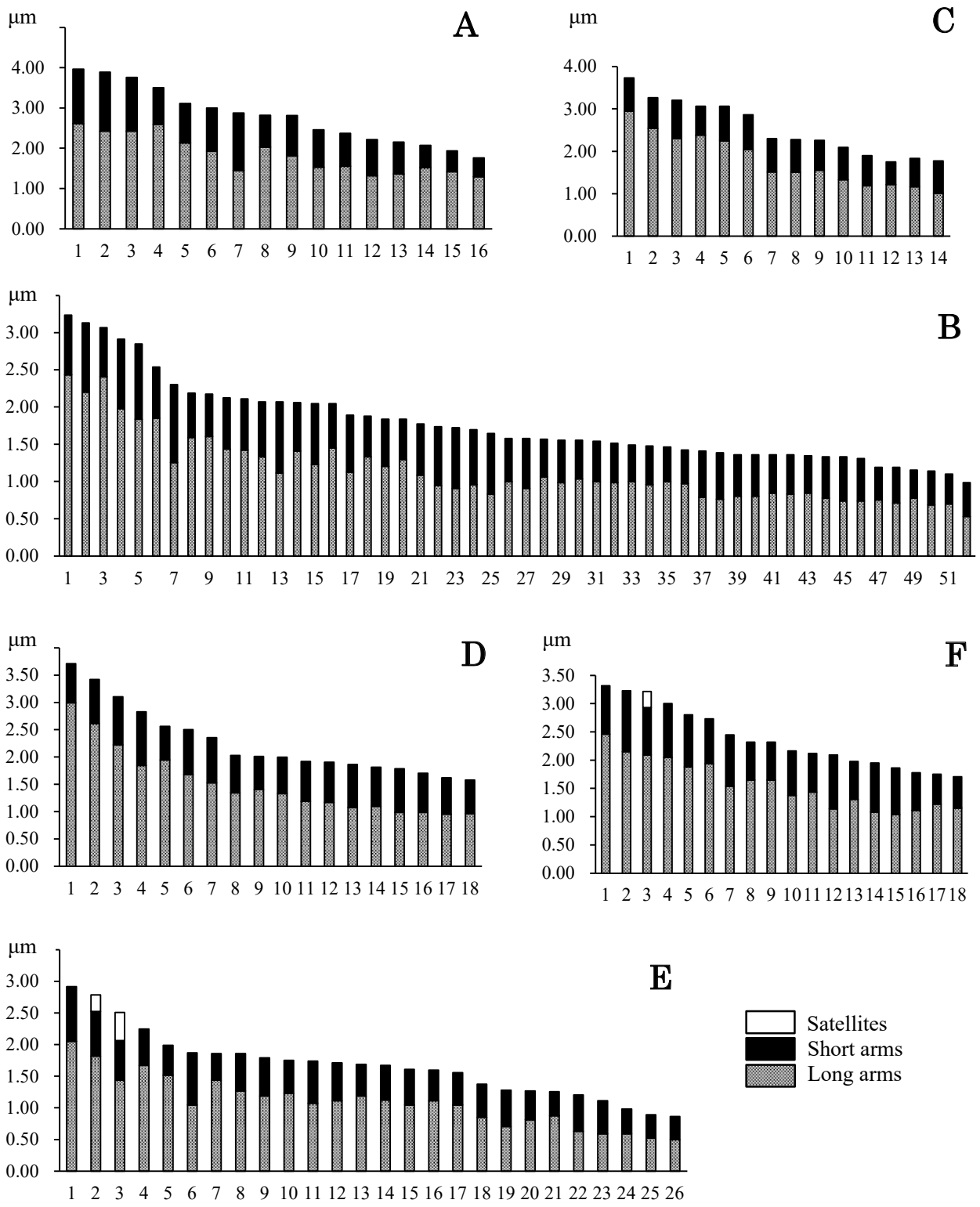

Figure 4. Chromosome length of *Lachenalia* studied.

A: *L. barkeriana*, B: *L. calcicola*, C: *L. callista*, D: *L. canaliculata*, E: *L. ensifolia* var. *maughanii*, F: *L. haarlemensis*. Horizontal axes show the chromosome numbers of each species. Vertical axes show chromosome length.

Table 2. The results of karyomorphological studies of *Lachenalia.*

Species	Information of mitotic metaphase			Polyploidy	Basic chromosome number (x)
	Chromosome number (2n)	Expression from chromosome length*	Expression from arm ratio*		
Lachenalia barkeriana	16	mono-modal (gradual)	symmetric (4m+12sm)	2x	8
Lachenalia calcicola	52	bi-modal (6L+46S)	symmetric (24m+26sm+2st)	4x ?	13 ?
Lachenalia callista	14	bi-modal (6L+8S)	symmetric (2m+9sm+3st)	2x	7
Lachenalia canaliculata	18	mono-modal (gradual)	symmetric (8m+7sm+3st)	2x	9
Lachenalia ensifolia var. *maughanii*	26	bi-modal (3L+23S or 4L+22S)	symmetric (9m+15sm+2st)	2x	13
Lachenalia haarlemensis	18	mono-modal (gradual)	symmetric (6m+12sm)	2x	9

*The mitotic metaphase chromosomes were characterized by centromeric position followed Levan et al. (1964). Symbols show regions of centromeres. m: median region, sm: submedian region, st: subterminal region. The karyotype formulas based on the positions of centromeres and chromosome length according to Tanaka (1980).

L. barkeriana (Fig. 2A, 3A, Table 3) which was classified under the section Lachenalia, subsection Inflatae (Duncan et al. 2022) showed 2n = 16 chromosomes and a mono-modal karyotype, with a gradual decrease in size from the largest to the smallest chromosomes. All chromosomes were metacentric (m) or submetacentric (sm) and showed a symmetric karyotype in the arm ratio. This study suggests that this taxon is diploid, with a basic chromosome number of x = 8 (Table 2).

Hamatani (2011) reported *L. pusilla* which is discussed in the same subsection, shows a bi-modal or mono-modal karyotype with a gradual decrease in size from the largest to the smallest chromosomes. *L. pusilla* (2n = 14) showed different chromosome numbers from *L. barkeriana* (2n = 16), although each species showed similar minority characters in the genus *Lachenalia*, which spreads rosette-forming with more than three leaves and does not stand up slower stalks. The speciation of *L. barkeriana* and *L. pusilla* is an interesting topic for future research.

L. calcicola (Fig. 2B, 3B, Table 4) which was classified under the section Polyxena (Duncan et al. 2022) showed 2n = 52 chromosomes and a bi-modal karyotype in length, with six relatively long and 46 relatively short chromosomes. Two long chromosomes were subtelocentric (st), and the other 50 chromosomes were “m” or “sm”; then, it showed a symmetric karyotype in arm ratio. And, *L. ensifolia* var. *maughanii* (Fig. 2E, 3E, Table 7) which were classified under the same section, showed 2n = 26 chromosomes and a bi-modal karyotype in length with three or four relatively long chromosomes and 23 or 22 relatively short chromosomes. The two chromosomes were “st”, and the other 24 chromosomes were “sm” or “m”. A symmetric karyotype was observed for the arm ratio. Two chromosomes (Nos. 2 and 3) contained satellites in their short arms.

According to Hamatani (2011), the *L. ensifolia* var. *ensifolia* (2n = 26), *L. longituba* (2n = 28), and *L. paucifolia* (2n = 26) which were classified in the same section, were diploids, although they showed bi-modal karyotypes with three relatively long chromosomes. Molecular cytogenetic observations using FISH showed that *L. longituba* and *L paucifolia* exhibit 5S rDNA signals on two other chromosomes and 18S rDNA signals on two other chromosomes (Hamatani 2011). These results suggested that *L. ensifolia* var. *maughanii* which is the same species and different subspecies as *L. ensifolia* var. *ensifolia* was diploid, with a basic chromosome number of x = 13 (Table 2). *L. calcicola*

has 52 chromosomes, six of which are relatively long and are likely regarded as tetraploid (x = 13) (Table 2); however, it might be better to decide whether it is diploid or tetraploid based on further molecular cytogenetic observations because *L. calcicola* is another species from the species already made about molecular cytogenetic observations.

L. callista (Fig. 2C, 3C, Table 5) which was classified under the section Lachenalia, subsection Lachenalia (Duncan et al. 2022) showed 2n = 14 chromosomes and a bi-modal karyotype with six relatively long and eight relatively short chromosomes. The three long chromosomes were "st", and the other 11 chromosomes were "sm" or "m". A symmetric karyotype was observed for the arm ratio. This study suggests that this taxon is diploid, with a basic chromosome number of x = 7 (Table 2).

Given that numerous aneuploids and high-order polyploids are included in this subsection and that their chromosome numbers have been reported as 2n = 10, 12, 14, 15, 16, 17, 24, 28, 29, and 56, it was hypothesized that most species in the section Lachenalia subsection Lachenalia are taxa with a basic chromosome number of x = 7 (Table 2). However, several types (mono-modal, bi-modal, and tri-modal) of karyotypes in size from the largest to the smallest chromosomes are shown in this subsection (Hamatani 2011), and it is difficult to show the features of the karyotypes of the species in this subsection based on their chromosome length.

L. canaliculata (Fig. 2D, 3D, Table 6) and *L. haarlemensis* (Fig. 2F, 3F, Table 8) which were classified under the section Lachenalia, subsection Coriaceae (Duncan et al. 2022) showed 2n = 18 chromosomes and a mono-modal karyotype with a gradual decrease in size from the largest to the smallest chromosomes. The three chromosomes were "st", and the other 15 chromosomes were "m" or "sm" in *L. canaliculata*. A symmetric karyotype was observed for arm ratio. Furthermore, in *L. haarlemensis*, all chromosomes were "m" or "sm" and showed symmetric karyotype in arm ratio. One chromosome (No. 3) had a satellite on its short arm. This study suggests that these taxa are diploid with a basic chromosome number of x = 9 (Table 2).

The chromosome numbers of 2n = 14, 16, 18, 20, 36, and 40 were reported in the aforementioned subsection. However, there are still numerous species for which the chromosome numbers are unknown. In addition, there is limited availability of karyomorphological information. Further research is required to elucidate this specification.

Authors reported that all taxa already studied showed symmetric karyotype in arm ratio (Hamatani 2011; Hamatani and Tagashira 2019), and the present report shows the same result.

In the genus *Lachenalia*, basic chromosome numbers of x = 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 18, 20, 21, 22, and 28 have been confirmed, and it has been suggested that the primary basic chromosome numbers are x = 7, 8, 9, and 11 (Kleynhans et al. 2012; Spies et al. 2011). We aimed to reveal the speciation of this genus through detailed karyomorphological and molecular cytogenetic observations.

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摘 要

ラケナリア属（*Lachenalia*）6 種について核形態学的観察を行った．染色体数は 2n=14, 16, 18, 26, 52 が観察された．*L. calcicola* の 2n = 52，*L. callista* の 2n = 14，*L. canaliculata* の 2n = 18，*L. ensifolia* var. *maughanii* の 2n = 26 は初の報告で，*L. barkeriana* の 2n = 16，*L. haarlemensis* の 2n = 18 は過去の報告を裏付ける染色体数であった．

キーワード：核型，染色体数，*Lachenalia calcicola*, *Lachenalia callista*, *Lachenalia canaliculata*, *Lachenalia ensifolia* var. *maughanii*

Appendix：Measurements of somatic chromosomes at mitotic metaphase of *Lachenalia* studied.

Table 3. *L. barkeriana*, 2n = 16

Chromosome	Length (μm)	Relative length (%)	Arm ratio	Form
1	1.35 + 2.61 = 3.96	8.87	1.93	sm
2	1.47 + 2.42 = 3.89	8.71	1.65	m
3	1.33 + 2.42 = 3.76	8.41	1.82	sm
4	0.92 + 2.59 = 3.51	7.85	2.83	sm
5	0.98 + 2.13 = 3.11	6.96	2.18	sm
6	1.07 + 1.93 = 3.00	6.71	1.80	sm
7	1.43 + 1.45 = 2.88	6.43	1.01	m
8	0.79 + 2.03 = 2.82	6.31	2.57	sm
9	1.00 + 1.81 = 2.81	6.29	1.81	sm
10	0.93 + 1.53 = 2.46	5.50	1.65	m
11	0.82 + 1.55 = 2.37	5.31	1.89	sm
12	0.89 + 1.32 = 2.21	4.95	1.47	m
13	0.79 + 1.36 = 2.15	4.82	1.72	sm
14	0.55 + 1.52 = 2.07	4.63	2.75	sm
15	0.52 + 1.42 = 1.94	4.33	2.72	sm
16	0.47 + 1.29 = 1.76	3.93	2.76	sm

Table 5. *L. callista*, 2n = 14.

Chromosome	Length (μm)	Relative length (%)	Arm ratio	Form
1	0.78 + 2.95 = 3.73	10.55	3.76	st
2	0.72 + 2.54 = 3.26	9.24	3.53	st
3	0.91 + 2.30 = 3.20	9.06	2.53	sm
4	0.68 + 2.38 = 3.06	8.65	3.50	st
5	0.81 + 2.25 = 3.06	8.65	2.76	sm
6	0.82 + 2.04 = 2.86	8.10	2.48	sm
7	0.78 + 1.51 = 2.30	6.50	1.93	sm
8	0.77 + 1.50 = 2.27	6.44	1.95	sm
9	0.70 + 1.56 = 2.26	6.38	2.22	sm
10	0.76 + 1.33 = 2.09	5.91	1.74	sm
11	0.71 + 1.18 = 1.89	5.36	1.67	m
12	0.54 + 1.22 = 1.75	4.95	2.27	sm
13	0.67 + 1.16 = 1.83	5.19	1.74	sm
14	0.76 + 1.01 = 1.77	5.01	1.32	m

Table 4. *L. calcicola*, 2n = 52.

Chromosome	Length (μm)	Relative length (%)	Arm ratio	Form
1	0.80 + 2.43 = 3.23	3.52	3.03	st
2	0.93 + 2.20 = 3.13	3.41	2.36	sm
3	0.66 + 2.41 = 3.07	3.34	3.65	st
4	0.93 + 1.98 = 2.91	3.17	2.13	sm
5	1.01 + 1.84 = 2.85	3.10	1.82	sm
6	0.69 + 1.85 = 2.54	2.76	2.70	sm
7	1.05 + 1.25 = 2.30	2.50	1.20	m
8	0.60 + 1.59 = 2.19	2.38	2.67	sm
9	0.57 + 1.60 = 2.17	2.36	2.82	sm
10	0.69 + 1.44 = 2.12	2.31	2.09	sm
11	0.69 + 1.42 = 2.11	2.29	2.08	sm
12	0.74 + 1.33 = 2.07	2.25	1.81	sm
13	0.96 + 1.11 = 2.07	2.25	1.16	m
14	0.65 + 1.41 = 2.06	2.24	2.18	sm
15	0.82 + 1.23 = 2.04	2.22	1.51	m
16	0.60 + 1.46 = 2.04	2.22	2.43	sm
17	0.76 + 1.13 = 1.89	2.06	1.47	m
18	0.54 + 1.33 = 1.87	2.04	2.45	sm
19	0.63 + 1.20 = 1.83	2.00	1.90	sm
20	0.54 + 1.29 = 1.83	2.00	2.38	sm
21	0.69 + 1.09 = 1.78	1.93	1.58	m
22	0.79 + 0.94 = 1.73	1.89	1.20	m
23	0.82 + 0.91 = 1.71	1.87	1.11	m
24	0.74 + 0.96 = 1.70	1.84	1.30	m
25	0.82 + 0.83 = 1.65	1.79	1.02	m
26	0.58 + 1.00 = 1.58	1.72	1.71	sm
27	0.67 + 0.91 = 1.58	1.72	1.35	m
28	0.50 + 1.06 = 1.57	1.70	2.10	sm
29	0.57 + 0.98 = 1.55	1.69	1.73	sm
30	0.52 + 1.03 = 1.55	1.69	2.00	sm
31	0.54 + 1.00 = 1.54	1.67	1.83	sm
32	0.53 + 0.98 = 1.51	1.65	1.85	sm
33	0.49 + 1.00 = 1.49	1.62	2.03	sm
34	0.52 + 0.96 = 1.47	1.60	1.85	sm
35	0.47 + 1.00 = 1.46	1.59	2.14	sm
36	0.45 + 0.97 = 1.42	1.55	2.14	sm
37	0.62 + 0.79 = 1.41	1.53	1.27	m
38	0.62 + 0.76 = 1.38	1.51	1.23	m
39	0.56 + 0.80 = 1.36	1.48	1.44	m
40	0.56 + 0.80 = 1.36	1.48	1.44	m
41	0.52 + 0.84 = 1.36	1.48	1.63	m
42	0.53 + 0.83 = 1.36	1.48	1.56	m
43	0.50 + 0.84 = 1.34	1.46	1.67	m
44	0.56 + 0.78 = 1.34	1.45	1.40	m
45	0.60 + 0.74 = 1.34	1.45	1.24	m
46	0.57 + 0.74 = 1.31	3.83	1.28	m
47	0.44 + 0.75 = 1.19	1.29	1.71	sm
48	0.48 + 0.71 = 1.19	1.29	1.49	m
49	0.38 + 0.78 = 1.15	1.25	2.07	sm
50	0.45 + 0.69 = 1.14	1.24	1.51	m
51	0.40 + 0.70 = 1.10	1.20	1.74	sm
52	0.45 + 0.53 = 0.98	1.07	1.17	m

Table 6. *L. canaliculata*, 2n = 18.

Chromosome	Length (μm)	Relative length (%)	Arm ratio	Form
1	0.72 + 2.99 = 3.71	9.11	4.17	st
2	0.81 + 2.61 = 3.42	8.41	3.23	st
3	0.88 + 2.22 = 3.10	7.63	2.52	sm
4	0.98 + 1.84 = 2.82	6.95	1.88	sm
5	0.61 + 1.95 = 2.56	6.29	3.17	st
6	0.82 + 1.68 = 2.50	6.14	2.05	sm
7	0.83 + 1.53 = 2.36	5.79	1.84	sm
8	0.69 + 1.34 = 2.03	4.98	1.96	sm
9	0.60 + 1.40 = 2.00	4.92	2.32	sm
10	0.67 + 1.33 = 2.00	4.92	2.00	sm
11	0.73 + 1.19 = 1.92	4.71	1.63	m
12	0.74 + 1.17 = 1.91	4.68	1.58	m
13	0.79 + 1.08 = 1.87	4.58	1.36	m
14	0.72 + 1.10 = 1.82	4.46	1.53	m
15	0.80 + 0.98 = 1.78	4.38	1.23	m
16	0.72 + 0.98 = 1.70	4.18	1.37	m
17	0.67 + 0.95 = 1.62	3.98	1.43	m
18	0.61 + 0.96 = 1.57	3.88	1.57	m

Table 7. *L.ensifolia* var. *maughanii*, 2n = 26.

Chromosome	Length (μm)	Relative length (%)	Arm ratio	Form
1	0.86 + 2.05 = 2.92	6.72	2.38	sm
2	0.26 + 0.71 + 1.82 = 2.79	6.42	1.88	sm
3	0.44 + 0.63 + 1.44 = 2.51	5.79	1.34	m
4	0.58 + 1.67 = 2.25	5.19	2.91	sm
5	0.47 + 1.52 = 1.99	4.58	3.22	st
6	0.82 + 1.05 = 1.87	4.31	1.27	sm
7	0.42 + 1.44 = 1.86	4.28	3.44	st
8	0.59 + 1.27 = 1.86	4.28	2.16	sm
9	0.60 + 1.19 = 1.79	4.13	1.98	sm
10	0.52 + 1.23 = 1.75	4.04	2.35	sm
11	0.67 + 1.07 = 1.74	4.01	1.61	m
12	0.60 + 1.11 = 1.71	3.95	1.85	sm
13	0.50 + 1.19 = 1.69	3.89	2.39	sm
14	0.55 + 1.12 = 1.67	3.86	2.05	sm
15	0.56 + 1.05 = 1.61	3.71	1.86	sm
16	0.48 + 1.11 = 1.59	3.68	2.30	sm
17	0.51 + 1.05 = 1.56	3.59	2.05	sm
18	0.52 + 0.85 = 1.37	3.17	1.63	m
19	0.58 + 0.71 = 1.29	2.95	1.23	m
20	0.46 + 0.81 = 1.27	2.92	1.77	sm
21	0.38 + 0.88 = 1.25	2.89	2.31	sm
22	0.58 + 0.63 = 1.21	2.77	1.09	m
23	0.52 + 0.59 = 1.11	2.56	1.13	m
24	0.39 + 0.59 = 0.98	2.26	1.50	m
25	0.37 + 0.52 = 0.89	2.05	1.43	m
26	0.37 + 0.50 = 0.87	1.99	1.36	m

Table 8. *L.haarlemensis*, 2n = 18.

Chromosome	Length (μm)	Relative length (%)	Arm ratio	Form
1	0.85 + 2.46 = 3.31	7.75	2.88	sm
2	1.08 + 2.15 = 3.23	7.55	1.99	sm
3	0.28 + 0.84 + 2.09 = 3.21	7.52	1.86	sm
4	0.95 + 2.05 = 3.00	7.02	2.15	sm
5	0.92 + 1.88 = 2.80	6.55	2.03	sm
6	0.80 + 1.93 = 2.73	6.39	2.43	sm
7	0.91 + 1.54 = 2.45	5.72	1.69	m
8	0.67 + 1.65 = 2.32	5.42	2.47	sm
9	0.67 + 1.65 = 2.32	5.42	2.47	sm
10	0.78 + 1.38 = 2.16	5.05	1.76	sm
11	0.68 + 1.44 = 2.12	4.96	2.10	sm
12	0.95 + 1.14 = 2.09	4.89	1.19	m
13	0.67 + 1.31 = 1.98	4.62	1.96	sm
14	0.87 + 1.08 = 1.95	4.56	1.25	m
15	0.83 + 1.04 = 1.86	4.36	1.26	m
16	0.67 + 1.11 = 1.78	4.16	1.66	m
17	0.53 + 1.22 = 1.75	4.09	2.32	sm
18	0.55 + 1.15 = 1.71	3.99	2.08	sm