
CYTOLOGICAL
VARIABILITY IN THE
AFRICAN GENUS
LAPEIROUSIA
(IRIDACEAE–IXIOIDEAE)¹

Peter Goldblatt²

ABSTRACT

The African genus *Lapeirousia* (Iridaceae–Ixioidae) comprises two subgenera each with two sections. The basic chromosome number for the genus is postulated to be $x = 10$ in a strongly bimodal karyotype with one long and nine much smaller pairs. This karyotype occurs in at least some species of three sections and is exclusive in subg. *Paniculata* Goldbl. & Manning sect. *Fastigiata* Goldbl. In subg. *Lapeirousia* the bimodality is preserved in all species, but chromosome number ranges from $n = 10$ to 8. Genera most closely allied to *Lapeirousia* also have $x = 10$ and asymmetric but less strongly bimodal karyotypes. Sect. *Paniculata*, which is entirely tropical in distribution, has species with $n = 8, 7, 6, 5, 4,$ and 3. Species of the section with the highest chromosome numbers have bimodal karyotypes with one longer chromosome pair. Total chromosome length, a crude measure of genome size, is similar in all except two species, which have $n = 6$ and approximately twice the total chromosome length compared with all other species examined. Polyploidy appears to have been involved in the evolution of only these two species. Dysploid reduction is thought to have been responsible for the variation in chromosome number noted in other species. Evidence from comparative morphology suggests that descending dysploidy occurred repeatedly in the genus and that low numbers, $n = 4$ and 3, were achieved in separate lineages.

Lapeirousia Pourret, a genus of Iridaceae–Ixioidae (cf. Goldblatt, 1990a), comprises some 35 species (Goldblatt, 1972, 1990b; Goldblatt & Manning, 1990) distributed in two subgenera each with two sections. The genus is widespread in Africa south of the Sahara, with centers in the winter-rainfall zone of the southern African west coast and in the drier parts of tropical Africa, particularly Namibia. This pattern is unusual for Iridaceae, in which most African genera are either restricted to the Cape region of South Africa or extend into the wetter parts of eastern southern Africa, some as far north as Ethiopia. Only *Gladiolus* (Ixioidae), *Moraea* (Iridaceae), and *Aristea* (Nivenioideae) have ranges comparable to *Lapeirousia*, but they are absent or poorly represented in areas of tropical Africa where *Lapeirousia* is best developed (Goldblatt, 1990b).

Chromosome cytology of *Lapeirousia* in southern Africa is moderately well documented, with nine species counted, about half the total (Goldblatt, 1971, 1972), but until now there have been no

counts for any tropical African species. The karyotypes of 13 species in tropical Africa (of a total of 16) and an additional seven in southern Africa are described here. The cytology of only five species remains unknown. Data indicate that *Lapeirousia* is unusually variable cytologically. Haploid numbers of $n = 10, 9, 8, 7, 6, 5, 4,$ and 3 have now been recorded in the genus. This contrasts with the majority of Ixioidae, which are cytologically uniform (Goldblatt, 1971) and typically have only one base number and relatively little polyploidy. Only *Romulea* and *Crocus* have until now been exceptions to this pattern in the subfamily (De Vos, 1972; Brighton, 1976a, b, 1977).

Variation in chromosome number in *Lapeirousia* is accompanied by major differences in karyotype. Strong bimodality appears to be the rule (Goldblatt, 1972), with one long chromosome pair and a variable number of much smaller pairs (Goldblatt, 1971, 1972). The bimodality encountered in all southern African species examined also occurs in some of the tropical species. The patterns

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² B. A. Krukoff Curator of African Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.

of variation in form and overall size of the chromosome complements in *Lapeirousia* and in closely allied genera suggest that the direction of chromosome change has been from high to low numbers and that polyploidy has played only a minor role in the evolution of the genus.

MATERIALS AND METHODS

Wild-collected seeds or corms (Table 1) were sprouted in the greenhouse. Root tips, harvested when 1–2 cm long, were pretreated either in 0.003 M hydroxyquinoline for 6–8 hours at refrigerator temperature or in saturated aqueous 1-bromonaphthalene at room temperature for 3 hours, and then fixed in 3:1 absolute ethanol–glacial acetic acid for 1–2 minutes. Tips were then stored in 70% ethanol or immediately macerated in 10% HCl at 60°C for 6 minutes, washed in tap water, and later squashed in lactopropionic orcein (Dyer, 1963) or FLP orcein (Jackson, 1972). This method differs from the paraffin-section technique I previously used for *Lapeirousia* (Goldblatt, 1971, 1972) and has yielded more satisfactory results. Difficulties, noted previously, in growing corms were still encountered and an adequate number of root tips for study could be obtained only with difficulty in several species. Seeds, however, germinate easily and provide ample material for examination.

Total length of the chromosome complement was determined in selected species (Table 2) by linear measurement of camera-lucida-drawn chromosomes in karyotypes of estimated comparable degree of contraction and figured at the same magnification. Error in this type of estimation of genome size is considerable, but the results appear internally consistent so that some confidence can be attached to the results.

OBSERVATIONS

SUBGENUS *PANICULATA* SECTION *PANICULATA*

Restricted to tropical Africa and previously uncounted, sect. *Paniculata* is remarkably variable cytologically. The two putatively most primitive members of the section and the only ones with actinomorphic flowers, *L. avasmontana* and *L. coerulea*, have $2n = 16$ and 8, respectively. The karyotype of *L. avasmontana* (Fig. 1A) consists of one long acrocentric chromosome pair ca. 8 μm long and seven short acrocentric to submetacentric pairs ca. 3 μm long. No satellites were noted.

Lapeirousia coerulea, for which there are counts for seven populations, has a very different karyotype (Fig. 1B). In all populations there are two

pairs of longer acrocentric pairs 5–6 μm long (up to 7 μm in some preparations where the chromosomes are less contracted), and two pairs of acrocentric to submetacentric chromosomes 2.3–3 μm long. When satellites are visible (three of the seven populations examined) they are small and situated on the end of a short arm of one of the small chromosome pairs. In one population, *Lavranos & Pehlemann 21101* (Table 1), small constrictions are present near the ends of the long arms of a long chromosome pair, and no satellites were noted in these plants.

The widespread *Lapeirousia erythrantha* has $2n = 12$ in all eight populations examined, these covering a substantial part of the range of the species from southern Malawi to northern Zambia. The karyotypes are similar in all plants examined, with the exception of those with B chromosomes, and consist of three longer acrocentric pairs 6–7 μm long and three shorter acrocentric pairs 3.3–4 μm long (Fig. 1C). Size differences are not as sharp as in the preceding two species. Small satellites are present on the ends of the short arms of one of the longer pairs. One to three B chromosomes were noted in plants from Mufulira, Zambia (*Goldblatt 7575*). The B chromosomes varied in number in different plants and are identified by their particularly small size, ca. 1 μm smaller than the next smallest chromosomes. A collection from eastern Zambia (*Faden et al. 74/83*), which has $2n = 14$, is probably best interpreted as having $2n = 12 + 2B$. There are four small pairs in this collection and the smallest of these are probably B chromosomes.

Lapeirousia rivularis, evidently closely related to *L. erythrantha*, also has $2n = 12$ (Fig. 1D), although one seedling examined had $2n = 18$ and is apparently triploid. The karyotype of the $2n = 12$ plants closely resembles that of *L. erythrantha*. Total chromosome length in these two species (Table 2) is close to twice that of all the other species studied, suggesting their possible polyploid origin.

Two species apparently closely related to *Lapeirousia erythrantha*, *L. abyssinica* and *L. setifolia*, have $2n = 8$. They have similar karyotypes with two long acrocentric pairs 5.5–6.5 μm long (to 9 μm in preparations of less contracted chromosomes) and two much shorter pairs ca. 3 μm long. Small satellites are located on the end of the long arm of a long pair in *L. abyssinica* (Fig. 1E) and on the end of the short arm of a long pair in *L. setifolia* (Fig. 1F). In the latter, one of the small chromosome pairs is metacentric. Total chromosome length in *L. abyssinica* and *L. setifolia* (Table 2) is similar and about two-thirds that of *L. ery-*

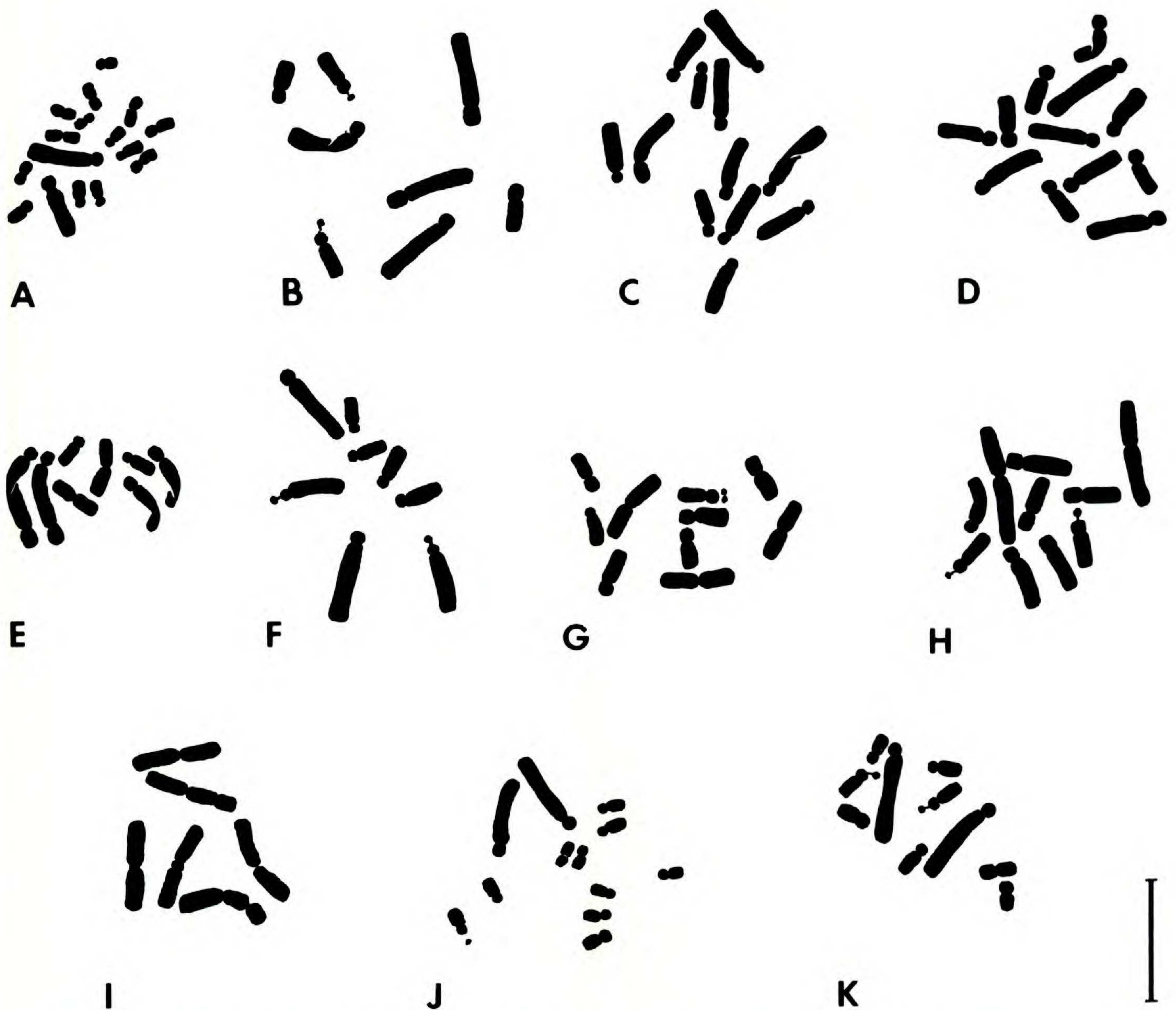


FIGURE 1. Mitotic metaphase in *Lapeirousia* subg. *Paniculata* sect. *Paniculata*.—A. *L. avasmontana*.—B. *L. coerulea*.—C. *L. erythrantha*.—D. *L. rivularis*.—E. *L. abyssinica*.—F. *L. setifolia*.—G. *L. otaviensis*.—H. *L. schimperi*.—I. *L. bainesii*.—J. *L. gracilis*.—K. *L. sandersonii*. Vouchers are given in Table 1. Scale bar, 10 μm .

thrantha (and *L. rivularis*). Other species closely allied to *L. erythrantha* are unknown cytologically, and there are no counts for *L. erythrantha* from Mozambique, Zimbabwe, or Zaire. Counts for this species, however, include both major variants, the small- and crimson-flowered typical form from the southeast part of its range and the blue-flowered form (corresponding to the type of *L. briartii*) from northern Zambia. The lack of any obvious structural variation among the populations examined is notable in view of the morphological variability and wide distribution of *L. erythrantha*.

Three of the six long-tubed species of sect. *Paniculata*, *Lapeirousia otaviensis*, *L. bainesii*, and *L. schimperi*, have similar basic karyotypes with $2n = 10$. Their karyotypes consist of one pair of long submetacentric (almost metacentric) chromosomes 8–10 μm long (depending on the degree

of contraction), and four shorter pairs 3.5–6 μm long that show no sharp size discontinuities (Fig. 1G, H). The longest of the latter four pairs is nearly metacentric, and the others are acrocentric. Satellites are present on the ends of the short arms of one of the shorter acrocentric pairs in *L. otaviensis* and *L. schimperi*. Satellites were not seen in populations of *L. bainesii* with this karyotype. Two populations of *L. bainesii* (Table 1) have $2n = 6$ (Fig. 1I) and nearly equal metacentric chromosome pairs 7.5–8 μm long. There are secondary constrictions close to the centromere in one pair and in the midpart of an arm on another.

Two other long-tubed species, *Lapeirousia gracilis* and *L. sandersonii*, have $2n = 12$ and 10, respectively, but otherwise identical bimodal karyotypes with one long acrocentric pair ca. 8 μm long and either five or four much shorter acro-

TABLE 1. Chromosome numbers in *Lapeirousia*. Original counts are marked with an asterisk. The taxonomy used here is based on the revisions of Goldblatt (1972, 1990b). Previous counts were reported by Goldblatt (1971, 1972). Acronyms (abbreviated according to Holmgren et al., 1981) following the collection data refer to the herbaria in which the vouchers are housed. Presence of a bimodal karyotype indicated by Y, absence by N.

Species	Diploid number	Karyo- type	Collection data
Subgenus <i>Paniculata</i>			
Section <i>Paniculata</i>			
<i>L. abyssinica</i> (A. Rich.) Baker	8*	N	Ethiopia, Muger valley, <i>Edwards et al.</i> 97 (MO)
<i>L. avasmontana</i> Dinter	16*	Y	Namibia, near Windhoek, <i>Goldblatt & Manning</i> 8798 (MO)
<i>L. bainesii</i> Baker	10*	N	Namibia, ENE of Otjiwarongo, <i>Lavranos & Pehlemann</i> 21031 (MO)
	6*	N	Namibia, farm Norabis, <i>Goldblatt & Manning</i> 8826 (MO); Steinhausen road E of Windhoek, <i>Goldblatt & Manning</i> 8808 (MO)
<i>L. coerulea</i> Schinz	8*	N	Namibia, Ameib, <i>Giess</i> 15284 (WIND); Ameib, <i>Goldblatt & Manning</i> 8811A (MO); Grootfontein, Valhal, <i>Goldblatt & Manning</i> no voucher; NW of Omaruru, <i>Wanntorp</i> 805 (S); Etosha Pan, <i>Giess</i> 15283 (MO); N of Tsumeb, <i>Lavranos & Pehlemann</i> 21101 (WIND); W of Otavi, J. <i>Lavranos & I. Pehlemann</i> no voucher
<i>L. erythrantha</i> (Klotzsch ex Klatt) Baker	12*	N	Malawi, University of Malawi, Zomba, <i>Goldblatt</i> 7521 (MO); Thondwe W of Zomba, <i>Goldblatt</i> 7575 (MO); Old Naisi Road, Zomba, <i>Goldblatt</i> 7514 (MO); near Ncheu, <i>Goldblatt</i> 7534 (MO); near Chileka, <i>Goldblatt</i> 7524 (MO); Chongoni Forest, <i>La Croix</i> 2698 (MO); Zambia, Chati Reserve, <i>Gold-</i> <i>blatt</i> 7567 (MO); Mufulira, <i>Goldblatt</i> 7575 (MO).
	14(? = 12 + 2B)		Zambia, Sanje Hill, <i>Faden et al.</i> 74/83 (MO)
<i>L. gracilis</i> Vaupel	12*	Y	Namibia, Asab, <i>Goldblatt & Manning</i> 8870 (MO)
<i>L. otaviensis</i> R. Foster	10*	N	Namibia, Auros farm, <i>Goldblatt & Manning</i> 8837 (MO)
<i>L. rivularis</i> Wanntorp	12, 18*	N	Zambia, Lusaka, <i>Goldblatt</i> 7537 (MO)
<i>L. sandersonii</i> Baker	10*	N	South Africa, Transvaal, E of Pretoria, Anon sub <i>Goldblatt</i> 5490 (MO)
<i>L. schimperi</i> (Asch. & Klatt) Baker	10*	N	Namibia, farm Vaalwater, <i>Goldblatt & Manning</i> 8831 (MO); Zambia, Mufulira, cultivated Missouri Botanical Garden, <i>Goldblatt s.n.</i> (MO); Zimbabwe, Victoria Falls, G. <i>McNeil</i> no voucher; Malawi, Nyika, I. <i>La Croix</i> no voucher
<i>L. setifolia</i> Harms	8*	N	Malawi, Nyika Plateau, <i>La Croix</i> 4321 (MO); Nyika, <i>Pawek</i> 6674 (MO)
Section <i>Fastigiata</i>			
<i>L. corymbosa</i> (L.) Ker			
subsp. <i>corymbosa</i>	20	Y	<i>Goldblatt</i> (1971, 1972)
subsp. <i>fastigiata</i> (Lam.) Goldbl.	20	Y	<i>Goldblatt</i> (1971)
<i>L. falcata</i>	20	Y	<i>Goldblatt</i> (1972)
<i>L. micrantha</i> (Klatt) Baker	20	Y	<i>Goldblatt</i> (1971, 1972)
	20*	Y	South Africa, Cape, Cedarberg, near Algeria, <i>Goldblatt</i> 5150 (MO)
Subgenus <i>Lapeirousia</i>			
Section <i>Sophronia</i>			
<i>L. anceps</i> (L.f.) Ker	20	Y	<i>Goldblatt</i> (1971)
	20*	Y	South Africa, Cape, S of Piekeniers Kloof, <i>Goldblatt</i> 3026 (MO); Koeberg, <i>Goldblatt</i> 5105 (MO)
<i>L. exilis</i> Goldbl.	18*	Y	South Africa, Cape, N of Springbok, <i>Goldblatt</i> 2649 (MO)

TABLE 1. Continued.

Species	Diploid number	Karyo- type	Collection data
<i>L. jacquinii</i> N.E. Br.	ca. 20	Y	Goldblatt (1971)
	18*	Y	South Africa, Cape, near Trawal, <i>Goldblatt</i> (no voucher)
	18(-20)*	Y	South Africa, Cape, near Klawer, <i>Goldblatt</i> 2266 (MO)
<i>L. littoralis</i> Baker			
subsp. <i>littoralis</i>	16*	Y	South Africa, Cape, E of Springbok, <i>Wisura s.n.</i> (NBG)
subsp. <i>caudata</i> (Schinz) Goldbl.	16*	Y	Mozambique, near Maputo, <i>Goldblatt</i> 6585 (MO)
<i>L. odoratissima</i> Baker	16*	Y	Namibia, Gobabis district, <i>Tölken s.n.</i> (BOL); ENE of Otjiwarongo, <i>Lavranos & Pehlemann</i> 21059 (WIND); E of Windhoek, <i>Goldblatt & Manning</i> 8803 (MO)
	18*	Y	Namibia, Palmfläche, <i>Merxmuller & Giess</i> 30147 (M); Malawi, <i>Pawek</i> 8166 (MO)
<i>L. oreogena</i> Goldbl.	ca. 18; 16- 18	Y	(Goldblatt, 1971, 1972)
<i>L. plicata</i> (Jacq.) Diels			
subsp. <i>plicata</i>	16*	Y	South Africa, Cape, Matjesfontein, <i>Goldblatt</i> 6091 (MO)
<i>L. pyramidalis</i> (Lam.) Goldbl.	ca. 18 20*	Y Y	(Goldblatt, 1971) South Africa, Cape, foot of Gifberg, <i>Goldblatt</i> 2196 (MO)
<i>L. silenoides</i> (Jacq.) Ker	20*	Y	South Africa, near Garies, <i>Goldblatt</i> 2767 (MO)
<i>L. verecunda</i> Goldbl.	18*	Y	South Africa, Cape, Spektakel Pass, <i>Goldblatt</i> 5710 (MO)
Section <i>Lapeirousia</i>			
<i>L. arenicola</i> Schltr.	16*	Y	South Africa, Cape, near Hondeklipbaai, <i>Goldblatt</i> 4242 (BOL)
<i>L. divaricata</i> N.E. Br.			
subsp. <i>divaricata</i>	ca. 20 20*	Y Y	(Goldblatt, 1972) South Africa, Cape, origin unknown, cultivated Missouri Botanical Garden, <i>Goldblatt s.n.</i> (MO)
subsp. <i>grandiflora</i> Goldbl.	16*	Y	South Africa, Cape, Richtersveld, <i>Goldblatt</i> 5716 (MO)
<i>L. dolomitica</i> Dinter			
subsp. <i>dolomitica</i>	16-18 16*	Y Y	(Goldblatt, 1972) South Africa, Cape, Richtersveld, <i>G. Delpierre</i> 380 (no voucher); <i>Williamson</i> 3606 (NBG)
subsp. <i>lewisiana</i> (B. Nord.) Goldbl.	16*	Y	South Africa, Cape, near Komkans, <i>Nordenstam & Lundgren</i> 1715 (S); Kamiesberg, <i>Goldblatt</i> 3980 (MO)
<i>L. fabricii</i> (de la Roche) Ker	16 + 1B*	Y	South Africa, Cape, near Alpha, <i>Goldblatt</i> no voucher
<i>L. violacea</i> Goldbl.	16*	Y	South Africa, Cape, Botterkloof, <i>Goldblatt</i> no voucher

Uncounted species: *L. angolensis* Goldbl.; *L. barklyi* Baker; *L. masukuensis* Vaupel; *L. montana* Klatt; *L. teretifolia* (Geerinck et al.) Goldbl.

to metacentric pairs 2.5–3 μm long (Fig. 1J, K). In both species satellites are located on the end of a short arm of a short acrocentric chromosome pair. Total chromosome length in these two species is similar (Table 2) and in the same range as that for most species of *Lapeirousia*, including those with low numbers such as 2n = 4 and 3.

type matching that already described for this and the two other species of sect. *Fastigiata*. There are one long acrocentric pair ca. 8 μm long and nine short acrocentric to metacentric pairs 2–2.5 μm long. Satellites, when observed, are always located on the short arm of a short acrocentric chromosome pair.

SUBGENUS PANICULATA SECTION FASTIGIATA

The bimodal karyotype (Goldblatt, 1971, 1972) already described for sect. *Fastigiata* is confirmed. *Lapeirousia micrantha* (Fig. 2A), counted here from a third population, has 2n = 20 and a karyo-

SUBGENUS LAPEIROUSIA

Sections *Lapeirousia* and *Sophronia*, including the two tropical African species of the latter, have similar karyotypes (Fig. 2B–H), closely resembling the karyotype described above for *L. micrantha*

TABLE 2. Total length of the chromosome complement in selected *Lapeirousia* species. Measurements were made from illustrations of karyotypes of estimated comparable degree of contraction, drawn at the same magnification. Species are grouped in subgenus and section by chromosome number to facilitate comparison.

Species	Diploid number	Total chromosome length (μm)
Subgenus <i>Paniculata</i>		
Section <i>Paniculata</i>		
<i>L. avasmontana</i>	16	40.0
<i>L. erythrantha</i>	12	57.3
<i>L. rivularis</i>	12	59.5
<i>L. gracilis</i>	12	34.1
<i>L. otaviensis</i>	10	46.8
<i>L. sandersonii</i>	10	38.2
<i>L. schimperi</i>	10	49.1
<i>L. abyssinica</i>	8	40.5
<i>L. coerulea</i>	8	40.7
<i>L. setifolia</i>	8	38.2
<i>L. bainesii</i>	6	45.5
Section <i>Fastigiata</i>		
<i>L. micrantha</i>	20	41.2
Subgenus <i>Lapeirousia</i>		
Section <i>Sophronia</i>		
<i>L. littoralis</i>		
subsp. <i>littoralis</i>	16	43.6
subsp. <i>caudata</i>	16	40.6
<i>L. odoratissima</i>	16	39.5
<i>L. anceps</i>	20	43.5
Section <i>Lapeirousia</i>		
<i>L. arenicola</i>	16	38.8
<i>L. dolomitica</i>	16	34.1

except for variation in the number of small chromosome pairs (Table 1).

In sect. *Sophronia* there are new counts for nine species, six of which are the first records for these species. Numbers range from $2n = 16$ to 20. *Lapeirousia littoralis* subsp. *littoralis* (Fig. 2B) and the tropical African *L. littoralis* subsp. *caudata* have $2n = 16$. The same number is also found in two acaulescent species, the southern African *L. plicata* subsp. *plicata*, and in two populations of the tropical African *L. odoratissima* (Fig. 2C). A third has $2n = 18$. It is also likely that $2n = 16$ is the correct number for *L. oreogena*, previously reported as ca. 18 and 16–18 (Goldblatt, 1972), an acaulescent species closely related to *L. plicata*. I have been unable to obtain sufficient root tip material of this species to confirm its chromosome number.

In the caulescent members of the section, $2n = 20$ is confirmed for *Lapeirousia anceps* (Fig. 2D) and *L. pyramidalis* (Fig. 2E) and reported for the first time in *L. silenoides*. A diploid number of $2n = 18$ was found in *L. exilis* and in two separate populations of *L. jacquinii*, previously reported as $2n = \text{ca. } 20$.

Counts here for sect. *Lapeirousia* include the first records for three species and additional counts for three more, leaving only one species uncounted. A diploid number of $2n = 16$ is the most common and the only one recorded for *L. arenicola*; *L. divaricata* subsp. *grandiflora*; both subspecies of *L. dolomitica* (Fig. 2F, G), previously reported as $2n = 16\text{--}18$ (Goldblatt, 1972); and *L. violacea* (Fig. 2H). The single count for *L. fabricii* is $2n = 16 + 1B$. Only *L. divaricata* subsp. *divaricata* differs in the section with two counts of $2n = 20$. It is possible that $2n = 16$ is basic for sect. *Lapeirousia* and *L. divaricata* and that the additional two pairs in subsp. *divaricata* represent B chromosomes.

DISCUSSION

The extensive variation in chromosome number and karyotype in *Lapeirousia* is puzzling. The patterns of variation are particularly difficult to assess in the tropical sect. *Paniculata*, which is so chromosomally diverse yet appears to comprise a monophyletic assemblage (Goldblatt & Manning, 1990). There is no reason to doubt that the only two actinomorphic-flowered species of the section are similar to the ancestral type of the section. Yet at the chromosomal level these two species, *L. avasmontana* and *L. coerulea*, differ surprisingly. The former has a bimodal karyotype with $2n = 16$, and the latter has $2n = 8$ and weak bimodality. No direct polyploid relationship appears to link them and polyploidy seems an unlikely explanation for the numerical difference. Cells of *L. avasmontana* have about the same amount of chromosome material as *L. coerulea*, based on measurement of total chromosome length (Table 2). More likely, *L. coerulea* is dysploid and its lower chromosome number is the result of chromosome fusion by unequal translocation and loss of centromeres and other nonessential genetic material (Jones, 1974, 1977; Goldblatt, 1979).

I suggest that the basic karyotype in *Lapeirousia* is the strongly bimodal type that occurs in all sections, and exclusively in all but sect. *Paniculata*. Basic number may be $x = 10, 9$, or 8, most likely 10. Base numbers in other genera in Watsonieae (Goldblatt, 1971, 1989; Goldblatt & Ma-

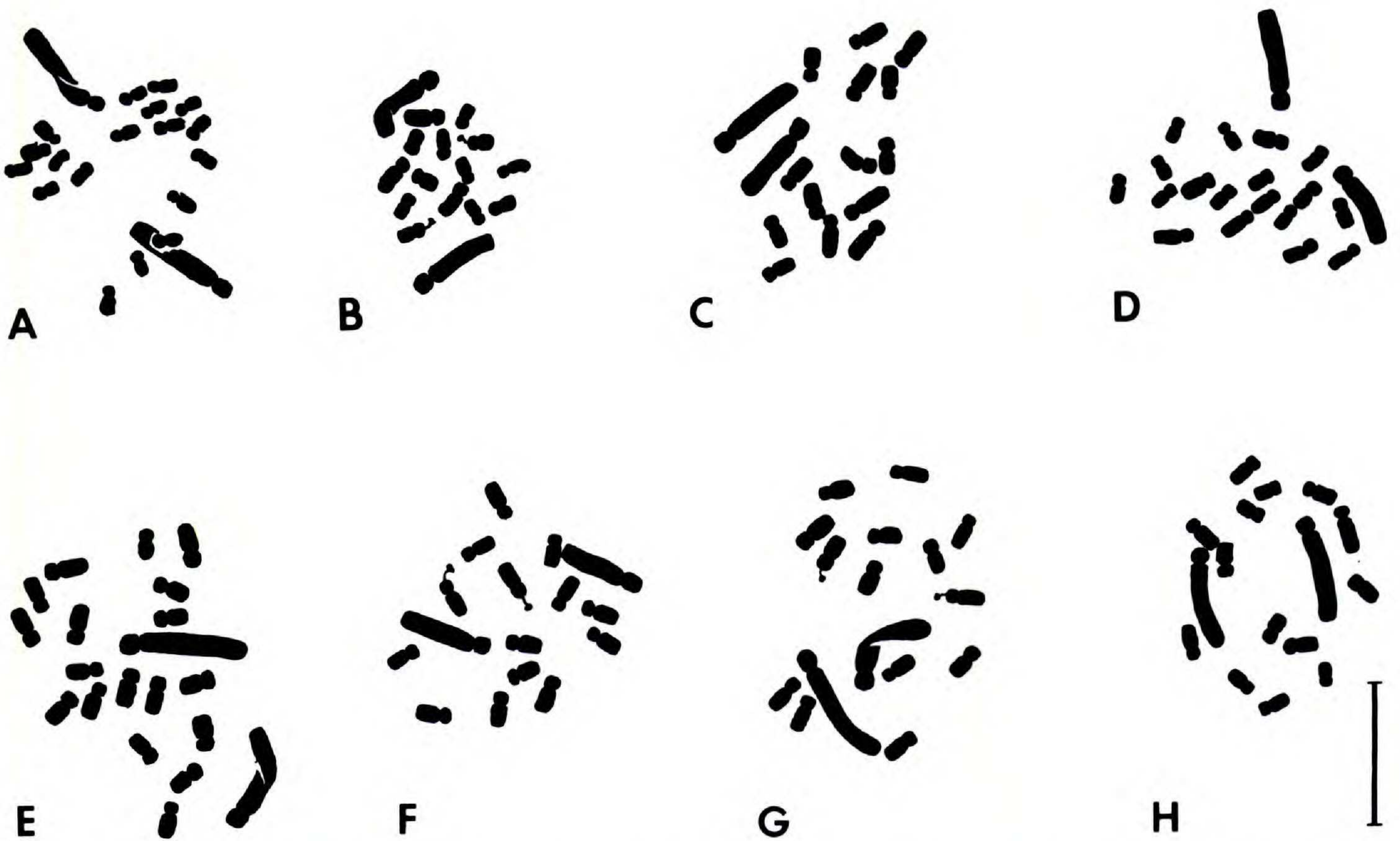


FIGURE 2. Mitotic metaphase in *Lapeirousia* subg. *Paniculata* sect. *Fastigiata* (A) and in subg. *Lapeirousia* sect. *Sophronia* (B–D) and sect. *Lapeirousia* (F–H).—A. *L. micrantha*.—B. *L. littoralis* subsp. *littoralis*.—C. *L. odoratissima*.—D. *L. anceps*.—E. *L. pyramidalis*.—F. *L. dolomitica* subsp. *dolomitica*.—G. *L. dolomitica* subsp. *lewisiana*.—H. *L. violacea*. Vouchers as given in Table 1. Scale bar, 10 μm .

rais, 1976) are $x = 10$ (*Thereianthus* and *Micranthus*), $x = 9$ (*Watsonia*), and $x = 8$ (*Savannosiphon*). The two first mentioned have a bimodal karyotype with one long and nine shorter pairs, and *Watsonia* has two long and seven shorter pairs (Goldblatt, 1971). In all three genera the degree of bimodality is less pronounced than in *Lapeirousia*. *Savannosiphon* (Goldblatt & Marais, 1976) does not have a bimodal karyotype. It seems reasonable to suggest that the ancestral base number and karyotype of *Lapeirousia* were similar to those in *Thereianthus* and *Micranthus*, which probably have the basic karyotype for Watsonieae. The karyotype in *Watsonia* is also probably derived from the *Thereianthus* type (Goldblatt, 1971, 1989).

Structural change appears to have proceeded in both subgenera of *Lapeirousia* toward reduction in number by fusion. The situation in subg. *Lapeirousia* is somewhat confused by the occurrence of two numbers in some species, and this may be the result of the presence of B chromosomes or other types of supernumeraries, which are not uncommon in strongly bimodal karyotypes.

The karyotype appears to be particularly unstable in sect. *Paniculata*. Rapid structural change

and accompanying decrease in chromosome number, such as postulated above in *Lapeirousia avas-montana* and *L. coerulea*, appears to be frequent. It is presumed to have occurred within *L. bainesii*, in which $x = 5$ is probably basic. This base number and a similar karyotype are shared with the allied *L. otaviensis* and *L. schimperi*. The low $n = 3$ in two populations of *L. bainesii* can best be explained by so-called Robertsonian fusion of small acrocentric chromosomes to form correspondingly larger metacentrics. Significantly, the measures of total chromosome length (Table 2) are similar in the dysploid *L. bainesii*, and in *L. otaviensis* and *L. schimperi*, which have the presumed basic karyotype for *L. bainesii*.

Strongly bimodal karyotypes are present in *Lapeirousia gracilis*, $n = 6$, and *L. sandersonii*, $n = 5$, both with long-tubed flowers. At least the former appears on morphological grounds (Goldblatt, 1990b) to be closely related to *L. bainesii* and *L. otaviensis*, and this suggests the possibility that the bimodal karyotype may also be ancestral to the rather different basic karyotype in *L. bainesii*, *L. otaviensis*, and *L. schimperi*. Their distinctive karyotype, with its long submetacentric chromosome pair, is presumably the result of ex-

tensive chromosomal rearrangement and fusion. There seems little doubt that the karyotype shared by these three last-mentioned species is a synapomorphy indicating common ancestry.

In *Lapeirousia rivularis* and the species of the *L. erythrantha* group the basic number is difficult to determine. These two species have $2n = 12$ and a total chromosome length half again as much as in *L. abyssinica* and *L. setifolia*, which have $2n = 8$. It seems reasonable to assume that the higher number, $n = 6$, in *L. rivularis* and *L. erythrantha* is polyploid (either dysploid from ancestors with $2n = 16$ or derived from dysploid ancestors with $2n = 6$) and that $n = 4$ in *L. setifolia* and *L. abyssinica* is basic for the alliance. Possibly, $n = 4$ in the latter two species indicates a common ancestry with the actinomorphic-flowered *L. coerulea*, which also has this number. However, there are significant differences in the karyotypes of *L. setifolia*, *L. abyssinica*, and *L. coerulea* so that if this hypothesis is correct, then their karyotypes have diverged appreciably. This model depends very much on crudely determined estimates of genome size (i.e., total linear measurement of illustrated chromosomes; Table 2), and this requires further investigation. Critical measurement of genome size would be particularly useful in evaluating the relationships of the species of sect. *Paniculata*.

The available data suggest that the unusually low numbers for Iridaceae, $n = 4$ and 3, may have been achieved independently in at least two separate lines in subg. *Paniculata* ($n = 4$ in *L. coerulea*, *L. setifolia*, and *L. abyssinica*; $n = 3$ in a population of *L. bainesii*) and possibly more than twice if the hypothesis that *L. abyssinica* and *L. setifolia* are directly related to *L. coerulea* is not correct. Such parallels in dysploid reduction are also known in Iridaceae in *Moraea*, in which $n = 10$ is basic and $n = 6$ (or 5) has evolved in at least four lines independently (Goldblatt, 1976, 1986, unpublished data) and in three with the loss of all intermediate numbers.

The possession of a bimodal karyotype in *Lapeirousia* may be related to its success in particularly arid habitats, among the most extreme in Iridaceae. The frequency of bimodal karyotypes is highest in plants of arid habitats (C. G. Vosa, pers. comm.), prominent examples being Agavaceae and the succulent Asphodelaceae–Alooideae. Numerical instability in bimodal karyotypes is also known, although the reasons are not. The repeated patterns of more than one number in some species of *Lapeirousia* and in all sections except sect. *Fastigiata* may be another example of this phenomenon. In short, the variation in chromosome number and relative size

in *Lapeirousia* are remarkable in Iridaceae and for plants in general and merit further investigation for they may lead to a better understanding of the ways in which dysploidy occurs and its adaptive significance. More counts from new populations and methods such as photometric measurement of genome size and Giemsa banding may be useful in understanding better the cytological evolution in the genus.

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