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# NOTES ON *ARISTEA* AITON (IRIDACEAE: NIVENIOIDEAE): TAXONOMY, CHROMOSOME CYTOLOGY, AND PHYLOGENY

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## ABSTRACT

Capsules with long pedicels, a thicker stem, wider leaves, and inflorescences borne on long leafless scapes confirm the current taxonomy that maintains *Aristea alata* separate from *A. abyssinica* and *A. cognata*. The two latter, however, are difficult to distinguish. Although some southern African plants referred to *A. cognata* are smaller than tropical African *A. abyssinica*, variation within and between populations suggests that smaller individuals are depauperate, due to local edaphic or seasonal conditions. I conclude that *A. cognata* and *A. abyssinica* are best treated as conspecific, and I do not recommend recognition of infraspecific taxa. Section *Ancipites*, to which these species belong, is probably heterogeneous, and the removal of *A. nitida* to section *Cladocarpae* is recommended. Three species of section *Pseudaristea* should also be added to section *Cladocarpae*. Lectotypes, lacking for sections *Ancipites* and *Pseudaristea*, are designated here. New collections of southern African *A. singularis*, only species of section *Singulares*, change our understanding of the species. It is probably not primitive in the genus, but appears specialized in growth form, inflorescence structure, seed morphology, and number of seeds per locule. The species is most likely related to, and perhaps nested within, section *Aristea* (= section *Cyaneae* Weim.). Original chromosome counts for seven species, five not before counted, confirm a base number of  $x = 16$  for *Aristea*.

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*Aristea* Aiton, the largest genus of Nivenioideae, one of four subfamilies of Iridaceae currently recognized (Goldblatt, 1990), comprises some 50 species of sub-Saharan Africa and Madagascar (Weimarck, 1940). An estimated 44 species of *Aristea* occur in Africa, of which 40 are found in southern Africa, and at least 8 occur in tropical Africa. Five of the tropical African species are shared with southern Africa, and three are endemic. The six species that occur in Madagascar are endemic to the island (Goldblatt, 1991). The systematics of the genus is fairly well understood (Weimarck, 1940; Vincent, 1985; Goldblatt, 1991), but some aspects of the taxonomy of the genus in Africa require attention.

In particular, the circumscription of taxa of the tropical and southern African *Aristea abyssinica*–*A. alata*–*A. cognata* complex is confused, and section *Ancipites* Weim., to which they belong, is probably heterogeneous. I suggest the removal of the Madagascan *A. nitida* Weim. from section *Ancipites* to section *Cladocarpae* Weim. *Aristea nitida* resembles closely *A. cladocarpa* Baker, also Madagascan, the type and currently only species of this section. I also recommend the inclusion of

three species of section *Pseudaristea* Pax, *A. ecklonii*, *A. ensifolia*, and *A. pusilla*, in section *Cladocarpae*. This leaves section *Pseudaristea*, which is lectotypified here, more narrowly circumscribed and exclusively southern African. Section *Ancipites* as understood here is also morphologically uniform as regards its defining features and is evidently monophyletic. The expanded section *Cladocarpae* appears morphologically coherent, despite the addition of both African and Madagascan species.

In southern Africa, new collections of *Aristea singularis* Weim., thought by Weimarck (1940) to be the most primitive species of the genus, and only member of section *Singulares* Weim., indicate a need for a reappraisal of its relationships. *Aristea singularis* is probably most closely related to species of section *Aristea* (= section *Cyaneae* Weim.), one of the more specialized of the eight sections of the genus recognized by Weimarck (1940). Original chromosome counts, made by M. Takei, Biological Institute, Oita University, Japan, are also reported here for seven species of *Aristea*, five of which have not before been counted. The new counts include the first cytological reports for the Madagascan members of the genus.

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1. *ARISTEA ABYSSINICA* AND *A. COGNATA* AND  
ASSOCIATED SECTIONS

Species of section *Ancipites* are apomorphic in *Aristea* in having a semi-scapose habit. The flowering stem, surrounded by a basal cluster of leaves, consists of a single long internode terminating in one or two apical inflorescences subtended by a short subterminal leaf. In addition the stem is strongly compressed and 2-winged (ancipitous according to Weimarck), also a derived condition. The section was treated by Weimarck (1940) as comprising *A. anceps* Eckl. ex Klatt, *A. alata* Baker, *A. alata* subsp. *abyssinica* (Pax) Weim. (based on *A. abyssinica* Pax), *A. alata* subsp. *bequaertii* (De Wild.) Weim. (based on *A. bequaertii* De Wild.), *A. goetzei* Harms, *A. cognata* N. E. Br. ex Weim., and *A. nitida* Weim. A few additional named species were regarded by Weimarck as conspecific with *A. alata* and need not be discussed further. Marais (1987) has already pointed out problems in Weimarck's treatment of *A. abyssinica* as a subspecies of *A. alata*. Marais considered *A. abyssinica* as resembling more closely the largely southern African *A. cognata* than the East African *A. alata* subsp. *alata*, and he regarded *A. abyssinica* and *A. cognata* as conspecific but separable at subspecific rank (his error in choosing to use the later synonym *A. cognata* for the species was corrected by Goldblatt (1993a)).

*Aristea alata* is readily distinguished from the remaining species (and subspecies) of section *Ancipites* by its more robust appearance, with stems 4–5 mm wide and leaves usually 4–5 mm wide. The terminal flower cluster is usually borne some distance above the subterminal (and only) cauline leaf, and the rhipidial spathes and bracts are reddish brown and 12–15 mm long (rarely almost 20 mm). The capsules are 9–12 mm long, and borne on long pedicels normally 5–12 mm long.

Plants of *Aristea abyssinica* sensu Marais are less robust, have stems 1–4 mm wide and leaves 1.3–3(–4) mm wide, and the terminal flower cluster is often nearly sessile or borne close to the cauline leaf. The capsules are 5–8 mm long and subsessile (the pedicels usually less than 2 mm long). The rhipidia have spathes 6–9 mm long, and the floral bracts are about the same length. Both the spathes and the bracts are scarious and have the median part reddish brown and the edges nearly transparent, and evidently readily torn, for they are often somewhat lacerated in plants collected late in the season. As noted by Goldblatt (1993a), subspecies *abyssinica* and subspecies *cognata* are not easily distinguished, and at least provisionally I preferred

not to recognize them as separate subspecies. Marais regarded subspecies *cognata* as restricted to southern Africa and Zimbabwe, and subspecies *abyssinica* as extending from Zambia and Malawi northward into Kenya and Ethiopia (where *A. alata* also occurs), but he did not enumerate their differences.

I have examined plants from across the entire range of *Aristea abyssinica* and find only weak support for maintaining *A. cognata* as separate at any taxonomic level. Consistent differences, if indeed any exist, between southern and tropical African members of the species are not evident in the mass of herbarium material available, much of it lacking well-preserved flowers. Floral differences, if there are any, remain to be demonstrated. Plants of *A. abyssinica* (including the type) in tropical Africa are 15–40 cm high, have capsules 6–8 mm long, and the leaves are about half, less often two-thirds, as long as the stems and 3–4 mm wide. In southern Africa, plants Marais regarded as subspecies *cognata* are 8–35 cm high, have stems 1–2 mm wide, capsules 5–8 mm long, and in shorter plants the leaves are as long as the stems. The leaves are also often narrower than in plants from tropical Africa, 1.3–3 mm wide.

The differences fail to separate specimens from the two areas consistently. Even in the same collection southern African plants may range from 8 to 35 cm high, and taller plants in general have stems exceeding the relatively broader leaves. Dwarfed individuals are probably depauperate due to edaphic or environmental conditions. For example, in the plants growing along paths where there is only low, trampled ground cover, *A. abyssinica* is usually 8–12 cm high, while plants nearby growing among taller grasses are 25–30 cm high. Weimarck's (1940) key to *A. cognata* and *A. alata* subsp. *abyssinica* also demonstrates the problem of overlapping vegetative characters. He separated *A. cognata* from subspecies *abyssinica* on the basis of a stem 1–1.8 mm wide (actually they may be up to 2 mm wide) vs. 2–5 mm wide, and capsules 5–8 mm long vs. 6–9 mm long. Additionally, Weimarck regarded the flowers as differing in size, those of *A. cognata* having tepals 2.8–3.5 mm wide vs. 6–7.5 mm in subspecies *abyssinica*. This reflects poor preservation of the material available to him. In fact, the tepals of plants he would have referred to *A. cognata* are 4.5–6.5 mm wide, while those of plants from tropical Africa are 4–7 mm wide.

Strictly southern African *Aristea anceps* is readily separated from *A. abyssinica* by its substantially longer rhipidia, 12–15 mm long, and



capsules (6–)9–12 mm long. The light rusty brown rhipidial spathes and floral bracts, sometimes green in the midline, and larger flowers than those normally found in *A. abyssinica* also help distinguish *A. anceps*.

The taxonomy of *Aristea abyssinica* is as follows:

***Aristea abyssinica* Pax in Engler, Hochgebirgsfl.**

Trop. Afr. 173. 1892. *Aristea alata* subsp. *abyssinica* (Pax) H. Weim., Acta Univ. Lund, new ser. 36(1): 44. 1940. *Aristea cognata* subsp. *abyssinica* (Pax) Marais, Kew Bull. 42: 932. 1987. TYPE: Ethiopia. Tigre and Begemder, Schimper 279 (holotype, B not seen; isotype, K).

*Aristea johnstoniana* Rendle, Trans. Linn. Soc. ser. 2, Bot. 4: 48. 1895. TYPES: Malawi. Mt. Mulanje, June 1891, Whyte 14 & 81 (syntypes, BM, K).

*Aristea bequaertii* De Wild., Feddes Repert. Sp. Nov. Regni Veg. 11: 509. 1913. *Aristea alata* subsp. *bequaertii* (De Wild.) H. Weim., Acta Univ. Lund, new ser. 36(1): 46. 1940. TYPE: Zaire. Shaba, Lubumbashi (Elisabethville), 3 Apr. 1912, Bequaert 303 (lectotype, designated by Weimarck (1940), BR not seen).

*Aristea homblei* De Wild., Feddes Repert. Sp. Nov. Regni Veg. 11: 509. 1912. TYPE: Zaire. Shaba. Welgelegen, in 1912, Corbusier sub Homblé 615 (holotype, BR not seen).

*Aristea cognata* N. E. Br. ex H. Weim., Acta Univ. Lund, new ser. 36(1): 39. 1940. TYPE: South Africa. Transvaal, Houtbosch, 1875–1880, Rehmann 5769 (holotype, K).

I have not been able to examine the types of either *Aristea tayloreana* or *A. goetzei*. The former was included by Weimarck in *A. alata* subsp. *abyssinica*, and the latter was maintained as a separate species. From the description this plant, restricted to the Lukwangule Plateau in the Uluguru Mountains of eastern Tanzania, may be very close to typical *A. alata*.

The last species in section *Ancipites*, *Aristea nitida*, from Madagascar, was imperfectly known to Weimarck. Later collections indicate that it does not accord with the definition of section *Ancipites*. The stems bear 2–3 leaves and 3–8 flower clusters, evenly spaced along the upper part, some of them subtended by short leafy bracts. Morphology supports Goldblatt & Le Thomas (1992) in regarding *A. nitida* as most closely resembling *A. cladocarpa*, a species referred by Weimarck to a monotypic section *Cladocarpae*. The main difference between the two species is actually in the capsules, those of *A. nitida* being ovoid and nearly sessile, whereas those of *A. cladocarpa* are cylindric and shortly

pedunculate. The resemblance between the two species is so strong that in the absence of capsules it is difficult to distinguish them, and separation at the sectional level seems inappropriate.

In turn, *Aristea cladocarpa* resembles fairly closely the tropical and southern African *A. ecklonii*, placed by Weimarck in section *Pseudaristea*. Like *A. cladocarpa*, *A. ecklonii* has cylindric capsules borne on short pedicels, and compressed 2-winged stems with leaves and branches along the axis. I propose modifying the current infrageneric classification by expanding section *Cladocarpae* to include *A. nitida*, *A. ecklonii*, and at least *A. pusilla* and *A. ensifolia*; the two latter are currently assigned to section *Pseudaristea* and evidently closely allied to *A. ecklonii*. Both sections *Cladocarpae* and *Ancipites* appear to be closely allied to section *Eucapsulares* Goldblatt (= section *Euaristea* Weim.), a fairly large and diverse assemblage including both African and Madagascan species. Further study is needed to determine their mutual relationships, including the possibility that sections *Cladocarpae* or *Ancipites* are nested within *Eucapsulares*.

Section *Pseudaristea* is consequently circumscribed more narrowly to include only those species with apomorphic cylindric, deeply 3-lobed capsules of a more or less woody texture. These capsules are also derived in *Aristea* in being tardily dehiscent, possibly serotinous. Species of the section also have unusually large flowers for the genus and relatively long anthers (Weimarck, 1940), both of which are probably apomorphic states, as are the distinctive capsules. When described by Pax (1888) section *Pseudaristea* included three species, only two of which were specifically named, *A. pusilla* and *A. spiralis*. I designate the latter as lectotype for the section because it is closer to the definition of the section than the poorly understood *A. pusilla* (neither Pax nor Weimarck indicated types for the sections they described). Section *Pseudaristea* as redefined includes only four western southern African species. In addition to *A. spiralis* these are *A. biflora* Weim., *A. lugens* (L.f.) Weim., and *A. simplex* Weim. I am uncertain of the affinities of the two remaining members of section *Pseudaristea* sensu Weimarck: both *A. zeyheri* Baker and *A. pauciflora* Wolley-Dod should provisionally remain in section *Cladocarpae* until and unless they can be placed elsewhere with more certainty. Their floral and capsular features are poorly known, and do not appear to accord with section *Pseudaristea* as redefined here. Lectotypes, not previously selected, are designated here for sections *Ancipites* and *Pseudaristea* as follows:



**Aristea** section **Ancipites** Weim., Acta Univ. Lund new ser. 36(1): 36. 1940. TYPE: *A. anceps* Ecklon ex Klatt (lectotype, here designated).

The first species of the section to be discovered, *A. anceps* also accords unambiguously with the characters of the section and there seems no doubt or confusion about its status or circumscription.

**Aristea** section **Pseudaristea** Pax, Nat. Pflanzenf. edition 1, 2(5): 153. 1888. TYPE: *A. spiralis* (L.f.) Ker Gawl. (lectotype, here designated).

## 2. *ARISTEA SINGULARIS* WEIMARCK

*Aristea singularis*, until now poorly understood, is a rare endemic of the northern Cedarberg Mountains in the northwestern Cape, South Africa. It was regarded by Weimarck (1940) as the sole species of his section *Singulares*. He interpreted it as one of the most unspecialized species in the genus and used this as justification for placing it at the beginning of his treatment, before three fairly generalized sections, mostly of tropical Africa and Madagascar. Study of new collections of *Aristea singularis* suggests that its true affinities probably lie with the specialized, predominantly southwestern Cape section *Aristea* (= section *Cyaneae* Pax).

The type and only collection of *Aristea singularis* known to Weimarck in 1940 when he described the species is from Boontjiesrivier, at the northern end of the Cedarberg (*Leipoldt s.n.* BOL 18888). Additional collections have now been made near Pakhuis Pass, both near the top of the Pass and along the track to Heuningvlei (*Barker 10453 NBG, Taylor 11001 NBG, Goldblatt 7253A MO*). Plants appear to be relatively uncommon and occur in fairly sheltered sites in the shade of rocks, but not in close proximity to streams or pools. The type collection is thought to have been made along a stream bank, which may explain its particularly robust and foliose appearance compared to all later collections (Weimarck, 1940: tab. 1).

**Vegetative form.** The most striking feature of *Aristea singularis* is the aerial stolons that give the species its characteristic appearance. The stolons consist of long, fairly thick and hard (but without secondary thickening) internodes produced from the base of the parent plant, which consists of a small dense tuft of lanceolate, equitant leaves and a number of short flowering stems. The ends of the stolons bear clusters of short leaves and under suitable conditions roots are produced, an-

choring the stolons some distance from the parent plant. The stolons persist for several years so that discrete tufts of leaves and flowering stems remain attached to one another in mature individuals. *Aristea singularis* is thus neither normally an erect nor a weakly climbing plant, as Weimarck supposed.

This growth form is not common in *Aristea* nor in other Iridaceae, but it is not significantly different from that in a few other species of the genus. *Aristea dichotoma* (section *Aristea*) has aerial and branched rhizomes that may root a short distance from the parent plant, and subsequently give rise to a tuft of leaves. Elongate rhizome-like underground stolons are also produced by some other species of section *Aristea*, including *A. africana* and *A. glauca*, both of which may form sparse or even dense mats of what seem to be several plants, all connected by rhizomes just below the soil surface. This is presumably comparable and homologous with the condition in *A. singularis* and *A. dichotoma*, which have aboveground stolons or rhizomes.

**Inflorescence and flowers.** The flowering stems of *Aristea singularis* are relatively short and generally do not exceed the leaves. They are laxly branched and each branch arches outward, terminating in an inflorescence of two, or occasionally one, pendulous flower, the pedicel of which is subtended by opposed coriaceous bractlike structures. Like other species of *Aristea*, the flowers are blue and consist of 6 subequal tepals, which in *A. singularis* are united basally for ca. 2 mm. The stamens are short, straight, and symmetrically disposed. The style reaches only to mid anther level and seems hardly, if at all, lobed at the apex. The pendent flower is unique in *Aristea*, but is otherwise unremarkable. The inflorescence is either a binate rhipidium, with each of the two rhipidial units bearing a single flower, or the whole inflorescence consists of a single flower, subtended by two bractlike structures. The latter is remarkable, for inflorescence units with one flower are rare elsewhere in *Aristea*, although they are known in a few species where they are the exception (Weimarck, 1940: 105–107).

A binate rhipidium is apomorphic for Nivenioideae (Goldblatt, 1990; Manning & Goldblatt, 1991) and is a structure believed to be the result of the union of two rhipidia (an inflorescence type characteristic of Iridaceae). In most species of *Aristea* the binate rhipidia have four or more flowers; in a few species, by reduction, they have only two. Two-flowered binate rhipidia are regarded as plesiomor-



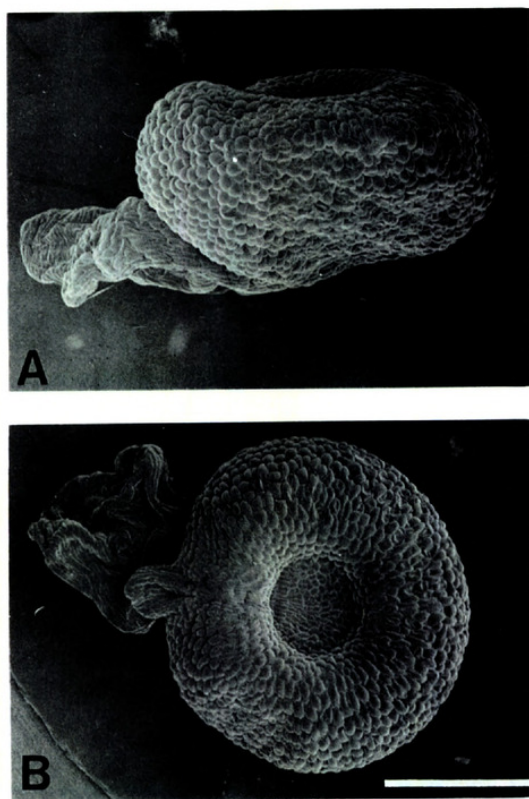


FIGURE 1. Seed morphology of *Aristea singularis*. — A. Lateral view, showing the compressed-spherical shape, and funicular nature of the elaiosome. — B. Dorsal view, showing the collapsed chalazal tissue. Scale bar, 1 mm.

phic for three genera of Nivenioideae, *Nivenia*, *Klattia*, and *Witsenia* (Goldblatt, 1993b), but in some species of *Nivenia* the binate rhipidia are one-flowered. The binate nature of the inflorescence units in these species is maintained except that one of the rhipidial units is represented only by its subtending bract (spathe), which lacks a flower or floral bract. In *A. singularis* there is only one rhipidial spathe and one floral bract. The binate ancestry of the inflorescence is then not evident when the inflorescences are one-flowered.

**Capsules and seeds.** The pendent capsules are deeply and narrowly 3-lobed along their entire length, an apomorphic condition very closely resembling the narrowly winged capsules of sections *Aristea* and *Racemosae*. Unlike the radially compressed seeds of these two sections, the seeds of *A. singularis* are radially compressed spheres, on the chalazal side of which there is a deep invagination (Fig. 1A, B). The seeds are not numerous, as Weimarck (1940) believed, based on his examination of immature capsules. There are normally two seeds per locule or, apparently by reduction, only one. The seeds are also remarkable in having a large cream to yellowish elaiosome-like appendage, unique in the genus (Fig. 1A, B). The

elaiosome appears to be an elaboration of the funicle. Both the capsules and the seeds of *A. singularis* are most likely derived in *Aristea*, and suggest a need for a reevaluation of its systematic position.

**Probable relationships.** The relatively short flowering stems of *Aristea singularis*, held not much above the level of the leaf apices, are similar to those of section *Aristea*, although binate rhipidia with one flower per unit or a solitary flower are not. Species of section *Aristea* typically have binate rhipidia with two flowers, one to each of the subunits. Weimarck, however, interpreted the single-flowered rhipidia as plesiomorphic because they resemble one flower and its associated bracts in the spikes of Iridaceae subfamily Ixioideae (individual flowers borne on a vertical axis, subtended by an outer and opposed inner bract). I disagree with this interpretation. Binate rhipidia are more likely to be the result of fusion of two multiflowered rhipidia, themselves the plesiomorphic inflorescence type in Iridaceae or at least in subfamilies Nivenioideae and Iridoideae (Goldblatt, 1990). The reduction in number of flowers per rhipidial subunit seems most likely to be apomorphic. Thus, the apomorphic 2- or 1-flowered binate rhipidia in *A. singularis* are consistent with its other specialized features, the apomorphic growth form, reduced number of seeds, strongly lobed capsules, and presence of an elaiosome on the seed.

*Aristea singularis* seems to be a relatively specialized member of *Aristea*, derived in several features. Its relationships probably lie with species of section *Aristea*. Except for the narrowly 3-lobed capsules (rather than 3-winged), rounded seeds (rather than radially flattened), and well-developed aerial stolons, it falls within the section. These discordant features are all apomorphic and reveal nothing about its relationships. The rounded seeds, in particular, may be a secondary condition associated with the presence of an elaiosome and a novel mode of seed dispersal, presumably by ants. Whether section *Singularis* still merits recognition is debatable, but it is certainly not basal in the genus. It is more likely nested within section *Aristea*, and its continued recognition would render that section paraphyletic. A decision about its sectional taxonomy must wait for a more detailed phylogenetic analysis of *Aristea*.

### 3. CHROMOSOME CYTOLOGY

Using a squash technique on root tips of germinating seedlings, fully explained elsewhere (Goldblatt et al., 1993), diploid numbers were established



TABLE 1. New chromosome numbers in *Aristea* with collection data. Vouchers are at the Missouri Botanical Garden (MO).

Species	Diploid number $2n$	Collection data
Section <i>Ancipites</i>		
<i>A. abyssinica</i> Pax	64	Zimbabwe, Nyanga, Goldblatt 9070
	32	S. Africa, near East London, Goldblatt & Manning 9532
<i>A. anceps</i> Ecklon ex Klatt	32	S. Africa, near Fish River mouth, Goldblatt 9053
Section <i>Eucapsularis</i> (= section <i>Euaristea</i> Pax)		
<i>A. angolensis</i> Baker	32	Malawi, Zomba Mt., Goldblatt 4528
<i>A. angustifolia</i> Baker	32	Madagascar, Andringitra, Goldblatt & Schatz 8971
<i>A. kitchingii</i> Baker	32	Madagascar, source unknown, no voucher
<i>A. schizolaena</i> Harvey	32 + 2B	S. Africa, Cape, near East London, Goldblatt & Manning 9531
Section <i>Racemosae</i>		
<i>A. juncifolia</i> Baker	32	S. Africa, Cape Point Reserve, Goldblatt 9056

by M. Takei for seven species of *Aristea*, five of these not before counted (Table 1). Results confirm earlier observations (Goldblatt, 1971) that  $x = 16$  is the basic chromosome number in *Aristea*. Six of the species examined, including one from tropical Africa and two from Madagascar, are diploid,  $2n = 32$ , and the seventh, *A. abyssinica*, has both diploid and tetraploid,  $2n = 64$ , populations. Additional counts in this widespread African species may be helpful in understanding its systematics. Two other species of the genus, the tropical and eastern southern African *A. ecklonii* and the Cape *A. glauca*, are also reported to have both diploid

and tetraploid populations (Goldblatt, 1971). Plants of *A. schizolaena* examined actually had  $2n = 34$ , but consistently had two small darkly staining chromosomes at mitotic prophase, and it seems likely that these represent B chromosomes. I assume that the correct way to view this karyotype is to record it as  $2n = 32 + 2B$ .

Chromosomes of *Aristea* are relatively small, 0.9–2.3  $\mu\text{m}$  long, and meta- to submetacentric (Fig. 2). The longest chromosome pair has large satellites 0.5–0.7  $\mu\text{m}$  long in all the species examined. The chromosomes stain uniformly at late mitotic prophase, excepting for the one extra pair

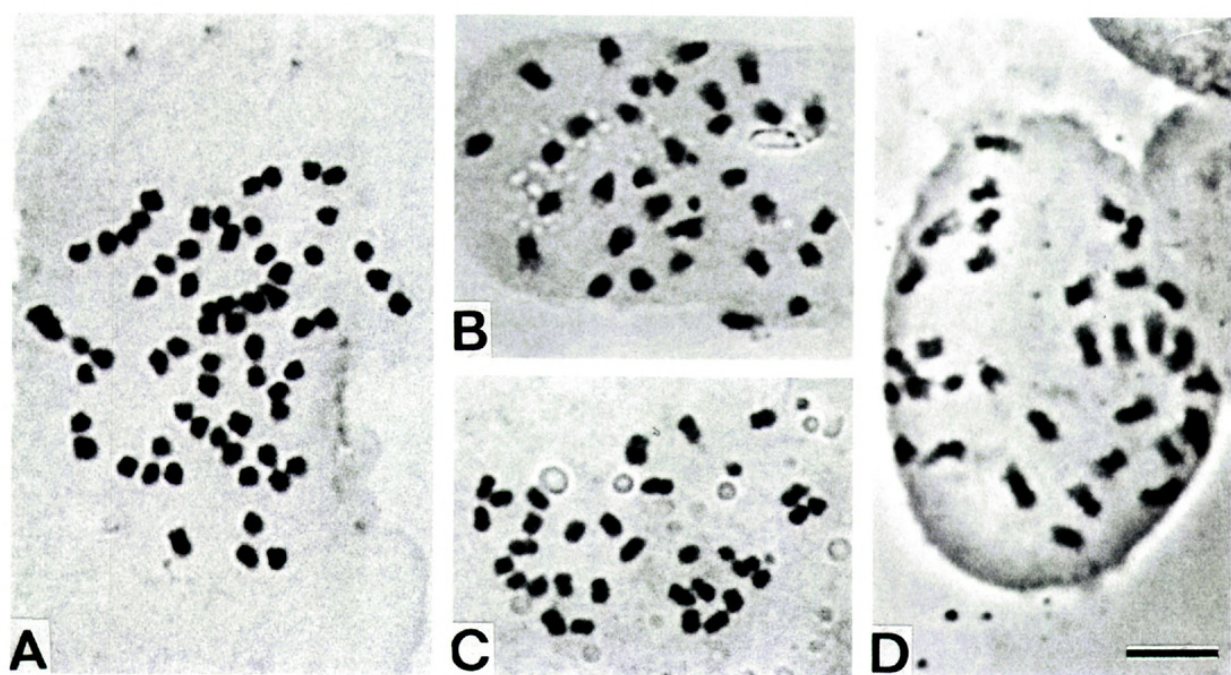


FIGURE 2. Mitotic metaphase in *Aristea*.—A. *A. abyssinica*.—B. *A. anceps*.—C. *A. angolensis*.—D. *A. angustifolia*. Scale bar, 5  $\mu\text{m}$ .



Goldblatt, Peter. 1995. "Notes on *Aristea* Aiton (Iridaceae: Nivenioideae): Taxonomy, Chromosome Cytology, and Phylogeny." *Annals of the Missouri Botanical Garden* 82, 139–145. <https://doi.org/10.2307/2399984>.

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