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Pollen morphology of Madagascan *Aristea* and *Geosiris* (*Iridaceae-Nivenioideae*) in relation to systematics and phylogeny

P. Goldblatt & A. Le Thomas

Summary : Specialization from the presumed basic monosulcate and semitectate-reticulate pollen grains of *Iridaceae* is evident in all six species of *Aristea* in Madagascar. Disulcate grains are characteristic of *A. cladocarpa* and *A. nitida*, and although the two species are currently assigned to different sections, morphology suggests that they are closely related, and perhaps most closely allied to the tropical African *A. ecklonii*, which has monosulcate grains. *Aristea humbertii* and *A. madagascariensis* have operculate (-pontoperculate) grains, while four samples of *A. kitchingii* exhibit variation ranging from predominantly disulcate in two samples to predominantly zonasulculate in the other two. Porate anther dehiscence is restricted in *Aristea* to these three species, which appear to comprise a monophyletic lineage. The disulcate grains of *A. angustifolia* may link these three species to tropical African members of section *Euaristea*, here renamed section *Eucapsulares* (*Euaristea* does not include the type of the genus). Pollen grains of *Geosiris* accord with the basic type in *Iridaceae*, but appear less specialized than those of the Madagascan species of *Aristea*. Pollen grains of *Aristea* are in general more variable than in most other genera of *Iridaceae* and need further investigation. *Patersonia*, included in the study because it is the only Australasian genus of *Nivenioideae* and may be closely related to *Aristea*, has inaperturate, intectate pollen grains with an unusual sculpturing.

Résumé : Les types polliniques dérivés des grains monosulqués et semi-tectés réticulés, primitifs chez les *Iridaceae*, sont particulièrement diversifiés dans les six espèces malgaches d'*Aristea*. *Aristea cladocarpa* et *A. nitida* sont caractérisés par un pollen disulqué ; bien que ces deux espèces appartiennent actuellement à deux sections différentes, la macromorphologie suggère qu'elles sont très affines et probablement les plus proches de l'espèce africaine *A. ecklonii* dont le pollen est monosulqué. Le pollen d'*A. humbertii* et *A. madagascariensis* est monosulqué operculé (ou pontoperculé), tandis que celui d'*A. kitchingii* est particulièrement diversifié. En effet, parmi les quatre spécimens étudiés pour cette espèce, deux d'entre eux ont une majorité de grains disulqués, alors que dans les deux autres les grains sont en grande partie zonasulculés. Seules ces trois dernières espèces d'*Aristea*, qui apparaissent constituer une lignée monophylétique, possèdent des anthères à déhiscence poricide. Le pollen disulqué d'*A. angustifolia* pourrait constituer un lien entre cette lignée et les espèces tropicales africaines appartenant à la section *Euaristea*, nommée ici *Eucapsulares* (*Euaristea* ne renferme pas le type du genre). Le pollen de *Geosiris* ressemble au type de base des *Iridaceae* ; il est moins spécialisé que celui d'*Aristea* dont la variation est en général plus importante que dans la plupart des autres genres d'*Iridaceae* et qui nécessite de futures investigations. Le pollen de *Patersonia* est inclus dans cette étude comme seul genre australien appartenant aux *Nivenioideae* et proche des *Aristea*. Il est inaperturé, presque intecté, à ornementation inhabituelle dans la famille.

Peter Goldblatt, Missouri Botanical Garden, P. O. Box 229, St. Louis, Missouri 63166-0229, U.S.A.
Annick Le Thomas, E.P.H.E., Laboratoire de Phytomorphologie, Muséum national d'Histoire naturelle, 16, rue Buffon, 75005 Paris, France.

The African and Madagascan *Aristea*, with ca. 50 species, is the largest and most widespread genus of *Nivenioideae*, one of four subfamilies of *Iridaceae* currently recognized (GOLDBLATT, 1990, 1991*a*). Of the remaining five genera of *Nivenioideae, Nivenia, Klattia* and *Witsenia* are southern African, *Patersonia* is Australasian, and *Geosiris* is a monotypic saprophyte endemic to Madagascar. Available evidence indicates that although *Geosiris* has been regarded as a separate family or a member of *Burmanniaceae*, it is well placed in *Iridaceae-Nivenioideae* (GOLDBLATT et al., 1987), in which it appears to be most closely related to *Aristea* (MANNING & GOLDBLATT, 1991). Pollen grains of *Geosiris, Nivenia, Klattia* and *Witsenia* (SCHULZE, 1983; GOLDBLATT & MANNING, 1989) are monosulcate and semitectate reticulate. Only *Witsenia* diverges in having distinctive supratectal gemmae superimposed on a basal reticulum. According to present knowledge, *Aristea* is also one of the most palynologically diverse genera in the family (RADELESCU, 1970; SCHULZE, 1971). Some African species have monosulcate, reticulate pollen grains, while others, mostly from the Cape Region of southern Africa, have different apertures, so far incompletely characterized owing to the method used by SCHULZE (1971) to prepare grains for observation.

Pollen of four of the six Madagascan species of *Aristea* (GOLDBLATT, 1991*b*) have been examined by STRAKA & FRIEDRICH (1984), and they appear to differ from all those in Africa both in their apertures and in sculpturing. Again, however, the apertures were not satisfactorily described. In this study we attempt to characterize palynologically all the Madagascan species of *Aristea* and to compare them with the African members of the genus, *Geosiris*, and the remaining *Nivenioideae*. Because the pollen grains of *Patersonia* are unknown, we have included a sample of this genus in our study.

MATERIALS AND METHODS

Pollen samples were taken from dried specimens at the Paris (P) and Missouri Botanical Garden (MO) herbaria (Table 1). Fourteen samples of the six Madagascan species of *Aristea, Geosiris* and *Patersonia* were examined. Samples were rehydrated in a wetting agent and after washing were treated in 2.5 % glutaraldehyde and then dehydrated and critical-point dried. In some cases, pollen grains were examined without critical-point treatment drying with satisfactory results. Pollen grains mounted in glycerine jelly were measured using the light microscope; measurements are based on a sample size of 10 grains.

Pollen of *Aristea* is particularly difficult to study owing to the fragility of the exine, of which the foot-layer is extremely thin. It is best observed in rehydrated condition, without being acetolysed, so that the apertures can be distinguished under the light microscope by the presence of the thickened intine. In some of the species in our study, the variation in the pollen grains is extensive and numerous grains had to be examined. Pollen grains of *Patersonia* posed even more problems than those of *Aristea*, and, because of the apparently fragile nature of the exine and a very thin nexine, we obtained satisfactory preparations only with untreated grains. With other treatments the exine became detached from the surface of the grain.

GENERAL DESCRIPTION

Pollen grain size, aperture number and form, and details of exine sculpturing are recorded in Table 1.

TABLE 1. — Pollen grain characters and voucher information for ***Geosiris*** and species of ***Aristea*** and ***Patersonia*** examined. Abbreviations : 1s = monosulcate, 2s = disulcate, zs = zonasulculate, op = operculate, o = inaperturate, pt = pontoperculate, ru = rugulate, re = reticulate, p = perforate, mr = microreticulate, ar = areolate, ei = islands of exine, in = intectate (* more fully explained in text, – not observed). Voucher specimens are at the Paris Herbarium (P).

TAXON	SULCUS	EXINE SCULPTURING	APERTURE MEMBRANE	GRAIN SIZE µm	VOUCHER INFORMATION
Aristea (ca. 50)					
angustifolia Baker	2s	ru	ei	44.1 × 35.8	*Perrier 8349*
	(1-)2s	ru	ei	45.3 × 38.1	*Rakotovao 9930*
cladocarpa Baker	2s	ru	ei	37.5 × 35.1	*Humbert 11124*
	(1s-)2s	ru	ei	47.6 × 36.7	*Bosser 16695*
humbertii Perrier	1s	ru	op/pt	48.5 × 39.6	*Humbert 3790*
kitchingii Baker	zs(-1s-2s)	mr/p	smooth	48.5 × 43.2	*Bosser 13374*
	zs(-2s)	ru-ar	ei	48.5 × 40.5	*Peltier & Peltier 1193*
	1s-2s(-zs)	re/p	*ei	40.2 × 29.4	*Miller & Phillipson 3714*
	2s(-zs)	ru-ar	*ei	45.3 × 38.1	*Keraudren-Aymonin & Aymonin 25146*
madagascariensis Baker	1s	re-ar	op/pt	48.9 × 45.3	*Dorr et al. 2880*
	1s	re-ar	pt	—	*Peltier & Peltier 1866*
	1s	re-ar	pt	46.2 × 37.8	*Bosser 13018*
nitida Weim.	*(1s-)2s	ar	ei	43.5 × 41.4	*Humbert 6938*
Geosiris (1)					
aphylla H. Baillon	1s	mr	smooth	28.0 × 19.3	*Bosser 18900*
Patersonia (ca. 20)					
sericea R. Br.	o	in	—	78.9 × 72.3	*Arnoux 1844*

SHAPE

Grains mostly elongate (boat-shaped) in *Geosiris*, most often spherical in *Aristea*, but sometimes ellipsoidal in polar view, especially when grains are mono- or disulcate, spherical in *Patersonia*.

Size

Mean sizes for species are presented in Table 1; for genera, means and extremes are as follows :

— *Aristea* : length (48.9-)45.3(-37.5); width (43.2-)38.4(-29.4) µm.
— *Geosiris* : length (31.5-)28.0(-25.5); width (22.5-)19.3(-15.0) µm.
— *Patersonia* : length (87.0-)78.9(-60.0); width (82.5-)72.3(-67.5) µm.

Apertures

In *Geosiris* apertures are consistently monosulcate with a smooth membrane (Fig. 1, *1*). In *Aristea* apertures are extremely variable; monosulcate apertures are relatively uncommon, and then the aperture is very wide, reaching the ends of the grain and covered by an operculum or pontoperculum in *A. humbertii* and *A. madagascariensis* (Fig. 1, *4-5*; 2, *1-2*), exceptionally zonasulculate (Fig. 1, *3*); apertures are both mono- and disulcate in *A. nitida*, extending beyond the equator and always covered by thick pieces of exine of the same structure as that on the extra-apertural surface (Fig. 3, *5-6*). *A. kitchingii* has an unusual degree of apertural variation (Table 1) : zonasulculate grains (i.e., with ring furrow parallel to the equator (Walker & Doyle, 1975) are most frequent, and occurred in all four samples (Fig. 2, *6, 8, 12*), but some grains are also mono-or disulcate (Fig. 2, *10-11*); all three apertural types were noted in one sample (*Bosser 13374*); the apertural membrane is smooth or most often with scattered or loosely aggregated exine elements. In *A. cladocarpa* and *A. angustifolia* grains are almost always disulcate (Fig. 3, *1, 3*), with a very small proportion of monosulcate grains. In *Aristea* the aperture margins are diffuse, often very irregular. Grains are inaperturate in *Patersonia* (Fig. 3, *8*), with a very thick intine all around the grain.

Surface sculpturing

Unlike most *Iridaceae*, the exine is seldom reticulate, but then the sexine is simplicolumellate and microreticulate (or reticulate), as in *Geosiris* (Fig. 1, *3*) and two of four samples of *A. kitchingii* (Fig. 2, *9, 11-12*). In the other species of *Aristea*, the sexine consists of short columellae standing on the nexine, and more or less strongly enlarged above, forming a sculptural pattern that is rugulate (*A. humbertii,* Fig. 1, *6*), rugulo-areolate (two samples of *A. kitchingii*, Fig. 2, *7*), reticulo-areolate (*A. madagascariensis*, Fig. 2, *4*), or areolate (*A. nitida*, Fig. 3, *7*). In *Patersonia* the exine is almost intectate (Fig. 3, *9*) and thin, consisting of more or less uniformly distributed verrucae and supported by very short columellae.

DISCUSSION

Although *Aristea* is only moderately known palynologically, available data indicate that it is one of the most variable genera of *Iridaceae* in this respect. The ca. 44 African and 6

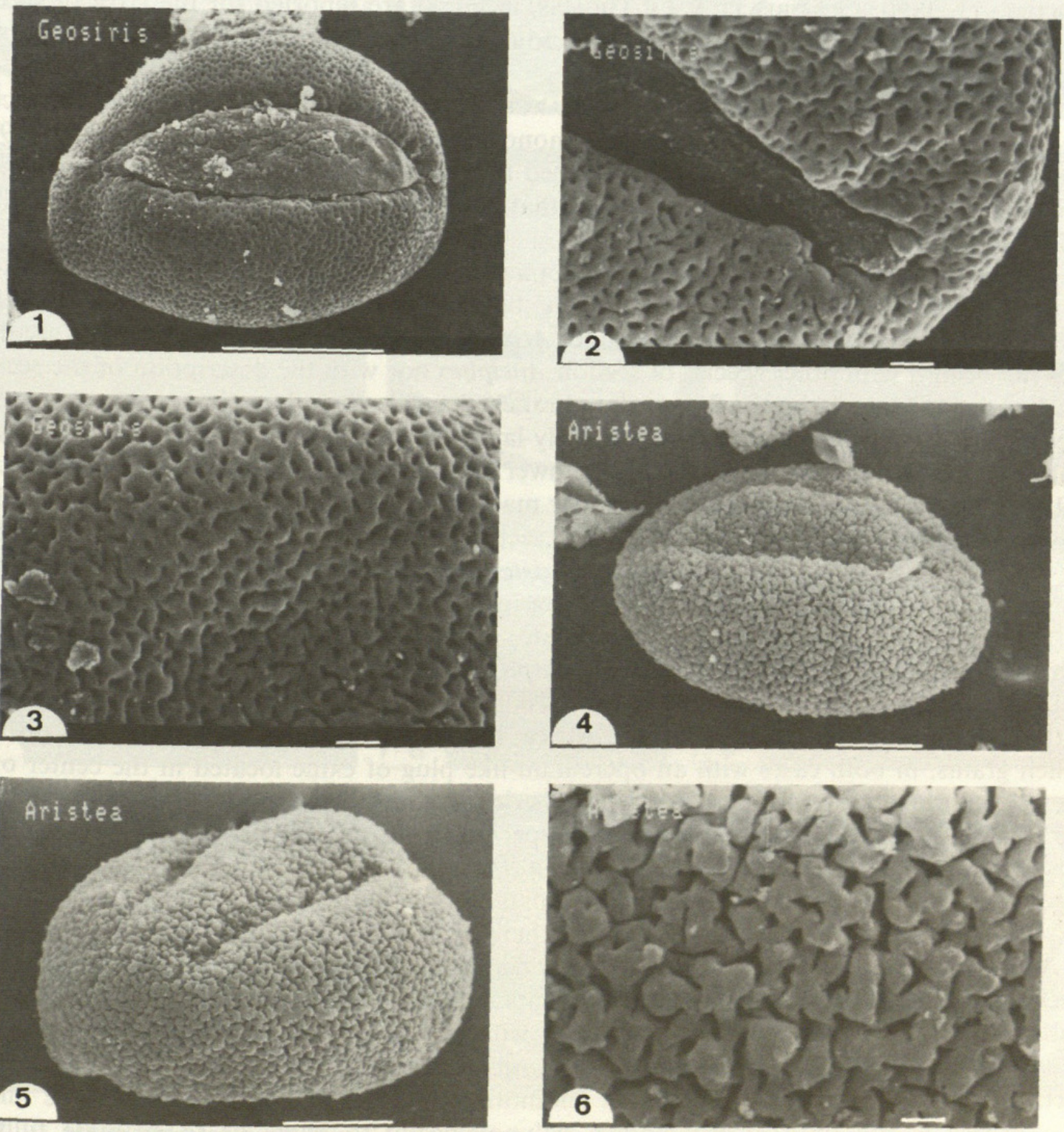

Fig. 1. — **Geosiris aphylla** Baillon : **1**, monosulcate grain; **2**, extremity of the sulcus; **3**, microreticulate exine. — **Aristea humbertii** Perrier : **4**, monosulcate operculate grain; **5**, pontoperculate grain; **6**, rugulate exine. (1-3, *Bosser 18900*; 4-6, *Humbert 3790*. — Scale : 1, 4, 5 = 10 μm; 2, 3, 6 = 1 μm).

Madagascan species are currently assigned to eight sections (WEIMARCK, 1940), based primarily on capsule and seed characters. Pollen grains have been examined for species of five sections : *Eucapsulares nom. nov.* [1] (= section *Euaristea* Pax, this does not include the type of the genus), *Racemosae, Aristae* (= *Cyaneae* Pax, but including the type of the genus, *A. africana* (L.) Hoffmsg.), *Pseudaristea*, and *Cladocarpae*. In section *Eucapsulares* monosulcate and semitectate-reticulate grains of the type that are thought to be basic in *Iridaceae* (GOLDBLATT, 1990; GOLDBLATT & LE THOMAS, in press) are reported for the African species, *A. angolensis* (SCHULZE, 1971). Grains of the four Madagascan species assigned to the section differ in both aperture and sculpturing.

Aristea cladocarpa, treated by WEIMARCK (1940) as the sole member of section *Cladocarpae*, was also described as having monosulcate reticulate grains by SCHULZE (1971), whereas STRAKA & FRIEDRICH (1984) described the grains of this species as atreme or dilept. However, in the two samples of this species that we examined the pollen is predominantly or entirely disulcate.

Pollen grains of *Aristea nitida* (section *Ancipites*), not previously examined, are notable for their spherical shape and are also disulcate, but very different from grains of *A. cladocarpa* in their comparatively thick, areolate exine. *Aristea nitida*, imperfectly known to WEIMARCK, does not accord with other species of section *Ancipites* nor with the description of the section, which is defined largely by the flattened, unbranched and leafless flowering stem, and terminal one(-two) flower clusters subtended by a fairly large leafy bract. The stem of *A. nitida* has 2-3 well developed leaves and several axillary flower clusters along its upper length (GOLDBLATT, 1991*b*). The species seems to us fairly similar macromorphologically to *A. cladocarpa* and the two should probably be referred to the same section. The most appropriate sectional position for the two species may be section *Pseudaristea*, in which they resemble most closely the widespread African species *A. ecklonii*. Pollen grains of *A. ecklonii* have been described by SCHULZE (1971) as monosulcate and reticulate, thus differing notably from the disulcate or areolate grains of *A. nitida* and *A. cladocarpa*.

Two other species of section *Pseudaristea, A. spiralis* and the closely related *A. lugens*, both from the Cape Region of southern Africa, have what may best be described as disulcate pollen grains, in both cases with an operculum-like plug of exine located in the center of the aperture. Both species stand out in having spherical grains, like *A. nitida*. The areolate exine in the latter, however, is not matched in these species. *Aristea lugens* has a reticulate exine with very large lumina (SCHULZE, 1971), and *A. spiralis* has an exine with large supratectal gemmae superimposed on an apparently microreticulate surface (RADELESCU, 1970).

The remaining two sections for which there are palynological data are *Racemosae* and *Aristea* (section *Cyaneae* of WEIMARCK), both derived in their narrowly 3-winged capsules and laterally flattened seeds. These specialized fruits and seeds are apomorphic and make it seem unlikely that either has a close relationship with the Madagascan species. SCHULZE (1971) described the pollen grains of section *Racemosae* as monosulcate and reticulate, and those of section *Aristea* (as section *Cyaneae*) as anomotreme and reticulate with very large lumina.

Aristea is still insufficiently known palynologically to allow us to evaluate fully the systematic significance of the data here for the Madagascan species of the genus. We suggest,

1. **Aristea** section **Eucapsulares** Goldbl. *nom. nov.* pro section *Euaristea* Pax, Nat. Pflanzenf. ed. 1, 2 (4) : 152 (1888). Lectotype here designated : *Aristea angolensis* Baker.

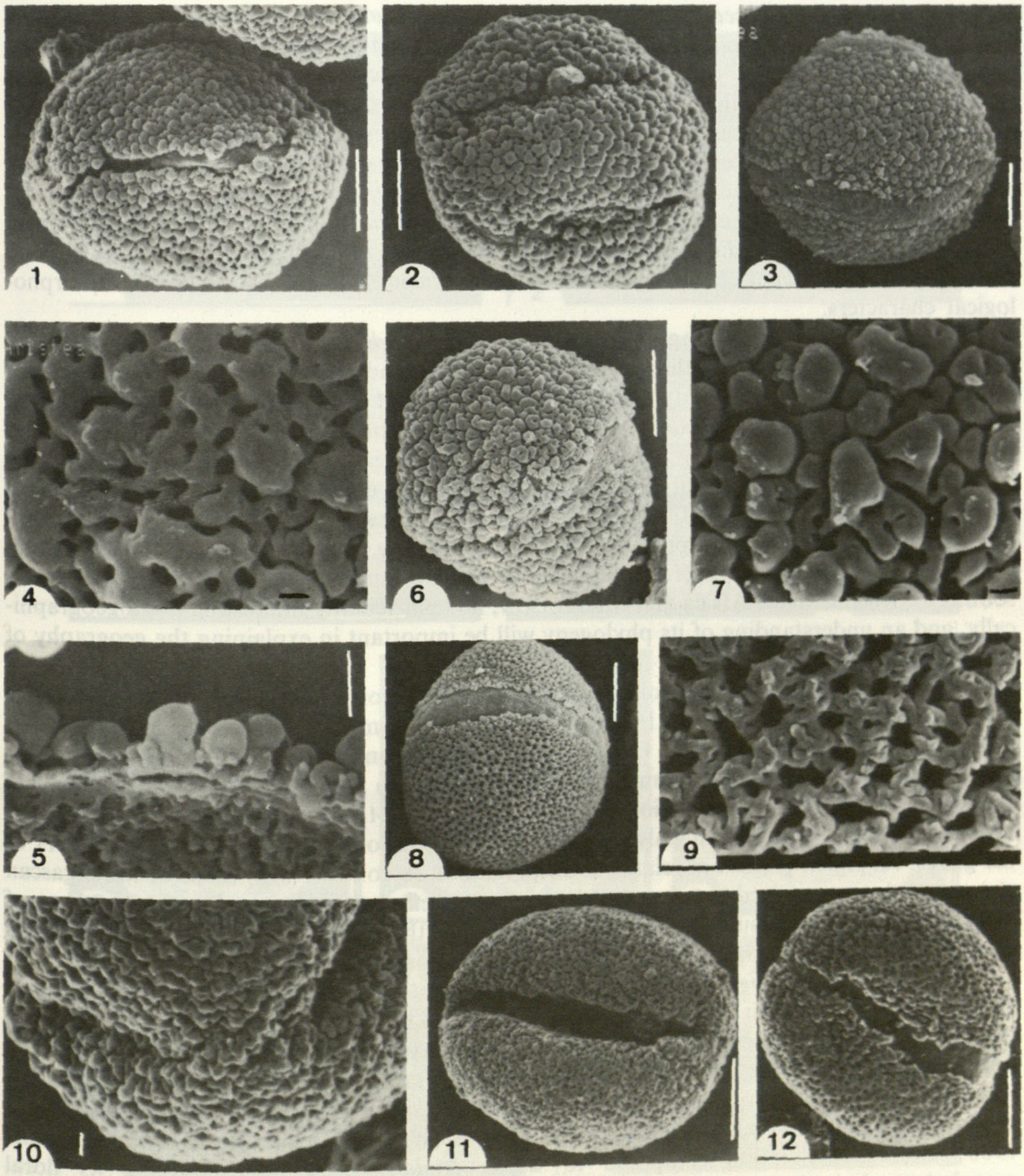

Fig. 2. — **Aristea madagascariensis** Baker : **1**, monosulcate operculate grain ; **2**, pontoperculate grain ; **3**, zonasulculate grain ; **4**, reticulo-areolate exine ; **5**, exine section. — **A. kitchingii** Baker : **6**, zonasulculate grain ; **7**, rugulo-areolate exine ; **8**, zonasulculate grain ; **9**, reticulate exine with bipartite and perforate muri ; **10**, disulcate grain ; **11**, monosulcate grain ; **12**, zonasulculate grain. (1-2, *Bosser 13018* ; 3-5, *Dorr et al. 2880* ; 6-7, *Keraudren-Aymonin & Aymonin 25146* ; 8-9, *Miller & Phillipson 3714* ; 10-12, *Bosser 13374*. — Scale : 1-3, 6, 8, 11, 12 = 10 µm ; 4, 5, 7, 9, 10 = 1 µm).

however, that *A. madagascariensis, A. kitchingii* and *A. humbertii* constitute a clade, on the basis of both their complex and variable apertures and generally rugulate to areolate, comparatively thick exine, correlated with an unusual macromorphological synapomorphy, porate anthers. Whether they correctly belong in section *Eucapsulares*, which includes the majority of tropical African *Aristea* species awaits further SEM examination.

Aristea angustifolia seems to accord well morphologically with section *Eucapsulares*, as does its finely rugulate exine, but its disulcate grains are not yet matched in any African species of the section. All that we can say at present is that *A. angustifolia* seems to link the tropical African species of section *Eucapsulares* with the apparently monophyletic Madagascan group consisting of *A. kitchingii, A. madagascariensis* and *A. humbertii* based on both macromorphological characters.

The remaining two Madagascan species, *Aristea cladocarpa* and *A. nitida*, appear to constitute a second lineage of the genus in Madagascar, and seem, at least on morphological grounds (elongate capsules, leafy stems), to be linked to *A. ecklonii*, currently assigned to a second African section *Pseudaristea*, which is itself palynologically diverse, but still inadequately known.

Clearly, *Aristea* is unusual in *Iridaceae* in being so diverse palynologically. Accurate characterization of the African species will undoubtedly assist in developing a more natural classification of the genus and promises to provide valuable data for phylogenetic reconstruction. Because *Aristea* is widespread, and one of the few genera of *Iridaceae* shared between southern Africa, tropical Africa and Madagascar, it is particularly interesting phytogeographically, and an understanding of its phylogeny will be important in explaining the geography of the genus.

The description of *Geosiris* pollen grains given above corresponds with those of SCHULZE (1983) and STRAKA & FRIEDRICH (1984), and does not confirm ZAVADA's (1983) indication that the pollen is sulcoidate-ulcerate. Our observations are consistent with the presumed basic monosulcate type for *Iridaceae* and supports its inclusion in *Iridaceae* (GOLDBLATT et al., 1987). The postulated close relationship of *Geosiris* with *Aristea* (MANNING & GOLDBLATT, 1991) is, however, not evident palynologically in comparison with Madagascan members of the genus. Its pollen grains are relatively unspecialized, in contrast with those of Madagascan *Aristea*. If they are indeed closely related, this is not reflected in their pollen grains, those of Madagascan *Aristea* presumably having diverged from the ancestral state in *Iridaceae*. Grains similar to those of *Geosiris* do, however, occur in some African species of *Aristea*.

Pollen grains of *Patersonia* are unique for *Nivenioideae* and fairly unusual in *Iridaceae*. Inaperturate grains occur in a few *Ixioideae* (SCHULZE, 1971; GOLDBLATT et al., 1991), but they generally have the perforate exine with supratectal verrucae typical of the subfamily. The only other member of the family known to have inaperturate grains is the ditypic Australasian genus *Diplarrhena* (GOLDBLATT & LE THOMAS, in press). The latter, generally assigned to subfamily *Iridoideae*, is currently considered to be most closely related to *Libertia* (RUDALL, 1986; GOLDBLATT, 1990), compared to which *Diplarrhena* is specialized in its floral morphology. It is the only member of the subfamily with a zygomorphic flower and only member of *Iridaceae* with two stamens. In neither respect does it resemble *Patersonia*. Nevertheless, the similarity of the pollen grains of these two genera suggests that the possibility of their being closely related should be borne in mind in future studies. Pollen morphology of *Patersonia* provides no support for the inclusion of the genus in *Nivenioideae*, suggested largely

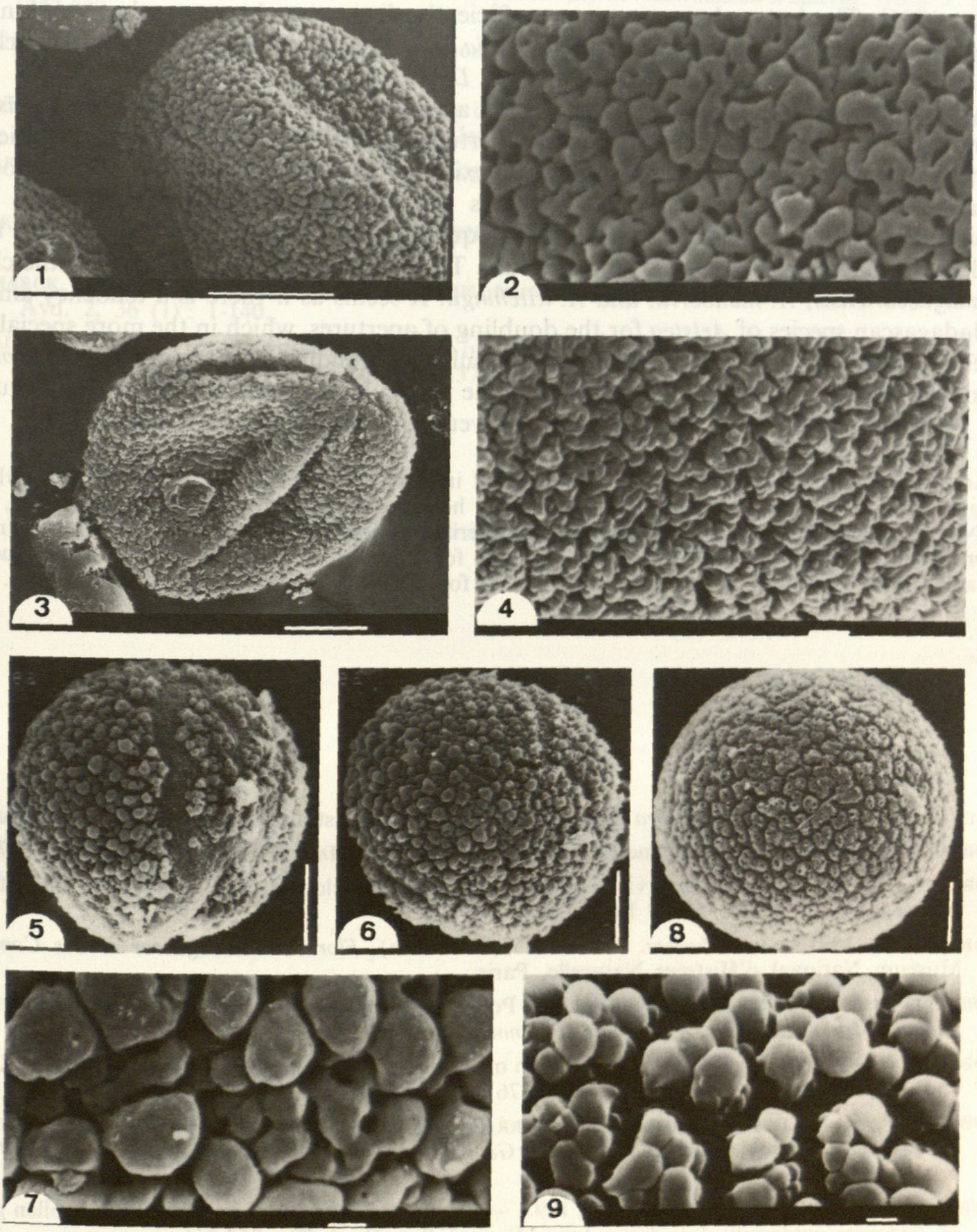

Fig. 3. — **Aristea angustifolia** Baker : **1**, disulcate grain ; **2**, rugulate exine. — **A. cladocarpa** Baker : **3**, disulcate grain ; **4**, microrugulate exine. — **A. nitida** Weim. : **5**, monosulcate grain, the apertural membrane covered by exine elements ; **6**, disulcate grain ; **7**, areolate exine. — **Patersonia sericea** R. Br. : **8**, inaperturate grain ; **9**, intectate exine. (1, *Rakotovao 9930* ; 2, *Perrier de la Bâthie 8349* ; 3-4, *Bosser 16695* ; 5-7, *Humbert 6938* ; 8-9, *Arnoux s. n.* — Scale : 1, 3, 5, 6, 8 = 10 μm ; 2, 4, 7, 9 = 1 μm).

on the basis of shared fugacious flowers (GOLDBLATT, 1990) and binate rhipidial inflorescences (COOKE, 1986). The latter character seems sufficiently distinctive, however, that we think it unlikely to have arisen independently in *Patersonia* and other *Nivenioideae*. Hence we conclude that the inaperturate grains of *Patersonia* and *Diplarrhena* are convergent.

An evolutionary trend can be traced in the apertural variation in Madagascan *Aristea*, beginning with a true operculum covering the aperture, followed by fusion of the extremities of the operculum with the adjacent extra-apertural exine to form a pontoperculum. Reduction of the intine under the pontoperculum then leads to the disulcate condition, with the two apertures more or less displaced towards the equator. Their enlargement and fusion then would give rise to a truly zonasulculate aperture. This pattern is well represented in the clade *A. madagascariensis, A. humbertii*, and *A. kitchingii*. It seems as if there is a tendency among the Madagascan species of *Aristea* for the doubling of apertures, which in the more specialized species of the group fuse, resulting in the zonasulculate condition. We know of no *a priori* reason why the Madagascan *Aristea* species, none particularly specialized within the genus in other respects, should have evolved such a diversity of pollen grain specializations.

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