

Pollen morphology in *Tigridieae* (*Iridaceae*)

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Summary. The pollen morphology of the New World tribe *Tigridieae* is examined in the context of a literature survey. Pollen is normally sulcate in subtribe *Cipurinae* (as in other *Iridaceae*) and bisulcate in subtribe *Tigridiinae*, with occasional exceptions. There is some variation in surface sculpturing between taxa, and within an anomalous species, *Tigridia pavonia*.

INTRODUCTION

Although sulcate (monosulcate) pollen is the most common type in *Iridaceae*, various other forms have been reported, such as bisulcate, inaperturate and spiraperturate (Erdtman 1952). Both sulcate and bisulcate forms occur in the *Tigridieae*, a New World Tribe of the subfamily *Iridoideae*, and this has been used together with other characters (e.g. floral morphology and chromosome numbers) to subdivide the tribe into two subtribes: *Cipurinae*, with sulcate pollen, and *Tigridiinae*, with bisulcate pollen (Goldblatt 1982). However, information on Tigridioid pollen is relatively scanty and scattered throughout the taxonomic literature (Table 1). As part of a current systematic investigation of the tribe, we have undertaken a brief survey of the pollen morphology in order to test its taxonomic value.

MATERIALS AND METHODS

Pollen samples were taken from either living material in the Kew collection or Kew Herbarium material. Details of species and specimens examined are given in Table 2. Altogether 38 specimens were examined, representing 15 species from 11 genera of subtribe *Cipurinae*, and 7 specimens from 3 genera of *Tigridiinae*, in some cases with more than one specimen per species.

Living material was dehydrated through an alcohol series and mounted on microscope slides in glycerine jelly for light microscopy, and on stubs for scanning electron microscope (SEM) observation. Herbarium material was mounted directly onto stubs and slides. SEM stubs were coated with gold and observed using a JEOL JSM-35 SEM.

Measurements of pollen grains were taken using light microscopy and are based on a sample size of 20 grains.

OBSERVATIONS

Information on number of sulci and grain size in individual specimens is given in Table 2. Because of the difficulty in determining pollen orientation and consequently the polar and equatorial axes, measurements were made of the axis parallel to the sulcus ('length') and the axis at right angles to the sulcus ('breadth').

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TABLE 1. Summary of previous information on pollen morphology in *Tigridiidae*

Genus	Author	No. spp examined	No. sulci
<i>Calydorea</i>	Schulze (1971)	2	1
<i>Catila</i>	Ravenna (1983)	1	2
<i>Cobana</i>	Ravenna (1974)	1	2
<i>Cypella</i>	Schulze (1971)	1	1
<i>Eleutherine</i>	Erdtman (1952)	1	1
	Schulze (1971)	1	1
<i>Fosteria</i>	Molseed (1970)	1	2
	Schulze (1971)	2	2
<i>Nemastylis</i>	Schulze (1971)	1	1
<i>Rigidella</i> (= <i>Tigridia</i>)	Cruden (1971)	4	2
	Erdtman (1952)	1	2
	Molseed (1970)	1	2
	Schulze (1971)	1	2
<i>Sessilanthera</i>	Molseed & Cruden (1969)	2	2
<i>Tigridia</i>	Erdtman (1952)	1	2
	Molseed (1970)	16	2
	Schulze (1971)	1	2

General description:

Shape: Pollen in subtribe *Tigridiinae* commonly elliptic in outline in polar view, or rarely spheroidal (in 2 out of 4 specimens of *Tigridia pavonia*). Pollen in subtribe *Cipurinae* spheroidal or rarely elliptic.

Size: Variable between (and sometimes within) species (Table 2).

Cipurinae: Length (36.7–)48.9(–61.7) μm , breadth (33.1–)42.1(–55.0) μm .

Tigridiinae: Length (39.9–)45.8(–55.3) μm , breadth (29.7–)36.3(–43.9) μm , except *Tigridia pavonia*: length (72.2–)89.0(–104.2) μm , breadth (59.4–)69.4(–77.3) μm . Grains in *Cipurinae* generally larger than in *Tigridiinae*, except *T. pavonia*, where grains 1.5–2.5 times larger than in any other species.

Sulci (Table 2): Grains bisulcate in *Cipura campanulata* (Figs. 1A, 1B) and in most *Tigridiinae* (Figs. 1C, 1E, 3C), except 2 out of 4 specimens of *T. pavonia* (Figs. 3A, 3B); otherwise sulcate (Fig. 1D). In bisulcate grains sulci parallel to long axis of grain, on opposite sides or occasionally closer together; in all bisulcate species except *T. pavonia* sulci with scattered 'islands' of exine (Figs. 1E, 1F), and connected by a narrow channel, effectively forming a single sulcus encircling grain (Fig. 1C). In sulcate grains sulcus lacking 'islands' of exine.

Surface sculpturing: A complex continuous reticulum, the bases of the lumina with or without granules. Muri simplibaculate; bacula usually fused, or in *T. pavonia* and *Cipura flava* sometimes separate (Fig. 3F). Muri sometimes thin in *T. pavonia*, thick in all other species. Several patterns of lumina observed: (1) Small psilolumina (i.e. without granules) ranging from polyhedral to rounded, in all *Tigridiinae* (except *T. pavonia* and one specimen of *Fosteria*), and in *Eleutherine* and *Nemastylis* (2 spp.) (Fig. 2A, 2E). (2) Very large polygonal lumina in *Cipura flava* and most *T. pavonia* specimens. In *T. pavonia*: 2 specimens with straight muri (rectimurrate) and sparse granules (Fig. 3D), 3 specimens with curved muri (curvimurrate) and numerous granules (Fig. 3E), one specimen with discontinuous muri with numerous granules (Fig. 3G). (3) Large polygonal psilolumina present in *Calydorea campestris*, *Cypella* sp., and 1 of 2 specimens of *Herbertia pulchella*. (4) Lumina similar in *Ennealophus euryandrus*, *Catila amabilis* and *Cipura campanulata* but with granules (Fig. 2B, 2G). (5) Similar

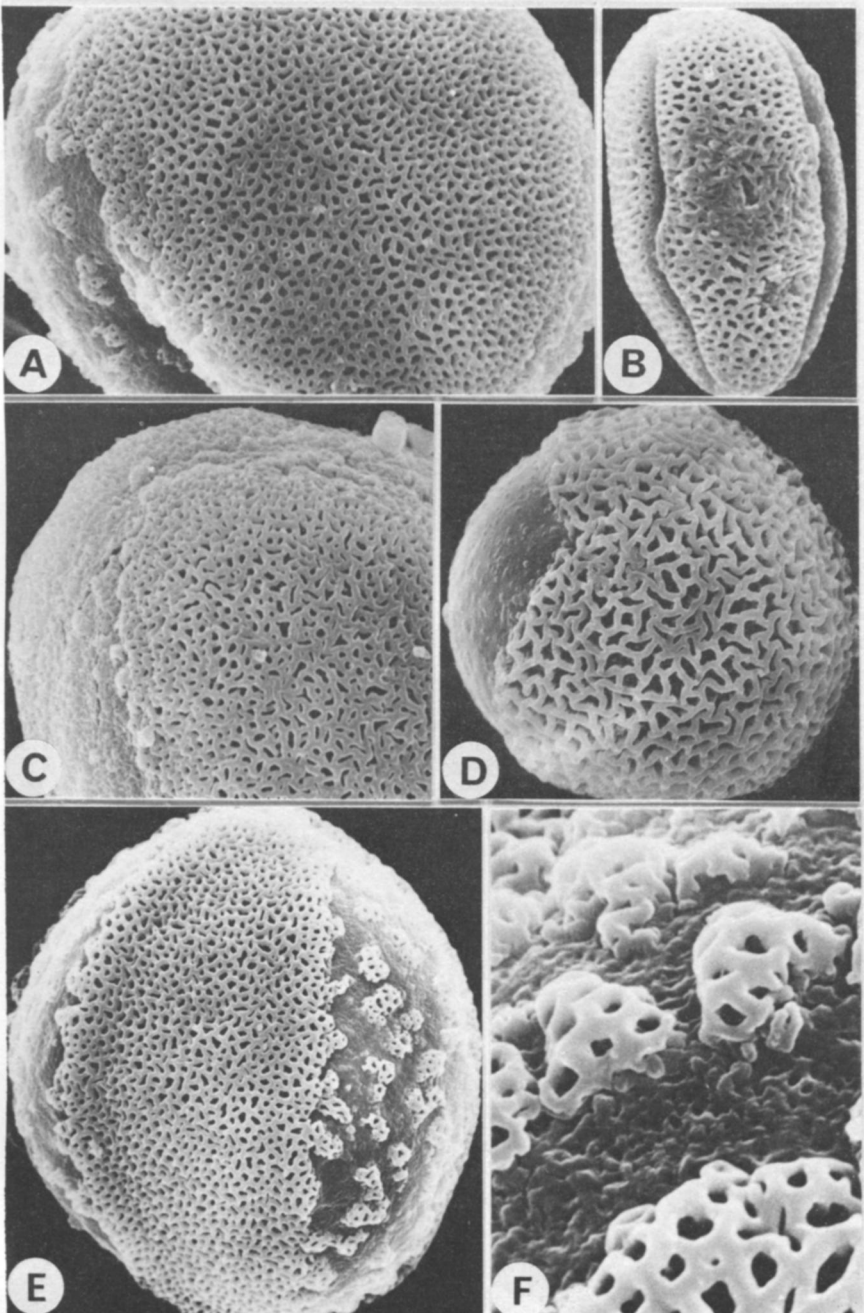


FIG. 1. Pollen (SEM). **A–B** *Cipura campanulata*, bisulcate grains; **A** *Kenton et al.* 33–201 \times 2000; **B** *Kenton et al.* 30–342 \times 3000; **C** *Alophia drummondi*, showing narrow channel connecting 2 sulci \times 320; **D** *Ennealophus euryandrus*, sulcate grain \times 2000; **E–F** *Tigridia galanthoides*: **E** bisulcate grain \times 2000; **F** detail of sulcus showing 'islands' of exine \times 10000.

TABLE 2. Details of species and material examined. Key: T—*Tigridiinae*; C—*Cipurinae*

Species	Collector/Origin	Subtribe	No. of sulci	Average grain size (μm)	
				Length	Breadth
<i>Alophia drummondii</i> (Graham) Foster	Anderson s.n., USA	T	2		
<i>Calydorea campestris</i> Baker	Donbrowski & Sito 55-344, Brazil	C	1	46.6	33.1
<i>Calydorea campestris</i>	Weir 1861-2, Brazil	C	1		
<i>Catula amabilis</i> Ravenna	*Ravenna 3, 1959, Argentina	C	1		
<i>Cipura campanulata</i> Ravenna	Kenton, Rudall & Howard 33-201, Mexico	C	2	59.8	55.0
<i>Cipura campanulata</i>	*Kenton, Rudall & Howard 50-342, Mexico	C	2	47.2	41.2
<i>Cipura campanulata</i>	*Kenton, Rudall & Howard 33-195, Mexico	C	2	61.7	51.6
<i>Cipura flava</i> Ravenna	*Philcox & Ferreira 3738, Brazil	C	1		
<i>Cypella</i> sp.	Cutler 26-207, Argentina	C	1	41.3	39.6
<i>Cypella herbertii</i> (Lindley) Baker	*Cutler & Lonsdale, Argentina	C	1	56.4	48.1
<i>Eleutherine latifolia</i> (Standley & Williams) Ravenna	Kenton, Rudall & Howard 50-349, Mexico	C	1		
<i>Ennealophus euryandrus</i> (Gris.) Ravenna	Cutler & Lonsdale 68-357, Argentina	C	1	36.7	34.9
<i>Fosteria oaxacana</i> Molseed	Kenton, Rudall & Howard 21-135, Mexico	T	2	44.0	36.6
<i>Fosteria oaxacana</i>	Kenton, Rudall & Howard 21-136, Mexico	T	2		
<i>Gelasine azurea</i> Herbert	Goldblatt s.n. (cultivated)	C	1	42.5	39.1
<i>Herbertia lahue</i> (Molseed) Goldblatt	Tubergen s.n. (cultivated)	C	1	49.8	41.8
<i>H. pulchella</i> Nichols.	Cutler & Lonsdale 15-91, Argentina	C	1		
<i>H. pulchella</i>	CAGS (cultivated)	C	1	52.2	36.8
<i>Hesperoxiphion huilense</i> Ravenna	Porter 124, Ecuador	C	1	50.0	39.6
<i>H. peruvianum</i> (Baker) Baker	Rudall & Kenton 84-646, Peru	C	1	54.0	49.9
<i>H. peruvianum</i>	Rudall & Kenton 112-713, Peru	C	1		
<i>H. peruvianum</i>	Rudall & Kenton 118-725, Peru	C	1	48.0	44.1
<i>H. peruvianum</i>	Rudall & Kenton 135-767, Peru	C	1		
<i>Mastigostyla cardenasii</i> Fos- ter	*Cardenas 2491, Bolivia	C	1		
<i>Nemastylis geminiflora</i> Nutt.	*Bush 603, USA	C	1		
<i>N. tenuis</i> (Herbert) Benth. ex Baker	*Pringle 11190, Mexico	C	1		
<i>Tigridia galanthoides</i> Molseed	Walker 74.008, Mexico	T	2	46.4	37.4
<i>T. meleagris</i> (Lindl.) Nichols.	Kenton, Rudall & Howard 52-367, Mexico	T	2	42.0	29.7
<i>T. meleagris</i>	Kenton, Rudall & Howard 57-414, Mexico	T	2	9.9	32.2
<i>T. multiflora</i> (Baker) Ravenna	*Hinton 17231, Mexico	T	2	1.2	32.3
<i>T. multiflora</i>	Walker s.n., Mexico	T	2		
<i>T. orthantha</i> (Lemaire) Ravenna	Kenton, Rudall & Howard 18-98, Mexico	T	2	55.3	43.9
<i>T. pavonia</i> (L.f.) DC.	*GBH 1432, Mexico	T	1	94.5	59.5

TABLE 2. Details of species and material examined. Key: T—*Tigridiinae*; C—*Cipurinae*

Species	Collector/Origin	Subtribe	No. of sulci	Average grain size (μm)		
				Length	Breadth	
<i>T. pavonia</i>	*Quero 3177, Mexico	T	1	1	04.2	77.3
<i>T. pavonia</i>	Kenton, Rudall & Howard 28-154, Mexico	T	1, 2		84.4	69.8
<i>T. pavonia</i>	Kenton, Rudall & Howard 28-155, Mexico	T	2		72.2	70.3
<i>T. pavonia</i>	?collector, s.n.	T	2			
<i>T. sp.</i>	Kenton, Rudall & Howard 4-8, Mexico	T	2		52.2	41.9

*indicates herbarium material

(psilolumina) in *Hesperoxiphion* (2 spp.), but interspersed with small rounded psilolumina (Fig. 2C). (6) rounded psilolumina present in *Mastigostyla cardenasii* and 1 of 2 specimens of *Fosteria oaxacana* (Fig. 2D). (7) Large circular psilolumina in *Cypella herbertii* (Fig. 2H). (8) Narrow psilolumina present in *Herbertia lahue*, *Gelasine azurea* and 1 of 2 specimens of *Herbertia pulchella* (Fig. 2F).

DISCUSSION

This investigation confirms the findings of Molseed (1970), Schulze (1971) and others (Table 1) that bisulcate pollen grains are highly characteristic of the subtribe *Tigridiinae*, with the exception of occasional specimens of *Tigridia pavonia*. This condition must be regarded as a synapomorphy for this subtribe, since sulcate pollen is the most common type in *Iridaceae*, and is considered primitive in Monocotyledons, and indeed among Angiosperms in general (Zavada 1983). In the other subtribe, *Cipurinae*, most species have sulcate pollen, but we have observed only bisulcate grains in *Cipura campanulata*, and Ravenna (1983) also recorded bisulcate pollen in *Catila*, a monotypic South American genus related to *Cypella* and *Calydorea*, although we found only normal sulcate grains in this species, perhaps indicating some variability. (Ravenna recorded that the sulci were often connected at the poles). These anomalies may be isolated instances of evolutionary divergence in these taxa, which on other grounds are firmly linked with *Cipurinae* (Goldblatt & Henrich 1987), but further research on this character in the *Cipurinae* may prove useful in indicating relationships, particularly in *Cipura*, a Central and South American genus of 5 species. Goldblatt has suggested a possible correlation between bisulcate grains and tetraploidy. Most *Cipurinae* are diploid with $2n = 14$, and most *Tigridiinae* amphidiploid with $2n = 28$ (Goldblatt 1982). Both loss of the sulcus and increase in number of sulci are common evolutionary trends in monocotyledons (Zavada 1983), and both occur in the *Iridaceae*: bisulcate grains in *Tigridiinae*, and inaperturate grains in *Syringodea* (Erdtman 1952). Variation in pollen surface sculpturing does not show a clear divergence between the two subtribes, although some differences exist, particularly in lumen size and occurrence of granules, but a great deal more research is needed to establish the significance of this in terms of relationships within and between genera. Our observation of occasional variation in exine pattern within species, especially in two specimens of *Fosteria oaxacana* (Figs. 2D, 2E) from plants collected in the same locality, underline the need for caution in this respect.

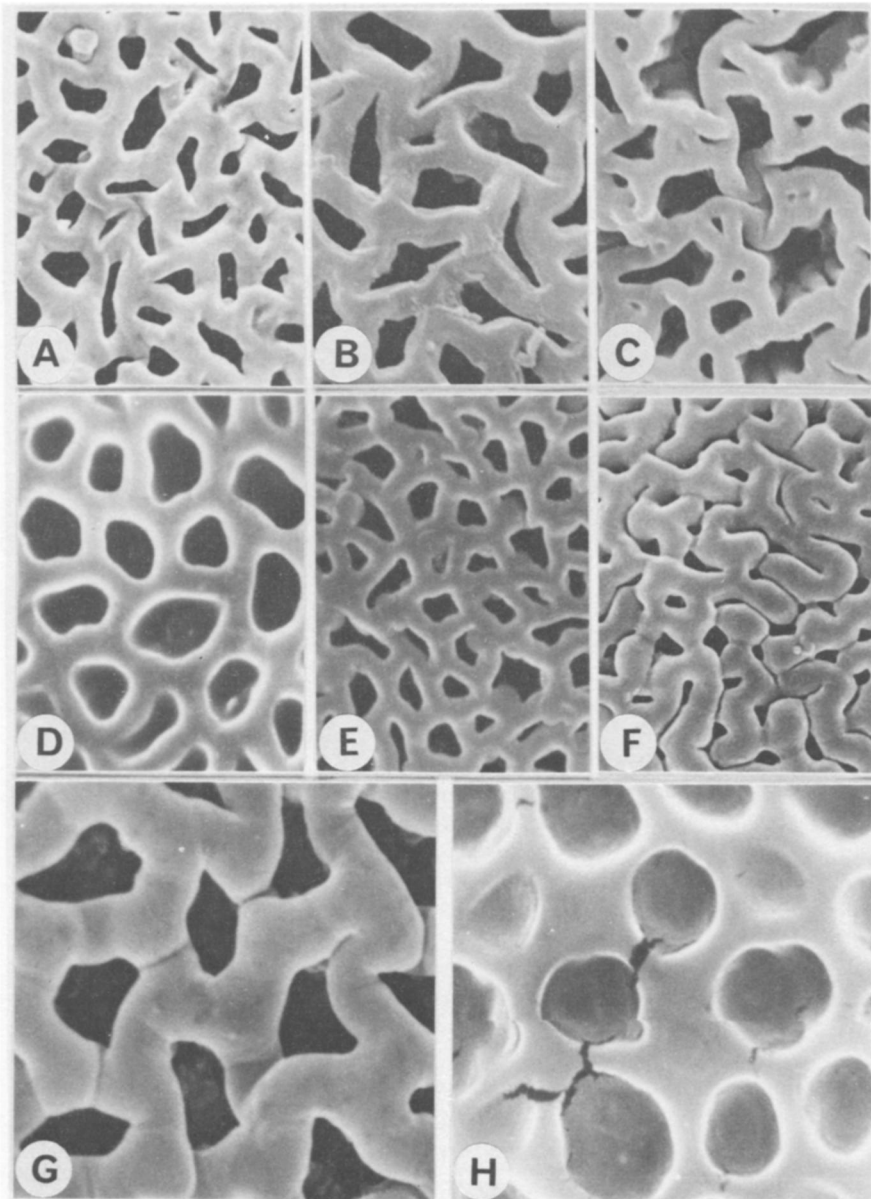


FIG. 2. Detail of exine sculpturing showing variation in lumina shapes and size. **A** *Tigridia galanthoides*; **B** *Ennealophus euryandrus*; **C** *Hesperoxiphion peruvianum* (Rudall & Kenton 84-646); **D** *Fosteria oaxacana* (Kenton, Rudall & Howard 21-136); **E** *Fosteria oaxacana* (Kenton, Rudall & Howard 21-135); **F** *Gelasine azurea*; **G** *Cipura campanulata* (Kenton, Rudall & Howard 50-342); **H** *Cypella herbertii*. (All SEMs $\times 10000$).

Relatively small variation in surface patterning (e.g. in lumen size) may reflect differences in degree of hydration, or even differences in conditions in the developing anther. Also method of preparation cannot be ruled out as a factor in variation, although small differences in grain size between different specimens of *Cipura campanulata* (Table 2) seemed to be unrelated to whether

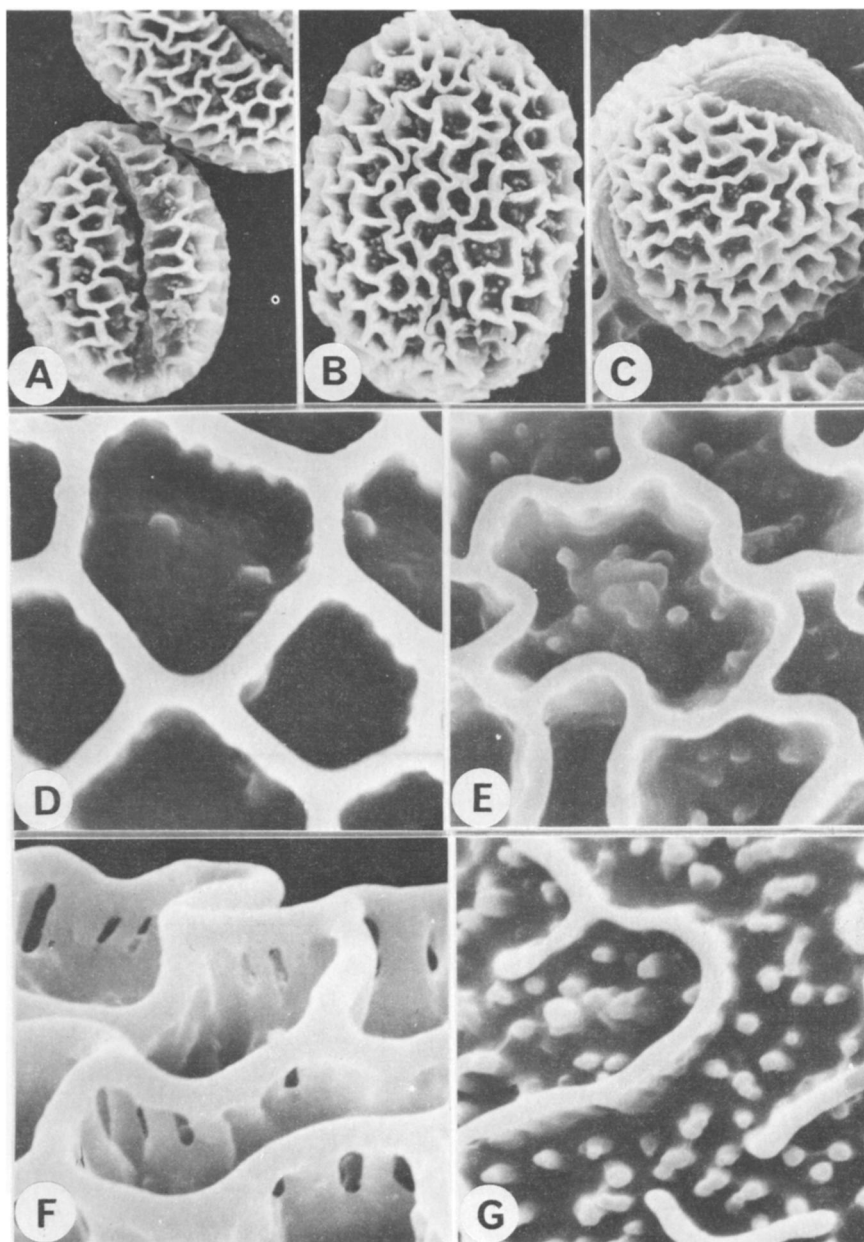


FIG. 3. Pollen (SEM). **A–C** *Tigridia pavonia* (Kenton, Rudall & Howard 28–154); **A, B** monosulcate grain; **A** distal face $\times 660$; **B** proximal face $\times 780$; **C** bisulcate grain $\times 720$; **D–E & G** *T. pavonia* showing variation in lumen shape and number of pila; **D** from Quero 3177 $\times 4000$; **E** from Kenton, Rudall & Howard 28–154 $\times 3600$; **F** *T. pavonia* (Kenton, Rudall & Howard 28–154) detail of muri showing individual bacula $\times 5400$; **G** from ?collector s.n. $\times 3600$.

fresh or herbarium material was used. The occurrence of widely different patterns of surface sculpturing in the two species of *Cipura* examined suggests a need for further work in this genus.

As Molseed (1970) and others have also observed, pollen in *T. pavonia* (Tiger

Flower) is significantly different from that of the rest of the tribe, particularly in size (grains up to 2.5 times larger) and surface sculpturing. Molseed pointed out that *T. pavonia* has much the largest flowers in the genus, which could account for the difference in pollen size, but he also noted that in other species with large flowers or long styles, pollen grain size does not increase accordingly. Similarly there is no correlation with chromosome size or ploidy level (Molseed 1970, and Kenton, pers. comm.); most species of *Tigridia* (including *T. pavonia*) have $2n = 28$ chromosomes. We have observed variability in pollen of *T. pavonia*, in surface sculpturing (Figs. 3D, 3E, 3G) and even some variation in number of sulci (Figs. 3A–C), and Molseed (1970) recorded viscin threads among grains, although we have not confirmed this in our material. Pollen variability within a single species is not uncommon; for example Ferguson (1980) found a high proportion of 'abnormal' pollen grains among two species of *Ceratonia*, and also noted that in species of this and other genera there is a difference in grain size between 'wild' and 'cultivated' specimens. Similarly Clarke (1975) recorded that in several species of *Hypericum* more than 10 per cent of pollen grains were irregular in aperture number and configuration, although they may still be fertile, and he related this variation to meiotic irregularities. Clarke found a higher degree of irregularity among cultivated than wild material of the same species. *T. pavonia* was cultivated for its large showy flowers by the Aztecs in Mexico almost 1000 years ago, and is now very common throughout Central America, although its natural distribution is unknown (Molseed 1970), and there are various colour forms. This long history of cultivation could well account for some of the 'atypical' characters and variability in this species.

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