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M. Chaturvedi<sup>a</sup>, K. Datta<sup>a</sup> & P. K. K. Nair<sup>b</sup>

<sup>a</sup> Palynology Laboratory, National Botanical Research Institute, Lucknow, U.P., 226 001

<sup>b</sup> Environmental Resources Research Centre, P.B. 1230 Peroorkada, Thiruvananthapuram, Kerala, 695 005, India

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# Pollen morphology of *Oryza* (Poaceae)

M. CHATURVEDI, K. DATTA and P. K. K. NAIR

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Pollen morphological studies of 19 species of *Oryza* (Poaceae) were carried out using LM and SEM. Eleven exine surface patterns are distinguished at  $\times 20,000$  magnification under SEM. These are categorised into three basic types: granulose, spinulose and insular. *O. brachyantha* – a genomically unrelated species, and two species (*O. granulata* and *O. meyeriana*) comprising the *O. meyeriana* complex have spinulose exine surfaces. The *O. ridleyi* complex which also contains two species (*O. longiglumis* and *O. ridleyi*) is characterised by a granulose exine pattern. In the *O. officinalis* complex and the *O. sativa* complex, both granulose and insular exine patterns have been observed in different species. The largest pollen grains occur in the *O. sativa* complex, which contains both cultivated species and their wild relatives.

M. Chaturvedi & K. Datta, Palynology Laboratory, National Botanical Research Institute, Lucknow-226 001, U.P.; P. K. K. Nair, Environmental Resources Research Centre, P.B. 1230, Peroorkada, Thiruvananthapuram-695 005, Kerala, India.

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The genus *Oryza*, named by Linnaeus (1753), belongs to the subfamily Oryzoideae of the family Poaceae (Duistermaat 1987) and includes *O. sativa* and *O. glaberrima* – the two cultivated species of rice. The enumeration and nomenclature of the species within the genus have been repeatedly revised (Tateoka 1962 a,b; 1963, 1965 a,b; Shastry & Sharma 1974, Duistermaat 1987), with the result that the number of recognised species has been variable. Launert (1965) transferred three African species: *O. angustifolia*, *O. perrieri* and *O. tisseranti* to the genus *Leersia* Swartzia. Tateoka (1963) enumerated 22 *Oryza* species, which included some synonyms and separated out *O. coarctata* from *Oryza* as *Porteresia coarctata* – a salt tolerant taxon growing in saline water. Vaughan (1989), in his publication on the taxonomy of *Oryza*, presented an updated enumeration of species and their synonyms, limiting the number of valid species to 22. He reviewed the relationship among the wild species, and between wild and cultivated species, and formed complexes of valid species of closely related genome groups, based on earlier works on *Oryza* (Tateoka 1963, IRRI 1964, Chang 1979, 1985; Duistermaat 1987). These species are distributed in Africa, Central and South America, Australia, and South-east Asia, as below:

## SOUTH-EAST ASIAN SPECIES

**Cultivated** (world wide): *Oryza sativa* (Race-Indica, Race-Japonica, Race-Javanica)

**Wild:** *Oryza granulata*, *O. longiglumis*, *O. meyeriana*, *O. minuta*, *O. nivara*, *O. officinalis*, *O. ridleyi*, \**O. rufipogon* (Distributed up to Australia), \**O. schlechteri*.

## AFRICAN SPECIES

**Cultivated** (West Africa): *Oryza glaberrima*

**Wild:** *Oryza barthii*, *O. brachyantha*, *O. eichingeri*, *O. longistaminata*, *O. punctata*.

**AMERICAN SPECIES (wild):** South America (Amazon

basin), *Oryza alta*, *O. grandiglumis*. Central & South America: \**Oryza glumaepatula*, *O. latifolia*.

**AUSTRALIAN SPECIES (wild):** *Oryza australiensis*, *O. meridionalis*.

(\*Species not covered in the present investigation)

Poaceae is a stenopalynous family characterised in all its taxa by 1-porate pollen with an annulate pore. However, scanning electron microscope studies on the pollen exine surface patterns in the genus *Sorghum* have provided features of taxonomic importance for distinguishing sections, subsections and series (Chaturvedi et al. 1994). The present study deals with the pollen morphology of 19 of the 22 valid species of *Oryza* and also provides information about the pollen exine surface patterns of these species as observed under SEM, as an additional parameter for taxonomic consideration.

## MATERIALS AND METHODS

Pollen of 19 wild and cultivated species of *Oryza* L. were obtained from plants growing in the International Rice Research Institute, Manila, Philippines (IRGC accessions), and the Central Rice Research Institute, Cuttack, Orissa (CRRRI accessions). The species of *Oryza* investigated, which are listed below, have been classified following the review published by Vaughan (1989).

- I. *Oryza brachyantha* A. Chev. et Roehr. (IRGC-100115)- Unrelated species
- II. *O. meyeriana* complex
  1. *O. granulata* Nees et Arn. ex Watt (IRGC-104611)
  2. *O. meyeriana* (Zoll. et Mor. ex Steud.) Baill. (IRGC-106473)
- III. *O. officinalis* complex
  1. *O. alta* Swallen (IRGC-101395)
  2. *O. australiensis* Domin (IRGC-103303)
  3. *O. eichingeri* A. Peter (IRGC-101424)
  4. *O. grandiglumis* (Doell) Prod. (CRRRI SD-1021)
  5. *O. latifolia* Desv. (IRGC-100962)
  6. *O. minuta* J.S. Presl. ex C.B. Presl. (CRRRI SD-1025)
  7. *O. officinalis* Wall ex Watt (IRGC-103802)

8. *O. punctata* Kotschy ex Steud. (IRGC-101441)
- IV. *O. ridleyi* complex
  1. *O. longiglumis* Jansen (IRGC-105148)
  2. *O. ridleyi* Hook f. (IRGC-100820)
- V. *O. sativa* complex
  1. *O. barthii* A. Chev. (IRGC-104981)
  2. *O. glaberrima* Steud. (IRGC-102226)
  3. *O. longistaminata* A. Chev. et Roehr. (IRGC-101741)
  4. *O. meridionalis* Ng (IRGC-105298)
  5. *O. nivara* Sharma et Shastri (CRRRI-Pot No.W-101)
  6. *O. sativa* L.
    - a. Race Indica (CRRRI-cv. Poorva)
    - b. Race Japonica (IRGC-244)
    - c. Race Javanica (IRGC-78809)

Pollen preparations for light microscopy were made according to the acetolysis method (Erdtman 1952). For scanning electron microscopy, acetolysed pollen grains were transferred to absolute alcohol, mounted on stubs, coated with gold and photographed at 10 kv using a Philips XL 20 scanning electron microscope.

The observations of the pollen morphology under the light microscope are based on 20 pollen grains in each sample. For a comparison of exine ornamentation in the different species, SEM photomicrographs were taken of the centre of the pollen in equatorial view (Fig. 1A) at a uniform magnification of  $\times 20,000$ . In order to categorize the excrescences on the exine surface the grain margin was also examined under SEM and representative photomicrographs of the margins showing spinules (Figs. 1B & D), granules (Fig. 2C), and fused granules (Fig. 1F), are provided.

## RESULTS

The pollen grains of *Oryza* are typically graminaceous, being monoporate with an annulate pore (Fig. 1A). Observations of the pollen morphological features, including pollen size, pore diameter, annulus diameter, exine thickness and ornamentation type are summarised in Table I. The exine ornamentation types, as resolved under SEM, are categorised in three basic types; granulose, spinulose and insular. Several forms of pattern within these three basic types have also been observed and are described below:

### 1. Granulose

- (i) Granulose-punctate: Granules scattered, intergranular region perforated (Fig. 4A)
- (ii) Densely-granulose: Granules densely placed (Figs. 2B & C)
- (iii) Sparsely-granulose: Granules sparsely placed (Fig. 4G)
- (iv) Grouped-granulose: Free or partially fused granules arranged in groups (Figs. 3B & E)
- (v) Mixed-granulose: Free granules interspersed with fused granules, generally in twos, threes and occasionally in fours. This ornamentation type may be further classified as: a. Granules large (Figs. 2D & 3C), b. Granules small (Figs. 2E & 3A)

### 2. Spinulose

- (i) Sparsely-spinulose (Figs. 1D & E): Spinules sparsely placed
- (ii) Grouped-spinulose (Fig. 1C): Spinules arranged in groups

### 3. Insular (insulae formed by the fusion of granules/spinules dividing the exine surface into small areas). The different forms of insular pattern observed in *Oryza* species are as follows:

- (i) Type-1. Insulae formed by widely spaced granules/spinules (Figs. 1G, 2G, 3D & 4E)
- (ii) Type-2. Insulae formed by compact granules, forming a mosaic pattern (Fig. 2A)
- (iii) Type-3. Mixed insular pattern having partially formed insulae interspersed with free granules (Figs. 3F & 4C)

## DISCUSSION

The prevalence of a stenopalynous condition in grasses with 1-porate-annulate pollen grains, although providing a characteristic feature for the family Poaceae, also constitutes a limiting factor when trying to distinguish the various taxa contained within the family. The study of pollen exine surface patterns under SEM has considerably broadened the scope of application of this pollen feature at a number of taxonomic levels in grasses (Andersen & Bertelsen 1972, Köhler & Lange 1979, Chaturvedi et al. 1994). In an earlier investigation seven exine surface patterns were distinguished in *Sorghum* at a magnification of  $\times 10,000$  and these have a taxonomic bearing at the section, subsection and series levels within the genus (Chaturvedi et al. 1994). In the present case of *Oryza*, exine patterns are distinguished at a much higher magnification:  $\times 20,000$ , as in some of the species of *Oryza* the exine surface has an extremely fine pattern (Figs. 1B, C & 2B, C), so that the distinguishing features are not convincingly discernible at a lower magnification. The analysis of the pollen characters in the *Oryza* species complexes, on the basis of 19 species, shows 11 exine surface patterns which can be categorised into three basic types: granulose, spinulose and insular. *O. brachyantha*, a genomically unrelated species is characterised by a grouped-spinulose exine pattern (Fig. 1C), and both species of the *O. meyeriana* complex: *O. granulata* and *O. meyeriana*, have sparsely-spinulose exine surfaces (Fig. 1E). In other species complexes, the exine surface exhibits a variety of granulose and insular patterns.

In the *O. officinalis* complex, the exine surface patterns are variable. *O. alta* and *O. punctata* have an Insular Type-1 exine pattern (Figs. 1G & 2G), and *O. australiensis* an Insular Type-2 pattern with insulae forming a mosaic pattern (Fig. 2A) – a feature which differs from all other patterns of the genus. Vaughan (1989) reported this Australian species as being different from all other species of *Oryza* on account of its strongly rhizomatous habits. Among other species of this complex, *O. eichingeri* has a densely-granulose exine surface (Fig. 2B). *O. alta* and *O. grandiglumis* – the two South American species, and *O. latifolia* which is distributed in Central-South America are distinguishable on the basis of their exine patterns. While *O. alta* has an Insular Type-1 exine surface (Fig. 1G), *O. grandiglumis* has a mixed-granulose exine with large granules (Fig. 2D), and *O. latifolia* has a mixed-granulose pattern with small granules (Fig. 2E). *O. latifolia* is also characterised by the smallest pollen size and the smallest pore diameter (Table I). An exine pattern similar to that of *O. latifolia* also occurs in *O. minuta* and *O. officinalis* – the two South-east Asian species of this complex. Duistermaat (1987) considered *O. officinalis* and *O. minuta*, to be the same species, calling it *O. minuta*. In the light of this the similarity in the exine patterns in these two species is significant.

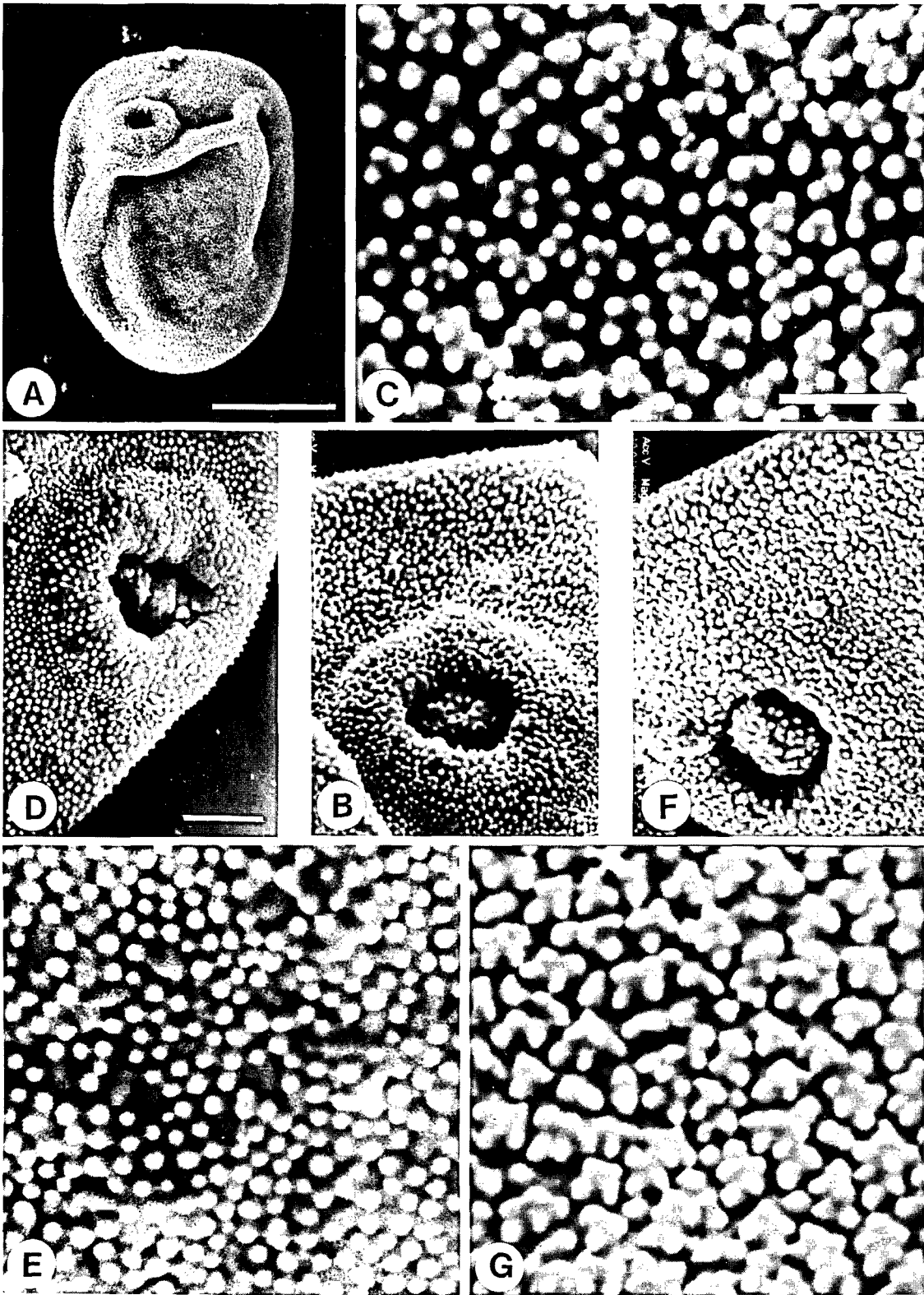


Fig. 1. Pollen grain, apertures and exine surface ornamentation in *Oryza* species (SEM photomicrographs). A–C. *O. brachyantha*. (A) Pollen grain, (B) Part of a grain showing the depth of the closely set minute spinules at the margin, and the operculate-annulate pore, (C) Grouned-spinulose exine surface. D–E. *O. meyeriana* complex (*O. granulata* and *O. meyeriana*). (D) Part of a grain showing the depth of the sparse spinules at the margin, and the operculate-annulate pore, (E) A sparsely-spinulose exine surface. F–G. *O. officinalis* complex. (*O. alta*) (F) Part of a grain showing the fusion of granules at the margin, and an operculate-annulate pore, (G) Insular Type-1 exine surface. Scale bars: A = 10  $\mu$ m; B, D, F = 2  $\mu$ m; C, E, G = 1  $\mu$ m.

Table I. Pollen morphology of *Oryza* species.

| Plant name                             | Pollen type       | Pollen size longest axis & range (µm) | Pore diameter (µm) | Annulus diameter (µm) | Exine thickness (µm) | Exine ornamentation (SEM)                                         |
|----------------------------------------|-------------------|---------------------------------------|--------------------|-----------------------|----------------------|-------------------------------------------------------------------|
| I. <i>Oryza brachyantha</i>            | 1-porate-annulate | 29 (28–34)                            | 2,3                | 6.5,7,8               | 1,1.5                | Grouped-spinulose                                                 |
| II. <i>Oryza meyeriana</i> -complex    |                   |                                       |                    |                       |                      |                                                                   |
| 1. <i>O. granulata</i>                 | -do-              | 35 (30–40)                            | 2.5,2.75           | 8,8.5,9               | 1,1.25               | Sparsely-spinulose                                                |
| 2. <i>O. meyeriana</i>                 | -do-              | 36 (30–42)                            | 2.5,3              | 8,8.5,9               | 1.25,1.5             | Sparsely-spinulose                                                |
| III. <i>Oryza officinalis</i> -complex |                   |                                       |                    |                       |                      |                                                                   |
| 1. <i>O. alta</i>                      | -do-              | 42 (34–51)                            | 3.5,4              | 9,11,13               | 1.5–2                | Insular Type-1                                                    |
| 2. <i>O. australiensis</i>             | -do-              | 39 (32–45)                            | 2,2.5,3            | 8,9,9.5               | 1,1.5,2              | Insular Type-2, insulae compact, forming a mosaic pattern         |
| 3. <i>O. eichingeri</i>                | -do-              | 32 (28–36)                            | 2.75,3             | 6,7,9                 | 1.5,1.75             | Densely-granulose                                                 |
| 4. <i>O. grandiglumis</i>              | -do-              | 43 (37–50)                            | 3,3.5,4            | 9,10,11               | 1,1.25,1.5           | Mixed-granulose, granules large                                   |
| 5. <i>O. latifolia</i>                 | -do-              | 29 (24–34)                            | 1.5,1.75,2         | 6,6.5                 | 1.25                 | Mixed-granulose, granules small                                   |
| 6. <i>O. minuta</i>                    | -do-              | 39 (33–45)                            | 3.75–4             | 9,10                  | <1, 1                | Mixed-granulose, granules small                                   |
| 7. <i>O. officinalis</i>               | -do-              | 33 (28–42)                            | 1.75,2             | 7.5,8.5               | 1–1.5                | Mixed-granulose, granules small                                   |
| 8. <i>O. punctata</i>                  | -do-              | 35 (34–37)                            | 2,2.5,3,4          | 7,10                  | 1,1.5                | Insular Type-1, insulae ruguloid                                  |
| IV. <i>Oryza ridleyi</i> -complex      |                   |                                       |                    |                       |                      |                                                                   |
| 1. <i>O. longiglumis</i>               | -do-              | 34 (29–39)                            | 1.75,2,2.5         | 7,7.5,8               | 1.5,1.75             | Mixed-granulose, granules small                                   |
| 2. <i>O. ridleyi</i>                   | -do-              | 37 (33–40)                            | 2.5,3,4            | 8.5,9                 | <1,1                 | Grouped-granulose, granules fused to form raised irregular groups |
| V. <i>Oryza sativa</i> -complex        |                   |                                       |                    |                       |                      |                                                                   |
| 1. <i>O. barthii</i>                   | -do-              | 44 (40–50)                            | 3,3.5,4            | 11,12                 | 1.5,1.75             | Mixed-granulose, granules large                                   |
| 2. <i>O. glaberrima</i>                | -do-              | 44 (38–50)                            | 3–3.5              | 9,10,11               | 1.75,2               | Insular Type-1                                                    |
| 3. <i>O. longistaminata</i>            | -do-              | 44 (36–53)                            | 3–4                | 9,10,11               | 1.5,1.75             | Grouped-granulose, granules uniform in size                       |
| 4. <i>O. meridionalis</i>              | -do-              | 42 (37–52)                            | 3–3.5              | 10,10.5,11            | 1,1.5                | Insular Type-3                                                    |
| 5. <i>O. nivara</i>                    | -do-              | 51 (45–62)                            | 4.5,5              | 10,12,15              | 1,1.25               | Granulose-punctate, granules scattered                            |
| 6. <i>O. sativa</i>                    |                   |                                       |                    |                       |                      |                                                                   |
| a. Race-Indica                         | -do-              | 50 (45–56)                            | 6,6.5              | 12,13                 | 1,1.25               | Insular Type-3                                                    |
| b. Race-Japonica                       | -do-              | 42 (36–48)                            | 4,5                | 11,11.5,12            | 1.25–2               | Insular Type-1                                                    |
| c. Race-Javanica                       | -do-              | 46 (36–51)                            | 4.5,5.25           | 11,12,14              | 1.5–2                | Sparsely-granulose                                                |

In the *O. ridleyi* complex although the exine surface is basically granulose, the two species of the complex show different patterns. While *O. longiglumis* has a mixed-granulose pattern with small granules (Fig. 3A), *O. ridleyi* has a grouped-granulose pattern (Fig. 3B).

The *O. sativa* complex includes both cultivated and wild species. The African cultivated species *O. glaberrima* and its wild relatives (Chang 1979) *O. barthii* (annual relative) and *O. longistaminata* (perennial relative) show variable exine surface patterns. In *O. glaberrima* the exine pattern is Insular Type-1 (Fig. 3D), in *O. barthii* it is a mixed-granulose with prominent large granules (Fig. 3C), and in *O. longistaminata* it is grouped-granulose (Fig. 3E). The other cultivated species of the genus *O. sativa* which is cultivated all over the world is polymorphic with three geographically identified

racess namely, Indica, Japonica and Javanica. Variability is also reflected in the exine surface patterns of these races. The race Indica has an Insular Type-3 pattern (Fig. 4C), Japonica has an Insular Type-1 pattern (Fig. 4E), and Javanica has a sparsely-granulose pattern (Fig. 4G). *O. nivara* with a granulose-punctate exine surface and scattered granules (Fig. 4A) differs from all the other species of the genus. *O. meridionalis* – an Australian species of this complex has an Insular Type-3 exine surface (Fig. 3F).

When all the species-complexes are considered together, it is apparent that the largest pollen grains occur in the *O. sativa* complex which comprises cultivated and allied species. The average pollen size in the species of this complex varies in the range 42–51 µm. The largest grains occur in *O. nivara*, with an average size 51 µm (45–62 µm). In *O. sativa* race

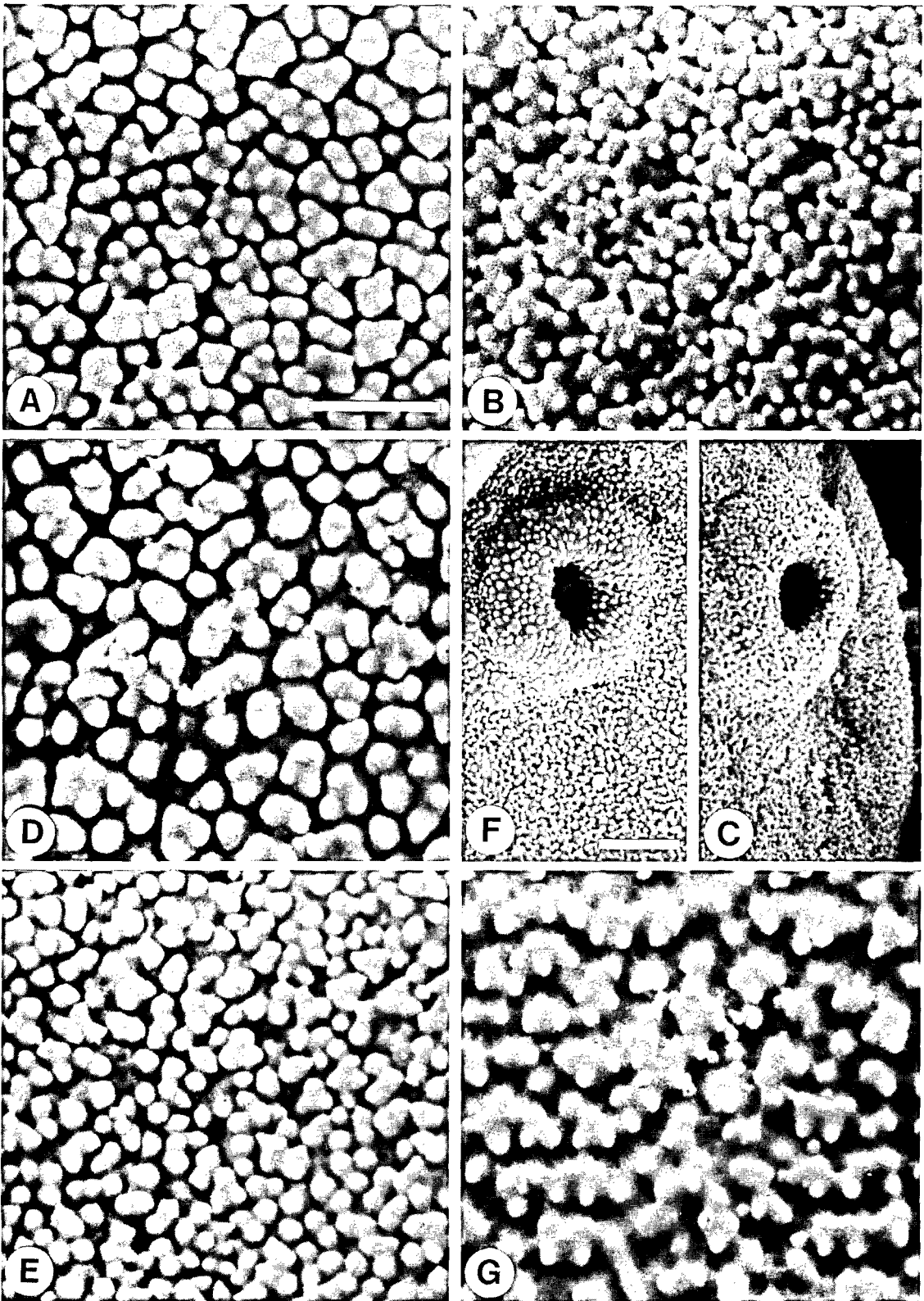


Fig. 2. *Oryza officinalis* complex (continued): A. *O. australiensis*: Insular Type-2 exine surface. The insulae form a mosaic pattern; B–C. *O. eichingeri*. (B) Densely-granulose exine surface, (C) Part of grain showing the densely placed minute granules at the margin, and an annulate pore; D. *O. grandiglumis*: Mixed-granulose exine surface with large granules; E. *O. latifolia*, *O. minuta* and *O. officinalis*: Mixed-granulose exine surface with small granules; (F) Part of grain in *O. latifolia* showing a small annulate pore; (G) *O. punctata*: Insular Type-1 exine surface, insulae ruguloid. Scale bars: A, B, D, E, G = 1  $\mu$ m; C, F = 2  $\mu$ m.

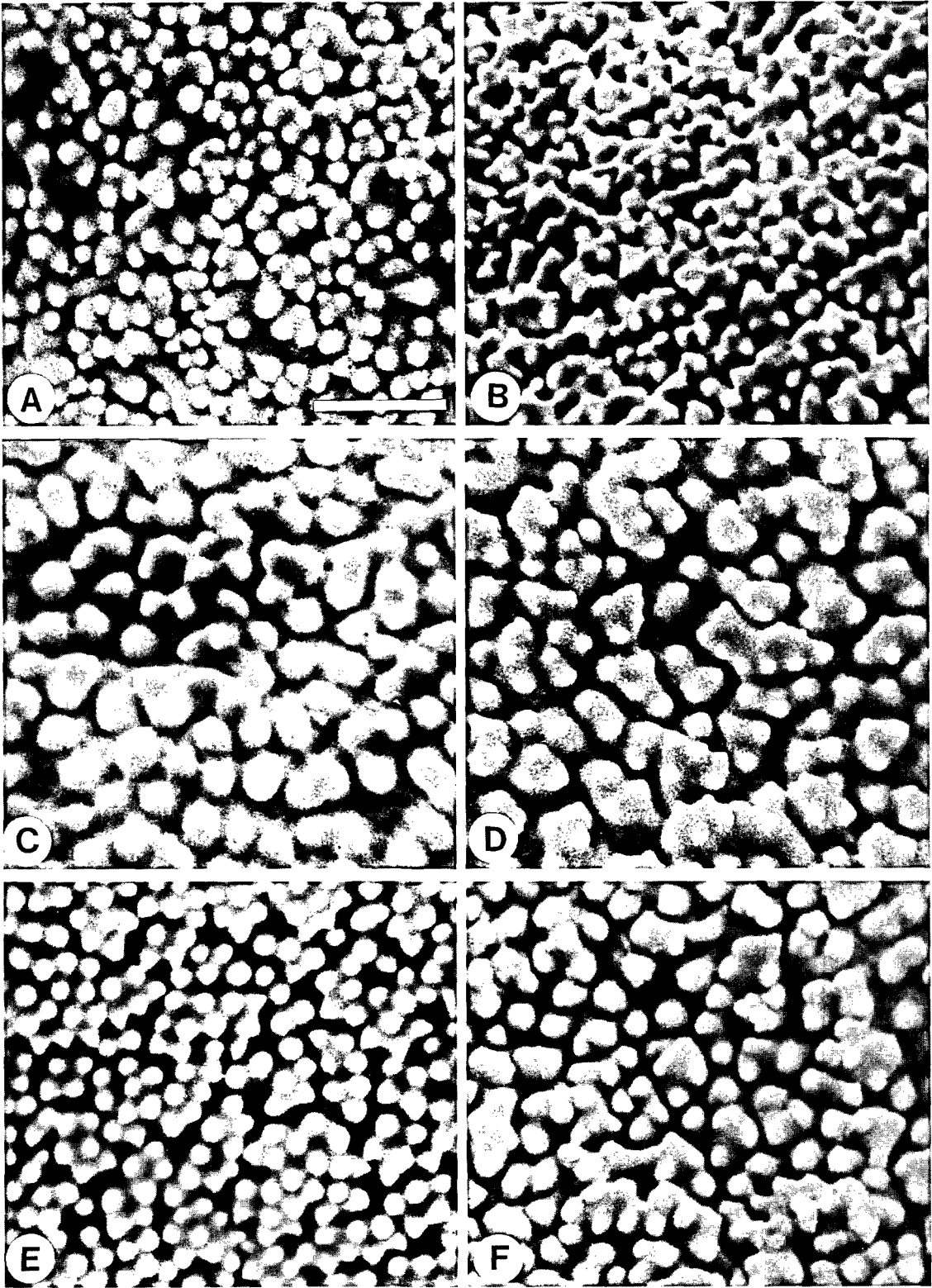


Fig. 3. Exine ornamentation types in *Oryza* species (SEM photo-micrographs). A–B. *O. ridleyi* complex: (A) *O. longiglumis*. Mixed-granulose exine surface with small granules; (B) *O. ridleyi*. Grouped-granulose exine surface, with granules fused to form raised irregular groups. C–F. *O. sativa* complex: (C) *O. barthii*. Mixed-granulose exine surface with large granules; (D) *O. glaberrima*. Insular Type-1 exine surface; (E) *O. longistaminata*. Grouped-granulose exine surface, with uniform-sized granules; (F) *O. meridionalis*. Insular Type-3 exine surface. Scale bar: A–F = 1  $\mu$ m.

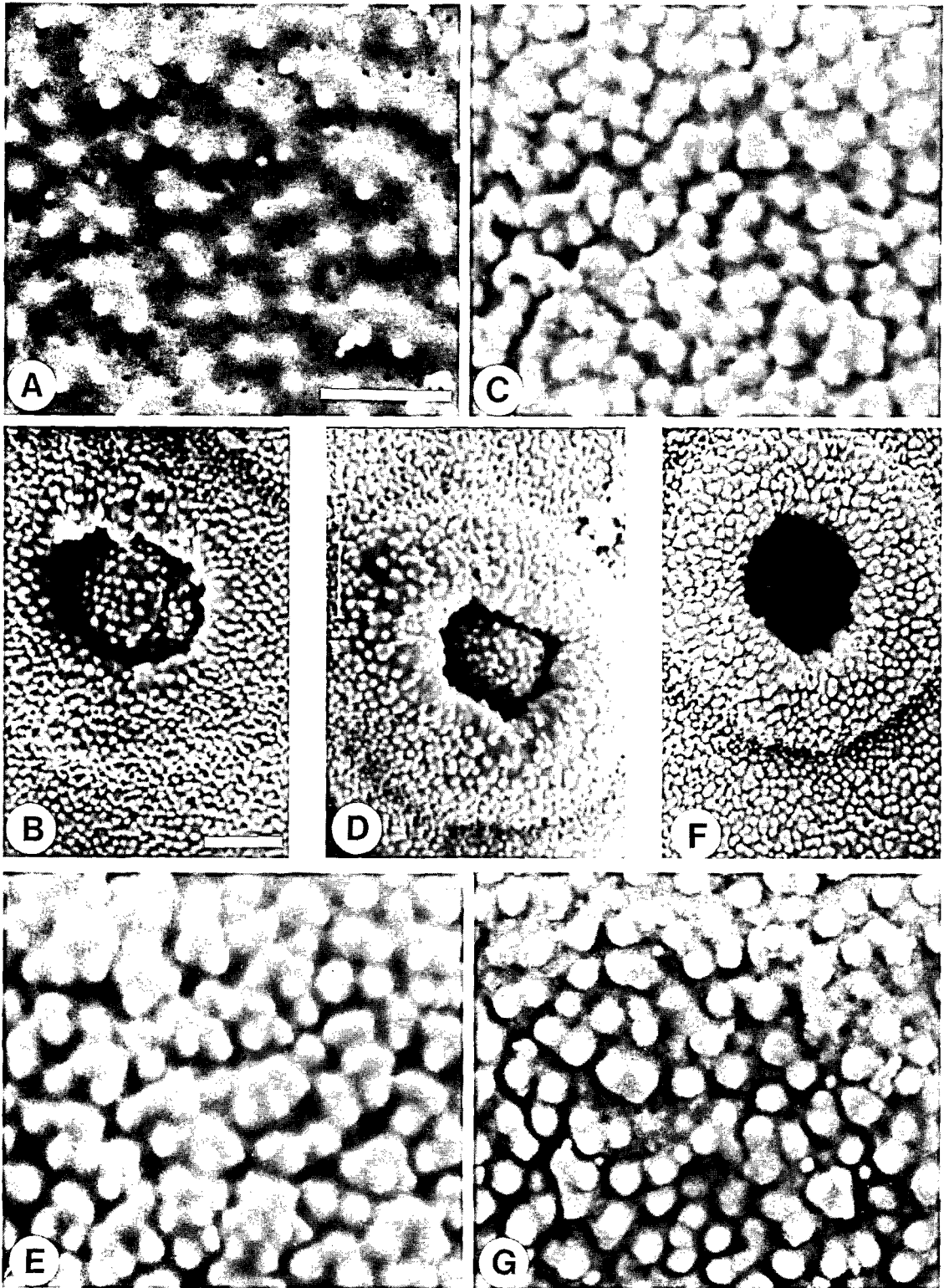


Fig. 4. *Oryza sativa* complex (continued): Exine patterns and pores. A. *O. nivara*: Granulose-punctate exine surface with scattered granules; B–C. *O. sativa* Race Indica. (B) Part of a grain showing the large, operculate-annulate pore, (C) Insular Type-3 exine surface, D–E. *O. sativa* Race Japonica: (D) Large operculate-pore, (E) Insular Type-1 exine surface; F–G. *O. sativa* Race Javanica. (F) Large pore with annulus (the operculum has fallen off), (G) Sparsely-granulose exine surface. Scale bars: A, C, E, G = 1 µm; B, D, F = 2 µm.

Indica, the pollen grains are larger than those of the other two races Japonica and Javanica, and the average pollen size is closer to that of *O. nivara* (Table I), which is considered to be the wild annual relative of *O. sativa* (Chang 1979). Similarly, in the cultivated African species *O. glaberrima* and its wild relatives *O. barthii* and *O. longistaminata* (Chang 1979), the pollen size shows a striking similarity, being 44 µm. The pollen size in the *O. officinalis* complex varies between 29–43 µm. In the *O. meyeriana* complex it is 35 and 36 µm, and in the *O. ridleyi* complex 34 and 37 µm. The unrelated species *O. brachyantha* has smaller pollen grains, their size being 29 µm.

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