POLLEN MORPHOLOGY OF FOUR SUCCULENT SPECIES OF EUPHORBIA (EUPHORBIACEAE)

M. O. WEBER EL GHOBARY

Laboratoire de Palynologie, Montpellier.
Departement de Biologie végétale. Institut de Botanique.
Systematique et de Biogeographie. Geneve.

(Recibido el 28 de Septiembre de 1984)

SUMMARY. The pollen morphology of four succulent species of Euphorbia L. from the Ivory Coast (E. ingens, E. kamerunica, E. milii and E. unispina), were studied for the first time using light and scanning electron microscopy. In general the pollen is isopolar, oblate spheroidal, medium size, tricolporate. Exine columellate, characteristic of angiosperms pollen. Differences in pollen characters between taxa were observed. Exine and aperture features are recognized here as practical taxonomic use in the delimitation of taxa. Based on the exine structure two types of pollen are recognized: tectate perforate and microreticulate. Intraspecific variation was encountered.

RESUMEN. La morfología polínica de cuatro especies suculentas del género Euphorbia L. de Costa de Marfil (E. ingens, E. kamerunica, E. milii y E. unispina), fue estudiada por primera vez utilizando microscopía óptica y electrónica de barrido. En general, el polen es isopolar, oblongo-esferoidal, de tamaño mediano, tricolporado. Exina con columelas, característico del polen de angiospermas. Se observaron diferencias en los caracteres polínicos dentro de los taxones. Las características de la exina y de sus aperturas son reconocidas como caracteres taxonómicos en la delimitación de las especies. Basándose en la estructura de la exina se pudieron distinguir dos tipos de polen: tectado-perforado y microperforado. Se encontró variación intraespecífica.

INTRODUCTION

The genus Euphorbia L. is a member of the tribe Euphorbiaceae within the Crotonoideae, and is represented by c. 2000 species, distributed in sub-tropical and warm temperate regions (HEYWOOD, 1979; HICKEY & KING, 1981). The succulent Euphorbia of Africa and adjacent islands have been classified primarily on morphological features associated with their habit (PAX, 1909; CHEVALIER, 1933; WHITE & al., 1941; HUTCHINSON & al., 1958; AUBREVILLE, 1959). The family Euphorbiaceae is distinctly eurypalynous (ERDTMAN, 1952; 1969). Previous studies have shown the great diversity of pollen characters of
the family (ERDTMAN, 1952; PUNT, 1962; KOHLER, 1965; LABOURIAU, 1967; MEWIJIS & PUNT, 1983). Phylogenetic trends in pollen morphology within Euphorbiaceae are reported by WEBSTER (1974). Despite the economic importance, the occurrence of latex (PONSINET & DURISSON, 1968) and widespread distribution of the genus Euphorbia (HICKEY & KING, 1981), there are only few scattered pollen data (PUNT, 1962; SCHILL, 1973). Sporoderm morphogenesis in E. obesa was recently studied by FREAN (1983) using first scanning electron microscope. No early study on pollen morphology of succulent Euphorbia from Ivory Coast has been reported. Therefore, this paper provides the first pollen data of the related taxa, observed by light and electron microscope.

The main purpose of this study is to observe whether the represented taxa exhibit pollen diversity. Together with other available data, the present results are employed to discuss evolutionary trends in four succulent Euphorbia from Ivory Coast.

MATERIAL AND METHODS

Fresh pollen was collected mainly from succulent plants growing in Ivory Coast. Besides, material from greenhouse and herbarium specimens was used. As a preliminary treatment, developing and mature anthers were placed in centrifuge tubes and softened for 2 hrs. in distilled water with 5% detergent. The material was poured through a fine mesh wire, then centrifuged for 5 min., decanted and washed once with distilled water with centrifugation, then kept for 15 min. in glacial acetic acid. Pollen slides for light microscope (LM) observation were prepared after the acetolysis (ERDTMAN, 1960) and paraffin embedding method described by SIVAK (1973). The slides are preserved at the Laboratoire de Palynologie, Montpellier and another set retained by the authors. The photomicrographs were taken with a ZEISS light microscope. For scanning electron microscope (SEM), the technique described by HIDEUX (1972) and includes the ultrasonic technique was used.

The terminology employed in this study follows that of ERDTMAN (1969), PUNT (1962) and PRAGLOWSKI & PUNT (1973). Polar (P) and equatorial diameter (E), and P/E ratios were calculated according to VAN CAMPO (1957). As far as possible, the means (X) and standard deviation (sd) of P and E are based on fifty measurements. For other pollen features twenty measurements were made, following PUNT (1962). The specimens examined and the quantitative data given in the Appendixes I and II. For taxonomic arrangement the synopsis (CHEVALIER, 1933; WHITE & al., 1941; HUTCHINSON & al., 1958; AUBREVILLE, 1959) were considered.

RESULTS

The pollen grains of four succulent Euphorbia studied in this paper are usually isopolar, radially symmetrical; shape in equatorial view prolate spheroidal, varying in some grains to oblate spheroidal or subprolate, outline in polar view three lobed or circular. Size medium to large. The most common pollen type within each species is tricolporate. Only two species are polymorphic with occasional 4 or 5-colporate pollen types. Pollen with compound apertures: colpi distinct, may be broad to
marrow, rather long, tapering meridionally to a small apocolpium. The margins regular, with a well developed margo. Ora small to medium, variable in shape from circular to lollongate and may be costate. Exine distinctly columellate, tectate perforate or semitectate microreticulate, without supratractectal ornamentation.

POLLEN DESCRIPTION

Euphorbia ingens E. Mey (Pl. I, Figs. 1-7).

Pollen tricolporate, shape in equatorial view prolate spheroidal to subprolate (P/E = 1.10-1.20), outline in polar view three lobed; mean polar axis 55 μm and mean equatorial diameter 49 μm. The breath of mesocolpium in polar view c. 29.5 μm; polar area, t = 9.8 μm. Apertures: colpi rather long, 45 μm, open, margin distinct, membrane persistent, smooth. Os medium (15 x 8.8 μm), lollongate no well delimited. Exine c. 3.7 μm thick in interapertural zone, semitectate microreticulate, distinctly columellate; lumina less than 1 μm, minute reticulum present in apocolpia. Infratectal columellae simple, 1.5 μm high, and 1.5 μm broad, homogeneous distributed, distinct with light microscope. The tectum smooth, c. 1.5 μm, equal thick as the foot layer.

E. kamerunica Pax (Pl. II, Figs. 1-8).

Pollen tricolporate to 4-5-colporate, shape in equatorial view prolate spheroidal to subprolate (P/E = 1.10-1.27), outline in polar view three lobed; mean polar axis 41 μm and mean equatorial diameter 37 μm. The breath of mesocolpium in polar view c. 22.5 μm, polar area, t = 8.5 μm. Apertures: colpi 35 μm long, open, narrow, conspicuously marginate, membrane present, smooth. Os medium (13.5 x 8.3 μm) lollongate or circular (8.3 x 8 μm) clear bordered towards the poles by thickened exine, sometimes equatorially constricted. Os well visible with light microscope. Exine c. 3.8 μm thick in interapertural zone, tectate densely perforate, distinctly columellate. Tectal perforations present in apocolpia. Infratectal columellae simple, 1.5 μm high, appearing uniform in size but irregularly spaced. Tectum smooth, without projections c. 1.2 μm thick like the foot layer.

E. milii Des Moulin (Pl. III, Figs. 1-7).

Pollen tricolporate, shape in equatorial view prolate spheroidal to slightly subprolate (P/E = 1.10-1.23); outline in polar view intersubangular. Mean polar axis 45 μm, and mean equatorial diameter 42 μm. The breath of mesocolpium in polar view c. 23.26 μm, aire polar, t = 9.8 μm. Apertures: colpi narrow, long 40 μm, about equal in length to grain, margin large with smooth membrane. Os obscure, medium, circular (7.3 x 8.4 μm) sometimes only towards the poles visible. Exine c. 3.3 μm thick in interapertural zone, tectate densely perforate. Widely spaced perforations present in apocolpia. Infratectal columellae, like in E. kamerunica.

E. unispina N. E. Br. (Pl. IV, Figs. 1-7).

Pollen highly polymorphic, may have tectate perforate or microreticulate exine, and variable ora. Mostly tricolporate and occasionally 4-colporate; shape in equatorial view oblate to prolate spheroidal (P/E = 0.97-1.08), outline in polar view circular or three
lobed. Mean polar axis 43 µm and mean equatorial diameter 41 µm. The
breath of mesocolpium in polar view c. 22.9 µm; polar area, t = 9.37
µm. Apertures: colpi narrow, long 38 µm, conspicuously marginate,
membrane smooth. Os medium circular (11.5 x 10.5 µm) or lalongate
(13.6 x 11.5 µm). Exine in interapertural zone c. 3.5 µm thick by
tectate perforate grains and 4 µm by semitectate microreticulate grains;
lumina dense, less than 1 µm in diameter. Exine structure well visible
in apocolpia. The tectum smooth, c. 1.2 µm, about equal thick as the
foot layer. Infratectal columnellae, like in E. ingens.

**DISCUSSION**

In a previous study (PUNT, 1962), has pointed out the relative
homogeneity of the pollen characters existing between taxa of the genus
Euphorbia. Tricolporate pollen grains with tectate columnellate exine
recognized in the genus are similar to those of Hippomaneae.

The exine in pollen of succulent E. obesa is classically tectate
perforate, considered with less advanced features (FREAN, 1983).
However, more evolved exine, semitectate reticulate was recognized in
some succulent Euphorbia from Madagascar (SCHILL, 1973). The present
data reveal pollen diversity, as regard in exine and aperture structures
which have been the basis for identifying pollen types.

Based on scanning electron microscope, two types of exine, tectate
perforate (type 1) and semitectate microreticulate (type II) were clearly
visible within the examined taxa. Furthermore, intraspecific variation
was apparent in E. unispina (Pl. IV, Figs. 1-7). This species shows
heterogeneous characters in its habit (CHEVALIER, 1933), which may
explain pollen diversity observed in the taxa. Pollen of candelabrous
succulent plants (samples, 29, 31), present tectate perforate exine (Pl.
IV, Figs. 3, 6, 7) while sarmentous plants (all other samples) differ in
having pollen with semitectate microreticulate exine (Pl. IV, Figs. 1, 2,
4, 5). The pollen of E. unispina is most variable, both in terms of its
size and ora configurations. The pollen diversity is so distinct, that the
systematic position of the varieties of E. unispina needs clarification.

The present pollen data may suggest relationship between the
taxa. Exine of E. milii and E. kamerunica pollen is closely related. E.
ingens and E. unispina (type II), pollen show similar semitectate
microreticulate exine. The structure of ora seems to be the only feature
of taxonomic significance. This observation coincide with previous
reports (PUNT, 1962; SCHILL, 1973). The observations made in this paper
on the general pollen shape, prolate spheroidal to subprolate, agree
with the description given by SCHILL (1973).

During this study variation in pollen size and shape was
encountered in all taxa, but was not considered as useful characters.
Conclusion from other data, involving morphological and anatomical
characters is given considerable support by the results of the present
study. The floral structure, the cyathium is rather uniform throughout
the succulent Euphorbia without great taxonomic value (WHITE & al.,
1941). However, ultrastructure differences in the nectaries of some
succulent Euphorbia were noted by GENC & RAUH (1984) and SCHNEPF &
DEIGHGRABEN (1984). Seed characters within the genus, are less useful
for distinguishing taxa (EHLER, 1976). Pollen data of succulent
Euphorbia from Madagascar (SCHILL, 1973), correspond with cytological

78
characters; large pollen grains with increased aperture numbers and lolongate ora indicate polyploidy (SCHILL, 1971).

The succulent Euphorbia presented in this paper are palynologically distinct taxa. The present data supported by other available informations permit to suggest progressive evolution in pollen morphology within the examined taxa. E. ingens and E. unispina pollen promote evolutionary trend in exine structure, semitectate microreticulate as been considered more advanced for angiosperms pollen (WALKER, 1974). This suggestion is also supported by their advances character of starch grains morphology within the taxa, reported by MAHLBERG & al. (1983). The remarkable lolongate ora and large pollen grains of E. ingens, may indicate polyploidy, but cytological data are not yet reported to allow a comparison. There is a discordance observed between the present pollen data of E. mili and E. kamerunica and their starch grains morphology reported by BIESBOER & MAHLBERG (1981). Both taxa show tectate perforate exine considered less advanced (WALKER, 1974), and apparently small circular ora, which for succulent Euphorbias appear less evolved (SCHILL, 1973). However, starch grains morphology detected in the taxa show evolutionary trends, in havin osteid shapes (BIESBOER & MAHLBERG, 1981). It is interesting to note that a striking resemblance was observed between pollen grains of E. ingens and those of Sebastiania fruticosa, recently described by LIEUX (1983). Sebastiania pollen was placed like the Euphorbia pollen to Hippomaneae type (PUNT, 1962). Therefore, intergeneric affinities in pollen characters can be suggested.

Based only on a limited number of individuals, the present data indicate, that pollen characters can be employed in taxonomic revision of the taxa belonging to this complex genus Euphorbia. This conclusion agree with previous report (SCHILL, 1973). In order to understand better taxonomic affinities and progressive evolution within the taxa, more extensive pollen survey of succulent Euphorbia from Ivory Coast is suggested.

ACKNOWLEDGEMENTS

I wish to thank Prof. M. M. Van Campo and Prof. M. Ph. Guinet, Lab. de Palynologie, Montpellier, for generously support. I am indebted to Prof. J. Miège (Univ. of Geneva) and various curators, who provided the material for study.

REFERENCES


APPENDIX I

(Material examined)


**APPENDIX II**

<table>
<thead>
<tr>
<th>sp.</th>
<th>sample</th>
<th>P</th>
<th>E</th>
<th>P/E</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. ingens</td>
<td>1</td>
<td>57 - 61</td>
<td>53 - 57</td>
<td>1.10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>59.60 - 1.34</td>
<td>53.66 - 0.70</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>55 - 62</td>
<td>47 - 52</td>
<td>1.20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>58.80 - 2.20</td>
<td>48.75 - 1.76</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>48 - 53</td>
<td>46 - 49</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td></td>
<td>51.36 - 1.66</td>
<td>47.95 - 1.20</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>40 - 49</td>
<td>42 - 47</td>
<td>1.08</td>
</tr>
<tr>
<td></td>
<td></td>
<td>47.39 - 0.96</td>
<td>43.84 - 1.60</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>60 - 64</td>
<td>51 - 56</td>
<td>1.18</td>
</tr>
<tr>
<td></td>
<td></td>
<td>62.75 - 1.57</td>
<td>52.75 - 1.09</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>49 - 55</td>
<td>45 - 49</td>
<td>1.08</td>
</tr>
<tr>
<td></td>
<td></td>
<td>51.94 - 1.68</td>
<td>47.98 - 1.18</td>
<td></td>
</tr>
<tr>
<td>E. kaerunica</td>
<td>7</td>
<td>35 - 39</td>
<td>35 - 37</td>
<td>1.10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>38.10 - 1.30</td>
<td>34.37 - 1.30</td>
<td></td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>31 - 47</td>
<td>28 - 44</td>
<td>1.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td>40.95 - 5.20</td>
<td>39.16 - 5.20</td>
<td></td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>35 - 43</td>
<td>33 - 42</td>
<td>1.05</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>38 - 42</td>
<td>35 - 31</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td></td>
<td>39.94 - 1.66</td>
<td>37.15 - 1.26</td>
<td></td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>39 - 44</td>
<td>35 - 49</td>
<td>1.11</td>
</tr>
<tr>
<td></td>
<td></td>
<td>41.15 - 1.40</td>
<td>37.06 - 1.60</td>
<td></td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>39 - 48</td>
<td>31 - 37</td>
<td>1.27</td>
</tr>
<tr>
<td></td>
<td></td>
<td>43.55 - 2.60</td>
<td>34.22 - 2.00</td>
<td></td>
</tr>
<tr>
<td>E. milli</td>
<td>13</td>
<td>40 - 45</td>
<td>39 - 42</td>
<td>1.06</td>
</tr>
<tr>
<td></td>
<td></td>
<td>43.15 - 1.51</td>
<td>40.47 - 0.99</td>
<td></td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>43 - 47</td>
<td>40 - 45</td>
<td>1.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td>44.27 - 1.87</td>
<td>42.95 - 1.81</td>
<td></td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>44 - 49</td>
<td>42 - 44</td>
<td>1.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td>48.60 - 1.50</td>
<td>44.20 - 1.39</td>
<td></td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>41 - 48</td>
<td>39 - 45</td>
<td>1.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td>44.40 - 2.55</td>
<td>42.27 - 2.10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>44 - 47</td>
<td>36 - 44</td>
<td>1.18</td>
</tr>
<tr>
<td></td>
<td></td>
<td>46.42 - 1.09</td>
<td>39.28 - 3.09</td>
<td></td>
</tr>
<tr>
<td></td>
<td>18</td>
<td>45 - 49</td>
<td>43 - 47</td>
<td>1.04</td>
</tr>
<tr>
<td></td>
<td></td>
<td>46.71 - 1.70</td>
<td>44.71 - 1.07</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>sp.</th>
<th>sample</th>
<th>P</th>
<th>E</th>
<th>P/E</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. unispina</td>
<td>19</td>
<td>44 - 47</td>
<td>37 - 42</td>
<td>1.18</td>
</tr>
<tr>
<td></td>
<td></td>
<td>46.21 - 1.25</td>
<td>36.85 - 1.30</td>
<td></td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>37 - 42</td>
<td>35 - 40</td>
<td>1.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td>38.38 - 1.79</td>
<td>36.28 - 1.79</td>
<td></td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>42 - 45</td>
<td>40 - 44</td>
<td>1.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>43.36 - 1.51</td>
<td>41.01 - 1.77</td>
<td></td>
</tr>
<tr>
<td></td>
<td>22</td>
<td>37 - 43</td>
<td>35 - 40</td>
<td>1.10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>41.25 - 2.30</td>
<td>37.33 - 2.16</td>
<td></td>
</tr>
<tr>
<td></td>
<td>23</td>
<td>44 - 48</td>
<td>42 - 46</td>
<td>1.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>45.85 - 1.21</td>
<td>44.14 - 1.34</td>
<td></td>
</tr>
<tr>
<td></td>
<td>24</td>
<td>44 - 50</td>
<td>38 - 43</td>
<td>1.23</td>
</tr>
<tr>
<td></td>
<td></td>
<td>48.83 - 1.50</td>
<td>39.58 - 1.80</td>
<td></td>
</tr>
</tbody>
</table>

Pollen grain dimensions of the examined samples (mean (\(\bar{x}\)), standard deviation (s d), P = polar axis, E = equatorial diameter, all measurements are in micron).

82
PLATE 1.- Euphorbia ingens. Figs. 1, 3, 6, SEMG: 1, Polar view; 3, Microreticulate surface in mesocolpium; 6, wall cross section. Figs. 2-7, PhMG: 2, 4, Polar view; 4, Optical section; 5, 7, Equatorial view; 5, Upper focus; 7, Optical section.

Scale: Fig. 1 x 6.56 μm; Fig. 3 x 1.65 μm; Fig. 6 x 1.83 μm; Figs. 2, 4 x 11.35 μm; Figs. 5, 7 x 11.80 μm.
PLATE II.—Euphorbia kamerunica. Figs. 1-2, SEMG: 1, Polar view; 2, Tectate perforate surface in apocolpium. Figs. 3-8, PhMG: 3-5, Polar view; 3, Uppermost focus; 4, Upper focus; 5, Optical section; 6-8, Equatorial view; 6, Uppermost focus; 7, Upper focus; 8, Optical section.

Scale: Fig. 1 x 7.20 μm; Fig. 2 x 1.46 μm; Figs. 3-5 x 10.88 μm; Figs. 6-8 x 9.53 μm.
PLATE III.—Euphorbia milii. Figs. 1, 2, SEMG: 1, Oblique equatorial view; 2, Tectate perforate surface. Figs. 3-7, PhMG: 3, 4, Polar view; 3, Upper focus; 4, Optical section; 5-7, Equatorial view; 5, Large mesocolpium; 6, Optical section on endoaperture; 7, Optical section.

Scale: Fig. 1 x 7.20 μm; Fig. 2 x 1.44 μm; Figs. 3, 4 x 9.38 μm; Figs. 5-7 x 9.22 μm.
PLATE IV.—Euphorbia unispina. Figs. 1-3, 6 SEMG: 1, Polar view; 2, Microreticulate surface in mesocolpium; 3, Tectate perforate surface in mesocolpium; 6, Polar and equatorial view. Figs. 4, 5, 7, PhMG: 4, 5, Polar view; 4, Upper focus; 5, Optical section; 7, Equatorial view optical section.

Scale: Fig. 1 x 6.25 μm; Fig. 2 x 1.85 μm; Fig. 3 x 2.59 μm; Figs. 4, 5 x 7.52 μm; Fig. 7 x 7.76 μm; Fig. 6 x 8.32 μm.

86