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Contributions to the palynology of hydrophytic, non-entomophilous angiosperms. 1. Studies with LM and SEM

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ABSTRACT

DÍEZ, M. J., S. TALAVERA & P. GARCÍA-MURILLO (1988). Contributions to the palynology of hydrophytic, non-entomophilous Angiosperms. 1. Studies with LM and SEM. *Candollea* 43: 147-158. In English, English and Spanish abstracts.

The pollen morphology of 15 species of aquatic Angiosperms belonging to the genera *Althenia* Petit, *Callitriche* L., *Ceratophyllum* L., *Elatine* L., *Lemna* L., *Myriophyllum* L., *Najas* L., *Potamogeton* L., *Ruppia* L., *Zannichellia* L. and *Zostera* L. have been studied with light and scanning electron microscopy. The pollen of *Callitriche*, *Myriophyllum* and *Potamogeton*, in particular, has taxonomic importance owing to its unusual morphology, in particular, shape, apertural system and exine. Furthermore the relationship in these species between floral morphology and pollination system is of particular interest. Problems encountered during the studies are emphasized.

RESUMEN

DÍEZ, M. J., S. TALAVERA & P. GARCÍA-MURILLO (1988). Contribución a la palinología de los hidrófitos, Angiospermas no-entomófilas. 1. Estudios con MO y MEB. *Candollea* 43: 147-158. En inglés, resúmenes inglés y español.

En base a observaciones efectuadas con ayuda del microscopio óptico y electrónico de barrido, se describe la morfología polínica de 15 especies de Angiospermas hidrófitas presumiblemente no entomófilas incluidas en los géneros *Althenia* Petit, *Callitriche* L., *Ceratophyllum* L., *Elatine* L., *Lemna* L., *Myriophyllum* L., *Najas* L., *Potamogeton* L., *Ruppia* L., *Zannichellia* L. y *Zostera* L. Asimismo, se observa la utilidad del polen como caracter taxonómico (*Myriophyllum*, *Callitriche*, *Potamogeton*), las características polínicas tan peculiares de estas especies, fundamentalmente en lo que respecta a la forma, sistema apertural y exina, así como su relación con el sistema de polinización. Se pone de manifiesto la dificultad del estudio tanto al MO como MEB de estos granos de polen.

Introduction

In the Palozoic, presumably between the Silurian and the Devonian, plants begin to colonize the terrestrial environment. Many changes occur in their structures. One group of plants, the Angiosperms, will dominate the environment. These plants expand and diversify to occupy all possible habitats, gradually becoming better and better adapted to them. At the same time selective pressure pushes various groups of these plants towards an invasion of the aquatic environment which their ancestors originally inhabited. During this transition they also develop some differences in structure; aeriferous channels and lose others, the cuticle, the conducting system, the stomata and the roots. The chloroplasts shift and some modifications to the metabolism take place. In this way the adaptation to the environment becomes increasingly effective. Despite these modifications the pollination system of the greater part of these groups remains the same as that of their terrestrial forbears and includes entomophily and anemophily. The most specialized, however, utilize water as their

pollination agent. Of the 102 known hydrophytic genera, belonging to almost subclasses of Angiosperms, only 25 from 11 families, have representatives with hydrophilous pollination. Hydrophyly represents only 0.05% (COX, 1983) of all Angiosperms. This fact provides clear evidence of the slight success of water as a pollination vector. WILLDENOW (1806) and CAVOLINI (1806) in DUCKER & KNOX (1985) each, in different plants, discovered that there are species that live under water and have highly specialized pollen and pollination mechanisms. Since then several writers have devoted themselves to this subject including DUCHARTRE (1873), ROZE (1887, 1892), SCULTHORPE (1969, in COX, 1983), GAMERRO (1968), SCHWANITZ (1968), PETTITT & JERMY (1975), PETTITT & al. (1981), VAN VIERSSEN & al. (1982) and COX (1983) but the number of species that has been studied is limited owing, not only to the fact that most of these species are almost inaccessible but also, that because of their very specialized morphology, the pollen grains are difficult to examine.

The purpose of this study is to show the characteristics of the pollen of both hydrogamous and anemogamous hydrophytes and to compare these with attributes of the floral morphology of each species in order to ascertain whether there is a correlation between pollen, floral morphology and pollination vector.

Materials and methods

Pollen material was obtained from the Herbarium of the Department of Botany, Faculty of Biology, Seville University (SEV) or directly in the field where it was fixed in glacial acetic acid or "Kew mix" (35% industrial spirit, 37% water, 5% glycerol and 5% formaldehyde solution (H.CHO).

Previous studies in the genus *Ceratophyllum* (*C. demersum* L. and *C. submersum* L.), *Ruppia* (*R. cirrhosa* (Petagna) Grande, *R. drepanensis* Tineo ex Guss. and *R. maritima* L.), *Potamogeton* (*P. fluitans* Roth., *P. lucens* L., *P. natans* L., *P. nodosus* Poiret, *P. panormitanus* Biv., *P. pectinatus* L., *P. polygonifolius* Pourret and *P. trichoides* Cham. & Schlecht.), *Althenia* (*A. filiformis* Petit and *A. orientalis* (Tzvelev) García-Murillo & Talavera) and *Zannichellia* (*Z. contorta* (Desf.) Cham. & Schlecht., *Z. obtusifolia* Talavera, García-Murillo & Smit, *Z. palustris* L., *Z. pedunculata* Reichenb. and *Z. peltata* Bertol.) showed similar pollen grains, so, from each of genera only one species has been taken as the representative type, except in *Potamogeton* where two different types have been selected: *P. lucens* (where all the species are included) and *P. pectinatus*.

Both acetolysed and unacetolysed pollen was studied according to whether or not the exine was acetolysis resistant (the pollen grains often desintegrate using conventional techniques). Acetolysed pollen was prepared using Erdtman's method (1960) but paying particular attention to the modifications suggested by REITSMA (1969). Non acetolysis resistant pollen was prepared following the method of WODEHOUSE (1935). In the genus *Callitriche* the proportion of acetic anhydride to sulphuric acid was increased to 18:1. Pollen material for the genus *Elatine* is, with few exceptions, non-acetolysis resistant, therefore the Wodehouse method was used for all the species examined in the present study.

Material was prepared for scanning electron microscopy (SEM) by suspending unacetolysed or acetolysed pollen grains in 95% ethanol on specimen stubs on which small coverslips had been mounted. The ethanol was allowed to evaporate at room temperature. Pollen grains of *Althenia orientalis* and *Zannichellia peltata* were critical point dried (CPD) in a BALZER'S UNION CPD 020, using 100% ethanol as the exchange liquid. The specimens were sputter-coated and examined in a JEOL T100 SEM.

The polarity, symmetry, shape in equatorial view (e.v.) meridional optical court (m.o.c.) and polar view (p.v.) equatorial optical court (e.o.c.), size (twenty measurements of pollen grains were made from each specimen), apertural system and exine are described from light microscopy (LM). The ornamentation: surface of the tectum and suprategal elements and occasionally the exine structure are described from SEM.

The terms of WODEHOUSE (1935), ERDTMAN (1944, 1945, 1948, 1966, 1969), VAN CAMPO (1957), FAEGRI & IVERSEN (1975), REITSMA (1970), HIDEUX & FERGUSON (1975) and DÍEZ & al. (1985) are followed.

Pollen morphology

Ceratophyllum submersum L. (non-acetolysis resistant, pollen very delicate and easily damaged, even using the Wodehouse method).

Pollen isopolar or apolar, bilateral symmetry (Fig. 1) or radial. Shape elliptic or circular in both m.o.c. and e.o.c. Breviaxe or equiaxe, semitransverse-adequate, $P/E_1 = 0.73-1$ ($\bar{X} = 0.85 \pm 0.07$). Size large $P \times E_1 = 35-52$ ($\bar{X} = 39.15 \pm 4.30$) \times $37-59$ ($\bar{X} = 45.70 \pm 6.14$) μm . Inaperturate. The sporoderm is ca. $0.5 \mu\text{m}$ thick, without exine or with endexinous exine. The surface ornamentation seen with SEM is psilate (Fig. 2).

Samples studied. — **Huelva.** Laguna de las Madres, 19.8.1986, Díez & P. García (SEV 119779).

References. — WODEHOUSE (1935), ERDTMAN & al. (1961), ERDTMAN (1966), PETTITT & JERMY (1975), WALKER (1976).

Elatine alsinastrum Guss. (acetolysis resistant).

Pollen isopolar, radial symmetry (Figs. 3-5). Shape elliptic in m.o.c. (Fig. 3) and in e.o.c. circular-triangular, angulaperturate (Fig. 4). Longiaxe, adequate-pererect, $P/E = 1-1.91$ ($\bar{X} = 1.25 \pm 0.21$). Size small, $P \times E = 16-23$ ($\bar{X} = 19.17 \pm 1.69$) \times $10-21$ ($\bar{X} = 15.55 \pm 2.03$) μm . Trizonocolporate; colpi long, ending near poles; endoapertures $3-7 \mu\text{m}$ in size equatorially positioned. The exine is ca. $1 \mu\text{m}$ thick in the mesocolpium, the sexine and nexine are the same thickness; with costae. Partial tectum, infratectum columellate. The surface ornamentation seen with SEM is reticulate (Fig. 6); small lumina, less than $1 \mu\text{m}$; muri similar in width to the lumina at surface level, however the muri are wider at the base of the infratectum.

Samples studied. — **Huelva.** Almonte: Doñana, 25.5.1974, Cabezudo (SEV 18390); Almonte: Doñana, 9.11.1966, Novo (SEV 17525); Almonte: Doñana, 6.4.1966, Novo (SEV 72268).

References. — ERDTMAN & al. (1961), ERDTMAN (1966), FAEGRI & IVERSEN (1975), MOORE & WEBB (1978).

Myriophyllum alterniflorum DC. (acetolysis resistant).

Pollen usually symmetrical, isopolar with radial symmetry. Circular or slightly elliptic in m.o.c. (Figs. 7 and 8) and circular in e.o.c. Breviaxe, transverse-semitransverse, $P/E = 0.71-0.88$ ($\bar{X} = 0.97 \pm 0.03$). Size small, $P \times E = 20-24$ ($\bar{X} = 21.73 \pm 1.12$) \times $25-29$ ($\bar{X} = 27.26 \pm 1.36$) μm . Tetra or hexazonoporate, sometimes penta or polizonoporate, strongly aspidate; the pores are circular in shape, ca. $5 \mu\text{m}$ in diameter, surrounded by a very obvious annulus, $3-4 \mu\text{m}$ in width. They are usually arranged either in two groups of two or two groups of three. The exine is ca. $1.5 \mu\text{m}$ thick in the mesopodium, with the sexine thicker than the nexine. Tectum complete, infratectum columellate; columellae difficult to observe, very short and irregularly spaced (Fig. 10). The surface ornamentation seen with the SEM is perforate and scabrate (Fig. 9).

Samples studied. — **Huelva.** Almonte, 23.3.1966, Novo (SEV 17789); entre Villablanca y San Silvestre de Guzmán, 18.5.1979, Silvestre & al. (SEV 51496).

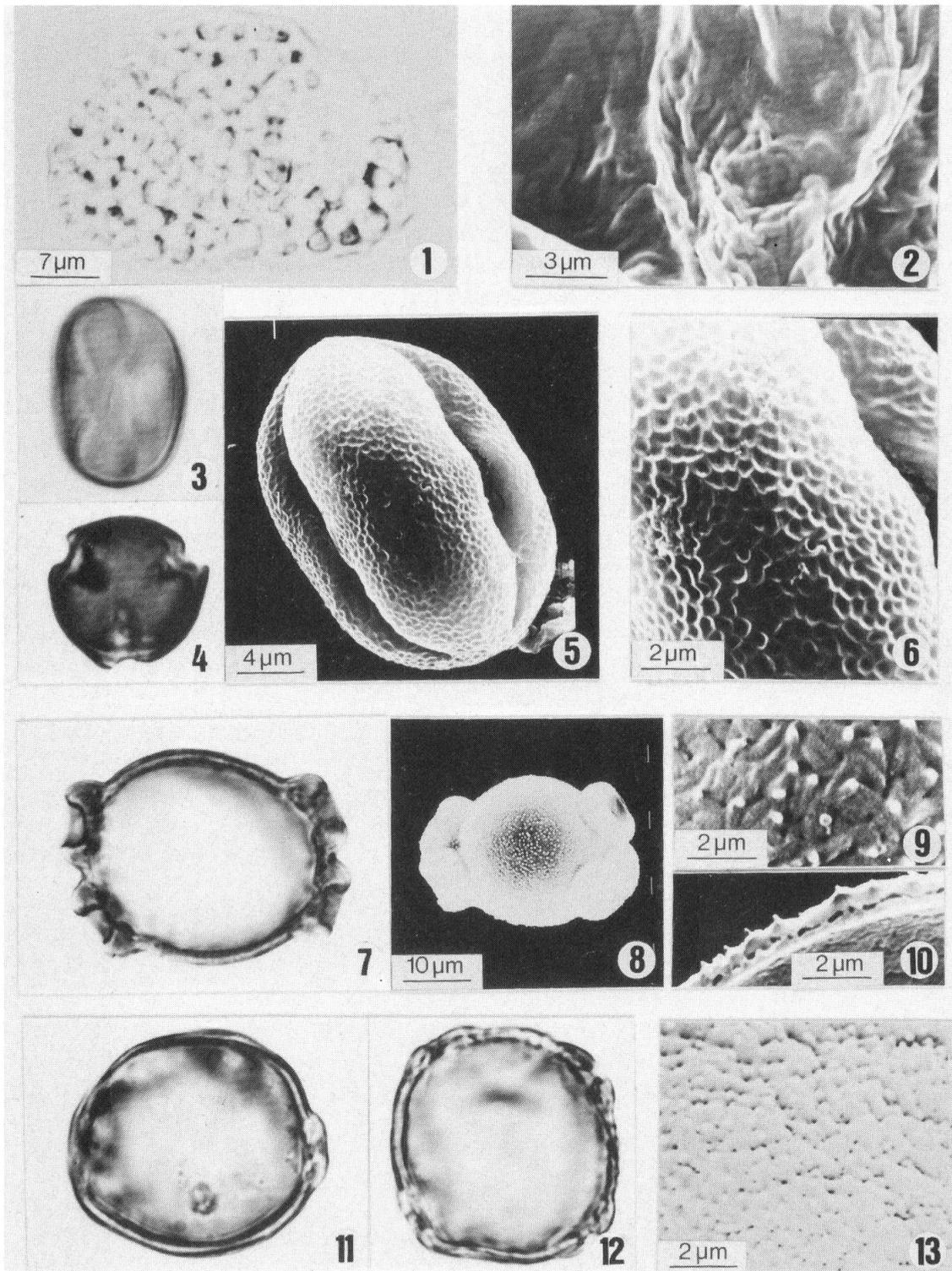
References. — WODEHOUSE (1959), ERDTMAN & al. (1961), PRAGLOWSKI (1970), NILSSON & al. (1977), MOORE & WEBB (1978), ENGEL (1980), LEWIS & al. (1983).

Myriophyllum spicatum L. (acetolysis resistant).

Pollen subisopolar (Fig. 11), radial symmetry (Fig. 12). Circular or more or less circular in m.o.c., quadrangular in e.o.c. (Fig. 12). Breviaxe, transverse-semitransverse, $P/E = 0.60-0.84$ ($\bar{X} = 0.76 \pm 0.05$). Size small-medium, $P \times E = 14-26$ ($\bar{X} = 20.54 \pm 2.95$) \times $21-33$ ($\bar{X} = 26.73 \pm 2.82$) μm . Tetrazonoporate, sometimes pentazonoporate; pores slightly elongate in meridional plane, ca. $4 \times 2 \mu\text{m}$ and surrounded by an annulus $2 \mu\text{m}$ wide. The exine is ca. $2 \mu\text{m}$ thick in the mesopodium, with sexine thicker than the nexine. Tectum complete, infratectum apparently without columellae. The surface ornamentation seen with SEM is scabrate (Fig. 13).

Samples studied. — **Huelva.** Punta Umbría, 28.6.1982, Furest & Amat (SEV 9097). **Sevilla.** Las Cabezas de San Juan, 6.11.1980, Aguilar (SEV 57658); Puebla del Río, 17.5.1979, Silvestre & al. (SEV 52579).

References. — ERDTMAN (1966), PRAGLOWSKI (1970), MOORE & WEBB (1978).



Figs. 1-2. — *Ceratophyllum submersum* L.

Figs. 3-6. — *Elatine alsinastrum* Guss.

Figs. 7-10. — *Myriophyllum alterniflorum* DC.

Figs. 11-13. — *Myriophyllum spicatum* L.

1, e.v. in m.o.c.; 2, ornamentation; 3, e.v. in m.o.c.; 4, p.v. in e.o.c.; 5, e.v.; 6, ornamentation; 7, e.v. in m.o.c.; 8, e.v.; 9, ornamentation; 10, exine; 11, e.v. in m.o.c.; 12, p.v. in e.o.c.; 13, ornamentation.

Callitriche stagnalis Scop. (only slightly acetolysis resistant).

Pollen heteropolar (Fig. 14), radial symmetry. Circular in both m.o.c. and e.o.c. (Fig. 14). Equiaxe. Size small, $D = 15-23$ ($\bar{X} = 19.98 \pm 1.88$) μm . Monoanaporate (Figs. 14 and 15); the pores are circular in shape and the margin is only indicated slightly. The exine is ca. 1 μm thick, the sexine and nexine are very difficult to discern. Tectum complete, infratectum apparently without columellae. The surface ornamentation seen with SEM is verrucose (Fig. 16).

Samples studied. — **Cádiz.** Sierra de la Gallina, 6.6.1973, Silvestre & Valdés (SEV 105232); Los Barrios, 27.3.1977, Silvestre (SEV 108656); Alcalá de los Gazules, 2.5.1980, Martínez (SEV 111953). **Huelva.** Villanueva de los Castillejos, 20.3.1976, Galiano & al. (SEV 108658).

References. — SHOSTSMAN (1954), ERDTMAN (1966).

Callitriche obtusangula Le Gall (only slightly acetolysis resistant).

Pollen isopolar (Fig. 17), bilateral symmetry. Elliptic in both m.o.c. and e.o.c. Breviaxe, pertransverse-semitransverse, $P/E_1 = 0.47-0.76$ ($\bar{X} = 0.60 \pm 0.06$). Size small-medium, $P \times E_1 = 18-28$ ($\bar{X} = 24.46 \pm 2.06$) \times $27-53$ ($\bar{X} = 40.51 \pm 5.31$) μm . Inaperturate. The exine is 1-1.5 μm thick, the sexine and nexine are very difficult to discern. Tectum partial, infratectum columellate. The surface ornamentation seen with SEM is reticulate (Fig. 18); lumina around 1 μm in size, approximately twice the width of the slightly striate muri.

Samples studied. — **Huelva.** Doñana, 24.4.1983, Smit (SEV 112056); Almonte, 24.4.1983, Smit (SEV 112058); Almonte, 28.4.1983, Smit (SEV 112059).

References. — SHOSTSMAN (1954), ERDTMAN (1966).

Callitriche brutia Petagna (only slightly acetolysis resistant).

Pollen isopolar (Fig. 19), bilateral symmetry. Elliptic in both m.o.c. and e.o.c. Breviaxe, pertransverse-transverse, $P/E_1 = 0.41-0.65$ ($\bar{X} = 0.56 \pm 0.06$), Size medium, $P \times E_1 = 18-23$ ($\bar{X} = 20.66 \pm 1.34$) \times $30-46$ ($\bar{X} = 37 \pm 4.86$) μm . Inaperturate. The exine is ca. 0.5 μm thick, the sexine and nexine are very difficult to discern. Tectum partial, infratectum columellate. The surface ornamentation seen with SEM is reticulate (Fig. 20); lumina ca. 1.5 μm in size, muri narrow and psilate; lumina/muri more than two.

Samples studied. — **Huelva.** Almonte: Doñana, 24.4.1983, Valdés (SEV 111780).

References. — None.

Ruppia cirrhosa (Petagna) Grande (only slightly acetolysis resistant).

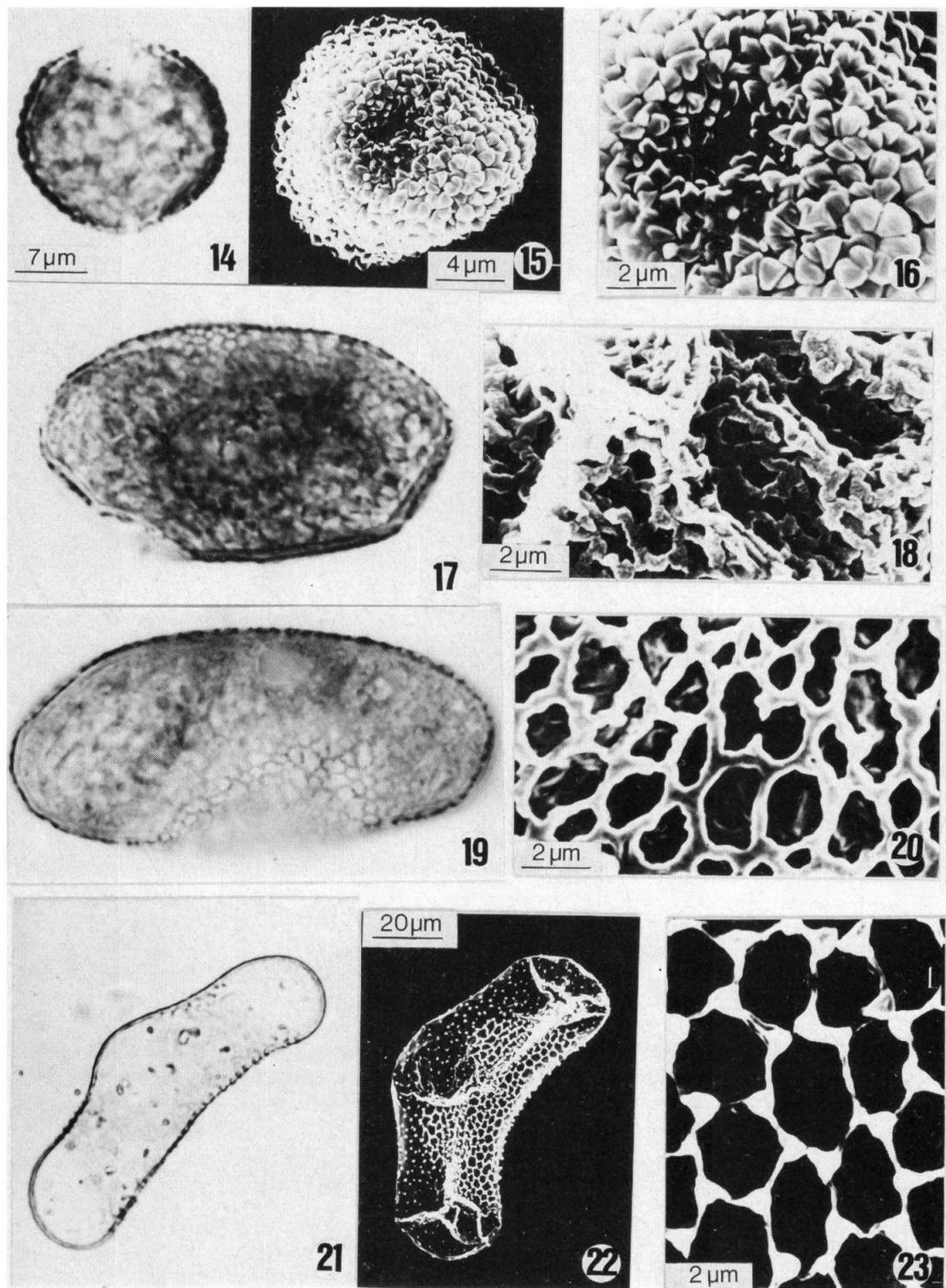
Pollen heteropolar (Figs. 21 and 22), bilateral symmetry. Faintly arcuate in m.o.c. and elliptic in e.o.c. Breviaxe, pertransverse, $P/E_1 = 0.25-0.39$ ($\bar{X} = 0.30 \pm 0.03$). Size large, $P \times E_1 = 19-33$ ($\bar{X} = 23.61 \pm 3.40$) \times $68-86$ ($\bar{X} = 75.19 \pm 5$) μm . The apertural system is reduced to three tenuous, two in the ends and one in the area at convex pole; sometimes, the three tenuous are fused forming one very large "aperture"; apertural membrane with pointed ektexinous elements. The exine is ca. 1 μm thick, the sexine and nexine are very difficult to discern. Tectum partial, columellate infratectum. The surface ornamentation seen with SEM is reticulate (Fig. 23); the lumina are 3-5 μm in size and irregular in shape; the muri are very narrow.

Samples studied. — **Cádiz.** Zahara de los Atunes, 4.5.1983, Smit, Talavera & Valdés (SEV 113571). **Huelva.** Marismas del Odiel, 12.10.1983, Barrera, García & Moreno (SEV 113566).

References. — GAMERRO (1968), VIERSSEN & al. (1982).

Potamogeton pectinatus L. (only slightly acetolysis resistant).

Pollen isopolar (Fig. 24), bilateral symmetry. Elliptic or more or less elliptic in both m.o.c. and e.o.c. Breviaxe, transverse-semitransverse, $P/E_1 = 0.62-0.82$ ($\bar{X} = 0.70 \pm 0.09$). Size medium, $P \times E_1 = 20-30$ ($\bar{X} = 26.81 \pm 1.89$) \times $32-45$ ($\bar{X} = 37.41 \pm 2.83$) μm . Inaperturate. The exine is ca. 1 μm thick, with the sexine almost twice as thick as the nexine. Tectum partial,



Figs. 14-16. — *Callitriche stagnalis* Scop.

Figs. 17-18. — *Callitriche obtusangula* Le Gall

Figs. 19-20. — *Callitriche brutia* Petagna

Figs. 21-23. — *Ruppia cirrhosa* (Petagna) Grande.

14, e.v. in m.o.c.; 15, p.v.; 16, ornamentation; 17, e.v.; 18, ornamentation; 19, e.v.; 20, ornamentation; 21, e.v. in m.o.c.; 22, e.v.; 23, ornamentation.

infratectum columellate. The surface ornamentation seen with SEM is thinly reticulate (Fig. 25); the lumina are 3-4 μm in size, irregular in shape; the muri are very narrow.

Samples studied. — **Cádiz.** Puerto Real, sin fecha, Amat & Talavera (SEV 88096). **Córdoba.** Jauja, 26.6.1982, Furest & Amat (SEV 88111). **Huelva.** Almonte: Doñana, 15.5.1966, Novo (SEV 25858); Laguna del Portil, 7.5.1982, Amat & Furest (SEV 88093).

References. — ERDTMAN & al. (1961), ERDTMAN (1966), SCHWANITZ (1967), FAEGRI & IVERSEN (1975), PETTITT & JERMY (1975).

Potamogeton lucens (L. (only slightly acetolysis resistant)).

Pollen apolar (Fig. 26), radial symmetry. Circular in o.c. Equiaxe. Size medium, $D = 26-32$ ($\bar{X} = 28.77 \pm 1.49$) μm . Inaperturate. The exine is ca. 1 μm thick; the sexine almost twice thick as the nexine. Tectum partial, infratectum columellate. The surface ornamentation seen with SEM is reticulate (Figs. 27 and 28); lumina ca. 3 μm in size, irregular in shape; muri very narrow.

Samples studied. — **Huelva.** Almonte: Doñana, 24.6.1977, Valdés-Bermejo & Castroviejo (SEV 59909); Punta Umbría, 17.7.1978, Silvestre (SEV 87897); entre Mazagón y Bodegonas, 16.4.1982, Devesa & Talavera (SEV 88449).

References. — None.

Najas marina L. (non-acetolysis resistant).

Pollen isopolar, bilateral symmetry (Figs. 29 and 30). Elliptic in both m.o.c. and e.o.c. Breviaxe, pertransverse-transverse, $P/E_1 = 0.48-0.74$ ($\bar{X} = 0.57 \pm 0.06$). Size medium-large, $P \times E_1 = 27-34$ ($\bar{X} = 31.12 \pm 2.49$) \times $47-65$ ($\bar{X} = 53.87 \pm 4.62$) μm . Inaperturate. The sporoderm is ca. 1 μm thick, without exine or with endexinous exine. The surface ornamentation seen with SEM is psilate, although the sporoderm forms a more or less verrucate surface (Fig. 30).

Samples studied. — **Cádiz.** Jerez de la Frontera, 17.6.1982, Amat & Talavera (SEV 97329).

References. — ROZE (1892), HAYNES (1977, 1979).

Althenia orientalis (Tzvelev) García-Murillo & Talavera (non acetolysis resistant).

Pollen heteropolar, radial symmetry. Circular in both m.o.c. (Fig. 31) and e.o.c. Equiaxe. Size medium, $D = 30-39$ ($\bar{X} = 33.9 \pm 6.20$) μm . The apertural system is reduced to one tenuous, more or less circular in shape, completely occupying the distal pole (Fig. 32); apertural membrane psilate, with ektexinous elements similar to rugulate. The exine is 0.5-1 μm thick, with the sexine almost twice as thick as the nexine. Tectum partial, almost absent, infratectum columellate. The surface ornamentation seen with SEM is more or less rugulate (Figs. 32 and 33).

Samples studied. — **Málaga.** Alameda; laguna de la Ratosa, 14.6.1984, Arroyo, Mejías & Talavera (SEV 102136).

References. — ERDTMAN (1966), GARCÍA-MURILLO & TALAVERA (1986).

Zannichellia peltata Bertol. (non-acetolysis resistant).

Pollen apolar, radial symmetry. Circular in o.c. (Figs. 24 and 25). Equiaxe. Size small, $D = 16-21$ ($\bar{X} = 18.35 \pm 1.25$) μm . Inaperturate. The exine is 0.5-1 μm thick, the sexine and nexine are very difficult to discern. Tectum partial, infratectum apparently without columellae. The surface ornamentation seen with SEM is reticulate (Figs. 35 and 36); the lumina are 4 μm in size; the muri are very narrow, straight and usually smooth; lumina/muri more than ten.

Samples studied. — **Cádiz.** Zahara de la Sierra: río Guadalete, 4.5.1983, Smit, Talavera & Valdés (SEV 101868)

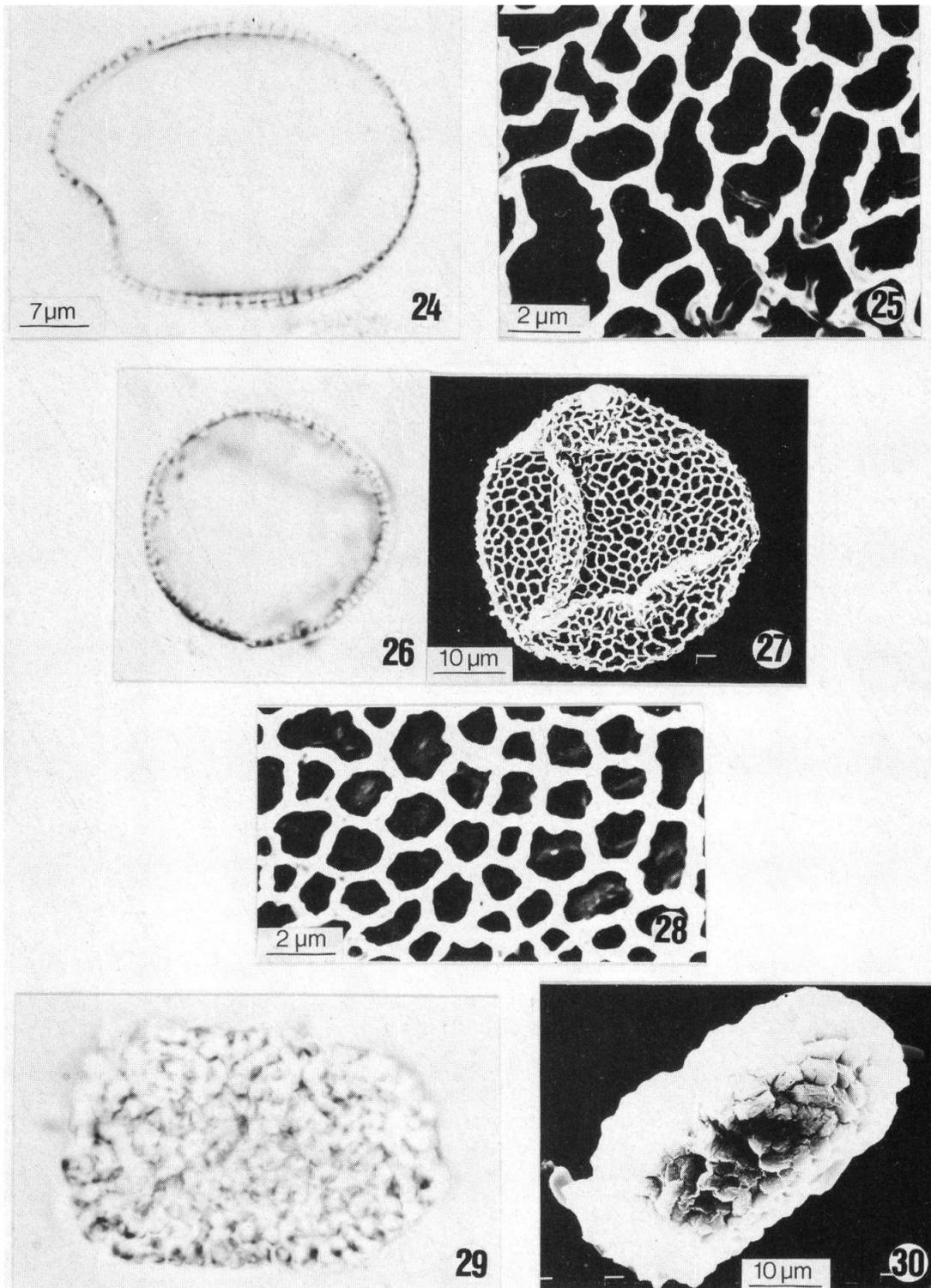
References. — VAN VIERSEN & al. (1982); TALAVERA & al. (1986).

Zostera marina L. (non-acetolysis resistant).

Pollen isopolar, bilateral symmetry. Filiform in shape (Fig. 37), more than $1.500 \times 9-10$ μm . The sporoderm is ca. 0.5 μm thick, without exine or with endexinous exine. The surface ornamentation seen with SEM is psilate (Fig. 38).

Samples studied. — **Pontevedra.** El Grove, 29.7.1972, E. Valdés (MAF 83215).

References. — WODEHOUSE (1935), ERDTMAN & al. (1961), PETTITT & JERMY (1975), COCK (1978).

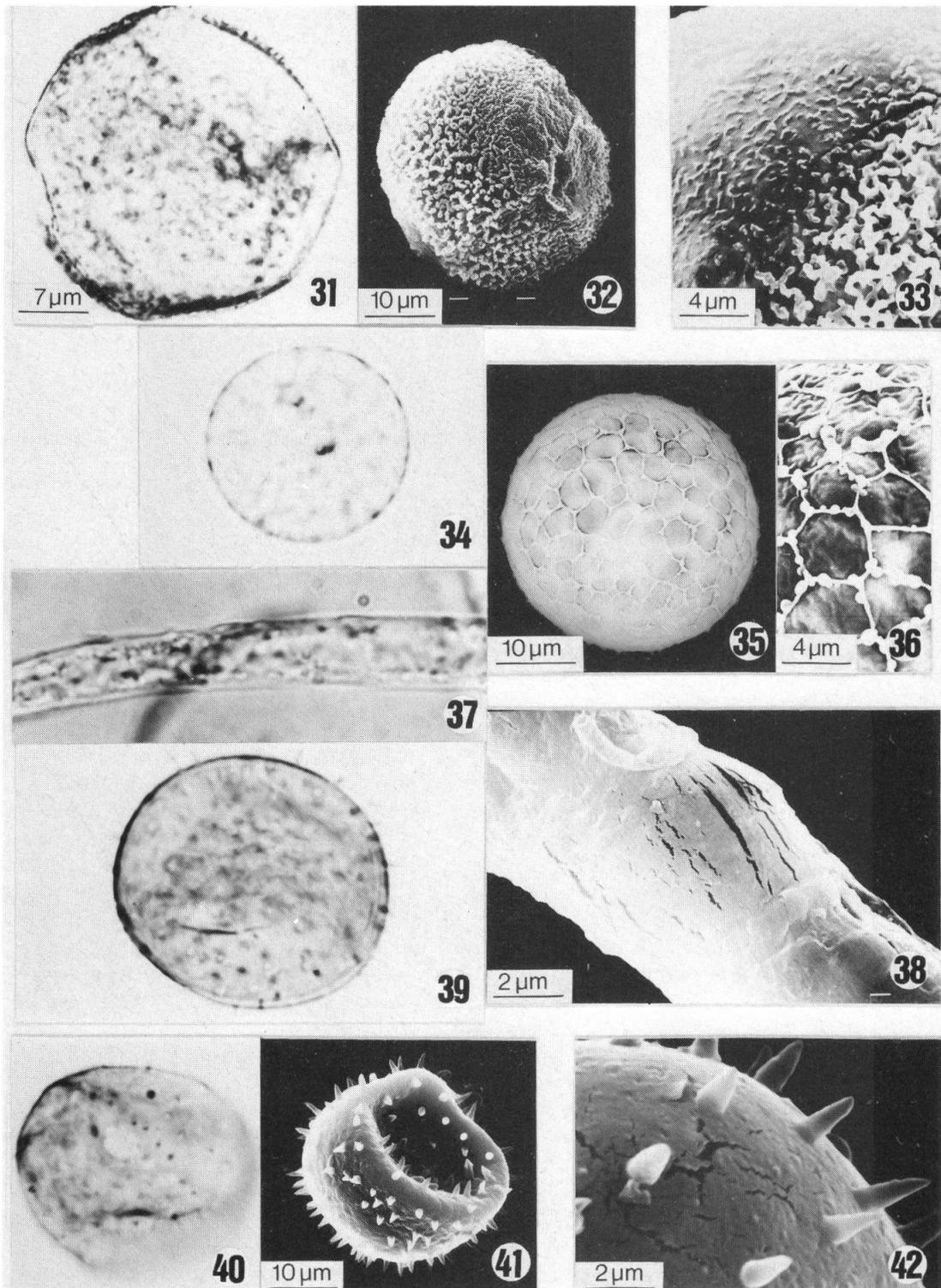


Figs. 24-25. — *Potamogeton pectinatus* L.

Figs. 26-28. — *Potamogeton lucens* L.

Figs. 29-30. — *Najas marina* L.

24, e.v. in m.o.c.; 25, ornamentation; 26, o.c.; 27-28, ornamentation; 29, e.v. in m.o.c.; 30, ornamentation.



Figs. 31-33. — *Athenia orientalis* (Tzvelev) P. García & Talavera

Figs. 34-36. — *Zannichellia peltata* Bertol.

Figs. 37-38. — *Zostera marina* L.

Figs. 39-42. — *Lemna gibba* L.

31, e.v. in m.o.c.; 32, e.v.; 33, ornamentation; 34, o.c.; 35-36, ornamentation; 37, o.c.; 38, ornamentation; 39, e.v. in m.o.c.; 40, p.v. showing the aperture; 41-42, ornamentation.

Lemna gibba L. (non-acetolysis resistant).

Pollen heteropolar, radial symmetry. Circular in both m.o.c. and e.o.c. (Fig. 39). Equiaxe. Size small-medium size, $D = 22-27$ ($\bar{X} = 24.05 \pm 1.2$) μm . Monoanaporate (Fig. 40); pore circular in shape with tenuous border. The exine is ca. $0.5 \mu\text{m}$ thick, the sexine and nexine are very difficult to discern, probably the exine is only endexinous and the ektextinous material is reduced to only the ornamental elements. The surface ornamentation seen with SEM is equinulate, with spinules $1.5-2 \mu\text{m}$ in height directly on the endexine; the space between the spinules is greater than their width (Figs. 41 and 42).

Samples studied. — **Huelva.** Sierra de Aracena: entre Las Chinas y la Nava, rivera del río Múrtigas, 7.8.1979, Rivera & Cabezudo (SEV 50184).

References. — PLA DALMAU (1961), ERDTMAN & al. (1961).

Discussion

As can be seen from the above descriptions, the pollen morphology of the 15 species of Angiosperms studied, offers further evidence of the variability of Angiosperm pollen grains, sometimes observed in species belonging to the same genus. This can be seen in the two species of *Myriophyllum* studied. *M. alterniflorum* with circular pollen grains in v.p. and e.o.c., and frequently a greater number of apertures, four or six, sometimes five or seven, grouped in two places, which are, furthermore, strongly aspidate, whilst *M. spicatum* pollen grains are quadrangular-angulaperturate, frequently with four apertures, rarely five (and these are not very significant). In the genus *Callitriche* we observe two different groups: *C. stagnalis* with spheroidal, monoporate pollen grains, belongs to the first and in the second, *C. obtusangula* and *C. brutia* with ellipsoidal, inaperturate pollen grains. The last two species can be differentiated by the ornamentation. In *C. obtusangula* both lumina and muri are ca. $2 \mu\text{m}$ in diameter and the muri are striate, whilst in *C. brutia* the diameter of the lumina is more than $2 \mu\text{m}$ and the muri are psilate. In *Potamogeton*, although the pollen grains are always inaperturate, the shape is spheroidal in *P. lucens* and ellipsoidal in *P. pectinatus*.

If we examined all the species, we can observe that practically all the characters show some degree of variability, although of these the shape, the apertural system and the exine are the most significant.

Four different types of pollen shape are observed: spheroidal or almost spheroidal, ellipsoidal in equatorial view, ellipsoidal in meridional view and filiform. The two species of *Myriophyllum*, *Callitriche stagnalis*, *Potamogeton lucens*, *Althenia orientalis*, *Zannichellia peltata*, *Lemna gibba* and some *Ceratophyllum* pollen grains are spheroidal or almost spheroidal; *Ceratophyllum submersum*, *Callitriche obtusangula*, *C. brutia*, *Ruppia cirrhosa*, *Potamogeton pectinatus* and *Najas marina* are ellipsoidal in equatorial view; *Elatine alsinastrum* pollen grains are ellipsoidal in meridional view and *Zostera marina* pollen grains are filiform.

There is more variability in the apertural system; inaperturate pollen is the predominant type; present in *Ceratophyllum submersum*, *Callitriche obtusangula*, *C. brutia*, *Potamogeton pectinatus*, *P. lucens*, *Najas marina*, *Zannichellia peltata* and *Zostera marina*; furthermore, pollen grains of these species are ellipsoidal in equatorial view. *Ruppia cirrhosa* and *Althenia orientalis* have three or one tenuous pollen grains respectively. *Callitriche stagnalis* and *Lemna gibba* have spheroidal pollen grains with one circular aperture. *Elatine alsinastrum* has three apertures, it is the only species with composite apertures. Finally the two species of *Myriophyllum* have 4-7 circular apertures.

We observed that some taxa are exineless or with endexinous exine only: *Ceratophyllum submersum*, *Najas marina* and *Zostera marina* or the exine is reduced to only the ornamental elements in *Lemna gibba*. The rest of the species have extensive exine. In most species it is reticulate with large lumina: *Callitriche obtusangula*, *C. brutia*, *Ruppia cirrhosa*, *Potamogeton pectinatus*, *P. lucens* and *Zannichellia peltata*, rarely with small lumina, *Elatine alsinastrum*. The exine in both species of *Myriophyllum* is perforate with suprategal elements; in *Callitriche stagnalis* it is verrucate and in *Althenia orientalis* it is rugulate.

Starch was found in the cytoplasm in all the species, except *Elatine alsinastrum*.

Using these characters it is possible to arrange to species studied into two groups. The first group includes those species which have inaperturate or tenuate pollen grains, elongated (*Ceratophyllum submersum*, *Callitriche obtusangula*, *C. brutia*, *Ruppia cirrhosa*, *Potamogeton pectinatus* and *Najas marina*), filiform (*Zostera marina*) and spheroidal (*Althenia orientalis*, *Zannichellia peltata* and part of *Ceratophyllum submersum*). The pollen of all these species is shed on the surface or below the water (ROZE, 1887, 1892; GAMERRO, 1968; PROCTOR & YEO, 1973; SCHOSTSMAN, 1954). Their flowers, are without or with a very reduced perianth. This type of the floral morphology and pollen morphology suggest a correlation with hydrophily. Within this group we find two groups of species. The epihydrophiles whose pollination takes place on the surface of the water as in *Potamogeton pectinatus* (PROCTOR & YEO, l.c.), *Callitriche obtusangula* and *C. brutia* (SCHOSTSMAN, l.c.) or *Ruppia cirrhosa* (GAMERRO, l.c.). In all cases the pollen grains settle on the water surface and it is noteworthy that there is a clear tendency towards lengthening of the pollen grains, a fact already observed by McLAUGIN (1974) and COX (1983). In hydrophiles like *Ceratophyllum* (ROZE, 1892), *Najas* (ROZE, 1892; HAYNES, 1977, 1979), *Zannichellia* (ROZE, 1887; TALAVERA & al., 1986) and *Althenia* (ROZE, 1887) where pollination takes place beneath the water, both elongated and spheroidal pollen grains occur. This diversity of shape in the pollen of hydrophilous plants is due to the two different stigmatic strategies for capturing pollen present in aquatic plants. Species with wide, infundibuliform or discoid stigmas such as those of *Zannichellia* (ROZE, l.c.), *Althenia* (from observations we believe that pollination in *Althenia* is similar to that in *Zannichellia*, because anthesis takes place under water, the stigmas are infundibuliform also we have never observed floating pollen grains) and *Ceratophyllum* (ROZE, l.c.) have spheroidal or spheroidal-ellipsoidal pollen grains which are captured by the stigmas sinking vertically into the water (TALAVERA & al., l.c.). In contrast species with filiform stigmas, such as *Najas* and *Zostera* have elongated pollen grains (filiform in *Zostera* and ellipsoidal becoming filiform during germination (PROCTOR & YEO, l.c.) in *Najas*). These are easily accepted by the filiform stigmas. Chemotactic factors may facilitate the rolling of the pollen grains on to the stigma (DUCKER & KNOX, 1976; PETTITT & al., 1981).

The second group comprising *Elatine alsinastrum*, *Myriophyllum alterniflorum*, *M. spicatum*, *Callitriche stagnalis*, *Potamogeton lucens* and *Lemna gibba* generally have more or less spheroidal and aperturate pollen grains (*Potamogeton lucens* and *Elatine alsinastrum* are exceptions). All these species appear to show an anemophilous syndrome, they have flowers with a distinct perianth which emerge from the water to form conspicuous spiciform inflorescences which are more or less rigid and pedunculate. *Lemna gibba* has pollen grains large spinules, which suggests entomophilous pollination as LUDWIG (in MÜLLER, 1883) states. However, the flowers are inconspicuous and naked. The male flower with one anther which protrudes out of the small spathe and the absence of lipidic coating on the surface of the pollen grains could be similar to the anemophilous flowers of other Angiosperms. On the other hand, the presence of both male and female flowers in the same spathe and the anthers above the stigma, would make possible the geitonogamy as it does in other genera of the Order *Arales* (TALAVERA, 1976) and/or an exogamy where the wind plays a possible role in the pollination of *Lemna gibba*.

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