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EMBRYOLOGICAL QUESTIONS: 13. CAN THE ATYPICAL 4-NUCLEATE EMBRYO SACS OF TAMARIX ASSIGNED TO THE PLUMBAGELLA TYPE (HAPLOID EGG) BE REINTERPRETED AS NEW TAMARIX TYPES (DIPLOID EGG)? (**)

Riassunto — *Interrogativi embriologici: 13. I gametofiti femminili atipicamente 4 nucleati, di Tamarix attribuiti al tipo Plumbagella (oosfera aploide) possono essere reinterpretati quali nuovi tipi Tamarix (oosfera diploide)?* I gametofiti femminili 4 nucleati (tricellulari) occasionalmente osservati in *Tamarix odessana* e *Tamarix parviflora* da Hjelmqvist & Grazi (1964) e da essi attribuiti al tipo Plumbagella (oosfera aploide) possono essere giustificatamente reinterpretati come i nuovi tipi Tamarix 1 oppure Tamarix 4 (oosfera diploide) a secondo del corredo cromosomico diploide oppure triploide dei due nuclei calazali.

I tipi Tamarix a causa della diploidia della oosfera sono potenzialmente apomittici. Poiché i tipi Tamarix sono stati stabiliti sulla base di reinterpretazioni dell'autore essi, attualmente, debbono essere considerati 'tipi di sviluppo del gametofito femminile in attesa di conferma'.

Abstract — The 4-nucleate and 3-celled embryo sacs occasionally observed in *Tamarix odessana* and *Tamarix parviflora* by Hjelmqvist & Grazi (1964) and assigned by these authors to the Plumbagella type (haploid egg) can be more justifiably reinterpreted as the new Tamarix 1 or Tamarix 4 types (diploid egg), according to the diploid or triploid chromosome complement of the two chalazal nuclei.

The Tamarix types owing to the occurrence of diploid egg are potentially apomictic. Since the Tamarix types are only the author's reinterpretations, at present, they must be qualified as «embryo sac types awaiting confirmation».

Key words — Angiosperm embryo sac - Plant embryology - Tamarix.

The author has assumed that the Plumbago and Plumbagella types basically would be the result of a new status of cellularization

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of the embryo sac (1) indicated as C^2 neocellularization (cf. BATTAGLIA, 1989, in preparation). The symbol C^2 has been adopted to signify that the phenomenon of cellularization of the embryo sac takes place when only 2 nuclei, instead of the usual 4 (= C^4 cellularization), are present in the micropylar part of the embryo sac.

As a regular neocellularization C^2 is strictly limited to a few genera of the Plumbaginaceae, the author has considered it necessary to check critically the attribution to Plumbagella type of some 3-celled embryo sacs which are occasionally observed in some cases apart from Plumbaginaceae, that is in a few species of the genus *Tamarix*. The embryo sac in the species of the genus *Tamarix* is tetrakaryosporic (2) and several different 8-16 nucleate types coexist in the same species as first described by the author (BATTAGLIA, 1941).

According to HJELMQVIST & GRAZI (1964), in *Tamarix odessana* and *Tamarix parviflora*, in relation to environmental variations of temperature, some 4-nucleate embryo sacs (3) (4), attributed by these authors to the Plumbagella type, would occur with the different per-

(1) For simplicity, the author adopts the terms embryo sac mother cell (E.M.C. or EMC), embryo sac (E.S. or ES) and megaspore. Nevertheless he considers the terms gynospore mother cell (Gs. M.C.), gynogametophyte (G.G.) or abbreviated gynophyte, and gynospore (Gs.), as more appropriate (cfr. BATTAGLIA, 1982).

(2) Tetrakaryosporic=Tetrasporic, cf. BATTAGLIA (1983).

(3) These 4-nucleate embryo sacs are characterized by the formule E + 2CN + A (egg cell + 2 central or polar nuclei + 1 antipodal cell). The author (cf. BATTAGLIA, 1987b) has proposed the terms central nuclei and central synkaryon in the place of today's polar nuclei and secondary nucleus.

(4) A four celled embryo sac (formula: E + 2CN + A) not ascribed to the Plumbagella type has also been found in Ulmus glabra by HJELMQVIST and GRAZI (1965). These authors write:

In one case a mature embryo sac was observed that had a peculiar structure, only 4 nuclei, one egg cell, two polar nuclei, and one antipodal (Fig. 8 *i*). Such an embryo sac is of the same organization as an embryo sac of the Plumbagella type, but a fusion of 3 nuclei according to the Bambacioni phenomenon, which is characteristic of the Plumbagella and Fritillaria types, has not been observed in the species, and nothing in the size of the nuclei indicates a precedent fusion. We should rather interpret this embryo sac as having arisen without reduction as a stage in a rare apomictic development. The meiosis is in *U. glabra* frequently

This abnormal case is very doubtful and its origin cannot be convincingly traced.

centages detailed below; cf. HJELMQVIST & GRAZI (1964) Tab. 1: p. 142; Tab. 2: p. 150; Tab. 3: p. 155.

Tab. 1. Temperature conditions (°C) the last 7 days before the fixations (according to measurements at the meteorological institute of the Geographical Institution, Lund).

	Max.	Min.	Middle		Max.	Min.	Middle
Aug. 30	17.3	11.2	14.3	Sept. 24	19.6	11.2	15.4
Aug. 31	18.2	9.8	14.0	Sept. 25	15.2	14.8	15.0
Sept. 1	15.9	13.4	14.7	Sept. 26	12.9	8.8	10.9
Sept. 2	18.3	12.2	15.3	Sept. 27	12.5	9.2	10.9
Sept. 3	21.6	13.8	17.7	Sept. 28	13.6	8.9	11.3
Sept. 4	17.7	11.0	14.3	Sept. 29	11.5	8.0	9.8
Sept. 5	19.1	11.2	15.2	Sept. 30	12.5	9.2	10.9

Tab. 2. Embryo sac types of Tamarix odessana at the two fixation dates.

Type	Sept. 5			Sept. 30		
	Early 4-nucl. stage	Later stages		Early 4-nucl. stage	Later stages	
		Number	Per cent		Number	Per cent
Fritillaria type		71	43		45	46
Chrys. cinerariifolium type	18	41	25	5	11	11
Drusa type		5	3		—	—
Plumbagella type		1	1		2	2
Adoxa type	4	48	29	3	40	41
Total	22	166	—	8	98	—

Tab. 3. Embryo sac types of Tamarix parviflora at different temperatures.

	About 25°C		About 15°C	
	Number	Per cent	Number	Per cent
Adoxa type	31	25	34	28
Fritillaria type	37	30	40	33
Chrysanthemum cinerariifolium type	37	30	14	12
Plumbagella type	3	2	14	12
Transitions between Fritillaria and Plumbagella types	4	3	12	10
Drusa type	3	2	—	—
Unclassified 4-nucleate embryo sacs with 1 : 3 arrangement	8	7	6	5
Total	123	—	120	—

In this connection the author has some critical observations to make, namely:

a) Are the 4-nucleate (3-celled) embryo sacs observed in *Tamarix* convincingly assignable to the Plumbagella type?

b) Which cytological abnormalities have induced the occurrence of a C^2 neocellularization in these embryo sacs?

The answer to the first question, which obviously conditions the legitimacy of the second, can only be carried out by a detailed cytomorphological examination of the embryo sacs ascribed to the Plumbagella type, cf. Plate 1.

It is almost superfluous to point out that HJELMQVIST & GRAZI (1964) interpreted these embryo sacs as the result of a cellularization which had already taken place during that stage of the embryo sac development, well known as the «secondary tetranucleate» stage[5].

The author on the other hand, taking into account the nuclear size and the number and nucleolar volume of these 4-nucleate embryo sacs, has reached a completely different interpretation.

Plant embryologists who have investigated the genus *Tamarix*, have always represented the haploid micropylar nuclei of the embryo sacs as having only one nucleolus each, cf. JOSHI & KAJALE (1936), MAURITZON (1936), PURI (1939), SHARMA (1939), PAROLI (1939), BATTAGLIA (1941), JOHRI & KAK (1954) etc.

On the contrary the micropylar nuclei of the 4-nucleate embryo sacs ascribed by HJELMQVIST & GRAZI to the Plumbagella type show

(5) This 4-nucleate stage is characterized by the formula 2'+2''', that is 2 micropylar haploid nuclei + 2 chalazal triploid nuclei.

PLATE I

Tamarix parviflora: figs. 5b, 5c, 5e, × 1020, from Hjelmqvist & Grazi (1964); figs. 1A, 1B, 1C, from Hjelmqvist (1967).

Tamarix odessana: figs. 3c, 3d, × 1020, from Hjelmqvist & Grazi (1964).

Tamarix pentandra: fig. 98, × 719, from Johri & Kak (1954, p. 243): «Embryo sac showing 1 large (diploid) micropylar and 2 smaller (haploid) chalazal nuclei».

Tamarix gallica: fig. 27, from Paroli (1939), p. 17: «Stadio con 3 nuclei dei quali 2 piccoli, macrosporiali, alla calaza ed 1 grande, probabilmente derivato dalla fusione degli altri 2 nuclei macrosporiali, verso il centro del sacco embrionale.

Figs. 5e, 98, 27. Embryo sacs showing 1 large (diploid) micropylar nucleus and 2 smaller (haploid) chalazal nuclei. Post-meiotic stage: 1''+2', cf. Text.

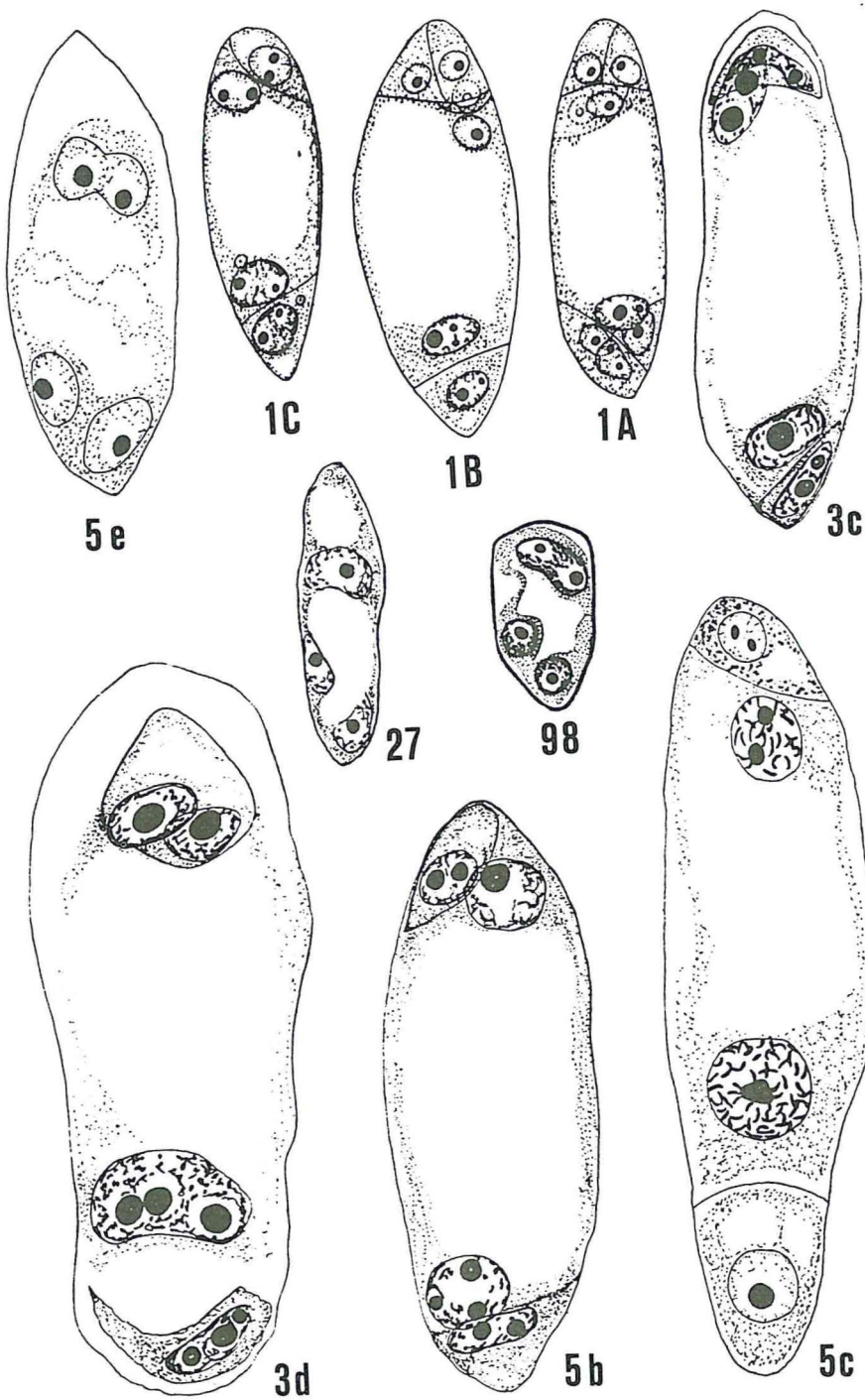
Fig. 1A. 8-nucleate embryo sac (Euphorbia dulcis type).

Fig. 1B. 6-nucleate embryo sac (Euphorbia type, 6-nucleate subtype).

Figs. 1C, 3c. Embryo sacs showing diploid egg cell + 2 diploid central nuclei + diploid antipodal cell. Formula: E''+2CN''+A''.

Figs. 5b, 5c, 3d. Embryo sacs of questioned interpretation, cf. Text.

PLATE I



2 nucleoli and a size larger than the size usual shown by the haploid micropylar nuclei of the *Tamarix* embryo sac. This worthwile difference can only mean that these nuclei are diploid.

On this basis the genesis for these embryo sac, according to the author, would be as follows:

a) 2+2 polarization of the spore nuclei; formula: 2'+2';

b) nuclear fusion of the 2 pair nuclei that is 2'+2' → $\hat{2}+\hat{2}$ → 1''+1'' (= «secondary binucleate» stage) (6);

c) first post-meiotic division followed by cellularization of the ES according to the formula 1''+1'' → 2''+2'' → E''+2CN''+A'' (7), cf. Plate 3, Tamarix 1 type.

The reliability of this interpretation is justified by the following considerations:

1) In the genus *Tamarix*, after an abnormal post-meiotic polarization 2'+2' (instead of the usual 1'+3'), the occasional nuclear fusion of the 2 micropylar nuclei, that is 2'+2' → $\hat{2}'+2'$ → 1''+2', has been observed by Paroli (1939, fig. 27 in *Tamarix gallica*), Johri & Kak (1954, fig. 98 in *Tamarix pentandra*) and Hjelmqvist & Grazi (1964, fig. 5e in *Tamarix parviflora*), cf. Plate 1;

2) A 1''+1'' stage, namely a binucleate stage characterized by dumb-bell shaped nuclei, cf. Tamarix 1 type (Plate 3) has been observed by the author in *Tamarix parviflora*. This observation which took place over 46 years ago has remained unpublished because after the embryological investigations on *T. gallica* and *T. africana* (Battaglia, 1941) the author had no opportunity to complete also the embryological investigation on *T. parviflora* owing to the state of war.

3) Hjelmqvist (1967, in *T. parviflora*) describes his figures 1A, 1B, 1C (cf. Plate 1) thus:

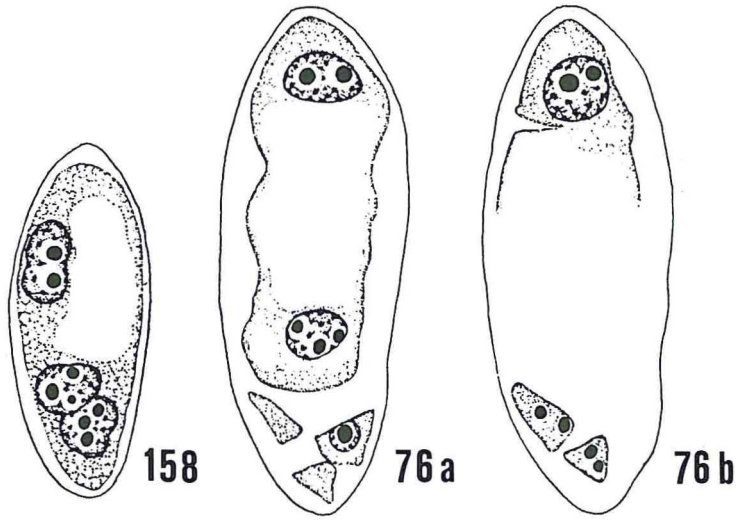
Figs. 1A-C - *Tamarix parviflora*, mature embryo sacs. *A*. Fritillaria type. *B*. Transitional type with reduction in the basal part. *C*. Plumbagella type (exceptionally with two micronuclei).

The author is not in agreement as regards the interpretation of fig. 1C. In fact since the 4 micropylar nuclei of figs. 1A & 1B, which show only one nucleolus each, are certainly haploid, the 2 micropylar nuclei of fig. 1C, characterized by larger size and two nucleoli each, cannot be considered haploid as well. Supposing that

(6) The sign ˆ has been chosen to indicate «nuclear fusion» (in a resting stage or in division); 2'=two haploid nuclei; 1''=one diploid nucleus.

(7) E''=diploid egg cell; 2CN''=two diploid central (polar) nuclei; A''=diploid antipodal cell.

PLATE II



Tamarix africana: fig. 158, × 800; from Battaglia (1941).
Tamarix gallica: fig. 76a, 76b, × 800; from Battaglia (1941, p. 588).

Fig. 158. Tri-nucleate embryo sac showing one dumb-bell shaped diploid sub-micropylar nucleus and two triploid chalazal nuclei. Stage 1''+2'''; cf. Text.

Figs. 76a, 76b. Six-nucleate embryo sac; stage 2''+4''', formula E''+CN''+CN'''+3A'''=diploid egg cell + diploid upper central nucleus + triploid lower central nucleus + 3 triploid antipodal cells, cf. Text.

the two chalazal nuclei of fig. 1C are diploid, a reasonable genesis of this embryo sac would be:
2'+2' (primary tetranucleate) → $\hat{2}'+\hat{2}'$ → 1''+1'' → 2''+2'', see Tamarix 1 type, Plate 3).

On the other hand, supposing that the 2 chalazal nuclei are triploid, the only genesis possible as regards this embryo sac, would be:
1'+3' (primary tetranucleate stage) → 2'+2''' (secondary tetranucleate stage) → $\hat{2}'+2'''$ → 1''+2''' (tri-nucleate stage) → 2''+2''' (tetranucleate stage owing to the failure of division of the chalazal nuclei), cf. Tamarix 4 type (Plate 3).

4 and 5) Hjelmqvist & Grazi (1964, *T. odessana*) ascribe to the Plumbagella type the two embryo sacs documented in their figs. 3c, 3d, cf. Plate 1.

Let us examine first the case of fig. 3d. As regards the 4 nuclei of this embryo sac the nuclear size and the number of nucleoli cor-

respond exactly with what is usually seen in the secondary tetranucleate stages (2'+2''') of this species, cf. HJELMQVIST & GRAZI (1964, p. 143). Assuming that after this stage cellularization takes place, the attribution of fig. 3d to the Plumbagella type would obviously be correct. However the author in his investigations on *Tamarix gallica* and *Tamarix africana* (BATTAGLIA, 1941) has sometimes noticed identical stages to those in Fig. 3d. Nevertheless these stages belonged to usual 8-nucleate embryo sacs (cf. Euphorbia dulcis type, BATTAGLIA, 1986b) subdivided into two subsequent sections. The first section contained the egg cell + two central nuclei + one antipodal cell (=E'+CN'+CN'''+A'''), as in the fig. 3d; the second section 2 synergids + 2 antipodal cells (=2S'+2A'''). The author favours the reinterpretation of fig. 3d as one of these cases on the basis of the shape of the upper part of the central cell, cf. fig. 3d. Indeed, if fig. 3d really documented the cellularization of a secondary tetranucleate stage the shape of the upper part of the central cell should be the same, or very similar, to that illustrated in fig. 1c, see Plate 1. On the contrary in fig. 3d the rather convex shape of the upper part of the central cell, entirely corresponds to the usual shape of the central cell of the 8-nucleate embryo sacs. Moreover in fig. 3d the egg cell has the pear-shaped appearance, typical of an egg-cell contiguous to 2 synergids. Consequently the author cannot consider fig. 3d as a reliable documentation of the occurrence of the Plumbagella type in *Tamarix odessana*.

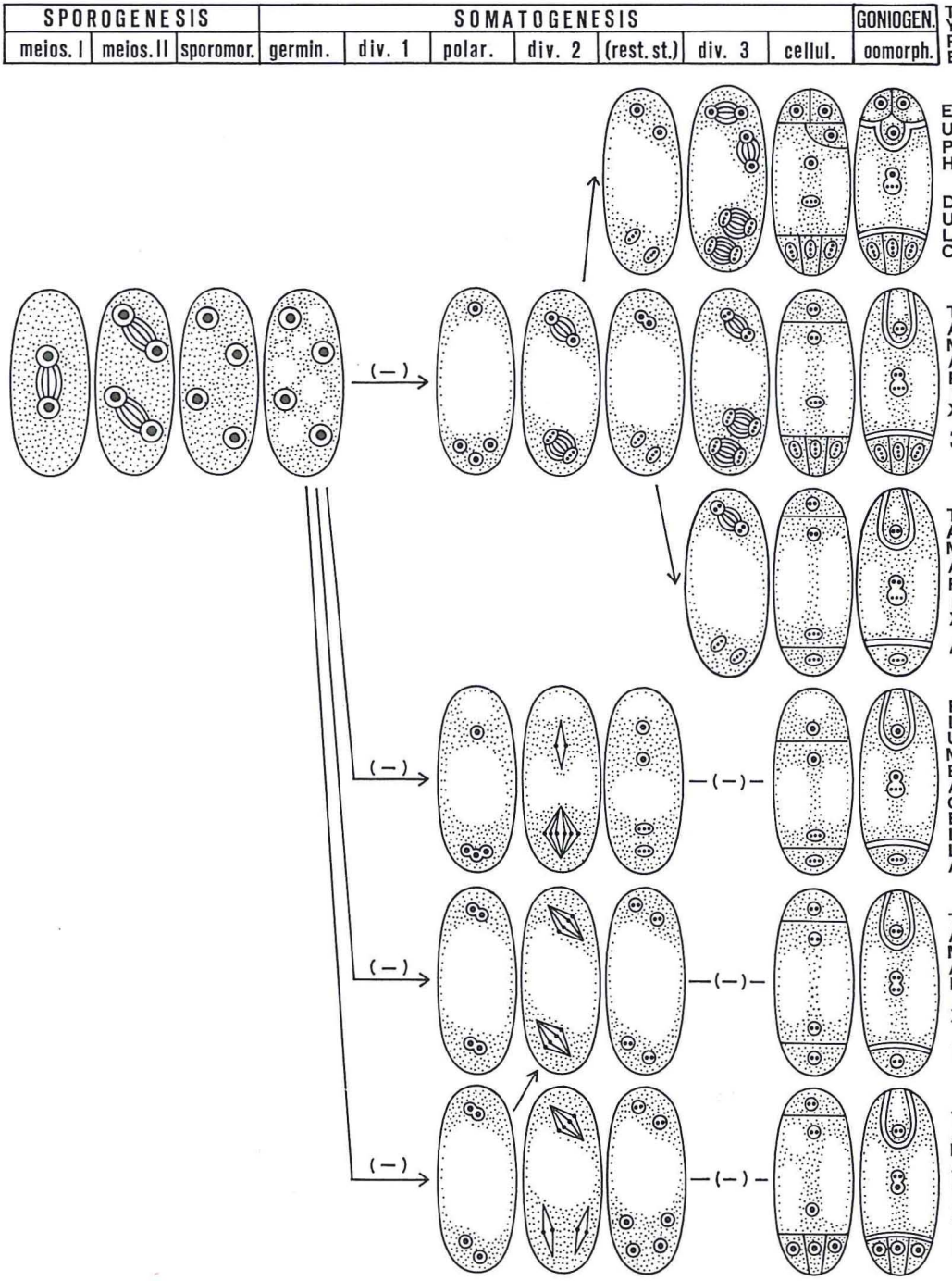
The case of fig. 3c is morphologically identical to the case of fig. 1c, discussed earlier. Therefore the author thinks that the more correct interpretation would be a 4-nucleate stage assignable to the Tamarix 1 type, or perhaps to the Tamarix 4 type, cf. Plate 3, owing to the uncertainty about the chromosome number of the chalazal nuclei.

PLATE III

Schemes of the embryo sac types discussed in the text.

The female gametophyte has been interpreted according to the gynogonial (archegonial) disappearance theory (cf. Battaglia 1951, 1963, 1980b, 1983) Meios. I = first meiotic division; meios. II = second meiotic division; sporomor. = sporomorphogenesis = spore differentiation; germin. = germination (formerly called vacuolization, cf. Battaglia 1951 or Growth, cf. Battaglia 1963); div. 1 (2) = first (second) somatogenic division; (rest. st.) = resting stage, a regular stage drawn only for didactic purposes; div. 3 = third somatogenic division; cellul. = Cellularization (formerly called wall formation, cf. Battaglia 1951, 1963); Goniogen. = Goniogenesis (cf. Battaglia 1980b, formerly called gametogenesis, cf. Battaglia 1951, 1963); oomorph. = oomorphogenesis. In all drawings a single nucleolus symbolizes the reduced (haploid) chromosome complement; two nucleoli the unreduced (diploid) chromosome complement etc. The sign (—) or (⟶) signifies suppression of division, cf. Battaglia, 1986 a.

PLATE III


SPOROGENESIS
SOMATOGENESIS
GONIOGEN.
TYPE
meios. I
meios. II
sporomor.
germin.
div. 1
polar.
div. 2
(rest. st.)
div. 3
cellul.
oomorph.
EUPH. DULC.
TAMARIX 3
TAMARIX 4
PLUMBAGELLA
TAMARIX 1
TAMARIX 2
(–)

6) The case of fig. 5b (*Tamarix parviflora)* is described by HJELMQVIST & GRAZI (1964) as «Mature embryo sac of the Plumbagella type». According to the author, on the contrary, the 2 micropylar nuclei are diploid and the 2 chalazal nuclei probably triploid (occurrence of 3 nucleoli in one of the chalazal nuclei), see Plate 3, Tamarix 4 type.

7) HJELMQVIST & GRAZI (1964, p. 152) ascribe to the Plumbagella type the case of fig. 5c (*Tamarix parviflora*). They write: «The Plumbagella type, only rarely met with in *Tamarix odessana,* occurred here in several cases (Fig. 5b, c), and in two of them the chromosomes were visible in the two polar nuclei and there proved to be about 3 times more in the lower than in the upper polar nucleus, which gave a certain proof of the presence of the Plumbagella type. In some cases the two upper nuclei in this type were about as big as the lower ones and had 2 nucleoli».

Apart from the fact that this last sentence is in itself a good reason for excluding the occurrence of the Plumbagella type, the author, on the basis of a morphological comparison, cannot consider *convincingly* haploid the two micropylar nuclei of fig. 5c. Moreover the «prophasic» aspect with which the two presumed polar nuclei have been depicted, is absolutely abnormal and unique in the embryological literature. Consequently the author considers the case of fig. 5c as a very rare anomaly and in any case not a *reliable documentation* of the occurrence of the Plumbagella type in *Tamarix parviflora.*

8) HJELMQVIST & GRAZI (1964) report, without documentation, that they observed in *T. parviflora* the occasional fusion of the 2 chalazal nuclei after a post-meiotic polarization 2+2. They also report the case of fig. 5e (Plate 1, compare with figs. 98 and 27) which according to the author is an example of a fusion, in a primary tetranucleate stage, polarized 2+2, of the two micropylar nuclei. On the contrary, HJELMQVIST & GRAZI (1964, p. 154), think that in fig. 5e the two chalazal nuclei, probably, have also been preceded by nuclear fusion; in fact they write:

> **An instance of such a fusion is shown in Fig. 5 *e*, where in a 4-nucleate embryo sac a fusion takes place between the two micropylar nuclei. The embryo sac is here possibly otherwise of Adoxa type, but it is perhaps more probable, with respect to the size and shape of the basal nuclei, that also these have resulted from a fusion, with a subsequent division. In one case, as a matter of fact, a 4-nucleate embryo sac of Adoxa type was observed, where the two basal nuclei were in fusion. In any case we have here an instance of automixis, the further development of which, however, is unknown.**

9) It is worth noting that HJELMQVIST & GRAZI (1964, p. 152), admit the possibility of the formation of 6-nucleate embryo sac with two micropylar diploid nuclei and four chalazal haploid nuclei, see Tamarix 2 type, Plate 3. HJELMQVIST & GRAZI write:

Also in the Adoxa type a reduction sometimes occurred of the nuclear number, so that the embryo sac was 6-nucleate. The reduction could here also occur either in the basal or the apical part, but was in both cases rare. A few embryo sacs were thus, observed where there were only two nuclei in the upper part. That these correspond to megaspore nuclei cannot, however, be maintained with certainty. In two of the cases the nuclei were big and 2-nucleolate, and with respect to the fusion phenomena that have been observed (see below) it is not impossible that here first there has been a fusion between two megaspore nuclei and after that a division. In two other cases the nuclei of the

HJELMQVIST & GRAZI (1964, p. 154) admit also the possibility of the fusion of two micropylar nuclei «also in the 4-nucleate embryo sacs classified as the Plumbagella type»; they, in fact, write:

As mentioned above, it is not impossible that similar fusions may have taken place in embryo sacs referred to the Adoxa type, and also in the 4-nucleate embryo sac classified as the Plumbagella type the nuclei of the apical part are often big and 2-nucleolate, so that it could be conceivable that they had arisen through a fusion and subsequent division. In such a case these embryo sacs should not belong to the Plumbagella type, but represent another, possibly auto- or apomictic development. The only cases that could be analyzed with certainty of these 4-nucleate embryo sacs proved, however, to belong to the Plumbagella type.

10) In his embryological researches on the genus *Tamarix* (1941), the author did notice two anomalous embryo sacs which deserve mention because they also confirm the possibility of the fusion of two micropylar nuclei ([8]).

([8]) This phenomenon is usually called *automixis* (THOMAS, 1940). Because Thomas was unaware of a formerly use of this term by HARTMANN (1909, Automixis: 1. Paedogamie, 2. Autogamie, 3. Pseudogamie; see also BATTAGLIA 1986a), the equivalent term *synkaryogenesis* (that is diploidization by synkaryogenesis), suggested the author in 1963, seems to be preferable.

In *Tamarix africana* the author observed a 3-nucleate stage cf. fig. 158, Plate 2, convincingly explainable in the following way: 2'+2''' (secondary tetranucleate) → $\hat{2}$'+2''' → 1''+2''' (see fig. 158, and Tamarix 3 and 4 types, Plate 3) ([9]).

The second anomalous case, see figs. 76a, 76b (*T. gallica*), Plate 2, can be now classified as Tamarix 3 type, cf. Plate 3, because it probably consists of 2 micropylar diploid nuclei + 4 chalazal triploid nuclei (1 lower central nucleus + 3 antipodal cells) ([10]).

The above observations justify the following conclusions:

— the 4-nucleate, later 3-celled, embryo sacs (E+2CN+A) occasionally observed in Tamarix odessana and Tamarix parviflora by HJELMQVIST & GRAZI (1964) and assigned by these authors to the Plumbagella type (haploid egg) are more likely classifiable as Tamarix 1 or Tamarix 4 type (diploid egg), according to the diploid or triploid chromosome set of the two chalazal nuclei (cf. antipodal cell and lower central nucleus;

— the status «2 diploid micropylar nuclei» is physiologically efficient to induce the cellularization of the embryo sac and therefore can be defined as neocellularization $C^{2''}$ (C=cellularization, 2''=two diploid nuclei). The cellularization $C^{2''}$ can be considered as intermediate between the usual cellularization $C^{4'}$ (occurrence of four haploid micropylar nuclei) and the cellularization $C^{2'}$ (occurrence of two haploid micropylar nuclei) recorded in the Plumbago & Plumbagella types only);

— the Tamarix types (cf. Plate 3) owing to the occurrence of diploid egg are potentially apomictic;

([9]) The author (BATTAGLIA 1941, p. 610) wrote: «Stadio tetranucleato secondario (Euphorbia dulcis) con i due nuclei micropilari in fusione».

([10]) The author (BATTAGLIA 1941, p. 588) wrote:

Nelle figg. 76 *a* e *b* ho riportato un gametofito nel quale si sono già separati sotto forma di cellule antipodali tre nuclei calazali probabilmente triploidi (tipo *Euphorbia dulcis*), mentre il quarto si comporta già come un unico nucleo polare inferiore (triploide) di una cellula proendospermatica non ancora perfettamente individuata; al micropilo in un citoplasma che inizia la sua divisione in cellule si trovano due voluminosi nuclei con due nucleoli ciascuno, certamente poliploidi (diploidi) e derivati probabilmente da precedenti fusioni di nuclei micropilari.

— since the Tamarix types are only the author's reinterpretations, at present, they must be qualified as «embryo sac types awaiting confirmation».

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