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E. BATTAGLIA (*)

# EMBRYOLOGICAL QUESTIONS: 16. UNREDUCED EMBRYO SACS AND RELATED PROBLEMS IN ANGIOSPERMS (APOMIXIS, CYCLOSIS, CELLULARIZATION...).

*Dedicated to the memory*
*of*
Prof. ALBERTO CHIARUGI
(1901-1960)

**Riassunto** — L'autore descrive dettagliatamente lo sviluppo e la morfologia (accertando inoltre le relative priorità) dei tipi ricorrenti di gametofito femminile angiospermico a corredo cromosomico non-ridotto. Tale analisi coinvolge necessariamente una preliminare riconsiderazione critica di numerose questioni relative ai concetti di spora, aposporia, apogamia, apomeiosi, ameiosi, apomissia, endosperma («trofofito») etc.

Si rivendica a WILHEM HAACKE (1893) la paternità sul termine apomissia ed a RENÉ MAIRE (1900) la prima reinterpretazione (in sede botanica) di tale termine. Non si accoglie l'uso (assai corrente) di termini quali diplosporia e apomissia gametofitica.

Viene valorizzata l'importanza del fenomeno (fino ad oggi minimizzato od ignorato, con riferimento al gametofito femminile) della ciclosi (correntemente «cytoplasmic streaming») endogametofitica a cui si attribuisce anche la responsabilità dell'incontro (seguito da fusione) dei nuclei polari («nuclei centrali») dando così origine al nucleo secondario («sincario centrale») del gametofito femminile maturo.

Viene descritto il meccanismo della cellularizzazione del gametofito femminile, sulla base dei dati della citologia classica, ma contemporaneamente si evidenzia la

(*) Dipartimento di Biologia Vegetale, Università «La Sapienza», Roma.

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necessità di un dettagliato riesame del fenomeno sulla base di tecniche moderne (TEM, fluorescenza etc.) *utilizzate congiuntamente e comparativamente* alle metodologie classiche.

Allo scopo di fornire una descrizione più ampia della variabilità embriologica relativa ai gametofiti femminili angiospermici non-ridotti, ed al tempo stesso per proporre una guida per future reinvestigazioni, vengono riassuntivamente analizzati (ed eventualmente reinterpretati) casi tanto classici e dubbi quali la divisione pseudoomeotipica (GUSTAFFSON) e la meiosi endo-duplicazionale (HÅKANSSON & LEVAN) quanto casi semplicemente occasionali, o comunque non ricorrenti, ascritti a fenomeni diversi di «diploidizzazione» (sensu lato) intrameiotica od intragametofitica (quest'ultimi, inesattamente secondo l'autore, attribuiti ad automissia).

**Abstract** — The author critically discusses the following topics:

## I. INTRODUCTION

## II. TERMINOLOGY AND RECOMMENDED DEFINITIONS

1. Basic type, main type, recurrent type, form and rearranged form.
2. Amphimixis (WEISMANN, 1891) and apomixis (HAACKE, 1893 *a*, *b*; MAIRE, 1900 *a*, *b*; WINKLER, 1906).
3. Apomixis referred to the egg.
4. Mixis and apomixis referred to the female gametophyte: dimictic, monomictic and apomictic embryo sacs.
5. A re-evaluation of the gamy-terminology (eugamy, aneugamy, apogamy...).
6. Criticism of the expression «gametophytic apomixis».
7. Criticism of the use of the term endosperm (secondary endosperm) in angiosperm embryology and its substitution by PEARSON's (1909) trophophyte. Zygotrophophyte and apozygotrophophyte.
8. Definition of the concept of spore and the related term apospory (VINES, 1878; DRUERY, 1885 *a*, *b*; BOWER, 1885).
9. The concept of spore conditioned by the occurrence of meiosis. CHIARUGI's (1926) distinction between «aposporia goniale» and «aposporia somatica». ROSENBERG's (1930) «generative» and «somatische Aposporie».
10. Criticism of the term «Diplosporie» (EDMAN, 1931).
11. Apomeiosis and ameiosis.
12. The relative uselessness of the term apospory and its derivatives (e.g. euapo-, pseudoapo- and hemiapo-spory).

13. Misuse of the non-synonymous terms meiosis and chromosome reduction, and apomeiosis and apospory.
14. Extension of the monokaryosporic and dikaryosporic terminology to non-reduced embryo sacs.

## III. Preliminary cytological considerations

1. Cytoplasmic cyclosis (protoplasmic streaming) and the related nuclear movement: a widely overlooked biological phenomenon occurring within the embryo sac.
2. Cellularization of the embryo sac: a cytological pattern requiring more detailed reinvestigation (e.g. by fluorescence microscopy coupled with electron microscopy).
3. The extent of correspondence between the cellularization pattern of the embryo sac and the post-meiotic simultaneous cytokinesis of female and male sporocytes. The rediscovery of the Helleborus type of ES development (cf. Mottier, 1897) e.g. a secondary monokaryosporiality owing to post-meiotic simultaneous cytokinesis.
4. Cellularization of the four-nucleate micropylar region of the embryo sac and of any four-nucleate coenocytic embryo sac (attaining the 4+0 nuclear polarization), according to the formulae «2S+E+CN» (ordinarily), «S+E+2CN» (occasionally), «E+3CN» (rarely) and «4CN» (rarely, non-recurrent anomaly: lack of embryo).

## IV. Recurrent types of unreduced embryo sac: recognized types

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|---|---|
| Ameiotic types: | IVa. HIERACIUM TYPE; |
| | IVb. PENNISETUM (PANICUM) TYPE; |
| Apomeiotic types: | IVc. ANTENNARIA TYPE; |
| | IVd. ERAGROSTIS TYPE; |
| Aneumeiotic types: | IVe. TARAXACUM TYPE; |
| | IVf. IXERIS TYPE. |

IVa. *HIERACIUM TYPE (ameiotic ES, 8-nucleate).*

IVb. *PENNISETUM TYPE (ameiotic ES, 4-nucleate; cf. Panicum type in Battaglia, 1963).*

1. The present Pennisetum type (ex-Panicum) and the question of Narayan's priority (1951: Pennisetum) versus Warmke's priority (1952, 1954: Panicum).
2. The Ph. D. thesis by Narayan (1951) and the validity of the Pennisetum (villosum) type.
3. The morphology of the ameiotic 4-nucleate Pennisetum (ex-Panicum) type. Regular occurrence of a mature ES showing the 4-celled form «2S+E+CN».
   Simultaneous development and coexistence, in the same ovule, of 4-nucleate (Pennisetum type) and 8-nucleate (Hieracium type) embryo sacs. Discovery of the cellularization processes corresponding to the formulae «S+E+2CN» (occasionally: 3-celled form) and «E+3CN» (rare: 2-celled form). Occurrence and meaning of the very rare non-celled ES (formula: 4CN).
4. Occurrence of the Pennisetum (ex-Panicum) type among plants retaining apomictic embryony.

IVc. *ANTENNARIA TYPE (apomeiotic ES, 8-nucleate).*

IVd. *ERAGROSTIS TYPE (apomeiotic ES, 4-nucleate).*

1. The development and morphology of the apomeiotic 4-nucleate Eragrostis type. Occurrence of the cellularization processes corresponding to the formulae 2S+E+CN (4-celled form: most cases) and S+E+2CN (3-celled form: very rare).
2. Occurrence of the Eragrostis type among plants retaining apomictic embryony.

IVe. *TARAXACUM TYPE (aneumeiotic ES, 8-nucleate, monokaryosporic).*

1. Restitution nucleus: definition.
2. Restitution nucleus: other interpretations and symbols.
3. Semiheterotypic division, restitution nucleus and the priority over the Taraxacum type.
4. Restitution nucleus: the need for further modern reinvestigation.
5. Occurrence of the Taraxacum type among plants retaining apomictic embryony.

IVf. *IXERIS TYPE (aneumeiotic ES, 8-nucleate, dikaryosporic).*

V. RECURRENT TYPES OF UNREDUCED EMBRYO SAC: DOUBTFUL CASES.

Va. *GUSTAFFSON'S* (1934) PSEUDOHOMOTYPIC DIVISION (type B in Battaglia, 1963).

Vb. *HÅKANSSON & LEVAN'S (1957) ENDO-DUPLICATIONAL MEIOSIS (Allium nutans types I & II in Battaglia, 1963).*

1. *Allium nutans types I & II: criticism and reinterpretation.*
2. *Allium odorum type versus Allium nutans type. Proposal for a new typology: Allium I type («reduced-tetraploid» & recurrent) and Allium II type («reduced-octoploid» & non-recurrent).*

*VI.* A SHORT LOOK AT THE NON-RECURRENT TYPES

VIa. *Datura type.*

VIb-VIe. *Rudbeckia I-IV types.*

VIf-g. *Antennaria carpatica I-II types*

VIh. *Leontodon II type*

VIi. *Instances of post-meiotic chromosome doubling or endogametophytic diploidization («Automixis», «Synkaryogenesis»).*

VII. SIMPLIFIED AND INTERPRETATIVE REPRESENTATIONS OF THE RECURRENT TYPES OF UNREDUCED EMBRYO SACS.

**Key words** — Apomixis, automixis, cellularization, cyclosis, diplospory, embryo sac, meiosis, Allium, Antennaria, Eragrostis, Helleborus, Hieracium, Ixeris, Pennisetum, Taraxacum.

## I. Introduction

For a more comprehensive account of two previous embryological papers (Battaglia, 1951 *a*, *b*), during the years 1954-1958 we carried out an extensive review on the types of the female gametophyte in apomictic Angiosperms. The up-dated and revised typescript was sent to the editor, the late Prof. P. Maheshwari, in the year 1959. This paper was published as Chapter 8 of Maheshwari's book «Recent Advances in the Embryology of Angiosperms» (Delhi, 1963).

Since 1958, although no new significant cytological phenomena have been discovered, a large amount of embryological work has been accomplished, mainly on the reproduction of apomictic grasses.

Further, there has been a recent increase in interest in all apomictic questions, both cytoembryological and terminological (1). This state of affairs, together with the consideration that several previous reports and problems now need to be reconsidered, has stimulated us to write the present contribution, albeit restricted to an up to date definition of the recurrent types of unreduced embryo sac development (2) of apomictic angiosperms (3).

## II. Terminology and recommended definitions

To stimulate pertinent studies and criticisms we assume the following terminology:

### 1. *Basic type, main type, recurrent type, form and rearranged form*

We use the term *type* for any pattern of embryo sac development, that is cytologically well established and described from the initial cell (gynospore sensu lato) to the last stage of development (the so-called mature embryo sac).

In a previous paper (Battaglia, 1989 p. 86), we have proposed

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(1) See 'Apomixis Newsletter' (1989 1990: Y.H. Savidan & C.F. Crane, eds.)

(2) For simplicity, we adopt the terms embryo sac mother cell (E.M.C. or EMC), embryo sac (E.S. or ES) and megaspore. Nevertheless we consider the terms gynospore mother cell (Gs. M.C.), gynogametophyte (G.G.) or abbreviated gynophyte, and gynospore (Gs.), as more appropriate (cfr. Battaglia, 1982). See also Dangeard (1902): andro(gyno) gaméte(gamie); Janet (1912): andro(gyno) gamétophyte (gaméte).

(3) We hope to be able to discuss in future articles many questions not considered here.

an evolutionary classification of the ES types of the extant Angiosperms and distinguished the basic types, the main forms of the basic type and the related rearranged forms, namely:

*Basic type*. An expression chosen to indicate the pattern of gametophyte development corresponding to the ten different formulae occurring in the sequence ($P^3C^{16}$)... ($P^mC^2$) = types VII..I;

*Main form* (of the basic type). An expression chosen to indicate, within each basic type, the pattern of gametophyte development characterized by the primary arrangement of polarization. For simplicity, the formula of the basic type coincides with the formula of its main form, thus, for instance, the formula ($P^3C^{16}$) also indicates the main form of this type, namely the development characterized by the primary arrangement of polarization i.e. «post-div. 3, (1+7) polarization»;

*Rearranged form* (of the basic type). An expression chosen to indicate, within each basic type, the pattern of gametophyte development characterized by any rearranged polarization. The rearranged forms have been indicated by adding one or more apostrophes to the top right of the basic formula.

We also use, descriptively, the term *form* to indicate morphological variations, as those, for instance, pertinent to the 4-nucleate gametophytes, that is the *4-celled form* (formula: 2S+E+CN = 2 synergids + egg cell + central nucleus), *the 3-celled form* (S + E + 2CN = 1 synergid + egg cell + 2 central nuclei), etc.

*Recurrent type*. In the present paper, we define as recurrent type a *regularly recurrent* pattern of development, occurring in nature in one species, or, at the very least, in one individual.

## 2. *Amphimixis* (Weismann, 1891) *and apomixis* (Haacke, 1893 *a*, *b*; Maire, 1900 *a*, *b*; Winkler, 1906).

As early as 1891, Weismann proposed the term *Amphimixis* [4], «*oder die Vermischung der Individuen*» together with «*der mixotische Kern, das Analogon des Keimkerns bei der Befruchtung*» [5].

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[4] See also *Amixie* in Weismann (1872, p. 49) and *Panmixie* in Weismann (1883, p. 35), a term related to the Darwinian *Pangenesis*, and later translated into the *Panmixia* by A.E. Shipley (cf. Weismann 1889, p. 90).

[5] Cf. Weismann (1891, p. 112, foot note 1):

«Unter einem «mixotischen» Kern verstehe ich einem durch Amphimixis entstandenen, also einen Kern, der zu gleichen Theilen aus dem Idioplasma zweier Individuen bestent».

Just two years later, HAACKE (1893 *a*, *b*) coined the term *Apomixis*, attributing to this term a singular meaning (see below). At the beginning of 1900, MAIRE (1900 *a*, *b*), citing the terminological priority of HAACKE, again used the terms «apomixie» and «mixie». Because these authors attribute to the term apomixis two remarkably different meanings, we believe that these two discordant interpretations of the same term apomixis, which are today injustifiably overlooked in the embryological literature, deserve and adequate citation not only from a historical point of view, but also for the sake of priority, namely:

From HAACKE, 1893 *a*, pp. 103-104:

Ich habe japanische Tanzmäuse, scharf charakterisierte Tiere, die sich dadurch auszeichnen, dass sie unsicheren Schrittes hin- und herlaufen und oft auf einem Flecke im Kreise herumwirbeln, mit anderen Mäusen gepaart, die ich, da sie besser klettern können als jene, Klettermäuse nennen will, und Kreuzungsmäuse erhalten, die nicht tanzten. Meine Versuche ergeben nun, dass in den von diesen Tieren erzeugten befruchtungsfähigen Keimzellen nur eine Art von Keimplasma enthalten ist, entweder Tanzmausplasma, das wir mit T bezeichnen wollen, oder Klettermausplasma, das wir K nennen wollen. Wenn man zwei solcher Kreuzungsmäuse miteinander paart, so sind demnach folgende Fälle möglich: 1) Ein Spermatozoon, das nur T enthält, kann sich mit einer Eizelle verbinden, die auch nur T enthält; wir erhalten dadurch wieder eine reine Tanzmaus. 2) Ein Spermatozoon aus T verbindet sich mit einer Eizelle aus K, wodurch wieder eine Kreuzungsmaus entsteht. 3) Wenn sich ein Spermatozoon aus K mit einer Eizelle aus T verbindet, entsteht ebenfalls wieder eine Kreuzungsmaus. 4) Dagegen entsteht wieder eine reine Klettermaus, wenn ein Spermatozoon aus K in eine Eizelle aus K eindringt. Nun gleichen zwar die Kreuzungsmäuse in Bezug auf ihr Verhalten den Klettermäusen; allein fortgesetzte Züchtungsversuche zeigen, dass aus Kreuzungsmäusen wieder reine Tanz- und reine Klettermäuse gezüchtet werden können, während das bei anderen, ihnen äusserlich gleichenden, die nur Klettermausplasma enthalten, nicht möglich ist. Hat man auf dem Wege des Rückschlags wieder reine Tanzmäuse erhalten, so kann man die Züchtung so lange fortsetzen, wie man Lust hat, ohne jemals wieder Klettermäuse zu erhalten, obwohl diese Tanzmäuse unter ihren Vorfahren Klettermäuse haben. Das Gleiche gilt mutatis mutandis von Klettermäusen. Die Reduktionsteilung bewirkt also keineswegs Amphimixis, Mischung verschiedener Plasmen, sondern vielmehr Apomixis, Entmischung zweier nicht zusammengehöriger Keimplasmen, wobei freilich nicht ausgeschlossen zu sein braucht, dass kleine Mengen fremden Plasma's dem Plasma einer im übrigen monoplasmatischen Keimzelle beigemischt sind.

Meine Versuche zeigen ausserdem, dass jedesmal, wenn zwei ungleiche Plasmen aufeinander einwirken, jedes der beiden etwas verändert wird, und zwar besteht die Veränderung in einer Ausgleichung von Ungleichheiten. So haben gescheckte Tanzmäuse oft Enkel, die zwar reine Tanzmäuse, im übrigen aber einfarbig sind. Da nun, wie sich später zeigen wird, die Scheckung eine Störung des plasmatischen Gleich-

gewichts bedeutet, so ist bei diesen Tanzmäusen eine Wiederherstellung des Gleichgewichts eingetreten. Geschlechtliche Fortpflanzung bewirkt also auch in dieser Beziehung die Ausgleichung ungleich abgeänderter Plasmen; sie arbeitet also auf Apomixis, nicht auf Amphimixis hin.

Es bleibt gewiss ein grosses Verdienst Weismann's, auf die Reduktionsteilung der Keimzellen als einen bedeutungsvollen Vorgang hingewiesen zu haben, aber die Bedeutung der Reduktionsteilung ist Entmischung, Apomixis, und nicht Vermischung zahlreicher Individuen oder Amphimixis. Letztere wird durch die Reduktionsteilung verhindert. Die Präformationstheorie kann aber, wie Weismann so schön ausgeführt hat, ohne die Annahme einer Amphimixis nicht bestehen, denn nach ihr ist jede Determinante jedes Ides für sich variabel, und da sie viel leichter in ungünstiger Weise als in günstiger Richtung abändern kann, so kann günstige Variation einer Zelle nur durch Zusammenhäufung einer Majorität günstig veränderter, aus verschiedenen Weismann'schen Iden stammender Biophoren zu stande kommen. Ohne Amphimixis kein Präformismus. Dementsprechend ist mit dem von uns in strengster Form geführten Nachweise, dass Amphimixis zum Untergange der Organismenarten führen müsste, wenn sie plötzlich eingeführt würde, dass es also keine Amphimixis geben kann, auch der Präformismus beseitigt.

So ergiebt sich denn aus der Gesamtheit unserer bisherigen Ausführungen, dass der Präformismus auf der ganzen Linie geschlagen ist. Um uns diese Thatsache noch einmal in eindringlicher Weise vor Augen zu führen, wollen wir die Ergebnisse, zu denen wir gelangt sind, kurz zusammenfassen.

From Haacke, 1893 *a*, pp. 233:

Dass aber mit dieser Variabilität im Weismann'schen Sinne nichts anzufangen ist, haben wir schon gezeigt. Die Individuenvermehrung der Organismenarten müsste eine über alle Begriffe ungeheuere sein, wenn überhaupt eine Anzahl zum Überleben tauglicher Individuen entstehen soll. Die Wahrscheinlichkeit, dass letzteres geschähe, erweist sich als verzweifelt gering, wenn wir konsequent, wie wir es gethan haben, auf den Weismann'schen Prämissen weiterbauen. Thatsächlich bewirkt aber auch das, was Weismann Amphimixis nennt, nämlich die Vermischung von Individuen, deren Keimzellen einer Reduktionsteilung unterworfen sind, nicht Variabilität, sondern Einförmigkeit unter den Individuen einer Art in einem Verbreitungsgebiete, wo nach allen Richtungen hin freie Kreuzung möglich ist. Freie Kreuzung arbeitet der Variabilität entgegen, sie macht die Individuen einander gleich, und dass sie das kann, verdankt sie der Reduktionsteilung der Keimzellen. Nicht eine Amphimixis, eine bunte Mischung verschiedener Vererbungstendenzen wird dadurch ermöglicht, sondern der Keimzellenreifungsprozess bedeutet eine Entmischung, für die ich den Namen Apomixis vorschlage.

From Haacke, 1893 *b*, p. 533:

Da das Ergebnis meiner Züchtungsversuche an mehr als 3000 Mäusen im schönsten Einklang mit meiner Ansicht über die Bedeutung der Reduktionsteilung der Keimzellen steht, welche Apomixis, Entmisch-

ung, nicht, wie Weismann will, Mischung, „Amphimixis“ ist, und da sie ebensosehr der Annahme entspricht, dass die morphologischen Eigenschaften an das Plasma, die chemischen, also auch diejenigen, welche die Farbe bedingen, an die Kernstoffe gebunden sind, so darf ich wohl einiges Zutrauen, zu meiner Deutung der verschiedenen Rollen, welche Plasma und Kern bei der Vererbung spielen, hegen. Stände Weismann Vererbungserscheinungen wie den von mir beobachteten, die man nur durch planmäßige Züchtungsversuche auf Grund einer leitenden Idee erhalten, aber nicht aus den Werken Darwin's und anderer Autoren zusammensuchen kann, nicht so ferne, so würde er seine Determinantenlehre und seine Idologie wohl nicht aufgestellt haben: Meine Versuche widerlegen diese Irrlehren direkt. Um das

From MAIRE, 1900 *a*, p. 93.

## L'ÉVOLUTION NUCLÉAIRE CHEZ LES *ENDOPHYLLUM*

Par M. René MAIRE

*(Suite)*

Ces considérations générales étant établies, si maintenant l'on jette les yeux sur des figures représentant la fécondation et la segmentation de l'œuf des *Cyclops strenuus* et *brevicornis* (1), on verra qu'à la fécondation il n'y a pas *fusion,* mais *association synergique* des pronuclei, c'est-à-dire des noyaux à *n* chomosomes du spermatozoïde et de l'ovule. Les noyaux à l'état de repos sont accolés mais séparés; ils se divisent simultanément en formant une seule et même figure mitotique dans laquelle on distingue cependant chaque individualité se divisant à part.

Ce n'est qu'au bout d'un grand nombre de divisions que l'individualisation morphologique des noyaux disparaît. Ce cas et d'autres encore conduisent à admettre que, dans les autres cas de fécondation où les noyaux paraissent se fusionner, cette fusion n'est qu'apparente, que si à l'état de repos les deux noyaux sont réunis sous la même membrane, leur chromatine répartie en karyosomes quelconques, ils n'en sont pas moins distincts, et ce qui le prouve, c'est qu'à chaque mitose ils affirment leur individualité par la formation de 2 *n* chromosomes.

Cette individualité ne disparaît qu'au moment de la réduction du nombre des chromosomes par ce pétrissage qui les unit par couples : c'est là seulement que se produit la *fusion,* processus très général que nous appellerons commodément *mixie* (2). On a alors : chromatine paternelle + chromatine

1. Par exemple, celles données par Wilson dans son traité classique *The Cellin Development and Inheritance.* Les figures de segmentation d'œufs d'*Ascaris megalocephala univalens* × *bivalens* données dans le même traité, et chez les végétaux une figure de mitose de l'embryon de *Ginkgo biloba* donnée par Hirase viennent aussi à l'appui des conclusions tirées de l'étude des *Cyclops.*

2. La réduction du nombre des chromosomes par mixie est bien nette chez les végétaux; chez les animaux, la formation des tétrades en complique le processus; mais bien que la question soit encore fort obscure, le phénomène de mixie s'y produit certainement.

From MAIRE, 1900 *a*, p. 377.

IX. — THÉORIE DE L'ÉVOLUTION NUCLÉAIRE CHEZ LES ENDOPHYLLUM.

Les *Endophyllum* envisagés selon les théories ci-dessus se présentent comme un cas particulier : il y a chez eux *apomixie*. [Je donne à ce terme d'apoximie uniquement la signification d' « absence de la mixie, de la réduction par fusion du nombre des chromosomes », et non le sens plus ou moins métaphysique que lui, attribué HAACKE (1) dans sa théorie des Gemmaires. L'apomixie pour Haacke serait le triage des Gemmaires opéré lors de la réduction et aboutissant à une épuration par suite de l'élimination d'un groupe de ces Gemmaires.]

To day, plant embryologists do not mention either HAACKE's nor Maire's terminologies and confine themselves only to WINKLER's (1908) definition of apomixis, (6), thus again overlooking not only the first

(6) WINKLER (1908, pp. 6-9), without citing the papers of WEISMANN, HAACKE and MAIRE, writes:

> Parthenogenesis und Apogamie sind zwei charakteristische Arten der Fortpflanzung, und es fragt sich daher zuerst, wie sie sich zu den anderen bei Pflanzen vorkommenden Fortpflanzungsweisen verhalten. Um darin einen klaren Einblick zu bekommen, teilen wir die bei Pflanzen überhaupt möglichen Vermehrungsarten in drei Unterabteilungen ein: die Amphimixis, die Pseudomixis und die Apomixis.
>
> Die Amphimixis ist die normale Art der geschlechtlichen Fortpflanzung, bei der also der Keim entsteht aus dem Verschmelzungsprodukt zweier Keimzellen, seien diese nun als Isogameten ausgebildet oder in Ei und Spermatozoon differenziert.
>
> Als Pseudomixis bezeichnen wir den Ersatz der echten geschlechtlichen Keimzellverschmelzung durch einen pseudosexuellen Kopulationsprozeß zweier nicht als spezifische Befruchtungszellen differenzierter Zellen. Was die Pseudomixis von der Amphimixis unterscheidet, ist also im wesentlichen nur der Umstand, daß die beiden miteinander verschmelzenden Zellen nicht als Gameten differenziert sind. Natürlich ist die Pseudomixis stets mit Autogamie verbunden; doch ist es wenigstens theoretisch auch nicht ausgeschlossen, daß sie mit Allogamie verbunden auftreten kann, wenn anders es sich bewahrheiten sollte, daß es Pfropfhybride gibt, die aus einer Zelle des Verwachsungsgewebes hervorgegangen sind, in die der Kern (und vielleicht auch Protoplasma) aus einer benachbarten artfremden Zelle hinübergewandert war.
>
> Bekannt ist pseudomiktische Fortpflanzungsweise bis jetzt vor allem bei einigen Farnen, so z. B. bei *Lastrea pseudomas* var. *polydactyla* Wills (Farmer, Moore und Digby 1903), wo der Sporophyt aus einer Prothalliumzelle hervorgeht, deren Kern mit einem aus einer Nachbarzelle herübergewanderten zweiten Kern verschmilzt, ehe die Entwicklung beginnt. Farmer und Digby (1907, p. 191) nennen diesen Vorgang Pseudapogamie.

definition of the same term by WINKLER (1906) (7) but also the large related terminology proposed later by this author in some outstanding articles, published in the years 1920, 1934 and 1942 (see for instance the terms *apogonosis, apomiktosis, aposporosis* and *zygogamosis*).

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Als Apomixis endlich bezeichnen wir den Ersatz der geschlechtlichen Fortpflanzung durch einen anderen, ungeschlechtlichen, nicht mit Kern- und Zellverschmelzung verbundenen Vermehrungsprozeß. Hierfür liegt an sich schon ein anderer Terminus vor, nämlich der der Apogamie. Dieser Ausdruck wurde von de Bary (1878, p. 479) für die Tatsache eingeführt, „daß einer Species (oder Varietät) die sexuelle Zeugung verloren geht und durch einen anderen Reproduktionsprozeß ersetzt wird". Die Apogamie im Sinne von de Bary deckt sich also genau mit dem, was wir Apomixis nennen, und wenn wir diesen neuen Terminus an Stelle des alten setzen, so geschieht es notgedrungen deshalb, weil, wie bereits anderwärts nachgewiesen wurde (Winkler 1906, p. 251ff.), alle neueren Autoren den Ausdruck Apogamie nicht mehr im de Bary'schen Sinne verwenden, sondern ihm eine andere engere Bedeutung zulegen, in der er allgemein gebräuchlich geworden ist. Als Beleg sei zunächst auf Juel (1900, p. 40) hingewiesen, der unter Apogamie nur die Erzeugung eines Sporophyten durch den Gametophyten ohne geschlechtliche Fortpflanzung versteht.

(7) Cf. WINKLER (1906, pp. 253-254):

Nur dürfte es sich empfehlen, beide zusammen unter einen Oberbegriff zu subsummiren, der gleichzeitig auch andere verwandte Fälle mit umfasst und damit als Ersatz für den Begriff der Apogamie im *de Baryschen* Sinne dienen kann. Diesen letzteren Terminus selbst wieder in seine alten Rechte einzusetzen, nachdem sich seine Bedeutung spontan so gewandelt hat, dürfte Schwierigkeiten unterliegen. Ich schlage daher den nach Analogie von Amphimixis gebildeten Terminus *Apomixis* vor, der also zu definiren wäre als: Ersatz der verlorenen geschlechtlichen Fortpflanzung durch einen anderen, ungeschlechtlichen Vermehrungsprocess. Als Unterarten der Apomixis wären dann zu unterscheiden

1.) vegetative Propagation, d. h. Ersatz der Befruchtung durch Ausläufer, blattbürtige Knospen, Adventivkeime aus Nucellarzellen u. s. w.
2.) Apogamie, d. h. apomiktische Erzeugung eines Sporophyten aus vegetativen Zellen des Gametophyten.
3.) Parthenogenesis, d. h. apomiktische Entstehung eines Sporophyten aus einem Ei, und zwar,
   *a*) somatische Parthenogenesis, wenn das Ei einen Kern mit unreducirter Chromosomenzahl besitzt,
   *b*) generative Parthenogenesis, wenn sein Kern die reducirte Chromosomenzahl enthält. —

Because we believe that the most correct terminological rule is the utilization of the terms according to their etymological meaning, we accept here *apomixis* as a shortened form of *apokaryomixis* ([8]) giving to this term the meaning of suppression of *karyomixis* ([8]) ([9]).

Actually, the gametic *mixis* ([9]) involves both *cytoplasmatic mixis* (currently *plasmamixis*) and *nuclear mixis* (*karyomixis*). However, the *cytoplasmic mixis* is irrelevant from the point of view of the terminology discussed here.

As mentioned in a previous paper (BATTAGLIA 1983, pp. 3-5), we assign to the prefix *apo* the meaning of absence by suppression (i.e. a secondary absence) leaving to the correlated prefix *a* the meaning of absence *'ab initio'* (i.e. a primary absence). Thus, for instance, we believe terminologically correct to write that the eggs *typically* ('by mixis', namely mictic eggs) develop 'mictic embryos' and *atypically* ('by apomixis', namely apomictic eggs) develop 'apomictic embryos'. By analogy, since the synergids (or the antipodals) *typically* ('by mixis') do not develop embryos, *atypically* ('by amixis, or primary absence of mixis) can develop amictic embryos (i.e. amictic embryogenesis *sensu lato*).

## 3. *Apomixis referred to the egg.*

As stated above, eggs develop embryos by mixis or apomixis. When apomixis occurs, the variable behaviour of the male counterpart, that is fertilization *sensu lato* ([10]), allows the following reproductive patterns to be distinguished:

*Parthenogenesis*

Here, the male counterpart is either absent, completely inoperative or simply unnecessary;

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([8]) We have not ascertained whether the terms *karyomixis* and *apokaryomixis* have been proposed earlier than in WOODRUFF & ERDMANN (1914: *'apocaryomictic'*, *'caryomictic'*) or in REGNARD (1914 *a*: *'caryomixie'*), see references in BATTAGLIA (1985).

([9]) As regards angiospermic reproduction, obviously *karyomixis* means *heterokaryomixis*. Some related and similar terms have been proposed by BURNETT (1956), i.e., for the mating systems of fungi, *heteromixis*, *homomixis* and *homo-heteromixis*.

([10]) Owing to tautology, we do not accept the term *syngamy*, suggested by HARTOG (1904) because syngamy is not different from *gamy*, nor *synmixis*, for example, from *mixis*. Further, HARTOG, proposing the term *syngamy* was probably unaware of the similar terms «Asyngamie» and «Asynchronogamie» proposed 30 years earlier by KERNER (1874).

*Pseudogamy* (FOCKE, 1881)

Here the male counterpart is necessary. Nevertheless the 'first' sperm nucleus ([11]) degenerates within or outside the egg cell.

The behaviour of the 'second' sperm nucleus is irrelevant to the definition of pseudogamy;

*Semigamy* («semigamia»: BATTAGLIA, 1945 *a*; cf. also BATTAGLIA, 1981).

Here, too the male counterpart is necessary. The 'first' sperm nucleus, although actually penetrating the egg, does not accomplish karyomixis and later divides independently thus contributing to the development of gynandrous embryos (occurrence of *gynandroembryony*). The behaviour of the 'second' sperm nucleus is again irrelevant to the definition of semigamy.

4. *Mixis and apomixis referred to the female gametophyte: dimictic, monomictic and apomictic embryo sacs.*

Owing to the so-called double fertilization, the karyomictic process occurs twice in the angiosperm embryo sac. Thus *dimixis* ([12]) (short for di-karyomixis) characterizes regular angiospermic reproduction and consequently the regularly fertilized embryo sac should also be called the dimictic embryo sac.

*Monomixis* (single karyomixis) is also known in angiospermic reproduction and this cytological pattern requires discussion.

A first case of monomixis, that is «mictic egg (zygote) and absence of central synkaryon» ([13]) ([14]), followed by development of embryos and lack of endosperm, (see next paragraph) takes place in the family Podostemaceae.

We consider this case to be strictly correlated with the non-differentiation of a true central cell ([15]). Mictic eggs and lack of en-

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([11]) We distinguish as 'first' the sperm 'destined' to fuse (plasmamixis and karyomixis) with the egg. Obviously the 'second' sperm nucleus should be that fusing with the 'central synkaryon' (cf. BATTAGLIA 1987b) currently referred to as the secondary nucleus.

([12]) BURNETT (1956, p. 51) ascribes to the term *dimixis* the following meaning: «The heteromictic condition where are two and only two types of complementary nuclei which control mating. The nuclear types are determined by two allelomorphs at a single locus», see also (9).

([13]) Zygote: cf. STRASBURGER (1877, p. 438), see also (19).

([14]) Central synkaryon (in place of secondary nucleus), cf. BATTAGLIA (1987 *b*).

([15]) See BATTAGLIA (1971, 1987 *c*). The fate of the second sperm nucleus within the embro sac of the Podostemaceae requires further investigations.

dosperm are also known, for instance, in the Orchidaceae. Nevertheless, in this case, the second sperm nucleus is able (always?) to fuse with chalazal nuclei, giving rise to a fertilized synkaryon (zygosynkaryon) ([16]) usually incapable (always?) of great mitotic activity ([17]).

A second case of monomixis, that is «apomictic egg and mictic central synkaryon (zygosynkaryon)» is a very frequent event in plants which are currently defined apomictic plants. Thus this definition should be abandoned in preference to other more correct phrases such as, for instance, apomictic embryony.

Necessarily, the term apomictic embryo sacs (in the sense of fully-apomictic embryo sac or holo-apomictic embryo sac), should be reserved to the case characterized by lack of karyomixis for both the egg nucleus and the central synkaryon.

5. *A re-evaluation of the gamy-terminology (eugamy, aneugamy, apogamy...)*

The fertilization process in the angiosperms is actually a dimictic process, therefore the terms amphimixis and apomixis cannot, descriptively, combine the karyological behaviour of the *two* sperms implied by the so-called «double fertilization». These considerations suggest the replacement of the terminological couplet «amphimixis & apomixis», as follows:

*eugamy*: the regular di-mictic fertilization;

*aneugamy*: any irregular (i.e. non-dimictic) fertilization, that is *semigamy*, *monomictic aneugamy* (i.e. non-mictic egg cell + mictic central synkaryon), *non-mictic aneugamy* (i.e. non-mictic egg cell + non-mictic central synkaryon; both sperms degenerate) and *androgenic aneugamy* (currently *androgenesis*);

*apogamy*: the loss of the fertilization process (sensu lato). Because pollination is the first step in the angiospermic double fertilization, the term apogamy would necessarily include the lack of pollination. Thus the present apogamy would correspond to the current concept of parthenogenesis.

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([16]) Zygosynkaryon (in place of primary endosperm nucleus), cf. BATTAGLIA (1987 *b*).

([17]) The behaviour of the second sperm nucleus within the orchid embryo sac deserves further investigation.

We believe that this terminological system, together with the terms *euspory* and *aneuspory* constitutes a comprehensive and linguistically homogenous treatment of the angiospermic fertilization.

## 6. *Critism of the expression «gametophytic apomixis»*

The term apomixis means loss of mixis and such a loss must be unequivocally referred to the gametophyte. Consequently it follows that «sporophytic apomixis» has no logical meaning and cannot be established.

Thus, we consider the widely accepted expression «gametophytic apomixis» (proposed by STEBBINS, 1950, p. 384, and conceptually alternative to «sporophytic apomixis»), to be nothing else than a pleonastic expression.

In this connection, and without any comment for the sake of simplicity, we cannot overlook KNIEP's (1928, pp. 464-470) terminological system, «gametische apomixis», «gametangische apomixis» and «somatogene apomixis» (cf. also «gametic, gametangial» and «somatogenous apomixis» in BULLER, 1941).

## 7. *Criticism of the use of term endosperm (secondary endosperm) in angiospermic embryology and its substitution by* PEARSON's (1909) *trophophyte. Zygotrophophyte and apozygotrohophyte.*

As regards angiospermic double fertilization, and following the current embryological terminology, we can say that the primary endosperm nucleus is formed when a sperm nucleus fertilizes the secondary nucleus.

This sentence clearly show the linguistic contrast between 'sperm' and 'endosperm'!

To avoid such great discrepancy, we have previously suggested (BATTAGLIA, 1987 *b* and 1989) the following terminology which revives the neglected term trophophyte (PEARSON, 1909, p. 335), namely:
*a*) *Zygotrophophyte* (in the place of the so-called secondary endosperm). This is the angiospermic trophophyte normally conditioned by the fertilization of the nucleus (usually a synkaryon) of the central cell:
*b*) *Apozygotrophophyte* This is the angiospermic trophophyte in all cases in which the central cell divide without karyomixis (namely by suppression of karyomixis) with a sperm nucleus.

8. *Definition of the concept of spore and the related term apospory* (VINES, 1878; DRUERY, 1885, *a*, *b*; BOWER, 1885).

We believe that the first question to be faced in embryological terminology is the definition of the concept of spore. The lack of such definition may explain the usage of such diverse terminologies as those, for instance, recently suggested for apomixis (*sensu lato*) by SOLNTZEVA (1989) and CRANE (1989) ([18]).

As early as 1877 Strasburger coined the term *zygote*, giving it the meaning of «Copulationsproduct» ([19]). Some years later, the meaning to be assigned to the term spore became a matter for reconsideration owing to the discovery of a singular reproductive deviation in ferns by DRUERY (1885 *a*, *b*) and named apospory by him. Actually, the term apospory was first introduced by VINES (1878) with reference to the reproduction of *Chara* and with a meaning qualified as symmetrical with apogamous (see details in BATTAGLIA 1983).

After the discovery (June 1884) of Druery's apospory, by the end of 1884 (DRUERY, 1885 *b*: THISELTON-DYER, 1885) the concept and definition of the term spore became indirectly as well as necessarily correlated to the new concept of apospory. Bower in December 1886 (cf. BOWER, 1887) summarized the relationship between spore and apospory as follows: cf. BOWER (1887, p. 301):

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([18]) It is a matter for the readers to make a comparative analysis, a criticism and a choice between the terminology presented here and those of the previous authors.

([19]) STRASBURGER (1877, pp. 438-439) writes:

> Dieses Copulationsproduct will ich hier als Zygote bezeichnen, um so die Zusammensetzung des Wortes mit „Spore" zu vermeiden. — Die Zygote entspricht einem Product aus Ei und Spermatozoid und darf daher nicht länger die Bezeichnung Spore tragen, die auf ungeschlechtlich erzeugte Reproductionszellen angewandt wird und auf diese beschränkt werden müsste.[1]) Die sich mit einander vereinigenden Protoplasmamassen will ich aber Gameten nennen.
>
> [1]) Das Weitere hierüber in einem demnächst in der botan. Zeitung erscheinenden Aufsatze.

# XVI. *On Apospory and allied Phenomena.* *By* Prof. F. O. Bower, *F.L.S.*

(Plates LVII.–LIX.)

Read 16th December, 1886.

THE term "spore" has been, and still is, used in so different senses by different writers that it will be necessary, in treating a subject such as the present, to define clearly which of its various senses will be adopted in this paper. The choice lies between two definitions given by two eminent botanists, Sachs and De Bary; the former, in his Textbook *, defines the spore, in a restricted sense, as "either a direct product of fertilization (zygospore, oospore) or the product of a vegetative act induced by fertilization;" that is, starting from the Mosses and Ferns, he applies the term exclusively to those reproductive cells which are *homologous* with the spores of those plants, while to others which are not homologous he applies other terms. De Bary, on the other hand, gives a wider significance to the term, and applies it quite generally to "any cell which, as a single cell, becomes free, and is capable of direct development into a new organism (Bion), without reference to its origin and homology" †. Since, in the description of the phenomena to be detailed below, it is of importance to avoid any confusion of view by the introduction of discussions as to the homology of the various reproductive cells of the Thallophytes with the spores of the Archegoniatæ, the narrower definition of the term, given by Sachs, will be adopted in this paper; but this is done rather with the object of clearing the ground of unwieldy discussion than as any expression of opinion as to the relative merits of the two definitions for purposes of general description. Accordingly, in discussing the phenomena of apospory, it will be understood that those cases only are taken into account in which the homology of the spores with those of the Mosses and Ferns is generally accepted ‡.

It is just ten years since Pringsheim § and Stahl ‖ found, independently of one another, that it is possible, by cultivation under abnormal circumstances, to induce a formation of protonema by direct vegetative growth from the sporogonium of certain Mosses. In such cases there is an excision of the spore from the cycle of life ¶. Writing in 1878,

* 4 Aufl. p. 237.

† Morph. und Biol. der Pilze, 1884, p. 139.

‡ *Cf.* De Bary, Morph. und Biol. der Pilze, pp. 130, 131. Compare also McNab, Proceedings of the Royal Dublin Society, n. s. vol. iv. part 9, p. 466 &c.

§ Monatsb. d. k. Akad. Wiss. zu Berlin, 10 July, 1876; also Jahrb. für wiss. Bot. Bd. xi. 1877, p. 1.

‖ Bot. Zeitg. 1876, p. 689.

¶ A peculiar abnormality is mentioned by Masters (Veg. Terat. p. 173). It was recorded as occurring in the Moss *Encamptodon* (*Weissia*) *perichætialis* by Dr. Montagne (Ann. Sci. Nat. 1845, pp. 119 and 366, plate 14). In

Vines * applied to this and similar modes of propagation the term "aposporous," which may be accepted as a useful one †. Further, the term "apospory," corresponding in form to "apogamy," may be adopted as expressing the phenomenon thus artificially induced in the Mosses. It will be well more clearly to define the use of these and other terms at the outset. In the following pages the term "*sporal arrest*" will be applied to all cases where spores do not come to functional maturity; this arrest may be partial or complete. Occasionally this sporal arrest is the only abnormal character; but in the most prominent of the abnormal examples of Ferns about to be described the phenomena are not simply those of arrest. The case is complicated by concomitant abnormalities, especially by a substitution of vegetative growth for the office of the spore. The vegetative growth, thus originating directly from the tissue of the sporophore, may at once assume the internal and external characters of the sporophore; this may be termed "*sporophoric budding*," where from the sporophore a fresh sporophoric bud is directly produced. With this might be compared "*oophoric budding*," a term which it is proposed to apply to those cases where from the oophore fresh individuals, showing oophoric characters, are produced by a vegetative process. Examples of this have been described by Cramer ‡ in the case of the Fern-prothallus, and by Treub § in the prothallus of *Lycopodium*. But the substitutionary growths from the sporophore following sporal arrest do not always assume the characters of the sporophore; they may show either at once or ultimately the characters of the oophore: to such a transition, by a direct vegetative process and without the assistance of spores, from the sporophore to the oophore, the term "*apospory*" is applied. This process may be regarded as the converse of that styled "*apogamy*," which consists essentially in a direct transition from the oophore to the sporophore without the intervention of a sexual process. It is important to note, however, that "sporal arrest" is not necessarily followed by any substitutionary vegetative growth; and cases will be cited of both partial and complete arrest of the spores, which show neither "apospory" nor "sporophoric budding" in the senses above defined; in fact, there is in such cases no substitutionary vegetative development, over and above those vegetative processes found in normal allied plants.

It is obvious that the most typical and prominent cases of the phenomena above defined

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this Moss the capsules were found to contain no spores, but in their place were "gemmæ of a kind analogous to those which are to be found in the cups of *Marchantia*." This was the case with all the capsules opened. The gemmæ were in the form of wedges or parallelograms, and multicellular. As they were not germinated, their real nature cannot be truly stated, but the comparison with the gemmæ of *Marchantia* would suggest a case of formation of oophoric gemmæ, in place of spores.

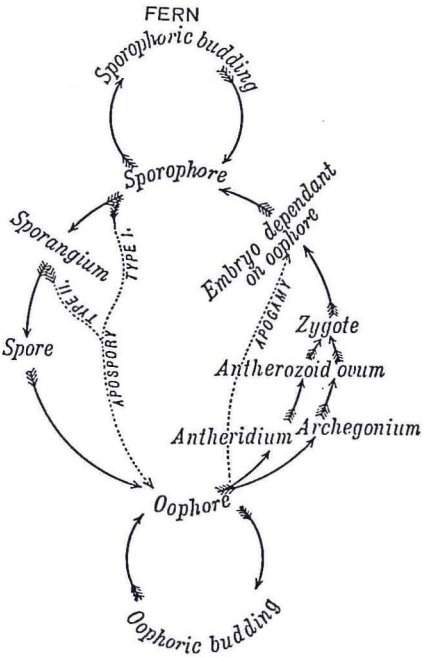
* Journal of Botany, 1878, p. 355.

† A reference to the preliminary paper on this subject (Journ. Linn. Soc., Bot. vol. xxi. p. 360) will show that though the source of the term "apospory" was not acknowledged, the word was not defined nor introduced as a new one. Compare 'Nature,' vol. xxxi. pp. 151, 216.

‡ "Ueber die geschlechtlose Vermehrung des Farnprothalliums," Denkschr. d. Schweiz. naturforsch. Gesellsch. Bd. xxviii. 1880.

§ Ann. Jard. Bot. de Buitenzorg, vol. v. 1886.

We also consider worthy of documentation in this context Bower's Fig. 1, showing the «Normal life-cycle of a Fern», comprehensive of both the aposporous and the apogamous additional phenomena.




Normal life-cycle of a Fern (see p. 326).

Fig. 1 - (from Bower 1887).

Also of considerable interest is the use by Bower of the self explanatory terminological couple 'oophore & sporophore' ([20]). In writing one of the most well-known botanical theoretical articles from the end of last century ('*On antithetic as distinct from homologous Alternation of Generations in Plants*', Annals of Botany, August 1890), Bower again wrote:

«Thus, where an antithetic alternation occurs (though not in all plants which show sexuality), there are two points in the life-cycle,

([20]) *Oophore* and *sporophore* were terms of common usage in those years, see for instance Thiselton-Dyer, 1885 p. 317: «...the sexual generation (oophore), the spore-bearing generation (sporophore)...». See also Balfour (1887).

which we may regard as fixed, and comparable in different plants, viz. the *zygote*, and the *carpospore*: the generation which intervenes (e.g. in the Fern or Moss) between the zygote and the carpospore, will collectively fall under the term *sporophyte*; that between the carpospore and zygote is termed the *gametophyte*».

This article, well-known in the last century but totally overlooked today, is also noteworthy because it introduces to current botanical usage, the terms gametophyte & sporophyte (cf. BOWER, 1890) ([21]) in place of the previous oophore & sporophore (cf. BOWER, 1887) or oophyte & sporophyte (cf. BOWER, 1888).

In conclusion, at least as regards angiospermic embryology, we believe that *the couplet 'spore & zygote' can be defined as respectively the initial cell of the gametophyte and the initial cell of the sporophyte* («Sporophyt»: DE BARY, 1884, p. 131).

9. *The concept of spore conditioned by the occurrence of meiosis.* CHIARUGI'S *(1926) distinction between 'aposporia goniale' and 'aposporia somatica'.* ROSENBERG'S *(1930) 'generative and somatische Aposporie'.*

After the discovery of chromosome reduction (cf. terminological details in BATTAGLIA, 1985 *a*) and, at the beginning of this century, owing to the exciting discovery of parthenogenetic reproduction in species of the genera *Antennaria*, *Hieracium*, *Taraxacum* etc., the concept of spore became strictly dependent on the occurrence of chromosome reduction ([22]) cf. SCHNIEWIND-THIES (1901), DAVIS (1904-1905), CHAMBERLAIN (1905), COULTER (1908), and more details in CHIARUGI (1926, 1927). However, on the basis of both physiological and morphological considerations, a few authors supported and emphasized the theoretical view of the independence of the concept of spore from the numerical reduction of chromosomes (cf. ERNST, 1908 *a*, *b*, and RUTGERS, 1923, both later criticized harshly by CHIARUGI, 1927). In any case, in the years 1900-1925, the recurrent reproductive deviations from amphimixis were almost unanimously ascribed to the joint occurrence of apospory and apogamy.

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([21]) Bower does not claim priority over the term gametophyte. We have left the question of priority over this term to future bibliographical research.

([22]) The term *maiosis* coined by FARMER & MOORE (1905) and soon modified, for linguistic reasons, into *meiosis* by KOERNICKE (1905), became popular almost immediately.

This terminological status changed abruptly in the years 1926-1931 together with a large realisation of the importance of a singular karyological mechanism, namely the semiheterotypic division and the correlated restitution nucleus, inducing a non-reductional meiosis, discovered and so named by OTTO ROSENBERG (1917, 1926 *a*, *b*, 1927 *a*, *b*). First, strictly relating the concept of apospory to the loss of chromosome reduction ([23]) however achieved, CHIARUGI (1926, p. 542-543) distinguished two cases of apospory: '*aposporia goniale*', (or '*aposporia diretta*') and '*aposporia somatica*' (or '*aposporia indiretta*').

In the case of 'aposporia goniale' the absence of chromosome reduction occurs in the '*cellule goniali dello sporofito destinate in origine alla formazione delle spore*'. In this case the initial cell of the embryo sac is named by CHIARUGI pseudospore ([24]). At the same time CHIARUGI established three different types of pseudosporic developments, namely '*gametofito monopseudosporiale*' (cf. *Alchemilla*), '*gametofito dipseudosporiale*' (cf. *Taraxacum*) and '*gametofito tetrapseudosporiale*' (cf. *Antennaria*).

In the other case of apospory, i.e. CHIARUGI's 'aposporia somatica', the absence of chromosome reduction takes place in the «*cellule somatiche dello sporofito trasformate, dalle quali si sviluppa indirettamente il gametofito*».

This second case «*...comprende i casi di aposporia nel senso classico di* ROSENBERG (1906, 1907)».

This classic subdivision of apospory deserves documentation, together with the general scheme of angiospermic apomictic reproduction, being unjustifiably overlooked by the embryological literature, see Fig. 2 ([25]).

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([23]) CHIARUGI (1926, p. 541) writes:

Con la parola *aposporia* devonsi intendere quindi tutti quei fenomeni che avvengono nello sporofito maturo, cioè la soppressione della riduzione cromatica, in qualunque cellula essa avvenga, con conseguente soppressione dell'alternanza del numero dei cromosomi. In altri termini un gametofito diploide di piante apomittiche è sempre aposporico riguardo all'origine, è sempre apogamico riguardo alla funzione e al destino.

([24]) The term *pseudospore* has earlier been used several times. The outstanding JACKSON's Glossary (1928) cites «Pseudospore, (1) a gemma or asexual vegetative bud; (2) Olive's term for Microcyst, the resting stage of Acrasieae». We have not ascertained the botanical priority over the term '*pseudospore*'.

([25]) The wrong establishment of the *Alchemilla* type became evident a few years later. The cytological details of the restitutional meiosis in *Taraxacum* were investigated several years later by GUSTAFFSON, FAGERLIND and BATTAGLIA. The last two authors also clarified apomictic reproduction in the genus *Erigeron*.

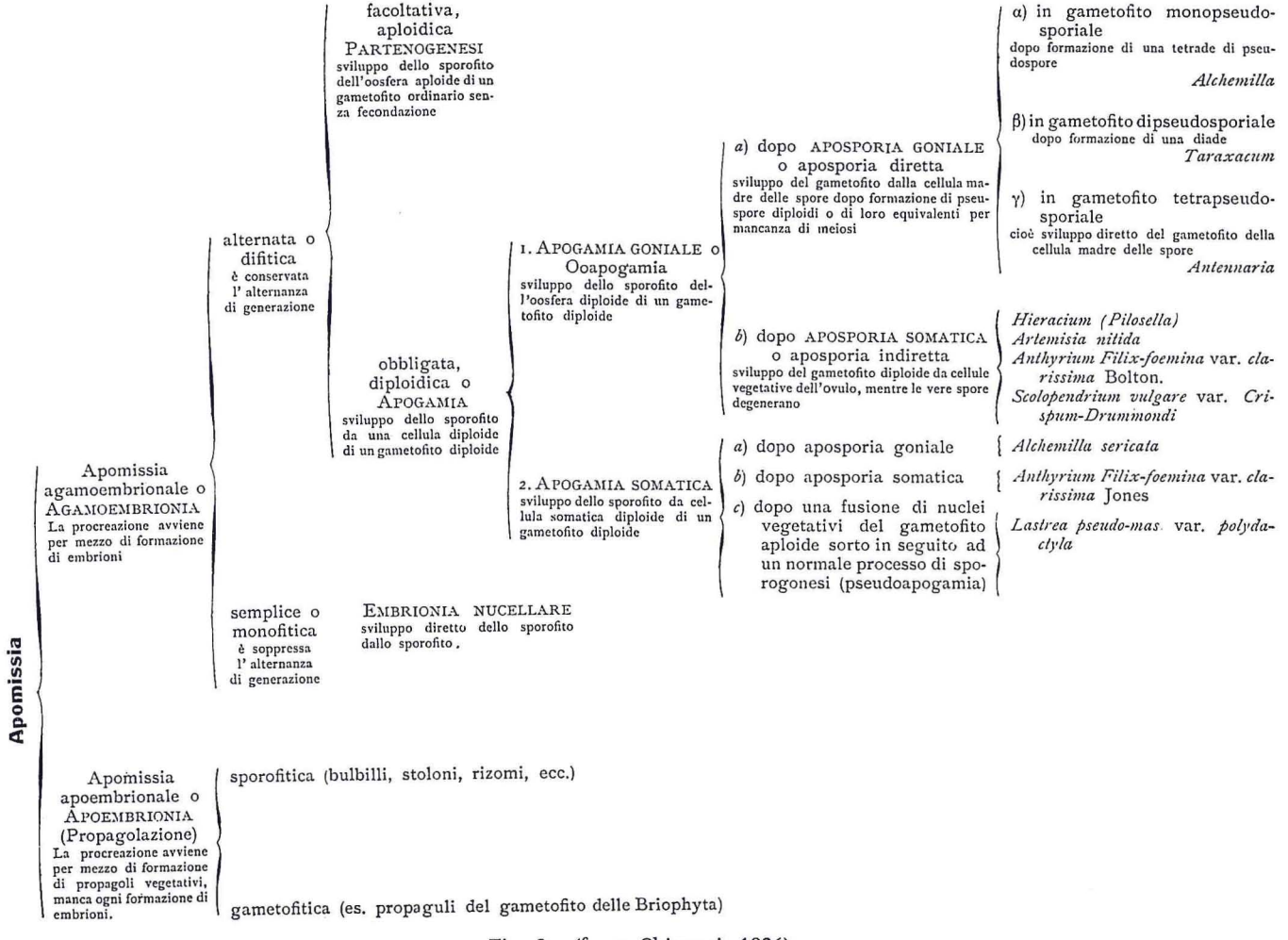


Fig. 2 - (from Chiarugi, 1926).

It is necessary to add that in the following year (1927) CHIARUGI published a most comprehensive scheme, together with an interpretative reconstruction of both amphimictic and apomictic female gametophytes of Angiosperms.

The distinction of apospory into 'goniale' and 'somatica', was almost immediately accepted by ROSENBERG (1930). However, this author modified CHIARUGI's terminological couplet 'goniale & somatica' into the well known and usual couplet 'generative & somatic'. In this context it is necessary to remember that, as early as 1884. Strasburger chose the couplet 'generative' and 'vegetative'. Since 1904, WINKLER adopted the couplet generative and somatic, first referred to 'Parthenogenesis' and later (1908) extended to 'Apogamie'. However, in successive papers, WINKLER (1920, 1934) gave his preference to another couplet, i.e. 'gamophasig & zygophasig'.

Finally in 1931, the apomictic terminology became enriched by the term *Diplospory* (EDMAN, 1931: *Diplosporie*), a term as lucky and easy to pronounce as it is linguistically and conceptually inadeguate. This term deserves as separate discussion.

## 10. *Criticism of the term «Diplosporie»* (EDMAN, 1931).

In his first embryological paper on *Oxyria digyna*, EDMAN (1929) published an unusual 'Tabelle II' on the apomictic reproduction of Angiosperms (cf. Fig. 3):

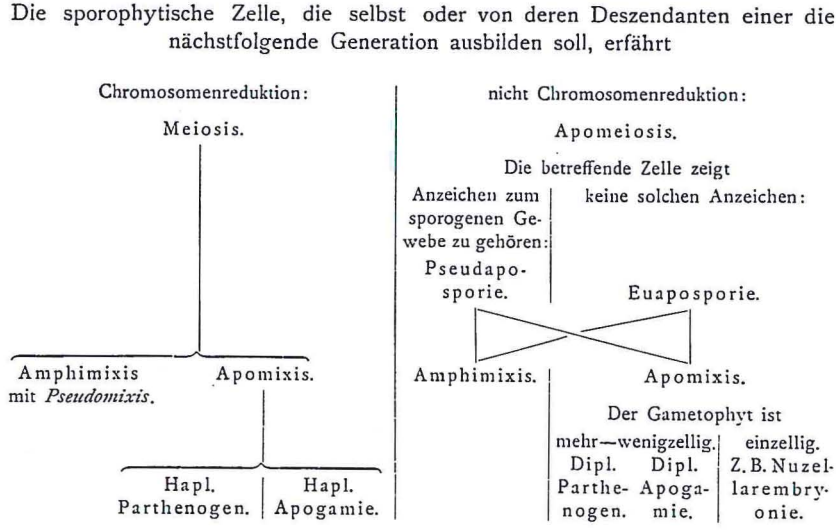


Fig. 3 - (from Edman, 1929).

This 'Tabelle' accepts RENNER's (1916) term *Apomeiose* and reintroduces two obsolete terms as *Pseudaposporie*, and *Euaposporie*, respectively referred by EDMAN to SHARP (1926) and SHARP (1921) ([26]).

However, EDMAN does not take into consideration RENNER's other similar and correlated term, *meiotische Hemiaposporie* ([27]). In the next embryological paper, EDMAN modifies his reproductive scheme and introduces (cf. Fig. 4) the terms *Diplospore* & *Diplosporie* to distinguish all cases in which, without chromosome reduction, the initial cell of the gametophyte is a cell belonging to the archesporial tissue ([28]), ([29]).

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([26]) EDMAN (1929, p. 210) writes:

> Die apogamen Fälle, d. h. diejenigen Fälle, wo der Embryosack aus einer nicht reduzierten »Spore» entsteht, sollten dagegen unter einer besonderen Bezeichnung zusammengefasst werden, z. B. Pseudaposporie (SHARP 1926, S. 355), welche Benennung für die Entstehung der diploiden Sporen bei *Marsilia Drumondii* vorgeschlagen ist; in diesem Falle könnte Aposporie mit Euaposporie ersetzt werden (SHARP 1921, S. 316).

Cf. SHARP (1921, pp. 315-317): «1. Pseudapospory: a spore is formed but without meiosis, so that it is diploid». ... «2. Eu-apospory: no spore is formed... (a) With meiosis... (b) Without meiosis». ...

([27]) Cfr. RENNER (1916, p. 364):

> Syngon ist auch der vierkernige Embryosack von *Cypripedilum*, aber nicht in der extremen Art wie bei *Tulipa* und *Plumbagella*, weil nur zwei Gonen statt vier sich an seiner Bildung beteiligen. Bis zur Sporenbildung kommt es auch hier nicht, doch wird wenigstens die heterotypische Teilung außerhalb des Gametophyten abgemacht: meiotische Hemiaposporie.
>
> . . . . . .
>
> vergleichen und seine Entstehung apospor nennen. Von den bisher allein als apospor bezeichneten *Hieracien* unterscheidet sich der *Antennaria*-Typus allerdings insofern, als bei *Antennaria* wenigstens das Archespor zur Bildung des Gametophyten herbeigezogen wird, während bei den *Hieracien* Zellen der Megasporangienwand (des Nucellus und des Integuments) eintreten. *Taraxacum* entwickelt seinen Embryosack ähnlich wie *Cypripedilum* aus zwei Gonen, also hemiapospor, aber dazu apomeiotisch.

([28]) Cfr. EDMAN (1931, p. 43):

> Aus dem Gesagten geht meines Erachtens hervor, dass die Gametophyteninitialen bei den *Marsilia Drummondii*-, *Taraxacum*- und *Antennaria*-Typen als Homologa der Sporen bei den meiotischen Pflanzen zu betrachten sind, und ich schlage vor, sie Diplosporen zu nennen. Dieser Ausdruck kann, wenn man so will, als eine Zusammenziehung aus diploiden Sporen betrachtet werden, und ist kein grösseres sprachliches Vergehen, als z.B. der Ausdruck Diplobiont. Jedenfalls sagt er deutlich aus, dass die fraglichen Zellen im sporogenen Gewebe entstandene, aber die sporophytische Chromosomenzahl enthaltende Gametophyteninitialen sind. In der Zusammensetzung Diplospore kann »Diplo» niemals — auch in Hinblick auf das Vorkommen polyploider Pflanzen — zu Missverständnissen führen.

([29]) Cfr. EDMAN (1931, p. 44)

> Die beiden Arten von Apomeiosis könnten als generativ und somatisch bezeichnet werden. Dadurch würden die Ausdrücke ganz unabhängig von der

EDMAN's couplet apospory and diplospory was later on accepted by all Swedish embryologists. The well-known review by GUSTAFSSON (1946-1947) on the apomixis of angiosperms ensured that these terms were widely circulated among botanists.

Today most embryologists and breeders follow EDMAN's terminology, sometimes with a little interpretative difference (i.e. apospory restricted to somatic apospory) and mainly for the sake of simplicity.

We do not agree with this terminological choice on the basis of the following considerations:

a). Diplospory, intended as diplo-sporogenesis, means double sporogenesis ('diplo' from the greek 'diploos' = double = twice, *sensu lato*);

b). *Diploid-spory* would be the only term exactly corresponding to the meaning assigned by EDMAN to his *diplospory*. However, because a close correlation between apomixis and polyploidy has been noted by all students of this subject, it is evident that the term *diploid-spory* is still not appropriate. Of course other phrases such as unreduced-sporogenesis (*unreduced-spory*) would be more suitable;

c). Diplospory intended as diplosporo-genesis means formation of diplospores. In this context, however, it would be necessary to consider the previous existence of the two strictly correlated terms *Diplosporen* and *Haplosporen* both cited and discussed by RENNER ([30]), ([31]). EDMAN (1931) overlooked this couplet Diplospore &

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Auffassung der Sporennatur oder Nicht-Sporennatur der Gametophyteninitialen. Den früher erwähnten Gründen zufolge dürfte indessen keine zu grosse Entstellung der morphologischen Fakta oder eine sprachliche Formlosigkeit begangen werden, wenn man die Entstehung von diploiden Gametophyteninitialen aus archesporialem Gewebe als Diplosporie bezeichnete.

([30]) Cfs. RENNER (1916, p. 361)

Für den Kernphasenwechsel bedeuten die beiden Sporenformen etwas sehr Verschiedenes. Die Tetrasporen sind wie sonst Gonen. Die Karposporen von *Polysiphonia* und den sich ähnlich verhaltenden Florideen dagegen bezeichnen keine Veränderung des Kernzustandes; wir können sie nach der Kernphase, der sie angehören, Diplosporen nennen. — Vermehrung der Gonosporen dürfte bei *Pleonosporium Borreri* vorkommen, dessen „Polysporen" (Nägeli) wohl den Tetrasporen der übrigen Formen entsprechen.

([31]) Cfs. RENNER (1916, p. 362)

Aber Ausnahmen sind da, und die Entdeckung von Svedelius hat uns mit einer besonders interessanten Abweichung bekannt gemacht. Wir haben hier einen zweigliedrigen Generationswechsel innerhalb der haploiden Phase, unabhängig vom Kernphasenwechsel, entfernt

Haplospore together with Dangeard's priority over the term *Diplospore* (see Jackson's Glossary, fourth edition 1928, p. 114: «Diplospore:, Dangeard's term for teleutospore»);

d). We also believe that the classical distinction of apospory into generative («goniale») and somatic apospory is still questionable from an organographic point of view. The case in which the normal embryo sac mother cell and the so-called aposporous initial lie contigously or very near each other is not rare. In this case they are in such a histological relation to make it difficult to distinguish them as, respectively, generative and somatic;

e). We further believe that the distinctive trait for any functional initial cell of the gametophyte, not preceded by normal or by abnormal meiosis (respectively eu-meiosis and aneu-meiosis), is precisely such an absence of meiosis. As we wrote in a earlier paper (BATTAGLIA, 1983), the absence of meiosis for the legitimate or true spore mother cell is a *suppression* of meiosis. On the contrary, for any cell other than the true spore mother cell, such an absence of meiosis is a primary absence and not a loss. Linguistically, a distinction between a primary absence and an absence by suppression, or a secondary absence, can be found in the two prefixes *a* and *apo*, i.e. ameiotic and apomeiotic sporogenesis (spory) in place of the somatic and gonial terminology.

Further, we also selected the adjectives primary and secondary to distinguish between the first or primitive pattern of sporogenesis (formation of *eumeio-*, *aneumeio-* and *apomeio-spores*, by the normal spore mother cell) and a second, derived or substitutive pattern of sporogenesis, that is the formation of *ameio-spores*, by a cell other than the true spore mother cell, as in the following scheme (cf. BATTAGLIA, 1983, p. 5):

| | |
|---|---|
| *primary sporogenesis*: (primary spores) | eumeiotic spory (eumeiospory), eumeiospores;<br>aneumeiotic spory (aneumeiospory), aneumeiospores;<br>apomeiotic spory (apomeiospory), apomeiospores; |
| *secondary sporogenesis*: (secondary spores) | ameiotic spory (ameiospory), ameiospores. |

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ähnlich dem, wie ihn die Zoologen seit lange als Metagenesis in der diploiden Phase kennen. Die Karposporen sind wieder echte Sporen, als Bindeglieder zwischen zwei Generationen, aber diesmal Haplosporen; Gonosporen fehlen ganz. — Biologisch entsprechen

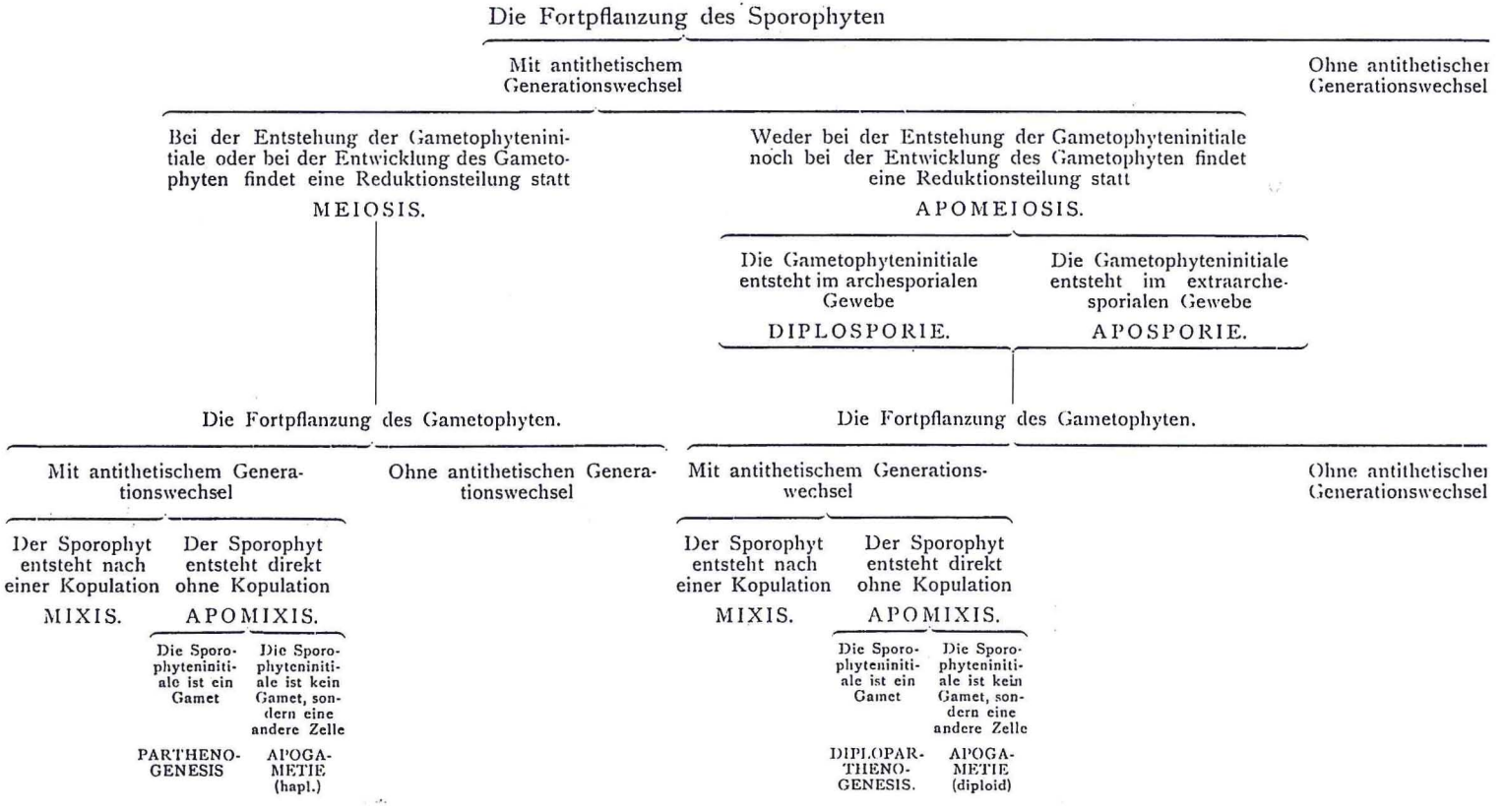


Fig. 4 - (from Edman, 1931).

## 11. *Apomeiosis and ameiosis*

RENNER (1916) probably has priority ([32]) over the term *Apomeiosis*, cf. RENNER, 1916 p. 351:

> Das Unterbleiben der Reduktionsteilung, das bei habitueller Apogamie notwendig eintreten muss, ist, soviel mir bekannt, noch nicht mit einem kurzen Terminus belegt worden. Das Wort, das sich für den längst vorhandenen Begriff von selber einstellt, ist Apomeiose. Die Keimzellen, d. h. die Sporen, können bei Apomeiose noch vollkommen ausdifferenziert werden, wie z. B. bei der habituell parthenogenetischen *Marsilia Drummondi*, wo sie sich von normalen Gonosporen durch nichts als durch die diploide Kernbeschaffenheit unterscheiden, auch in Tetraden aus den Sporenmutterzellen hervorgehen. Ebenso zerlegt sich bei den parthenogenetischen Alchemillen die Embryosackmutterzelle, wenn auch auf apomeiotischem Weg, in vier Megasporen[13]), von denen eine zum diploiden Embryosack, also zum Megaprothallium wird. In anderen Fällen tritt aber die Apomeiose als Sporenverlust auf, als Aposporie, wobei der Gametophyt aus vegetativen Zellen des Sporophyten hervorgeht, ohne den Umweg über die Spore. Die Aposporie steht also zur apomeiotischen Sporenbildung im selben Verhältnis wie die Apogametie zur Parthenogenesis; die Aposporie verwischt die Grenze des Sporophyten gegen den Gametophyten. Bei experimentell erzeugter Aposporie an Farnprimärblättern kommen sogar ausgesprochene Mittelbildungen zwischen Blatt und Prothallium vor.
>
> Bei habitueller Ausbildung sind Apogamie und Apomeiose natürlich immer miteinander verknüpft. Wenn aber festgestellt werden kann, ob die vorhandene Chromosomenzahl die haploide oder die diploide ist, lässt sich mit aller Sicherheit darauf schließen, auf welchem Weg die Anomalie erworben worden ist. Bei diploider Apogamie ist augenscheinlich primär die Meiose ausgefallen, und die Apomeiose hat Apogamie im Gefolge gehabt. Bei haploider Apogamie ist der primäre Verlust der der Gamie, und auf die Apogamie ist die Apomeiose gefolgt.

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([32]) In the present context, RENNER's terms *'Diplose'* and *'Apodiplose'* deserve adequate citation (cf. RENNER, 1916, p. 350-351):

> Hier liegt nichts als eine Verdoppelung des Chromatinbestandes der Zelle vor, das eigentliche Gegenstück zur Meiose, also wenn wir wollen die Diplose.
>
> Als ganz neutraler Ausdruck, eben als Korrelat von Meiose. ist der Begriff der Diplose vielleicht auch brauchbar, wenigstens für die Darstellung des Kernphasenwechsels. Der diploide Zustand wird ja, wie wir gesehen haben, nicht immer durch eine der Formen der Gamie hergestellt. Im engeren Sinn kann dann Diplose für den Typus *Hypochnus* — ob der Vorgang in der Spore oder in späteren Zellen des Mycels, wie vielleicht bei anderen Basidiomyceten, sich abspielt, ist natürlich nicht von Belang — verwendet werden. Apodiplose für Verlust der Chromosomenverdoppelung ist überflüssig, weil wir diesen Verlust von der Gamie herleiten — ebenso wie die Diplose sensu stricto — und deshalb als Apogamie bezeichnen.

However we have not ascertained the priorities of the two terms *apomeiosis* and *ameiosis*, owing to a quite large amount of both zoological and botanical literature utilizing these terms.

Both ameiosis and apomeiosis are cited in the older editions of SHARP's well-known 'Introduction to Cytology', (SHARP 1926, p. 350 and 396).

In this book these terms seem to be simply synonymous, both having the general meaning of absence of chromosome reduction. The latest Sharp's text-book (1943) however, cites only the term *ameiosis*.

The famous book 'Recent Advances in Cytology' (DARLINGTON 1937) records only *apomeiosis*, giving the meaning of a non-reductional cytological process to this term.

The very comprehensive dictionary HENDERSON & HENDERSON'S (1953) distinguishes between ameiosis and apomeiosis as follows:

*ameiosis* = «occurrence of only one division in meiosis, instead of two» (33);

*ameiotic* = «... ... Parthenogenesis in which meiosis is suppressed»;

*apomeiosis* = «sporogenesis without haplosis». («Haplosis = halving of the chromosome number during meiosis; reduction and disjunction» (34).

Independently of these disagreements and the uncertain terminological priorities, we have no doubt that, from a linguistical correct point of view, the unique difference between ameiosis and apomeiosis, depends on the concept of primary or secondary absence of meiosis.

## 12. *The relative uselessness of the term apospory and its derivatives (e.g. euapo-, pseudoapo-, and hemiapo-spory).*

Since we have qualified as a spore any initial cell of the gametophyte, the term apospory becomes relatively useless in angiospermic embryology. At best, this term might be confined to indicate the theoretical development of an embryo directly from a true embryo sac mother cell, (that is lack of spore and consequently no de-

(33) Approximately the same definition can be foun in WEBSTER's Dictionary (1976), namely: «*Ameiosis* = suppression of one of the meiotic divisions...».

(34) A quite different definition can be found in WEBSTER's Dictionary (1976), namely: «*Apomeiosis* = imperfect or suppressed meiosis».

velopment of the gametophyte). Obviously we also consider useless all apospory-derivatives as for instance *euapospory*, *pseudoapospory* (cf. SHARP, 1921; 1926), *hemiapospory* (cf. RENNER's 1916: 'Hemiaposporie'; CHIARUGI's 1927: 'emisporiale'; FAGERLIND's 1940: semiapospory; CHADEFAUD's 1975: 'demi-aposporie') etc.

In this context we cannot forget to mention, as conceptually incorrect, LOVE & LOVE's (1975, p. 69) *agamospory*, a term proposed to describe asexual reproduction in ferns ([35]), see also WALKER 1979, p. 113: «Apomictic Alternation of Generations (Agamospory)». Agamospory, indeed, means literally «agamous sporogenesis»! ([36]).

13. *Misuse of the non-synonymous terms meiosis and chromosome reduction, and apomeiosis and apospory.*

There are many terminological improprieties in the embryological literature, mainly due to inaccurate use of very common terms such as meiosis and chromosome reduction, apomeiosis and apospory.

Meiosis and chromosome reduction are very often improperly used as synonymous terms. It is superfluous to explain their difference. The same criticism if valid for the term apomeiosis (or ameiosis) intended as well for chromosome non-reduction (aporeduction would be, the right term here, cf. BATTAGLIA, 1955), as for apospory.

HAIR's (1956) paper on embryo sac development in *Agropyrum scabrum* (cf. *Elymus* complex in LÖVE & CONNOR, 1982; *E. rectisetus* *in* CRANE & CARMAN, 1987) represents a typical, example of such improper and questionable terminology. HAIR (1956, p. 136) writes:

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([35]) LOVE & LOVE (1975, p. 69) write:

> **III. Asexual spore formation in ferns**
>
> Apomixis other than vegetative reproduction has been reported from some algae and fungi, in which a gamete may directly give rise to a gametophyte. That was termed apomictosis by Winkler (1942), and it seems to be a very rare phenomenon, if the few reports are indicative of its frequency. In the true ferns, however, sexual reproduction without fertilization is known to be considerably more frequent than in the flowering plants (Manton 1950; Evans 1969), for reasons unknown. The mode of asexual reproduction in the ferns resembles the agamospermy of the angiosperms but it is not identical with it. Therefore, we propose for it the name agamospory. Whenever it occurs, it seems to be obligate and function similarly to diplospory in the higher plants.

([36]) It seems to us also as conceptually criticizable the use of the term *semi-agamospermy*, as suggested by K.N.N. NARAYAN (1955, p. 44) for the «Reproduction by seeds formed by circumventing either meiosis or fertilization».

*Ameiosis*, on the other hand, affected at least 96 per cent. of the total material. Two distinct processes, the second being the more frequent, were involved : (1) Dyad Formation following a suppressed meiosis and restitution, or (2) Simple Mitosis without any trace of a meiotic prophase (*cf.* table 3*b*).

*Dyad Formation.* In other apomictic plants this has been attributed to two kinds of antecedent processes. The mother nucleus, which is more or less asynaptic, undergoes either :

(*a*) An abortive " pseudo-heterotypic " division, which lapses at anaphase into a single restitution nucleus, and is followed by an effective equational division (Osawa, 1913 ; Okabe, 1932 ; Bergman, 1941 ; Rosenberg, 1927) ; or

(*b*) A " pseudo-homeotypic " division in which the unpaired chromosomes, contracted as in an ordinary meiosis, pass straight into division (Gustafsson, 1934).

Here both the di-karyocinetic restitutional meiosis, see case (1), and the so-called generative apospory (suppression of meiosis), see case (2), are enlisted under the same term Ameiosis!

## 14. *Extension of the monokaryosporic and dikaryosporic terminology to the non-reduced embyo sacs.*

As already stated in a previous paper (BATTAGLIA, 1983), the definition of the spore as a cell capable of functioning as the initial of the gametophyte allows us to extend to the non-reduced embryo sacs ([37]), the monokaryo... tetrakaryosporic terminology (these are more correct terms than the classic monosporic... tetrasporic terms which we believe would be abandoned).

As previously established, cf. BATTAGLIA (1983, p. 21), within the category of non-reduced embryo sacs, there have been recorded monokaryosporic types (the *Taraxacum* type owing to occurrence of aneumeiosis; the *Antennaria* type, owing to the occurrence of apomeiosis, etc.) and just one dikaryosporic type (the *Ixeris* type, owing to occorrence of aneumeiosis) ([38]).

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([37]) Here the term non-reduced means the occurrence of a non-reduced chromosome number resulting from any cytological process.

The series of symbols *r*, *2r*, *4r* etc. (*r* = reduced chromosome number) is useful to indicate the various chromosome numbers independently from the occurrence of polyploidy. We proposed the symbols *z* = zygotic number, *g* = gametic number, *r* = reduced number, *2r* = unreduced number as early as 1955 (BATTAGLIA, 1955a).

([38]) In this context we must mention that recently (SOLNTZEVA, 1989) has partial-

## III. Preliminary cytological considerations

### 1. *Cytoplasmic cyclosis (protoplasmic streaming) and the related nuclear movement: a widely overlooked biological phenomenon occurring within the embryo sac.*

It is almost superfluous to stress the importance of intracellular movements which represent a basic phenomenon of the living cell, and collectively, of the intracellular kinetics.

To this phenomenon belongs the so-called protoplasmic or cytoplasmic streaming, often referred to as cyclosis, (cf. Seifritz, 1943; Kamiya, 1959, 1981; Allen & Allen (1978, 1982, 1983); Allen (1983) etc.

The limits set to this paper preclude anything more than a passing brief mention of the occurrence of cytoplasmic cyclosis in the embryo sac, and the related nuclear movement which is to be considered as a partial expression of the more complex phenomenon of the endogametophytic kinetics.

Protoplasmic movement was discovered in *Chara* by Bonaventura Corti (1774) and later observed in several plants by such eminent scientists as Fontana, Treviranus, Amici etc.

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ly extended (i.e. with the exclusion of the ES-types corresponding to the classic somatic and gonial apospory) the mono-... tetrasporic terminology to the cases of non-reduced embryo sacs. She writes (Solntzeva, 1989, p. 5): «...it is very important to consider the ploidy of embryo-sac nuclei...»; «... a Roman numeral... designates the number of megaspores that contributes to the embryo sac». Thus, from her Fig. 1 we can see qualified as disporic (symbol II) both the 1-nucleate ES of the Taraxacum type and the 2-nucleate ES of the Allium nutans type, as tetrasporic (IV) both the 1-nucleate (owing to a birestitutional meiosis) ES of the Rudbeckia type and the 2-nucleate ES of the Ixeris type. Lastly we have also seen qualified as a disporic type (cf. Solntzeva, 1989, pp. 6-7) an occasional diploid embryo sac development in *Rubus nitidioides*. This was described by Thomas (1940) and ascribed by this author to the «fusion of haploid nuclei within the embryo sac» (Thomas, l.c. p. 123). Thomas ascribes to the autotetraploid *Rubus nitidioides* a «5% sexual» (obviously developing according to the Polygonum type) and a «95% apomictic (aposporous)» embryo sacs. Apart from the consideration that the roman numerals II, III, IV, in current cytology, are used to indicate respectively bi-, tri- and quadrivalent meiotic chromosome configurations, and that in Solntzeva's classification these *numerals* do not refer to the corresponding *numerical* nuclear condition of the ES, we simply note that such classification is not compatible with our definition of the concept of spore.

K.H. SCHULTZ suggested the term «cyklose» ([39]) to indicate intracellular streaming specifically. For the sake of correct terminology we adopt here the term *cytoplasmic cyclosis* ([40]) to indicate the movement of the cytoplasm within the embryo sac.

Since as far as we known there is no convincing or quantitative documentation of autonomous nuclear movement (such as rotation as an indirect function of the nuclear pores) we deduce that the nuclei *within the embryo sac* are moved passively by cytoplasmic movement. Thus, it is obvious that cyclosis is the main agent responsible for the movement of the central nuclei within the cellularized embryo sac.

Since the two touching central nuclei, very frequently show an outline resembling a letter O divided into two equal halves (i.e. Φ instead of the more simple OO configuration), it is probable that an additional nuclear-attraction force is involved.

Nothing is known of influence of cytoplasmic cyclosis on the position of the nuclei of the embryo sac immediately before the process of cellularization.

Nevertheless, since in the embryological literature most of the drawings of the nucleate embryo sac before the beginning of cellularization, show the 4 micropylar nuclei arranged in a Y configuration (which clearly preludes the usual S+S+E+CN cellularization) we think that the cytoplasmic cyclosis is not influential (at the micropyle) at the time of cellularization.

Conversely, because cellularization takes place shortly after the end of the last nuclear division (see the next paragraph), the orientation of the spindles of that division plays the main role in positioning the nuclei at the pre-cellularization stage of the gametophyte. Furthermore, the decisive influence of cytoplasmic cyclosis on the movement of the sperms during fertilization or on synkaryon for-

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([39]) The dictionary of BILANCIONI (1900), p. 120 cites: «Ciclosi: circolazione intracellulare, scoperta e così denominata dallo SCHULTZ 1820, per distinguerla dalla circolazione generale della pianta». For more details see SCHULTZ C.H. (1822; 1823-1828; 1828 *a*, p. 129: «Cyklose, oder das Kreisen»; 1831 p. 76: «J'ai vu pour la premiére fois, en 1820, le mouvement de circulation dans la chélidonine...»; 1842: «Die Cyklose...»).

([40]) A distinction of the term cyclosis into *cytoplasmic* and *nuclear* cyclosis, is justified by the occurrence of endonuclear kinetics specifically called *nuclear cyclosis* and observed in some dinoflagellates (cf. VON STOSCH, 1972: «cyclose nucléaire»). (It might be well to differentiate this phenomenon by another term, that is «cyclose endonucléaire»).

mation within the multinucleate antipodals, in the cases of polyantipody, can be easily assumed. However, such questions are beyond the subject of the present paper.

In conclusion we believe that the easiest way to understand the phenomenon of cyclosis, extending to the whole of cell-kinetics, is to study carefully any actual protoplasmic movement or any morphological change (of number, size and shape of vacuoles) by means of *in vivo* observations by microcinematographical techniques (see ERDELSKÀ 1973, 1974, 1983, 1985) or videomicrographs (videomicroscopy, cf. references in ALLEN 1983, TUCKER & ALLEN 1986, ALLEN & SCHUMM 1990) and fluorescence methods (cf. references in SCHMIT & LAMBERT 1990), see also next pages. We have written the present considerations in the hope that they will also be a stimulus for further investigation in the field of *in vivo* cytology of angiosperm gyno- and androgametophytes.

2. *Cellularization of the embryo sac: a cytological pattern requiring more detailed reinvestigation (e.g. by fluorescence microscopy coupled with electron microscopy).*

An extensive discussion of the pattern of cellularization of the angiosperm embryo sac is beyond the scope of this paper.

Nevertheless, we feel that we cannot overlook this problem since it is the key to a better understanding of the origin of some modified morphologies of the micropylar region of the mature ES (see next paragraph 4 and the 4-nucleate Pennisetum and Eragrostis types).

Firstly, we wish to state our present conviction as regards the cellularization of the female gametophyte in the angiosperms, namely that it is a fugaceous stage of the ES development, still unsatisfactorily known and awaiting reinvestigation with advanced techniques. More specifically, since this process is accomplished by the so-called secondary spindles ([41]), an up-to-date reinvestigation,

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([41]) Apart from the ultrastructural terminology, because the secondary spindles do not belong to the mitotic process (see FLEMMING' *mitosis* term in BATTAGLIA, 1985 *a*) we believe that the expression 'non-mitotic spindle' is preferable to the old 'secondary' terminology.

We have also distinguished (cf. BATTAGLIA, 1989) the non-mitotic spindles into «*effective*» or «*ineffective*» non-mitotic spindles according to the subsequent occurrence,

for instance by coupled Fl (fluorescence) and TEM techniques seems to be essential to achieve a more satisfactory knowledge of this process.

As far as we know there is no embryological account documenting the cellularization process by the traditional fixing and staining methods coupled and compared with Fl and TEM techniques.

Thus, the following considerations are mainly our present cytological opinion which has suggested the reconstruction of the different cellularization patterns summarized in Plate 1 (see also next paragraph 4).

a) The last coenocytic stage of the angiosperm embryo sac is achieved by 3 (or 1-2) rounds of *nuclear* divisions. At the end of each division the mitotic spindle is, as a rule, disorganized and disappears (see classic drawings such as Fig. 66, *Lilium Martagon*, in Guignard 1891) ([42]) ([43]).

b) *After the end* of last nuclear somatogenic division a system of non-mitotic spindles (secondary spindles) develops from all nuclei of the embryo sac and usually connects both sister and non-sister nuclei. Nuclei very far from each other or intercalated by vacuoles cannot be joined by a *full* secondary spindle.

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or non-occurrence, of persistent cell walls. Frequently ineffective non-mitotic spindles can be seen as fibre-systems connecting non-sister nuclei at the end of meiosis in the tetrakaryosporic types of embryo sac development. Ultrastructural investigations of these cases are very desirable.

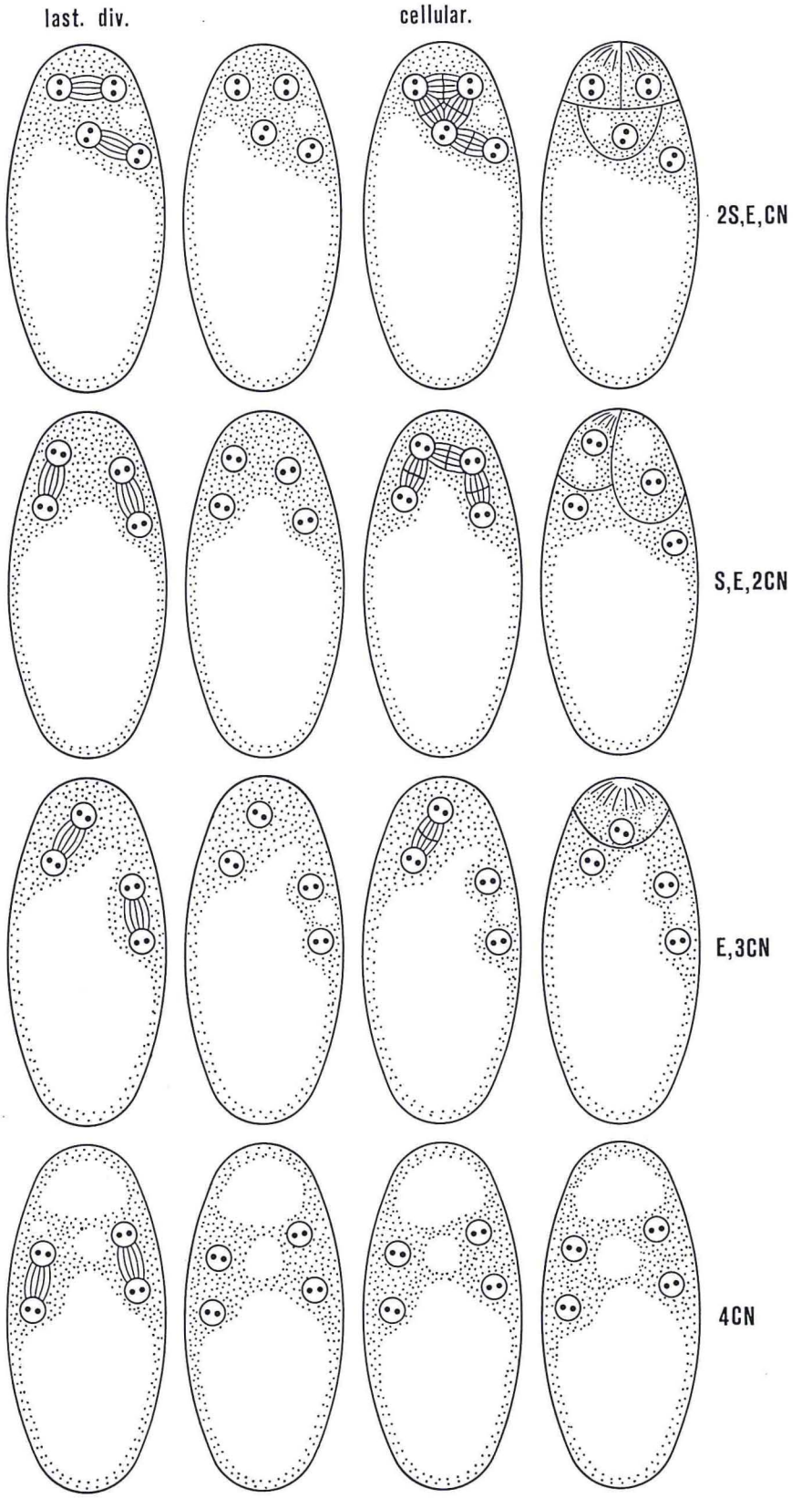
([42]) It is beyond the aim of this paper, and by contrast it may be the matter for a critical history of plant embryology, the discovery (?) by GUIGNARD (1889, 1891, etc.) of the 'spheres attractives', renamed 'spheres directrices', in the both plant sporophytic and gametophytic cells. See also 'centres cinétiques' in GUIGNARD (1898). Perhaps reinvestigation with the most advanced techniques would clarify GUIGNARD's incorrectness.

([43]) From this hypothesis it follows that we consider other statements to be cytologically wrong such as, for instance, those ascribing the cellularization of the ES to the spindles of the third somatogenic division (cf. COOPER, 1941: *Phryma*; SMITH, 1943: *Clintonia*; HOWE, 1975: *Grindelia*, etc.) or to the persistent spindles of the second somatogenic division (cf. SMITH, 1942: *Camassia*; etc.).

PLATE I

Four-nucleate embryo sac (polarization 4+0): patterns of cellularization. S = synergid, E = egg cell, CN = central nucleus. The synergids, and exceptionally the egg cell (see the pattern E, 3CN) show the apical filiform apparatus.

PLATE I



All non-mitotic *full* spindles develop cell-plates and are the sole agents inducing the cellularization of the ES.

c) The transitional stage between the coenocytic and the cellularized stages of the ES, is always characterized by secondary spindles, possibly connecting all the nuclei of the ES as can be seen in the following self-explanatory classical illustration from MOTTIER, 1897 (*Lilium Martagon* Figs. 21, 22, Pl. II); Guignard, 1900 *a* (*Tulipa sylvestris*, see Figs. 10, 11, in Battaglia, 1990); Schaffner, 1901 (*Erythronium*, Fig. 72, Pl. II); COOPER, 1935 *a* (*Lilium henry*, Figs 34,

PLATE II

Figs. 21, 22. *Lilium Martagon*, Mottier (1897, p. 158):
Fig. 21. Drei Kerne von der oberen Tetrade. Rechts unten die Eizelle; links der Polkern. (Weiteres im Text.).
Fig. 22. Ein späteres Stadium als in Fig. 21. Alle vier Kerne liegen fast vollständig in der Schnittfläche. Rechts oben die Synergiden; links unten die Eiselle und der Polkern».

Fig. 31. *Helleborus foetidus*, Mottier (1897, p. 158):
Fig. 31. Vier Kerne im oberen Ende der Embryosackmutterzelle, die simultane Zellplattenbildung zeigend».

Fig. 72. *Erythronium albidum*, Schaffner (1901, p. 380, 387): «Upper two spindles of the third division...». The uppermost nucleus gives rise to the two synergids, the one below this to the egg and upper polar nucleus. A typical arrangement of these divisions is shown in *fig. 72*. The old spindle has survived in this instance, and has separated into two limbs below».

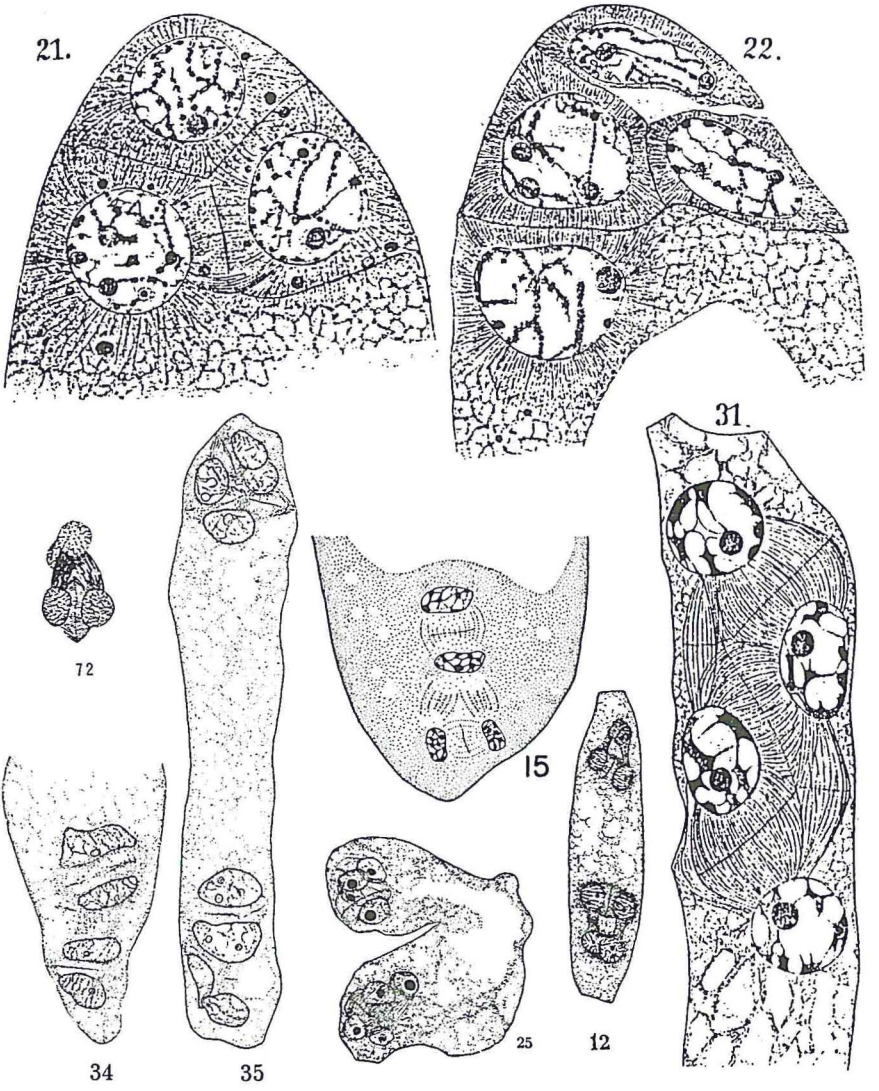
Figs. 34, 35, × 480, *Lilium henryi* (COOPER, 1935 *a*, p. 351): «The remnants of the spindles of the preceding division persist between the respective perinuclear zones. At the conclusion of the fourth division the four nuclei at each end of the embryo sac are held together by two prominent spindles and a less prominent one (figs. 34, 35). Cell plates are formed across these theree spindles in such a manner that three cells are formed at each end of the sac, leaving two nuclei, one small (n) and one large (3n), in the large central cell (figs. 35, 38)».

Fig. 15. *Camassia Leichtlinii* (Smith, 1942, p.: 661): «Cell plates are first formed across the spindles of the third nuclear division (fig. 15). Additional fibers appear in the region of the persistent fibers from the second divisions, and these soon also form typical cell plates».

Fig. 25, × 800, *Solanum tuberosum* (Rees-Leonard, 1935, p. 750).
Fig. 25. Division stages leading to 8-nucleate embryo sac; phragmoplasts between sister nuclei at chalazal end and one pair of sister nuclei at micropylar end of embryo sac; spindles present between remaining nuclei in micropylar region. Composite drawing from two serial selections of embryo sac. × 800».

Fig. 12. *Erythronium albidum* (Cooper, 1939, pp. 863-865): «Each spindle, during the third and last division in the megagametophyte, is surrounded by a dense layer of cytoplasma (fig. 7). Remnants of the spindles of the preceding division persist between the respective dense layers. The four nuclei at each end of the megagametophyte formed as a result of the final division are connected by two prominent spindles and by portions of a less prominent one (fig. 12), as described by Schaffner (13). The synergids and egg at the micropylar end and the antipodal cells at the chalazal end are delimited as a result of cell plate formation across the spindles of the last division, as well as across the persistent spindles of the preceding division».

PLATE II




35, Pl. II); COOPER, 1939 (*Erythronium*, Fig. 12, Pl. II); SMITH, 1942 (*Camassia*, Fig. 15, Pl. II) (44).

(44) We have not included some other similar instances because poorly illustrated or of minor interest, f.i. COULTER, 1898; STRASBURGER, 1905; BROWN, 1909; BROWN and SHARP, 1911; JOHANSEN, 1929; COOPER, 1941; etc.

d) The ultrastructure of the angiosperm embryo sac has extensively been investigated in the last 30 years. There are many hundreds of papers on this topic, see the most recent references in the Proceedings of Symposia on Sexual Reproduction by ERDELSKA (1983), WILLEMSE and VAN WENT (1985), CRESTI, GORI, PACINI (1988), TIKHOMIROV et al. (Leningrad, 1990).

Despite this vast literature, as far as we know, there are only two detailed accounts which describe and document the mechanism of transition from the free nuclear condition to the cellularized stage of the embryo sac, namely a first paper by CASS, PETEYA and ROBERTSON (1985, 1986) on *Hordeum* and another account by BHANDHARI and CHITRALEKHA (1989) on *Ranunculus*.

According to the account by CASS and collaborators (45), cell wall formation begins shortly after the third nuclear division and curved wall segments, associated with many orientated microtubules, can be clearly seen. Later a fusion takes place among actively growing wall segments.

It is worth mentioning that these authors have not seen «pegs» of wall material originating from the gametophyte wall and growing centripetally. They (CASS et al. 1985, p. 2170) write:

«In our opiniom the partitioning walls among the micropylar and chalazal quartets of nuclei in the barley megagametophyte are centrifugally growing cell plates exhibiting many features in common with cell plates described in various tissues (BAJER andMOLE-BAJER 1972; O'BRIEN 1972) and in a recent study of early cell partitioning in the endosperm of wheat (FINERAN et al. 1982).

.....

The first three cells of the antipodal apparatus are cut off by walls beginning in much the same way as those of the egg apparatus».

The CASS account (CASS et al. 1986) also describes the initial planes of wall deposition and the following geometry of the cellularization process, namely:

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(45) As far as we can deduce from the ultrastructural pictures obtained by this research, it illustrates a stage *towards the end* of the cellularization process. Further, we believe that the beginning of the transitional stage showing all nuclei of the ES connected by the secondary spindles (repeatedly documented in the old embryological literature), has not yet been illustrated in ultrastructural papers.

«The earliest observed stages of cell wall formation in the barley egg apparatus indicate that the initial wall between synergid nuclei is vertical (Fig. 1) and that the initial wall between the micropylar polar and egg nuclei is a discrete horizontal wall (Figs. 2, 3). Although the synergid wall remains unbranched, the wall between micropylar polar and egg nuclei branches (Figs. 2, 3). The originally horizontal component of this wall continues to grow horizontally (Figs. 4-6). We believe that this horizontal component will ultimately separate the egg apparatus from the rest of the megagametophyte. The other component of the polar nucleus — egg nucleus wall grows toward the micropylar megagametophyte wall. This vertical wall branch and the vertical wall between synergid nuclei fuse resulting in complete separation of the egg and synergid nuclei. At the conclusion of wall formation the barley egg apparatus consists of three cells separated from each other by two vertical walls, one of which is higly curved and separated from the rest of the megagametophyte by a flat wall contacting the megagametophyte wall circumferentially».

Some other considerations from this paper are worth commenting on because, in contrast with the drawings in the early embryological literature, they affirm that the partitioning process at each pole is achieved by 2 plates, one of which is branched and that there may be something unique about the nature of the plates, as follows:

«Our observations, which were not limited to just a few thin sections per stage in megagametogenesis, suggest that the original egg — micropylar polar nucleus cell plates branches. The ultrastructural basis for this is shown in Figs. 2 and 3 and is summarized by the diagram in Fig. 16. An additional relevant point here is that the two synergid nuclei and egg nucleus at the time of wall formation lie on the same horizontal plane (Figs. 4, 6, 16); the egg nucleus lies well behind the synergid nuclei as can be determined by examination of many sections of the same megagametophyte. The positioning of these nuclei along with that of the micropylar polar nucleus plays a substantial role in determining the geometry of partitioning. We agree with the concept that three walls or cell plates are required to accomplish the partitioning process. We have no evidence, however, that one of these arises de novo or across a persistent spindle from a previous division. Our interpretation is that there

are two plates, one of which is branched. The walls that these plates produce do not exhibit a typical middle lamella so that there may be something unique about the nature of the plates».

The cellularization pattern described by BHANDARI and CHITRALEKHA (1989) in *Ranunculus sceleratus* is appreciably different from that reported by CASS and collaborators as documented below:

«The four nuclei undergo mitosis simultaneously (Fig. 2), accompanied by cytokinesis and cell plate formation (Figs. 3-5). The cell plates are distinct, PAS-positive, and visible between the separating chromatin masses during early telophase (Figs. 3-5). At each of the two (micropylar and chalazal) ends, three cell plates are observed between the four organizing daughter nuclei .....

Of the three cell plates formed the two originating within the primary spindle of the dividing nuclei are larger (Figs. 4, 5). The large cell plate I (CPI) closer to the central vacuole is perpendicular to the long axis of the embryo sac and extends horizontally. The second large cell plate II (CPH), away from the central vacuole, appears to be horizontal (Figs. 4, 5, 7) or placed obliquely (Figs. 6, 8) to the long axis of the embryo sac. In addition, the third smaller but very distinct cell plate III (CPIII) (Figs. 4-8) is formed in the region between the two nonsister chromatin masses. It develops vertically at righ angles to the two large cell plates but parallel to the long axis of the embryo sac.

After their inception, the cell plates extend simultaneously. The initial growth results in the fusion of one side of the cell plates I and II with the lateral embryo sac wail (Figs. 6-8). Subsequently the other ends (not yet fused with the embryo sac wall) of the plates extend in the opposite direction (towards the other side of the embrio sac). By the time all the four chromatin masses become organized into nuclei. CPIII (vertical cell plate) is in contact with CPI (horizontal cell plate) and CPII (horizontal/oblique cell plate) (Figs. 7, 8). CPI grows towards the other side of the embryo sac wall along the cytoplasm lining the central vacuole (arrow, Figs. 9, 10). It separates the nucleus close to the central vacuole, from the remaining three nuclei. The free edges of CPII and CPIII (the vertical cell plate) between the three nuclei, extend towards the embryo sac wall and CPI (horizontal cell plate) (Figs. 6-8), to partition the nuclei. CPI is the largest and termination of its growth appears to be the final

event involved in the cellularization of the embryo sac. Thus, the fusion of the growing ends of the cell plates with each other, and with the embryo sac wall at their respective areas of contact, results in the delimitation of three incipient cells of the egg apparatus at the micropylar end (Fig. 11), antipodals at the chalazal end (Fig. 12), and a large central cell with two polar nuclei in the central region of the megagametophyte .....

The smaller size of the CPIII (vertical cell plate) present between the nonsister nuclei indicates that it may have arisen later than the two larger cell plates (CPI and CPII) between the sister nuclei. From an examination of serial sections it is evident that the cell plates appearing as thin strips in sectional view are in fact disclike three dimensionally».

We should also report the following comments by BHANDARI and CHITRALEKHA, on the previous literature, namely:

«CASS et al. (1985) observed the initiation of cell plates at the eight-nucleate stage, independent of and shortly after the last mitotic division, while the chalazal and micropylar nuclei are present as quartets. Though initially only two cell plates were observed at each pole of the embryo sac. CASS et al. (1986) suggested that the horizontal wall growing between the egg and polar nuclei, branches subsequently and one of these grows vertically. However, we found *de novo* origin of CPIII (vertical) in *R. sceleratus* and not by the bifurcation of CPI. Eventually, in barley, as in *R. sceleratus*, three walls at each of the two poles appear to be involved in the cellularization of free-nuclear megagametophyte.

On the contrary, in spinach the separating walls in the megagametophyte arise at the periphery of the embryo sac and grow centripetally (WILMS 1981). NEWCOMB (1973) observed a freely growing wall in the central cell of *Helianthus annuus* and likewise believed that is not formed during the actual process of cytokinesis».

We have intentionally not taken the accounts by NEWCOMB (1973 *a*, *b* [46]) and by WILMS (1981) into consideration since we believe that they have not observed the beginning of the cellularization process.

The available TEM data clearly do not agree with the classical

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[46] NEWCOMB (1973 *a*, p. 865) writes: «...the actual process of cell wall formation in the change from the coenocytic to the cellular condition has not been observed».

data, such as the convincing fig. 21 of MOTTIER (1897), which shows at least four distinct cell plates.

Since it is illogical to admit the occurrence of different patterns of cellularization (cf. data cited above for *Helianthus*, *Hordeum* and *Ranunculus*), we emphasize once more the need of further investigation with more advanced techniques.

It is obvious that the critical transitional stage needs to be first selected by suitable techniques such as those well-known ones developed by HERR, J.M. Jr. (1971-1985) or by STELLY et al. (1984), etc., and then stained by classic, fluorescence (etc.) methods, and finally reimbedded for TEM sectioning.

We firmly believe that only by this combination of old and new tecniques, and not by ultrastructural methods alone, the basic pattern as well as the details and perhaps the eventual variation of the cellularization process will be clearly and convincingly establised.

e) We believe that a «cellularization biochemical message» should start, as a rule, from the micropylar region of the ES, (see our hypothesis of the achievement of the $C^4$ cellularization status in BATTAGLIA, 1989). Thus, as a rule, the cellularization process should begin at the micropylar pole of the ES, (see further).

f) From an ultrastructural point of view, we must suppose that the «cellularization speed» or at least the consistency of the ultimate results of the cellularization process, should be strictly correlated with some factors such as the cytoskeleton (for instance as regards the orientation and distribution of MTs, the actin filaments etc.) and perhaps also with variable physiological conditions. Since the cytoskeleton-status, etc., may not be identical at the two opposite poles of the ES, the cellularization process might also be seen to be precocious at the chalazal pole or to proceed asynchronously as regards formation of cell plates. We believe that this asynchrony compelled some authors to deduce that the cellularization process also starts at the chalazal pole of the ES, cf. NEWCOMB (1973) etc. In this connection we would like to add that the perceptible cell plate might also be seen *at first* (regularly? occasionally?) within the secondary spindle connecting sister nuclei and *later* within the secondary spindle which connects non-sister nuclei (see for instance Smith's Fig. 15 for *Camassia* cf. Plate II).

Wada's researches on mitosis in living cells would support such statement.

According to BUNGO WADA (cf. 1981 and earlier papers) the nuclear

membranes do not break down before spindle formation as believed by cytologists using fixation. On the contrary, the nucleus increases its volume remarkably during prophase and transforms its outline from a sphere to a spindleform, the nuclear membrane trasformings itself into a spindle membrane.

Thus, at leat shortly after the end of each nuclear division of the embryo sac, the cytoskeleton structure (*sensu lato*) between two sister nuclei should be not the same as that existing between non-sister nuclei. Granted that the mitotic spindles of the last somatogenic division of the ES should be disorganized ([47]), the subsequent quick organization of the secondary spindles would logically be easily or rapidly achieved within the cytoskeleton between sister-nuclei than that between non-sister nuclei.

We also believe that these considerations account for the phrase «persistent spindle of the last division», so frequently found in early descriptions of the cellularization process.

3. *The extent of correspondence between the cellularization pattern of the embryo sac and the post-meiotic simultaneous cytokinesis of female or male sporocytes. The rediscovery of the Helleborus type of ES development (cf.* MOTTIER, *1897), i.e. a secondary monokaryosporiality owing to post-meiotic simultaneous cytokinesis.*

As mentioned before, the paper by MOTTIER (1897) clearly illustrates the simultaneous cellularization which takes place at the micropylar end of the coenocytic embryo sac of *Lilium martagon* (see Figs. 21, 22; Plate II). It also documents the existence of a post-meiotic simultaneous cytokinesis of the female sporocyte ([48]). This form of female sporogenesis, not mentioned in any of the embryo-

([47]) As matter of fact, hundreds of classical embryological papers show the occurrence of the 8-nucleate coenocytic stage *before* the start of the cellularization process.

([48]) The female sporocyte is usually called megasporocyte. Since the prefix 'mega' is very questionable (cf. BATTAGLIA, 1982) we would like suggest the term «gynosporocyte» in place of megasporocyte (similarly for compound terms as megasporogenesis etc.).

It is obvious that the same criticism can be made as regards the term microsporocyte, which should be replaced by the other term «androsporocyte».

logical text-books, occasionally takes place in *Helleborus foetidus* (see Fig. 31, Pl. II).

MOTTIER (1897, p. 144) writes:

> Häufig konnten bemerkenswerthe Abweichungen bei den Kerntheilungen in der primären Embryosackmutterzelle beobachtet werden. Manchmal scheint keine Zelltheilung unmittelbar auf die erste Kerntheilung zu folgen, wenn nämlich nach der zweiten Kerntheilung vier Kernanlagen zu sehen sind, die in einer geraden Reihe liegend, durch Verbindungsfäden miteinander zusammenhängen. In anderen Fällen können die vier Kerne im oberen Theile der Zelle liegen (Fig. 31, Taf. III), aber erst später werden die Zellwände angelegt. Dieses Bild ist lehrreich, indem es die eigenthümliche Anordnung der Verbindungsfäden zeigt, wenn die Zellplatten angelegt werden. Niemals konnten vier fast fertige Kerne ohne ein Anzeichen von folgender Zelltheilung angetroffen werden. Nach dem Verlaufe dieser zwei Theilungen in der primären Embryosackmutterzelle zu schliessen, scheint es ohne Zweifel, dass dieselbe mit der Pollenmutterzelle homolog ist.
>
> Die untere der vier Zellen nimmt auf Kosten der drei oberen nach und nach an Grösse zu und entwickelt sich in bekannter Art und Weise zum Embryosack. Ihr Kern, der in das Ruhestadium übergeht, nimmt etwas an Grösse zu, und je ein grosses Büschel Kinoplasmafasern strahlt von seiner oberen und unteren Seite aus. Die drei folgenden Kerntheilungen wurden nicht ins Einzelne verfolgt, da sich theilende Kerne wegen des verhältnissmässig langsamen Wachsens des Embryosacks nur selten angetroffen wurden. Nach den Zuständen, welche ich fand, scheint es mir sehr wahrscheinlich, dass die Theilung hier auf homotypischem, also gewöhnlichem Wege erfolgt. Nach jeder dieser Theilungen treten die Kerne in das Ruhestadium ein.

Further, the explanation of MOTTIER as regards his Fig. 31 is categorical: «die simultane Zellplattenbildung zeigend» (49).

Incidentally, we take this opportunity to establish the new Helleborus type of ES development (MOTTIER, 1897 and BATTAGLIA, this paper) since it is the first example (50) of a secondary

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(49) This simultaneous cytokinesis in *Helleborus* has not been recorded by any embryologist other than MOTTIER, see GUIGNARD (1882, cf. Fig. 81, 82, 83) or EYMÉ (1961, Planche III, Fig. 1).

(50) *Arabidopsis thaliana* seems to be the second case of the Helleborus type,

monokaryosporiality ([51]) due to post-metiotic simultaneous cytokinesis.

MOTTIER's fig. 31 shows four spore nuclei connected by five secondary (non-mitotic) spindles. The alternative interpretation of 3 non-mitotic spindles + 2 mitotic spindles seems to us very illogical.

The middle plane of each spindle shows a clear cell plate. Furthermore, two of the five cell plates present seem to be more developed than the remaining three ([52]).

The two better developed cell plates must be interpreted as those belonging to the secondary spindles organized between *pairs of sister nuclei*. This documentation, together with the above interpretation, describes the same morphological details so frequently described or recorded for the cellularization of the embryo sac and suggests strongly the hypothesis of the occurrence of an unique cellularization pattern for any female coenocytic stage due to a series (2 or more than 2) of nuclear divisions.

The comparison between MOTTIER's (1897) Fig. 31 and Smith's (1942) Fig. 15 (cf. Plate II), for instance, convincingly supports and strengthens such hypothesis.

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as very recently reported by WEBB and GUNNING (1990, p. 211): This interesting brief report deserves full citation:

> Aspects of megasporogenesis in Arabidopsis thaliana were investigated, using a variety of techniques including immunofluorescence microscopy of microtubules. The observations deviate from reports of preceding studies in that the megasporocyte was found to undergo both meiotic divisions followed by simultaneous cytokinesis (i.e. without an intermediate dyad stage) to give a multiplanar tetrad of megaspores. This variation of megasporogenesis has not been described previously. The microtubular cytoskeleton is extensive and largely cytoplasmic throughout megasporogenesis. The arrays suggest roles in maintenence of cytoplasmic integrity, organelle and nuclear positioning. There are no interphase cortical arrays of microtubules, suggesting that the role of internal influences on cell shape is small. Other phenomena observed during megasporogenesis will also be discussed.

([51]) We consider that the adjective monokaryosporic (etc.) is by far a more correct term than the current monosporic (cf. BATTAGLIA, 1983).

As regards the distinction between primary and secondary dikaryo-tetrakaryosporiality see the above mentioned paper.

([52]) This fine detail is appreciable only in the original documentation, see Fig 31, Taf. III (MOTTIER, 1897).

In this context the following consideration arises automatically: to what extent does the simultaneous cytokinesis during megasporogenesis (cf. *Helleborus*) differ from the simultaneous cytokinesis during microsporogenesi? From this point of view, we believe (and suggest) that the simultaneous cytokinesis in the coenocytic megasporogenesis of *Helleborus* deserves reinvestigation with modern techniques such as those applied to the simultaneous cytokinesis in the coenocytic microsporogenesis of orchids, *Impatiens, Lonicera* (etc.)y by BROWN and LEMMON (1988 *b*, 1989; indirect immunofluorescence), adequately coupled with complementary observations with the TEM (etc.).

4. *Cellularization of the four-nucleate micropylar region of the embryo sac, and of any four-nucleate coenocytic embryo sac (attaining the 4+0 nuclear polarization), according to the formulae «2S+E+CN» (ordinarily), «S+E+2CN» (occasionally), «E+3CN» (rarely) and «4CN» (rarely, non-recurrent anomaly: lack of embryo).*

We have earlier advanced and developed a theory assuming that the cellularization of the ES normally takes place when 4 nuclei are present in the micropylar end of the female gametophyte (BATTAGLIA, 1989). This status of cellularization was also indicated with the symbol $C^4$ («cellularization four micropylar nuclei) ([53]).

Since the morphology of the cellularized ES is strictly correlated with the number and position of the nuclei just before the beginning ot the wall formation ([54]), it is obvious to deduce (and to

([53]) The tetrakaryosporic (a term more correct than the usual tetrasporic) embryo sacs, after the 2 + 2 or 1 + 3 spore polarization, give rise, in most cases, to the well-known 8-nucleate or 16-nucleate cellularized gametophytes, respectively.

The rare polarizations 3 + 1 and 4 + 0 also occur, giving rise respectively to (6 + 2) and (8 + 0) nucleate stages, followed by specific pattern of cellularization distinguished by the formulae $C^{4(+2)}$ or $C^{4(+4)}$ cf. *Tulipa tetraphylla* and *T. sylvestris* types in BATTAGLIA (1989).

The cellularized embryo sacs in these last two types are qualitatively characterized by the occurrence of sterile micropylar cells called pseudo-eggs (cf. BATTAGLIA 1989, 1990).

We believe that the details of the wall formation in both *T. sylvestris* and *T. tetraphylla* types need further investigations, combining old and new techniques.

([54]) Since this paper is primarily morphological, is not intended to enter into a detailed discussion of subcellular structures. Nevertheless, it is obvious that we

observe as actually occuring) that the morphology of the cellularized micropylar region of the Polygonum type (4+4 nuclear polarization before wall-formation) would be identical to that of the cellularized ES of the Oenothera type characterized by the 4+0 nuclear polarization before wall formation. Further, there is no reason to hypothesize the occurrence of a different pattern of cellularization for any other (4+0) coenocytic ES, however attained, see further the unreduced Pennisetum and Eragrostis types.

Thus, any precellularization 4-nucleate micropylar stage will, after wall formation, achieve a morphology which can be summarized at least in most cases, by the formula «2S+E+1CN» (two synergids + one egg + one central nucleus).

Since the validity of classical light microscopy observations can not be denied, we feel justified in writing that the cellularization of the embryo sac is due to the occurrence of the so-called secondary spindles.

Each secondary spindle is able to induce its own middle *initial cell-plate* («efficient secondary spindle»). Initial cell plates actively grow and can meet and fuse with each other, thus originating the *definitive cell-plates* of the cellularized embryo sac.

Before going further into this topic, we must duly report at least a few sentences from an earlier description of the ES cellularization by HELEN GERASSIMOVA - NAWASHINA (1954 *a*, *b*; 1958, cf. 1961). She wrote (cf. GERASSIMOVA - NAWASHINA, 1961. p. 140-141 and Plate III):

«5. The interaction between the nuclei and the surrounding cytoplasm of the coenocyte results in the characteristics radiating organization of the cytoplasm between them («secondary spindles») where partition walls may be finally formed according to circumstances.

.....

An analysis of the organization of the «Normal type» embryo sac shows that it is a result of the operation of the general principles outlined above rather than a *sui generis* occurrence.

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consider that MTs act upon in the positioning of the ES nuclei in the precellularization stage; a phenomenon which was, for instance, described earlier for coenocytic dyads and tetrads during microsporogenesis (VAN LAMMEREN et al., 1985), and for the endosperm nuclei by VAN LAMMEREN (1988) etc.

Thus, in the course of the first mitosis in the *macrospore* the sister nuclei diverge to opposite poles of the elongated cell (principles 1, 2 and 3). The second and third divisions in the coenocyte take place synchronously (principle 4) and are oriented at right angles to each other (principle 2); this is the reason why the obligatory quartets of nuclei are formed at the micropylar and chalazal poles of the developing embryo sac. The nuclei composing a tetrahedrical quartet repel each other (principle 3) so that the following final arrangement is inevitably attained in each of them: three nuclei are pushed toward the arch-like apex of the coenocyte while the fourth becomes turned toward the centre which is occupied by a large vacuole. Somewhat later partition walls are formed in the quartet (according to principle 5), i.e. the egg apparatus and the antipodals are formed. Strong vacuolization prevents the formation of a cell wall between the distantly placed fourth nuclei of the quartets (the poiar nuclei), resulting in the formation of a large binucleate central cell. With the cessation of nuclear divisions, the polar nuclei soon come to a common dynamic centre (principles 1 and 6) where they may fuse (principle 8) to form the secondary nucleus (Fig. 1)».

Thirty years later, we have a somewhat different idea of the pattern of ES cellularization. We think, for instance, that more information is necessary on the question that the nuclei comprising a quartet repell each other.

In this context ultrastructural data should be adequately considered and the occurrence of cyclosis must not to be overlooked.

Granted that the *initial* cell-plates arise within each non-mitotic spindle (secondary spindle) and that they later on grow and fuse with other *initial* cell-plates giving rise to the *definitive* walls of the embryo sac, we cannot agree with the statement that 2 or 3 cell plates are required to accomplish the partitioning process at each end of the embryo sac, as has been reported in the most recent ultrastructural investigations.

In theory, 4 nuclei very near each other, without interposing vacuoles, can be *three-dimensionally* connected by 6 secondary spindles, but as far as we know there is no documentation in the embryological literature of the occurrence of this spindle-system between gynospore (megaspore) nuclei or embryo sac nuclei.

As regards the occurrence of 5 *initial* cell plates as a consequence of 5 secondary spindles, we believe that this case has been fully recorded by MOTTIER (1897) for the 4-nucleate gynospore of *Helleborus* (cf. Plate II, Fig. 31).

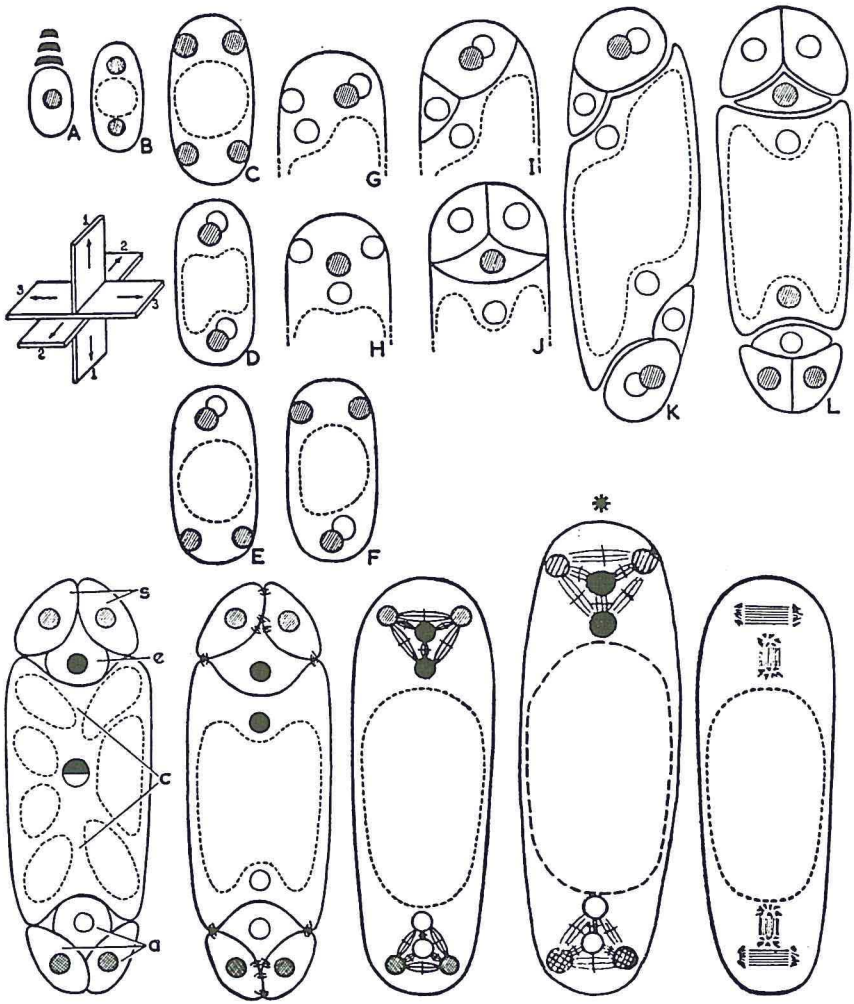



PLATE III

Fig. 1. (*a*, antipodals; *c*, central cell; *e*, egg cell; *s*, synergids). Diagram illustrating the development of the normal type of embryo sac. Top: the three nuclear division, their orientation and the resulting arrangements of nuclei followed by cell formation. The hatched nuclei are those nearer to the observer. A, the mature macrospore; above the three disintegrated ones. B, the binucleate coenocyte. C-F, the quadrinuceate coenocyte: C-D, square arrangement, face and side view; E-F, cross arrangement, face and side view. G-H, the micropylar tetrahedral quartets of nuclei resulting from the third (last)division, face and side view. I-J, same, after the formation of the partition walls. K-L, embryo sac organization, face and side view. The lower four figures mark the position of the spindles at the third division and the organization of the embryo sac; the pairs of sister nuclei are shaded identically (face view).

Fig. *. From Gerassimova-Navashina (1958, p. 138); figs. A, B etc. from Gerassimova-Navashina (1961, p. 142). Details in the Text.

The cellularization of the 4-nucleate micropylar region of the angiosperm embryo sac, giving rise to the usual morphology which corresponds to the formula 2S+E+1CN, seems as a rule, to be achieved by 4 secondary spindles, as documented, for instance by Figs 15 (*Camassia*), 35 (*Lilium*), 12 and 72 (*Erythronium*), (see the identical pattern of cellularization in our Plate I).

*At least* four cell plates can be seen at the micropylar end of the embryo sacs in Figs 21 and 22 (*Lilium*: MOTTIER, 1897). However, a comparison between Fig. 22 (*Lilium*) and Fig. 35 (*Lilium*) shows that in both cases the four micropylar nuclei display the same spatial arrangement. It follows that in Fig. 22, a secondary spindle connected the upper central nucleus to the non-sister nucleus positioned on the upper right side of the ES. Thus, the cellularization process at the micropylar end of Fig. 22 implies the occurrence of not less than five *initial* cell-plates.

It is evident from the cellularization in progress at the chalazal region of Fig. 34 (*Lilium*: COOPER 1935 *a*), that only three secondary spindles are involved in the case of the four superposed nuclei.

However Fig. 35 of the same paper records the occurrence of the usual four secondary spindles, with their *initial* cell-plates, at the chalazal region of the embryo sac.

We believe that the position of the nuclei at the beginning of the wall formation process depends mainly on the relationship between the direction of the spindles of the last nuclear division and the number, place and size of the neighbouring vacuoles.

Deviating from the most usual relationship cited above (including the usual Y arrangement of the 4 micropylar nuclei), we have drawn a micropylar partitioning of the embryo sac by three secondary spindles achieving the rare morphology summarized by the formula S + E + 2 CN, cf. Plate I. This micropylar cellularization occurs usually in the reduced embryo sac of *Allium mutabile* (PORTER, 1936).

In addition, 4-nucleate unreduced embryo sacs showing the normal cellularization 2S + E + 1 CN as well as the atypical one S + E + 2 CN, have frequently been observed in many grasses (f.i. Andropogoneae, Paniceae, etc) having the Pennisetum (ex-Panicum) or the Eragrostis type of ES development (cf. details and references in the next Chapters).

We cannot disregard the rare pattern of micropylar cellularization achieved by only a secondary spindle which gives rise to the

micropylar morphology summarized by the formula E + 3 CN ([55]) see Plate I.

In this case, the micropylar spatial relationship between nuclei and vacuoles allowed the development of only one secondary spindle.

Such very atypical micropylar cellularization is recorded in the embryological literature, for instance, as an occasional anomaly in *Pennisetum dubium* (GILDENHUYS & BRIX, 1959, p. 235). Plate I also shows the case in which the persistence of a large micropylar vacuole prevented any cellularization. We have earlier discussed (BATTAGLIA, 1989, pp. 44-47) the theoretical and embryological meaning of this case which confirms the pilot function that the micropylar region exerts on the differentiation of the angiosperm female gametophyte.

In this case, owing to the lack of cellularization, the embryo sac contains only four central nuclei (4 CN) and, later on, no more than the trophophyte (the usual endosperm). It is obvious that the lack of embryogenesis qualifies this case as an example of a non-recurrent type of ES development.

As regards the unreduced embryo sacs this non-recurrent anomaly has been rarely seen, cf. *Pennisetum dubium* (GILDENHUYS & BRIX, 1959, p. 237, Fig. 2k; see also NARAYAN, 1962).

([55]) We believe that in this case the egg cell would be equipped with the filiform apparatus, by analogy with the cellularization well-known in the reduced embryo sacs belonging to the Plumbago and Plumbagella types.

IV. RECURRENT TYPES OF UNREDUCED EMBRYO SAC: RECOGNIZED TYPES.

| | |
|---|---|
| Ameiotic types: | IVa. HIERACIUM TYPE;<br>IVb. PENNISETUM (PANICUM) TYPE; |
| Apomeiotic types: | IVc. ANTENNARIA TYPE;<br>IVd. ERAGROSTIS TYPE; |
| Aneumeiotic types: | IVe. TARAXACUM TYPE;<br>IVf. IXERIS TYPE. |

IVa. *HIERACIUM TYPE* (ameiotic ES, 8-nucleate).

This type was discovered by ROSENBERG (1906, 1907) in species of *Hieracium* subg. *Pilosella*.

In this case one or more cells, other than the normal EMC, usually nucellar cells, enlarge and function as ameiotic unreduced initial cells of the ES (i.e. the classical somatic apospory). Subsequent development by three nuclear divisions results in the usual 8-nucleate, 7-celled gametophyte.

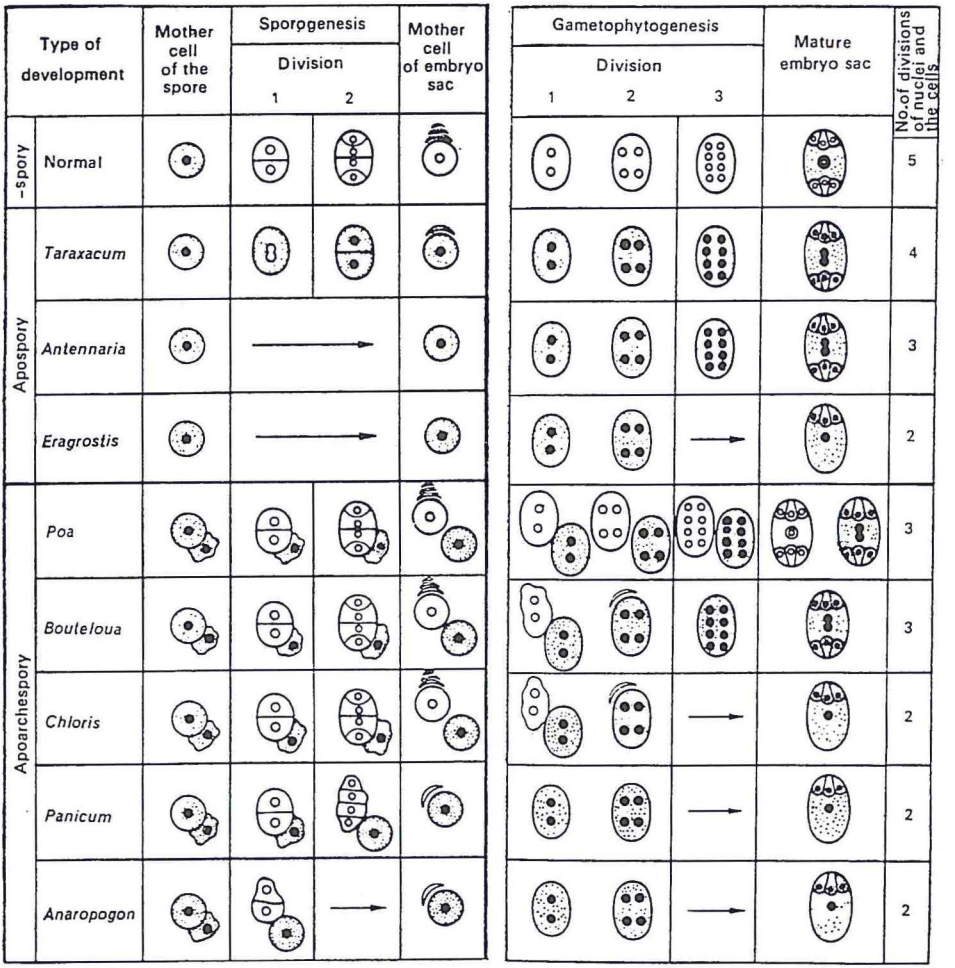
There is no detailed convincing documentation of a regular relationship between the differentation and development of the ameiotic initials and the cytological behaviour of the normal or legitimate EMC (precocious or late degeneration). The ameiotic ES development is completely independent from the meiotic ES development and when they coexist, the degree and the frequency of their coexistence can vary between different individuals of the same species.

Thus we cannot agree with the establishment of the new types, the Poa type and the Bouteloua type, etc. recently proposed by KHOKHLOV (1970, cf. 1976), see Plate IV. Indeed these types differ only in relative numbers of «reduced & unreduced embryo sacs».

The Hieracium type, recorded in the classical literature as somatic apospory is today simply defined as apospory. Lists of species (not a purpose of the present paper) having this type of ES development were given by STEBBINS (1941), GUSTAFSSON (1946, 1947); MAHESHWARI (1963), DAVIS (1963), RUTISHAUSER (1969) and most recent specialized papers.

## PLATE IV

From Khokhlov (1976, pp. 14-15).




Types of development of embryo sacs in apomixis in the different taxa of the grass family, illustrating a sequential deletion from the cycle of megagametophyte development. The dotted cells with four nuclei are unreduced elements; white cells with empty nuclei are reduced elements.

IVb. *PENNISETUM TYPE* (ameiotic ES, 4-nucleate; cf. Panicum type in BATTAGLIA, 1963).

1. *The present Pennisetum type (ex Panicum) and the question of* NARAYAN'S *priority (1951: Pennisetum) versus Warmke's priority (1952, 1954: Panicum).*

We established the Panicum type (BATTAGLIA, 1963 p. 248: «somatic apospory: (b) Panicum type, 4-nucleate unreduced embryo sac») on the basis of WARMKE'S paper (1954) on *Panicum maximum*. The Panicum type of ES development has been accepted by plant embryologists (see DAVIS, 1966; RUTISHAUSER, 1967... NOGLER, 1984 etc.). It is first necessary to recall that our review on «Apomixis» (BATTAGLIA, 1963) was actually written during 1954-1957, was revised in 1958-1959 and, was sent to the editor, of Phytomorphology the late prof. P. MAHESHWARI before the end of 1959. At that time we rejected the establishment of a Pennisetum type (NARAYAN, 1951; unpublished Ph. D. Thesis) in place of the Panicum type (WARMKE, 1954) since WARMKE himself had reported briefly and ambigously an ES development similar to that discovered in *Panicum*, occurring in apomictic species of the genus *Pennisetum*, cf. WARMKE (1954 p. 10):

> The production of large numbers of 4-nucleate and 4-celled mature embryo sacs in guinea grass, in addition to occasional embryo sacs of the normal type (eight nuclei and seven cells) is of interest. To the author's knowledge, this and another case in *Pennisetum*[2] are the only reports of mature, 4-nucleate embryo sacs outside the family Onagraceae.

[2] Personal communication from G. L. Stebbins, citing an unpublished thesis (Dept. of Genetics, University of California) by K. N. Narayan in which the mature embryo sacs of *Pennisetum rueppellii* and *P. villosum* are found to have only four nuclei.

The above sentences clearly gave rise to the following typological uncertainty: does the Pennisetum case belong to the somatic or to the gonial (generative) apospory?

Since in 1954-1958 we were unaware of any documentation on the occurrence of such unreduced 4-nucleate embryo sacs in both «Pennisetum rueppellii» and «P. villosum», we considered the Panicum type (WARMKE, 1954) to be rightly established.

Today, after a more complete perusal of the embryological literature published during the 1952-1959, we have quite a different opinion regarding the validity of the Panicum type, and believe that NARAYAN's (1951: Pennisetum) priority should be acknowledged and consequently the Panicum type changed to Pennisetum type.

First we wish mention that in those years (1954-1959) we were unaware of the existence of WARMKE's preliminary report on the «Apomixis... in Panicum maximum» published in 1952. WARMKE's full report (1954), and we will now say surprisingly, did not quote his preliminary account (1952). It is also worth mentioning that this preliminary report had also never been quoted in all the apomictic literature published in those years ([56]).

Only in subsequent years did we find that WARMKE's preliminary report was quoted by GILDENHUYS & BRIX (1959: «Apomixis in *Pennisetum dubium*»). However, this paper, although published in June 1959 (South Afric. J. Agric. Science), began to circulate only in 1960, too late for a critical consideration and inclusion in our review on «Apomixis». It is useful to add that WARMKE's preliminary report also escaped the attention of most embryologists; thus for instance, it is not recorded in the very comprehensive «Systematic Embryology of the Angiosperms» published by GWENDA DAVIS in 1966 nor in RUTISHAUSER's (1967) embryological text-book.

A second consideration concerning the present question is that WARMKE's preliminary report takes the establishment of the Panicum type back to the year 1952. This consideration is well worth making since SIMPSON & BASHAW (1969, p. 36) quote BASHAW's (1953) Ph. D. dissertation on apomixis in *Cenchrus* (*Pennisetum*) *setigerus* as well as a Ph. D dissertation (1953) by Fisher on apomixis in *Pennisetum ciliare* ([57]), ([58]). Obviously the preliminary report by WARMKE

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([56]) Cf. CELARIER & HARLAN (1955, 1956, 1957), HARLAN et al. (1958), SNYDER et al. (1955), SNYDER (1957), BROWN & EMERY (1957 *a*, *b*, 1958), EMERY (1957), EMERY & BROWN (1958), NYGREN (1954; see also 1967), NARAYANASWAMY (1953, 1954, 1955, 1956), FARQUHARSON (1955), HAIR (1956) etc.

([57]) The full report on apomixis in *Cenchrus* (Pennisetum) *setigerus* and *Pennisetum ciliare*, appeared in 1954 as a joint paper by FISHER, BASHAW & HOLT (1954). This deserves mention for the following explanation of the fig. 7: «Figs. 5-16. Photomicrographs of ovaries... of *Pennisetum ciliare* and *Cenchrus setigerus*... (7) Enlargement of nucellar cells surrounding gametophytic cavity at about the 4-nucleate stage». Nevertheless these authors do not explicitly write of the occurrence of mature 4-nucleate aposporous embryo sacs.

([58]) SIMPSON & BASHAW (1969 pp. 31, 35, 36), wrongly quoted NARAYAN's thesis (1951) as NARAYAN (1953) in both the text and references.

(1952) has priority over the above mentioned Ph. D. dissertations by BASHAW (1953) and FISHER (1953).

It follows that the choice between «Panicum type» or «Pennisetum type» concerns only two accounts, the Ph. D. thesis by NARAYAN (1951) and the preliminary report by WARMKE (1952).

A third consideration regards the short «Discussion» by G.L. STEBBINS at the end of WARMKE's preliminary report. It is obvious that WARMKE (1952), regarding the apomitic behaviour of *Panicum*, expressed himself in the same terms as those of his subsequent full report (1954). Stebbins took the chance of announcing the embryological findings of NARAYAN as regards the genus Pennisetum, see below (from WARMKE, 1952, p. 215):

DISCUSSION

G. L. Stebbins, Jr., U.S.A.:

Dr. Warmke stated that he did not know of autonomous parthenogenesis in the grasses. I would like to add the following three well-documented, but hitherto unpublished, examples: *Calamagrostis* spp. (Nygren), *Poa nervosa* (Clausen), *Pennisetum villosum* and *P. ruppellii* (Naragon). In *Pennisetum* Dr. Naragon also found the 4-nucleate embryo sac without antipodals. This is particularly interesting in view of the fact that *Panicum* and *Pennisetum* are rather closely related genera of the tribe *Paniceae*.

It is now not superfluous to add that the name «Naragon» stands for NARAYAN. This discussion does not settle the question: «does the Pennisetum 4-nucleate ES belong to the somatic or to the gonial apospory»? It follows that it is necessary to consider critically the Ph. D. thesis of K.N. NARAYAN (1951).

2. *The Ph. D. thesis by* NARAYAN *(1951) and the validity of the Pennisetum (villosum) type.*

The first observer and describer of a 4-nucleate unreduced pattern of ES development morphologically identical to the well-known 4-nucleate reduced Oenothera type (2S + E + 1CN) was NARAYAN (cf. «Cytogenetic Studies of Apomixis in Pennisetum», by KADUR NARASIMHAPPA NARAYAN, Ph. D. thesis, June 1951, Davis, California ([59]).

([59]) By courtesy of Prof. RUDOLF SCHMID (Dept. of Integrative Biology, Univ. of California, Berkeley).

The Pennisetum unreduced pattern differs from the Oenothera reduced pattern in that the initial cell of the *Pennisetum* embryo sac is formed by any cell of the ovule other than the true embryo sac mother cell, whereas the Oenothera ES develops from a normally reduced gynospore followed by the 1+0 nuclear polarization.

NARAYAN writes (p. 87, p. 63): «*P. villosum, P. setaceum*, and *P. orientale* are shown to be predominantly aposporous. Origin of apospory in these plants is not limited to the vicinity of the E.M.C. Aposporous initials take their origin in any part of the ovule such as the integument, chalazal, funiculus, and even the pericarpal region».

«*Four-Nucleate Embryo Sac.* Although *P. villosum, P. setaceum* and *P. orientale* resemble the other aposporous apomicts in the initial stages of development of aposporous cells, they differ from the rest in the formation of a 4-nucleate functioning embryo sac. Among normal sexual forms 4-nucleate functional embryo sacs are observed with certainty only in Onagraceae (MAHESHWARI, 1947)».

NARAYAN (1951, p. 32) also writes:

«Megasporogenesis and embryo-sac formation in *P. setaceum* and *P. villosum* offers an interesting contrast to that of *P. latifolium* since the former are obligate apomicts... Since there is very little difference between the life histories of these two plants, they are here considered together».

However, the documentation is mainly restricted to «Plate VI. Fig. 92-96. Megasporogenesis and embryo-sac formation in *P. villosum*» (cf. NARAYAN 1951, p. 106) ([60]). This documentation is reported here for the sake of embryological priority (see Plate V). It is quite evident that the ameiotic embryo sac initial cell of *Pennisetum* (i.e. somatic apospory of classical terminology) divides according to the scheme 1+0 → 2+0 → 4+0 and gives rise to a mature embryo sac with the morphology 2S + E + 1CN.

The main data from NARAYAN's thesis were published in 1962. This author wrote (cf. NARAYAN, 1962, p. 58): «Outside the Onagraceae the four-nucleate embryo sacs have been reported only in apomictic forms. Their presence was first recorded by NARAYAN (1951) in apomitcts like *P. villosum, P. setaceum* and *P. orientale*».

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([60]) In *Pennisetum setaceum* the 4-nucleate mature embryo sac (2S + E + 1CN) is documented by the «Plate IX. Fig. A: Ovule showing a tetranucleate embryo sac with a well-organized egg apparatus. The egg and synergid nuclei are seen. The endosperm nucleus lies adjoining the egg cell. There is no trace of antipodals».

Disappointingly, in NARAYAN's paper (1962) there is no embryological documentation, but the soundness of this account cannot be questioned because NARAYAN's embryological data were confirmed, together with a convincing documentation, by CHATTERJI & TIMOTHY (1969 *a*) in *P. orientale* and by SIMPSON & BASHAW (1969) in *P. setaceum* (P. ruppellii).

Because NARAYAN's (1951) embryological findings were later confirmed, it seems to us that NARAYAN's priority should be recognized and consequently the Panicum type renamed as Pennisetum type ([61]).

On the basis of both NARAYAN's (1951) data and the embryological documentation now available (see next pages) we have represented the Pennisetum type in our Plate 9.

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([61]) At the present we firmly believe that any real data which become known by public dissertation (as in the cases of Ph. D. theses) must be considered valid data in terms of priority, at least until a different decision is passed in future scientific congresses.

PLATE V

Figs. 92-96: *from Narayan (1951, p. 106); Figs. 13-20: from Warmke (1954, p. 7).*
Figs. 92-96: *Gynosporogenesis and ES development in Pennisetum villosum*; Narayan's *explanations:*

Fig. 92. Embryo sac mother cell in diakinesis showing 18 bivalents and 9 univalents. A cell immediately below the E.M.C. with a conspicuous nucleus is enlarging and vacuolating, showing the potentialities of an aposporic embryo sac. × 1200.

Fig. 93. Linear tetrad showing the degeneration of all the four megaspores. Adjoining nucellar cells are becoming prominent by enlargement and vacuolization. × 540.

Fig. 94. Four aposporous uninucleate cells prominent by their elongation with a conspicuous vacuole below the nucleus. × 540.

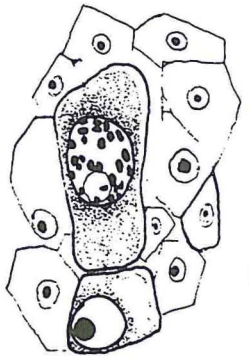
Fig. 95. A four-nucleate embryo sac. Three of the four nuclei are toward the micropyle, and the fourth lies in the center of the embryo sac. No signs of a well-organized egg apparatus. No antipodals are seen. × 190.

Fig. 96. Multiple aposporous embryo sacs, a complex of nine. Five of the nine sacs are binucleate. Both the nuclei are toward the micropylar end of the embryo sac with a prominent vacuole extending to the other end. A thin layer of cytoplasm intervenes between the vacuole and the cell wall. The other four are uninucleate. In all these embryo sacs a single large vacuole extends to the other end of the embryo sac. The nuclei in all the embryo sacs except the lowermost are toward the micropyle end. A few cells towards the micropylar end are becoming enlarged. × 540.

Figs. 13-20. *ES development in Panicum maximum; Warmke's explanations*:
Fig. 13-20: Embryo sac formation in *Panicum maximum*:

Fig. 13-16. Eight-nucleate embryo sac formation in the variety common guinea. Note separation of nuclei to opposite ends of cell as result of first division (fig. 13) and division of antipodals (fig. 16) to form a mass of antipodal tissue.

Fig. 17-20. Stages in development of mature 4-nucleate embryo sacs. Note orientation of first division figure, across the long axis of the cell, and at the micropylar end (fig. 17). Only one polar nucleus and no antipodals are formed in this type of embryo sac (fig. 20). × 130.



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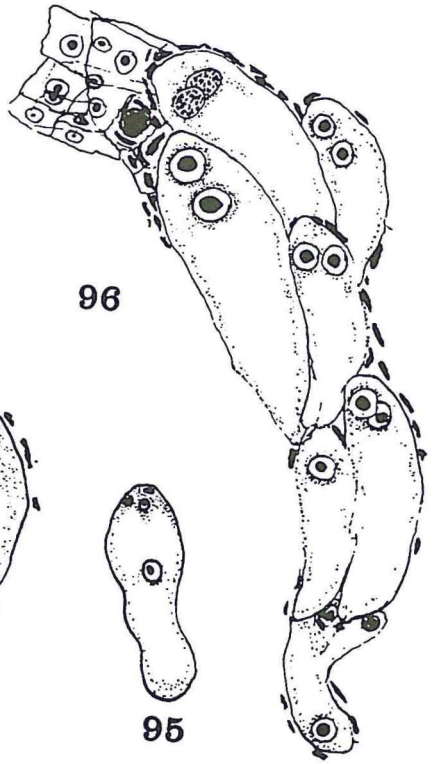

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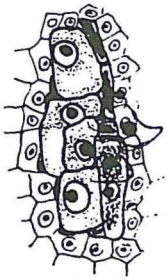

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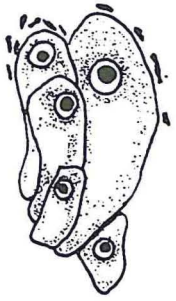

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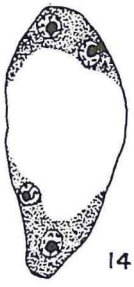

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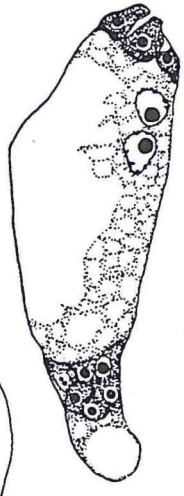

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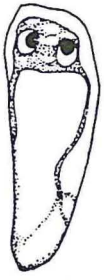

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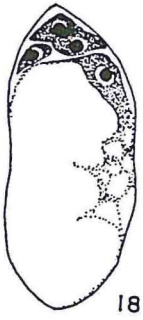

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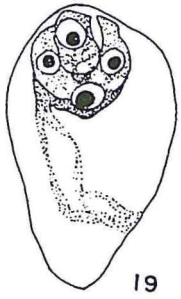

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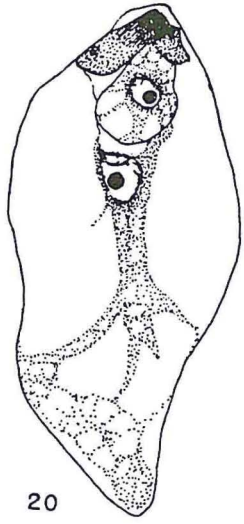

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Since there is only one Pennisetum type we can write simply Pennisetum type instead of Pennisetum villosum type.

Hypothetically, a pattern of embryological development strictly similar to that established here as the Pennisetum type has also been represented in the Plate X and called «Pennisetum II?» type. As far as we know this pattern of development has not yet been recorded in any angiosperm ES. Nevertheless, this type is very interesting from both the interpretative and the cytological points of view.

3. *The morphology of the ameiotic 4 - nucleate Pennisetum (ex Panicum) type. Regular occurrence of a mature ES showing the 4 - celled form «2S + E + CN».*
*Simultaneous development and coexistence, in the same ovule, of 4-nucleate (Pennisetum type) and 8 - nucleate (Hieracium type) embryo sacs.*
*Discovery of the cellularization processes corresponding to the formulae «S + E + 2CN» (occasionally: 3 - celled form) and «E + 3CN» (rare: 2 - celled form). Occurrence and meaning of the very rare non-celled ES (formula: 4CN).*

We established the Panicum type (BATTAGLIA, 1963) on the basis of WARMKE's (1954) well documented account (see Plate V, Figs 13-20: *Panicum maximum*).

By contrast, the contemporaneous paper by FISHER, BASHAW and HOLT (1954), «Evidence for Apomixis in *Pennisetum ciliare* and *Cenchrus setigerus*», which was incomplete as regards both embryo sac description and documentation, did not establish the occurrence of 4 - nucleate aposporous embryo sacs in the above mentioned species ([62]).

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([62]) FISHER, BASHAW and HOLT (1954, p. 402) write:

In both *P. ciliare* and *C. setigerus* the development of the embryo sac apparently follows a normal sequence up to the 4-nucleate stage. A subepidermal cell of the nucellus enlarges and differentiates as a megasporocyte (figure 5). This cell, by two successice divisions, forms a quartet of megaspores. The three nearest the micropyle disintegrate, the nucleus of the remaining cell divides into two nuclei (figure 6), and these divide again to give a 4-nucleate embryo sac. At approximately this stage of development, considerable abnormal enlargement is apparent in the nucellar cells surrounding the gametophytic cavity (figure 7). Examination of progressively older ovules reveals a continuation of this nucellar activity (figures 8-9) until a number of large vacuolate nucellar cells resembling embryo sac are formed. These are tentatively considered to be adventitious embryo sacs, aposporously produced from the nucellus (figures 10-11). While this nucellar activity is taking place, the normal em-

Apart from the question of NARAYAN's (1951) priority as regards the establishment of the Pennisetum type, we now think that WARMKE's paper (1954) deserves more critical consideration than that previously paid to it.

Warmke investigated different varieties of *Panicum maximum* and found the coexistence, in most of them, of 4-nucleate (aposporous) and 8-nucleate (both aposporous and sexual) embryo sacs.

The following sentences from his account deserve mention:

— from WARMKE (1954, pp. 7-8):

«*Formation of the embryo sac.* — The initials enlarge rapidly and their nuclei divide to produce 2- and then 4-nucleate embryo sacs. In some cases, however, nuclear division stops after the second division (fig. 17-20); in others it continues through the third division (fig. 13-16). This leads to the formation of two distinct types of mature embryo sacs: one with four nuclei and the other with eight nuclei. It appears that a developmental difference between the two types of embryo sacs may be detected as early as the first mitotic division in the young initials. In some cases the first division is parallel to the long axis of the cell, and the two daughter nuclei are separated — one going to each end — and a large cytoplasmic vacuole forms between them (fig. 13). Two more divisions follow in these embryo sacs, with the result that four nucleir are formed at each end. In other cases, the first division is at right angles to the long axis of the cell and occurs very close to the micropylar end (Fig. 17). The two daughter nuclei divide a second time to form four nuclei, all of which remain at the micropylar end of the embryo sac (Fig. 18) and differentiation begins.

As a result of this phenomenon, mature embryo sacs of quite different constitution are produced. The 4-nucleate type differentiates into an embryo sac with 2 synergids, 1 egg, 1 polar nucleus, and no antipodals (Fig. 19-20). This would appear to be comparable in all respects to embryo sac formation in the genus *Oenothera*. The 8-nucleate type differentiates into a normal embryo sac (*Polygonum*

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bryo sac becomes increasingly difficult to identify, indicating that the enlarged nucellar cells are completely crowding out the normal female gametophyte and taking over its function. In some instances the nucellar embryo sacs were seen to contain proembryos, even when located near the chalazal end of the ovule (figure 13). In several instances twin embryos (figure 15) were observed in the sectioned material, and when mature seeds were germinated, approximately 22% of them were found to have twin embryos.

type), with 2 synergids, 1 egg, 2 polar nuclei, and 3 antipodals (Fig. 15). As is common in grasses, the antipodal cells undergo additional divisions to form six or more cells (Fig. 16) which enlarge and invade the chalazal tissue. These two types of embryo sacs remain distinguishable until the time of anthesis, or later».

— From WARMKE (1954, p. 10):

«Although hundreds of ovules have been sectioned, it has not been possible to determine with certainty whether or not these two types of embryo sacs differ consistently in chromosome number. The evidence from chromosome counts in young embryo sacs, themselves, and in the dividing endosperm nuclei indicates strongly that the 4-nucleate types are usually or always unreduced. The evidence is not so clear for the 8-nucleate embryo sacs. There is some evidence that these are reduced: One 8-nucleate embryo sac (late prophase, 3rd division) was found with the reduced number of chromosomes, and one early endosperm division in an originally 8-nucleate sac (antipodals present) with the $3n$ number of chromosomes was found. Presumably $1n$ chromosomes had come from each of two polar nuclei and $1n$ from a sperm nucleus in this latter case. That 8-nucleate embryo sacs are not always reduced, however, is indicated by the finding ot two aposporic embryo sacs in the same ovule, both of wich apparently were destined to become 8-nucleate (nuclei separated to the two opposite ends of the cells). It seems possible in general, though, that the difference in shape and degree of vacuolation of megaspores and aposporic nucellar cells (the former being elongate and the latter shorter and more vacuolate) might well influence the direction of the spindle of the first embryo-sac division and thus tend to make those derived from megaspores 8-nucleate and those from nucellar cells 4-nucleate».

It is matter of minor criticism to state that WARMKE, disregarding or overlooking any ES - typology, early (CHIARUGI 1926, 1927; ROSENBERG, 1930) as well as recent (e.g. GUSTAFSSON, 1946, 1947; BATTAGLIA, 1951 *a*, *b*) mentions the Oenothera and the Polygonum types.

On the contrary we must say that the alternative development, or the coexistence, of 4-nucleate (4+0) and 8-nucleate (4+4) mature embryo sacs, cannot simply, or exclusively, be ascribed to the first (nuclear) division of the embryo sac.

It is quite evident that variations in general growth (e.g. ES-elongation and vacuolization) and spatial relationship with neighbouring cells, result in the development of binucleate embryo sacs show-

ing the main nuclear polarizations 2+0 and 1+1, (cf. Figs. 17, 13 Plate V) together with intermediate nuclear dislocations. It is now useful to recall that according to our recent hypothesis on the evolution of the female gametophyte of the angiosperms (BATTAGLIA, 1989), the cellularization process takes place only when the embryo sac has attained the 4-nucleate micropylar status (named $C^4$ cellularization or $C^4$ status).

Thus this hypothesis can explain why the nuclear divisions of the ES stop after the *chronologically second* mitosis in the case of 2+0 embryo sac (cf. Figs. 17-20: Pennisetum type, Plate V), while in the other case, that is the (1+1) embryo sac, they go through a third mitosis (cf. Figs. 13-16: Hieracium type, Plate V). Obviously such an embryological behaviour strongly supports the $C^4$ cellularization hypothesis mentioned above.

Furthermore there are several papers, published in 1955-1962, which document the occurence of some very unexpected embryological variations.

In 1955 SNYDER, HERNANDEZ and WARMKE (1955) again for *Pennisetum ciliare*, giving an adequate documentation, and for *Cenchrus setigerus*, (without any documentation), describe an embryological behaviour basically identical to that previously reported by WARMKE for *Panicum*. They also first document the occurrence of 2 juxtaposed 4-nucleate embryo sacs showing (2+2) and (4+0) nuclear dislocation respectively (see Plate VI fig. 14). SNYDER et al. consider the embryo sac having the 2+2 nuclear polarization as a reduced ES belonging to the Polygonum type, while the other one, although of nucellar origin, is qualified as a «mature gametophyte of the Oenothera type» (63).

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(63) SNYDER, HERNANDEZ and WARMKE (1955, p. 214-216) write:

MEGAGAMETOGENESIS. — Development of the embryo sac, or female gametophyte, apparently follows two distinctly different patterns, similar to those found in *Panicum maximum* (6). In the predominant behavior in the present material, the two nuclei resulting from division in the embryo-sac initial remain at the micropylar end of the developing embryo sac (fig. 11) — or at the end nearest the surface of the ovule in widely displaced embryo sacs. A second division of these nuclei results in a four-nucleate embryo sac in which the nuclei remain closely associated (fig. 12). Differentiation in these embryo sacs, without the occurrence of a third mitotic division, results in a mature gametophyte of the Oenothera type, with two synergids, an egg, and a polar nucleus (fig. 13).

In the second type of development the nuclei of a young two-nucleate embryo

This last conclusion is likely to be wrong since Snyder et al. (1955, p. 220):

a) do not provide any documentation of 2-, 4-nucleate reduced embryo sacs (i.e. Polygonum type);

b) state that «The products of meiosis in the ovules usually degenerate soon after formation» and such a sentence means that *usually* no 8-nucleate embryo sacs develop.

Nevertheless, they further write: «Both four-and eight-nucleate mature embryo sacs are produced, although the latter are *relatively* uncommon»;

c) their conclusion is influenced by WARMKE's previous opinion on the embryological behaviour of *Panicum* because they also write: «Evidence from *Panicum maximum* and from the present study strongly suggests... that eight-nucleate embryo sacs are typically reduced...».

According to our interpretation, the fig. 14 by SNYDER et·al. (1955) is the first documentation of the coexistence in the same ovule of both Hieracium (8-nucleate) and Pennisetum (4-nucleate) types (64). In any case, just two years later a clear documentation of such a coexistence in *Bothriochloa*, was presented by BROWN & EMERY (1957 *a*, see fig. 15, Plate VI). For the sake of simplicity we omit a discussion of other similar cases mentioned in the subsequent embryological literature.

Again in 1957 both Emery (march) for *Setaria villosissima* (Emery, 1957 microphotogr. fig. 7) and *S. leucopila* (without documentation) and BROWN & EMERY (1957 *a*, june) for *Themeda triandra* (see figs. 7, 8, Plate VI) and *Bothriochloa ischaemum*, (two forms called respectively «common» and «oriental» form, see figs. 17-18, Plate VI) dis-

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sac separate to opposite ends of the cell, and a large vacuole develops between them. These nuclei undergo a second division to form a four-nucleate embryo sac (fig. 14, *left*) and subsequently a third division to produce an eight-nucleate embryo sac having four nuclei at each end (fig. 15). The eight-nucleate embryo sac differentiates into a mature gametophyte of the Polygonum type, having two synergids, an egg, two polar nuclei, and three antipodals.

(64) Something very similar (or identical?) was also found by GILDENHUYS & BRIX (1959, figs. 2C, 2E) namely two juxtaposed embryo sacs respectively 4 + 0 (aposp.) & 4 + 4 (Polygonum type) and 1 + 1 (Polyg. type) & 4 + 0 (aposp.), see Plate VI. However, we believe that all these embryo sacs might be reinterpreted as aposporic embryo sacs (i.e. coexistence of the Pennisetum & Hieracium types). The nuclear & nucleolar sizes are identical in all juxtaposed embryo sacs, thus supporting the hypothesis of the occurrence in all nuclei of the same chromosome complement.

covered the occurrence of the atypical organization of the mature ES characterized by one synergid and two polar nuclei (S + E + 2CN). Unexpectedly all mature embryo sacs of *Setaria* showed the 3-celled form (S + E + 2CN), while in *Themeda* the embryo sacs «with one polar nucleus were approximately five times as frequent as those with two polar nuclei» (cf. BROWN & EMERY, 1957 *a*, p. 247).

As regards *Bothriochloa*, BROWN & EMERY state: «In the common form the ratio of embryo sacs containing two polar nuclei (fig. 18) to those with only one (fig. 17) was approximately one to seven, while in the oriental form the ratio was one to eight».

However, from the point of view of priority we cannot omit to mention that the occurrence of 2 polar nuclei (and thus, necessarily the occurrence of the 3-celled form of the mature ES) has been first recorded for *Dichanthium* and for *Bothriochloa* by CELARIER & HARLAN (1956, p. 20). These authors supply the following table (65):

TABLE V. FREQUENCY OF EMBRYO SAC TYPES IN DICHANTHIUM AND BOTHRIOCHLOA

| Species | A-No. | Chrom. No. | Breeding behavior | No. sacs analyzed | No. of sacs with 1 polar | 2 polar | others | No. of sacs per ovule (in %) 1 | 2 | 3 |
|---|---|---|---|---|---|---|---|---|---|---|
| D. sericeum | A-4610 | 20 | sexual | 23 | | 23 | | 100 | | |
| D. annulatum | A-3242 | 20 | sexual | 35 | | 35 | | 100 | | |
| D. annulatum | A-4083 | 60 | apomictic | 17 | 10 | 4 | 3 | 100 | | |
| D. annulatum | A-4099 | 40 | apomictic | 9 | 5 | 4 | | 88 | 12 | |
| B. venusta | A-2655 | 40 | apomictic | 60 | 50 | 10 | | 59 | 22 | 19 |
| B. ischaemum | A-1347 | 60 | apomictic | 63 | 31 | 5 | 27 | 29 | 37 | 34 |
| The following materials were analyzed early in the work and should be restudied in the light of our present information: | | | | | | | | | | |
| B. ischaemum* | A-2582 | 60 | apomictic | 20 | observed | observed | | All types observed. | | |
| B. ischaemum* | A-1359 | 60 | apomictic | 40 | | | var. | 1 and 2 sacs per ovule observed. | | |
| B. ischaemum* | A-729 | 50 | apomictic | 10 | all? | | | All types observed. | | |

* - studied early before present classification method was used.

(65) Apparently Table V is based on embryological observations by Mrs. Brooks. Indeed CELARIER & HARLAN (1956, pp. 19-20) write: «*Frequency of Embryo sac types.* From both preliminary embryological studies and crossing results it seemed more than likely that both sexual and asexual types of embryo sacs are produced and the frequency of production and survival of these types might vary between species, and accessions within species. Mrs M. Brooks undertook to check this hypothesis by detailed embryological studies... From the evidence now available the following correlations seem to offer a working hypothesis.

a) Sexual type sac — consists of two synergids, two polars, and one egg cell and in addition a cluster of antipodals.

The occurrence of the 3-celled form of the 4-nucleate mature ES was later recorded as a rare type of ES organization (together with the most common 4-celled case, see Table I) in several grass species, see Table II.

TABLE I - *(Pennisetum Type).*

**Genera showing the occurence of the «4-nucleate & 4-celled form» (2S + E + CN) of the Pennisetum type.**

*Anthephora*: Brown & Emery (1958);
*Bothriochloa*: Brown & Emery (1958); Gupta (1968, 1969); Christoff & Moskova (1972); Moskova & Yakovlev (1974); Seshavatharam (1983);
*Brachiaria*: Brown & Emery (1958); Pritchard (1967);
*Buchloë*: Brown & Emery (1958);
*Capillipedium*: Brown & Emery (1958); Bhanwra et al. (1982);
*Cenchrus*: Fisher et al. (1954); Snyder et al. (1955); Bashaw (1962: Penn. ciliare); Taliaferro & Bashaw (1966: Penn. ciliare); Islam & Das (1970); Gupta & Yashvir (1971); Young et al. (1979); Shanthamma (1982); Seshavatharam (1983);
*Chloris*: Brown & Emery (1958);
*Dichanthium*: Brown & Emery (1957, 1958); Knox & Heslop-Harrison (1963); Gupta (1968); Gupta, Roy & Singh (1969); Reddy & D'Cruz (1969 *a*); Saran & De Wet (1969); Faruqi (1975);
*Eriochloa*: Brown & Emery (1958); Seshavatharam (1983);
*Heteropogon*: Gupta (1968); Tothil (1968);
*Hyparrhenia*: Brown & Emery (1958); Mc William et al. (1970);
*Iseilema*: Seshavatharam (1983);
*Panicum*: Warmke (1952, 1954); Brown & Emery (1958); Pernes et al. (1975); Savidan 1875, 1978, 1980, 1982; Savidan et al. (1979); Seshavatharam (1983); Nakagawa (1990);
*Paspalum*: Brown & Emery (1958) (In *P. secans*, Snyder 1957, established the occurence of 8-nucleate unreduced embryo sacs); Burson & Bennet (1970 *a, b*; 1971);
*Pennisetum*: Narayan (1951, 1962); Brown & Emery (1958); D'Cruz & Reddy (1968); Chatterji & Timothy (1969 *a, b*); Simpson & Bashaw (1969); Sindhe (1976); Shanthamma & Narayan (1977); Birari (1981); Dujardin & Hanna (1984, 1988); Seshavatharam (1983);
*Themeda*: Brown & Emery (1958); Liebenberg & Pienaar (1962); Evans & Knox (1969), Faruqi et al. (1975); Birardi (1980); Liebenberg (1990);
*Tricholaena*: Brown & Emery (1958);
*Tripsacum*: cf. Savidan (1982, p. 49);
*Urochloa*: Brown & Emery (1958); Pritchard (1970).

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b) Apomictic type sac — consists typically of two synergids, one egg, and one polar with no antipodals. There is however some variation here and a more detailed study of this is needed.

Using these criteria a preliminary study of frequency has been made and the results are presented in table V».

TABLE II - *(Pennisetum Type).*

**Species showing the coexistence of the «3-celled» (S+E+2CN) and «4-celled» (2S+E+CN) forms of the Pennisetum type.**

*Apluda mutica*: Murty (1973);

*Bothriochloa ischaemum*: Celarier & Harlan (1956), Brown & Emery (1957 *a*);
*Bothriochloa venusta*: Celarier & Harlan (1956);
*Bothriochloa odorata*: Choda & Bhanwra (1977);
*Bothriochloa pertusa*: Gupta (1968, 1969);
*Capillipedium huegellii*: Choda & Bhanwra (1980);
*Dichanthium annulatum*: Celarier & Harlan (1956);
*Eremopogon foveolatus*: Bhanwra & Choda (1981); Satyamurty & Seshavatharam (1983);
*Heteropogon contortus*: Emery & Brown (1958);
*Pennisetum dubium*: Gildenhuys & Brix (1959, p. 235);
*Setaria leucopila* & *S. villosissima*: Emery (1957, fig. 7: *S. villosissima.* Both species show exclusively the occurrence of the 3-celled form);
*Themeda triandra*: Brown & Emery (1957 *a*).

TABLE III - *(Pennisetum Type).*

**Species showing the occasional occurrence of the 2-celled form (E+3CN) forms of the Pennisetum type.**

*Pennisetum dubium*: Gildenhuys & Brix (1959).

The very atypical embryo sac organization E + 3 CN, the 2-celled form, has also been observed, by GILDENHUYS & BRIX (1959) in *Pennisetum dubium* (see Table III).

We think that in this case, the egg-cell would bear the filiform apparatus, as in the well-known case of the Plumbago & Plumbagella types. Obviously a reinvestigation is desirable.

As far as we know, the 4-nucleate & non-celled mature ES, owing to a non-micropylar dislocation of the nuclei, has been observed in three cases, namely in *Pennisetum*, *Echinochloa*, cf. Fig. 19, Plate VI and *Cenchrus*, see Table IV.

This case is considered nothing other than a meaningless anomaly. However we cannot exclude, at least as a hypothetical occurrence, an endosperm (trophophyte) development giving rise to seeds without embryos although showing the usual morphology. In other words, we cannot exclude, theoretically, the occurrence of an «embryo-less agamospermy».

TABLE IV

**Species usually showing the Pennisetum type and occasionally the non-celled multinucleate mature embryo sac.**

*Cenchrus glaucus*: Shanthamma (1982, fig. 25: a 6-nucleate stage);
*Echinochloa stagnina*: Muniyamma (1978, fig. 19);
*Pennisetum dubium*: Gildenhuys & Brix (1959, fig. 2 k).

The cases of *Echinochloa stagnina* (MUNIYAMMA, 1978) and *Cenchrus glaucus* (SHANTHAMMA, 1982) are very interesting also from a theoretical point of view. In the ameiotic («aposporous») 4-nucleate embryo sacs of these species the nuclei are grouped in the centre of the ES and two large vacuoles occupy the opposite end. These embryo sacs lack any organization and are non functional. In addition, SHANTHAMMA (1982, p. 30) writes: «Occasionally, the 4-nuclei without organization undergo further divisions resulting in the formation of 6 to 8 nuclei all grouped together (figure 25)», cf. Fig. 25, Plate VI.

Likewise MUNIYAMMA (1978) records the occurrence of unorganized multinucleate embryo sacs, cf. Fig. 26, Plate VI which he ascribes to the occurrence of supernumerary amitotic divisions. Apart from the consideration that there is no documentation of amitotic divisions, we believe that these very atypical 4-nucleate embryo sacs divide further owing to the suppression of the «pilot function of the micropylar pole of the female gametophyte». Specifically, we consider these cases as «qualitatively identical» to that of *Inula helenium* discussed in a previous paper (BATTAGLIA 1989). Obviously, they also share and support the same theoretical considerations (i.e. actual occurrence of the «$C^4$ status» etc.).

4. *Occurrence of the Pennisetum (ex-Panicum) type among plants retaining apomictic embryony*

Although the provision of a full list of embryological references is beyond the purposes (and the limits) of the present paper, we have in any case summarized in Tables I-IV, almost all the occurrences of the Pennisetum (ex-Panicum) type with the typical ES-morphologies as the atypical ones and the interesting embryo-less mature embryo sacs following the 0 + 4 nuclear dislocations. In the compilation of Tables I-IV many embryological accounts lacking

an adequate, or at least convincing documentation, have been intentionally omitted (66).

Additional references can be found in the most recent contributions, for instance SESHARATHARAM (1978-1983) BHANWRA & CHODA (1984), BHANWRA (1988), SODERSTROM et al. (1986) NAGENDRAN & DINESH (1989) etc.

Finally, it must be noted that the Pennisetum type is confined to the grass family (Poaceae) and is very common among members of the Andropogoneae and Paniceae.

### IVc. *ANTENNARIA TYPE (apomeiotic ES, 8-nucleate)*

Thys type was discovered and rightly interpreted by Juel (1898, 1900) in *Antennaria alpina* and termed «Antennaria alpina» type by CHIARUGI (1926, 1927). Meiosis is completely suppressed in the regular gynospore mother cell, which then enlarges and functions as an apomeiotic unreduced initial cell of the ES. Subsequent development by three nuclear divisions results in the usual 8-nucleate stage but with the unreduced chromosome number.

The Antennaria type is very common in plants having unreduced embryo sacs, see references in CHIARUGI (1926, 1927), ROSENBERG (1930), SCHNARF (1936), GUSTAFFSON (1946, 1947), RUTISHAUSER (1967, 1969) etc.

### IVd. *ERAGROSTIS TYPE (apomeiotic ES, 4-nucleate)*

1. *The development and morphology of the apomeiotic 4-nucleate Eragrostis type. Occurrence of the cellularization processes corresponding to the formulae 2S + E + CN (4-celled form: most cases) and S + E + 2CN (3-celled form: very rare).*

In a very comprehensive and well-known account on «Apomixis in the Gramineae» BROWN & EMERY (1958, p. 253) wrote:

«The cytological report of apospory in a species does not prove that apomixis occurs. But, if all mature embryo sacs in the ovules of a plant are 4-nucleate rather than the typical 8-nucleate of relat-

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(66) Disappointingly most of these papers do not show a very detailed embryological documentation. Thus, for instance, the critical stage showing the first division of the vacuolized 1-nucleate ES, is frequently not reported.
It follows that, owing to the absence of this stage, the eventual occurrence of an ES-development according to the pattern here defined as the «Pennisetum II?» type, cannot be established (see Plate X).

ed sexual species, and especially if a proembryo and endosperm are present in an ovule lacking antipodals, the presence of 4-nucleate embryo sacs is strong evidence for apomixis.

This survey was designed especially to detect the aposporous method of apomixis. It is probable that diplospory, if present, would usually escape detection although two cases of probable diplospory were found and studied, one in a species of the Chlorideae and one in a species of the Maydeae».

The species belonging to the Maydeae is *Tripsacum dactyloides*. This species is «partially sexual and partially apomictic» (cf. FARQUHARSON, 1955) and according to BROWN & EMERY the EMC divides mitotically (diplospory) giving rise to embryo sacs that are 5-nucleate (formula 2S + E + 2CN) at maturity. These authors conclude that «since three antipodals wee seen in two young embryo sacs, it is probable that 8 nuclei are formed» ([67]).

The species belonging to the Chlorideae is *Fingerhutia africana* and BROWN & EMERY (1958) state that: «is probably apomictic by diplospory».

In spite of the previous sentence «two cases of probable diplospory were found and studied...», BROWN & EMERY write that three south african species belonging to the genus *Eragrostis* «very likely» are apomictic by diplospory ([68]). However the occurrence of diplospory (i.e. gonial aposporv) simply qualified as «probable» together with lack of any documentation did not allow to us to include in our review of apomixis a 4-nucleate Fingerhutia or Eragrostis type ([69]).

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([67]) It is disappointing to see that these authors disregard the correct embryological typology. Thus, for instance, on p. 260, they write: «There are also aposporous and diplosporous unreduced embryo sacs of the *Polygonum* type».

([68]) BROWN & EMERY (1958, p. 260) write:

The South African species *E. chloromelas, E. curvula,* and *E. heteromera* have one 4-nucleate embryo sac in each ovule. It is very likely that these species are apomictic by diplospory since there is no evidence of spores and the megasporocyte is vacuolate. An alternative possibility is that these species are sexual, having embryo sac development of a different «type» than is typical for the Gramineae in general. Final decision will depend on study of the nuclear division in the megasporocyte, the chromosome number of endosperm nuclei, and/or progeny tests. In this tribe 33 per cent of the species studied are possibly apomictic.

([69]) Unfortunately, in these years, we were unaware of a short note («Some South African Apomictic Grasses») published a few months earlier by BROWN & EMERY (October 1957) in J. South African Botany. This paper is noteworthy since they provide the following data:

Fingerhutia africana (diplospory perhaps),

In 1963 (STREETMAN, 1963 *a*) published the first (70) documentation of the occurrence of a «4-nucleate diplosporous embryo sac», that is the 4-nucleate apomeiotic ES of our terminology.

The occurrence of the apomeiotic development is unequivocally documented for *E. chloromelas*, *E. curvula* and *E. Lehmanniana*. Specifically:

*a*) In 3% of the mature embryo sacs the final stage is 4-nucleate (organized into 2 synergids + E + 1 polar nucleus), derived from two mitotic division of the EMC.

*b*) In 30% of the mature embryo sacs were 5-nucleate (that is the egg + 1 polar nucleus + 3 antipodals);

*c*) In 67% of the mature embryo sacs were 6-nucleate (that is the egg + 2 polar nuclei + 3 antipodals).

Streetman also writes: «Synergids were not observed in the 5- and 6-nucleate sacs, and conversely, antipodals were not found in 4-nucleate sacs», and concludes «The mechanism appears to be diplospory with an *Antennaria* type embryo sac resulting from two or more mitotic divisions of the megaspore mother cell».

In the second part of his research STREETMAN (1963 *b*) describes the normal ES development (Polygonum type) in four other species of *Eragrostis* and states «The synergids usually disintegrate soon after the mature embyo sac is complete».

Two papers by VOIGT (1971) & VOIGT & BASHAW (1972, 1976) improved our knowledge about reproduction in the apomictic species of *Eragrostis*.

VOIGT (1971) discovered «Sexuality in Eragrostis curvula» and states:

«The mode of reproduction of *E. curvula* appeared to parallel that found by BURTON (1948, 1955) in *Paspalum notatum* Flugge. In both species, the examined diploids were sexual and the natural polyploids were obligate apomicts».

VOIGT & BASHAW (1972, 1976) describe the occurrence of both

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Eragrostis curvula (diplospory probably),
Eragrostis chloromelas (diplospory probably),
Eragrostis heteromera (diplospory probably).

(70) VORSTER & LIEBENBERG (1977, 1984) report two accounts, namely LIEBENBERG (1961, unpublished M. Sc. thesis, Stellenbosch) and a brief communication by LIEBENBERG & PIENAAR (1962) recording the occurrence of apomixis in both ERAGROSTIS & THEMEDA.

obligate and facultative apomixis in this species. The ES development («diplospory») described by STREETMAN (1963) is confirmed. The four-nucleate condition, that is, «two synergids, an egg and a polar» was found to be the most common morphology of the mature ES. The eight-nucleate condition (that is our Hieracium type) also occurs. Specifically they write (cf. VOIGT & BASHAW, 1972, p. 844-855): «...at the immature two-nucleate stage, one of the nuclei frequently migrated to the chalazal end of the developing embryo sac (fig. 10). Development of this type usually resulted in a mature gametophyte of three nuclei and proliferated antipodals...».

Again for *E. curvula* (*E. curvula* complex) the occurrence of both obligate and facultative apomixis was described in those years by BRIX (1974) and by VORSTER & LIEBENBERG (1977). They pointed out the great difficulty in distinguishing between reduced and unreduced embryo sacs. Embryo sacs were often observed containing only two normal nuclei, that is the egg and one polar nucleus (or one secondary nucleus?), owing to the degeneration of the remaining nuclei.

Quite recently two embryological accounts by VORSTER & LIEBENBERG (1984: *Eragrostis curvula* complex) and by RABAU, LONGLY & LOUANT (1986) improved our knowledge as regards the cytological details which characterize the Eragrostis type. VORSTER & LIEBENBERG (1984) provide a very good documentation of both the «apomictic 4-nucleate diplosporic embryo sac» and «8-nucleate sexual monosporic Polygonum-type» ES which characterize the reproduction within the *Eragrostis curvula* complex.

With reference to the «diplosporic» development, the following sequence of embryo sac stages (1 + 0) → (2 + 0) → (4 + 0) → 2S + E + CN («polar nucleus») is adequately illustrated. Thus the embryo sac development follows the Eragrostis type just as shown in our Plate IX.

The classification of the embryo sac types and the occurrence of abnormal embryo sacs was also taken into consideration. The first question, «that young stages, classified as sexual, could just as well have been divergent diplosporic or abnormal embryo sac», led to the conclusion that: «The classification of 2- and 4-nucleate stages as being sexual, even when remnants of the degenerated megaspores are no longer visible, therefore seems to be justified». Disappointingly the chapter on abnormal embryo sacs («Only 3.5% of all the embryo sacs investigated, were abnormal or divergent») was not followed by any description or interpretation of the corresponding atypical morphologies.

The paper by RABAU, LONGLY & LOUANT (1986) is very useful since it illustrates an embryological research identical, as regards the subject (ES development), species (*Eragrostis curvula*), embedding & staining technique, (Haematoxylin), and documentation (photomicrographs), to that of VORSTER & LIEBENBERG (1984) and carried out independently and probably more or less contemporaneously. This consideration to a certain extent explains why RABAU et al. (1986) overlooked VORSTER & LIEBENBERG's (1984) account.

According to RABAU et al. (1986) about 99 per cent of the embryo sacs develop according to the «diplosporic» pattern.

Very good microphotographs illustrate the high percentage (74%) of the occurrence of the Eragrostis type corresponding to the sequence (1 + 0) → (2 + 0) → (4 + 0) → 2S + E + CN. (This type is called «non reduit monopolaire» or «type monopolaire»). There is also an adequate documentation of the 3-celled form of the mature ES (S + E + 2 CN) which was observed only once ([71]).

Similarly to most earlier embryologists, RABAU et al. (1986), also describe the occurrence of mature embryo sacs showing only one egg cell and one polar nucleus, owing to the degeneration and adsorption of the synergids.

In 26% of the embryo sacs the «diplosporic» pattern should follow a different developmental sequence summarized by the expression (1 + 0) → (1 + 1) → (2 + 2) and called by RABAU et al. «type bipolaire».

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([71]) STOVER (1937 p. 173) described an atypical cellularization of the normal 8-nucleate Polygonum type in *Eragrostis cilianensis*. In this case, «...the four chalazal nuclei are immediately separated from the rest of the embryo sac as four antipodal cells...»; «...The four nuclei at the micropylar end of the sac function as the egg, one synergid, and two endosperm nuclei (polar nuclei). (Figs. 10, 11). This organization of an embryo sac is a new type not only for the grasses but for all plants». Incidentally, as regards the last sentence, we must comment that an identical micropylar morphology (i.e. S + E + 2 CN) was described a year before in *Allium mutabile* by T.R. PORTER (1936). MAHESHWARI (1941) criticized STOVER's (1937) account («Unfortunately the figures are not convincing and a reinvestigation is necessary...») and SWAMY (1944) accomplished such a reinvestigation documenting the occurrence of the normal pattern of cellularization. Stover actually was wrong as regards the occurrence of four primary antipodal cells (this species shows the phenomenon of the polyantipody) however it is very likely that he saw the atypical micropylar morphology (S + E + 2 CN) documented by his fig. 10.

Thus, after PORTER (1936), STOVER was the second embryologist to record this atypical micropylar pattern of ES cellularization.

According to these authors, the 4-nucleate stage (2 + 2) very soon undergoes and accomplishes a cellularization process resulting in a 3-celled embryo sac characterized by the very atypic morphology one egg + one central cell (with 2 polar nuclei) + one antipodal cell. They also write that the antipodal cell is able to divide one (5-nucleate ES: E + 2 CN + 2 A) ([72]) or more times giving rise to 6-nucleate (E + 2 CN + 3 A) or 7-nucleate embryo sacs (E + 2 CN + 4 A).

RABAU et al. (1986) illustrate this new type of ES development and the related new form of cellularization with their microphotographs 8-9 and 10, which, being the unique documentation of a stated new type of ES development derserve critical consideration.

Let us first examine their fig. 10, described as follows (RABAU et al. 1986, p. 1781):
«SE hexanucléé non réduit (type bipolaire) contenent trois antipodes (A) au pôle chalazien».

This 5-nucleate figure clearly shows the egg, the upper polar nucleus (the second one is missing) and 3 uninucleate antipodal cells. The size, shape and position of the 3 antipodal cells require careful examination. At the chalazal end of this ES there are two juxtaposed antipodal cells equal in size and shape with a larger crescent-shaped one overlying them. This 3-celled group shows by far the most common arrangement of the 3 antipodal cells of the 8-nucleate cellularized embryo sac. Such a chalazal morphology has repeatedly been documented in apomictic and amphimictic embryo sacs of species belonging to the genera *Eragrostis*, *Pennisetum* etc. Furthermore, even the nuclear size and the morphology (chromatin s.l.) of these 3 antipodal cells, unequivocally exclude their origin from one antipodal cell following two successive mitoses. We have no doubt that this fig. 10 demonstrates the true further mitotic development of the «type bipolaire» that is the very common sequence (2 + 2) → (4 + 4) followed by the usual cellularization. Obviously, the well known precocious degeneration of the two synergids, justifies their absence from microphotograph 10.

Provided that the above reinterpretation represents the regular further development of the 4-nucleate stage, i.e. the (2 + 2) ES, or «type bipolaire», the old gametophyte documented by the Fig. 8-9,

([72]) A = antipodal cell.

cannot be considered a convincing proof of a quite different embryological development of the 4-nucleate (i.e. 2 + 2) embryo sacs.

Fig. 8-9 is described as a tetranucleate embryo sac «non réduit (type bipolaire), constitué d'une oosphère, de deux noyaux polaires (N) et d'une antipode en division, au pôle chalazien». This embryo sac is larger and probably, also older than that in fig. 10. Consequently, we cannot exclude an absence of synergids owing to degeneration. Because the phenomenon of polyantipody regularly occurs in the mature 8-nucleate embryo sacs of the genera *Eragrostis*, *Pennisetum* (etc.), there is nothing new in this «fig. 8-9» except the presence of one antipodal instead of theree or more than three. Logically this case cannot be recognized as an adeguate documentation of a new type of ES development.

2. *Occurrence of the Eragrostis type among plants retaining apomictic embryony*

As far as we know the Eragrostis type is confined to the non-amphimictic species of this genus (see Table V). Nevertheless, we cannot omit a very doubtful reference in *Chrysopogon serrulatus* by Faruqi et al. (1975, p. 135) who write: «In *C. serrulatus* tetranucleate embryo sacs with single polar nucleus were observed which showed diplosporous type of development (fig. 6)». Fig. 6 is poor and unconvincing. Obviously, a reinvestigation is necessary.

Table V - (*Eragrostis type*)

**Species showing the occurrence of the 4-nucleate & 4-celled Eragrostis type.**

*Chrysopogon serrulatus*: Very doubtful, cf. Faruqi et al. (1975, fig. 6);
*Eragrostis chloromelas*: Brown & Emery (1958: 4-nucleate, diplospory), Streetman (1963 *a*);
*Eragrostis curvula*: Brown & Emery (1958: 4-nucleate, diplospory); Liebenberg & Pienaar (1962); Streetman (1963 *a*) Voigt & Bashaw (1972, 1976); Brix (1974); Vorster & Liebenberg (1977, 1984); Rabau, Longly & Louant (1986: coexistence 4-celled & 3-celled form);
*Eragrostis heteromera*: Brown & Emery (1958: 4-nucleate, diplospory);
*Eragrostis lehmanniana*: Streetman (1963 *a*).

IVe. *Taraxacum type (aneumeiotic ES: 8-nucleate, monokaryosporic).*

Here the first meiotic division ends in a restitution nucleus. Meiosis II is regular and produces a dyad of unreduced cells of which the lower is the gametophyte «monokaryosporic» initial which ultimately forms a morphologically normal 8-nucleate unreduced ES. Priority over «Taraxacum type» and both definition and origin of the restitution nucleus deserve a comment.

1. *Restitution nucleus: definition*

First we must establish the following basic symbols:

m = mitosis; M = meiosis (MI = heterotypic, or first meiotic division; M II = homoeotypic or second meiotic division); R = restitution nucleus ([73]).

([73]) The term «restitution nucleus» was first proposed by ROSENBERG (1927). See also «nuclei di restituzione mitotici, eterotipici, omeotipici» in BATTAGLIA (1945 *b*).

PLATE VI

Fig. 14. *Pennisetum ciliare* from Snyder et al. (1955, fig. 14 reproduced here inverted: Fig. 14 (*right*), four-nucleate embryo sac with nuclei separated to opposite ends; note that nuclei are in prophase of third mitotic division; embryo sac on left is aposporic and has differentiated at four-nucleate stage.

Figs. E, C. *Pennisetum dubium.* From Gildenhuys & Brix (1959, p. 244, Figs 2A-2K): «E.-Haploid sac developing on left (2-nucleate stage), but inside aposporic sac. C.-Haploid (right) and aposporic sacs adjoning».

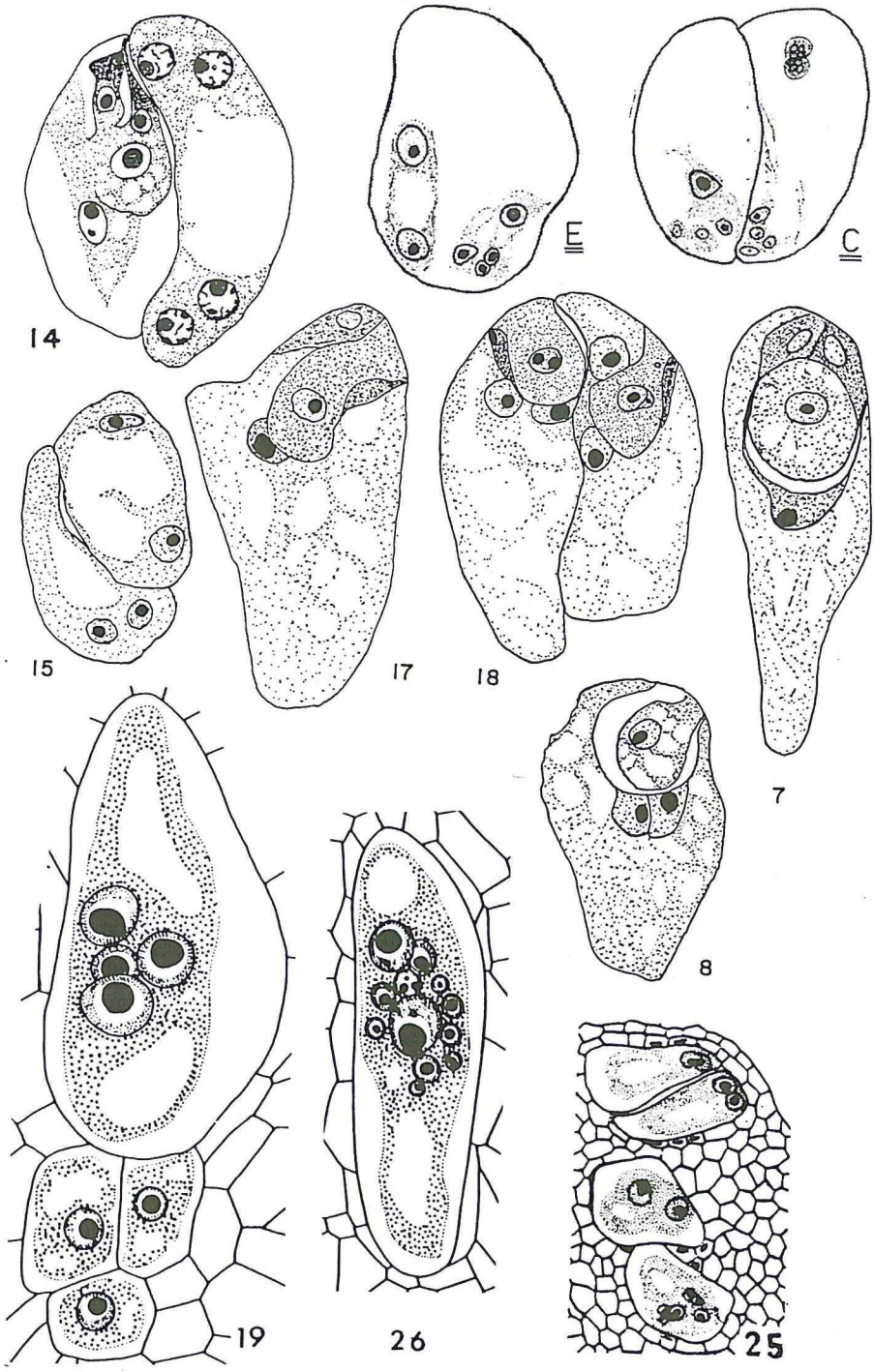
Figs. 15, 17, 18. *Bothriochloa ischaemum.* From Brown & Emery (1957a, p. 250): «Fig. 15, two 2-nucleate aposporous embryo sacs; sac on right is probably result of precocious division in aposporous embryo-sac initial. Figs. 16, 17, normal organization of 4-nucleate aposporous embryo sacs with 1 egg: 2 synergids: 1 polar. Fig. 18, two 4-nucleate aposporous embryo sacs organized with 1 egg: 1 synergid: 2 polars; note nucleus of male gamete lying against nucleus of egg cell».

Figs. 7, 8. *Themeda triandra.* From Brown & Emery (1957 a, p. 248): «Fig. 7, four-nucleate aposporous embryo sac containing 1 egg: 2 synergids: 1 polar nucleus. Fig. 8, aposporous embryo sac with 1 egg: 2 polar nuclei; no synergids were distinguishable in this embryo sac».

Figs. 19, 26. *Echinochloa stagnina.* From Muniyamma (1978, pp. 90, 91): «Fig. 19, Unorganized four-nucleate aposporous sac and three enlarging aposporous initials at the chalazal end. Fig. 26, Atypical embryo sac with centrally placed 12 nuclei of variable size».

Fig. 25. *Cenchrus glaucus.* From Shanthamma (1982, pp. 30, 35): «Occasionally, the 4-nuclei without organization undergo further divisions resulting in the formation of 6 to 8 nuclei all grouped together (figure 25)». «25. a group of 4-aposporous embryosacs, 3 embryosacs are binucleate and the remaining one showing unorganized 6-nucleate condition (× 1200)».

PLATE VI



We must also define the restitution nucleus as the formation, during a meiotic or a mitotic division, of a single nucleus in place of two sister nuclei. Thus, the following cases can be further differentiated:

m (R) = mitotic restitution (nucleus);

MI (R) = heterotypic restitution (nucleus) ([74]) ([76]);

MII (R) = homoeotypic restitution (nucleus) ([75]) ([76]).

The heterotypic restitution is the distinguishing feature of both the Taraxacum and Ixeris types. The occurrence, during female meiosis, of only the homoeotypic restitution has never been convincingly established. Double restitution ([77]) i.e. MI(R) + MII(R) is known (see further Rudbeckia IV type), however it gives rise to a non-recurrent type.

## 2. *Restitution nucleus: other interpretations and symbols*

We believe that it is terminologically exact to define as «restitution division» an abnormal division (meiotic or mitotic) which «restitutes» to form a single nucleus («the restitution nucleus») rather than two sister nuclei.

Thus, we are doubtful about the terminological legitimacy of the various interpretations (and symbols or abbreviations) of this concept, as discussed below.

Regarding the formation of *2n* nuclei (*Solanum*: microsporogenesis) by the mechanism of «parallel spindles» and «fused spindles» at MII ([78]), Mok & Peloquin, (1975 *b*, p. 295) write:

«The cytological event that leads to diplandroid formation is the parallel orientation of Anaphase II spindles during microsporogene-

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([74]) As regards the equivalent symbol FDR = «first division restitution», see next pages 81-82.

([75]) As regards the equivalent symbol SDR = «second division restitution» see next pages 81-82.

([76]) Although we accept the symbols MI & MII since they are of general acceptance, nevertheless we prefer to write heterotypic (homoeotypic) restitution in place of first (second) division restitution because in this way we can maintain and stress the qualitative difference existing between the two meiotic divisions.

([77]) Cf. «nucleo di birestituzione» in Battaglia (1945 *b*).

([78]) As early as 1927, for *Solanum tuberosum*, Yasona Fukuda described the occurrence of «fused spindles» during the second meiotic division of PMCs. Subsequently «fused spindles» have been reported in many potato cultivars, hydrids etc. by Bleier (1931), Meurman & Ranken 1932, (see references in Ramanna, 1979 etc.).

sis in contrast to *n* microspore formation where Anaphase II spindles are at an angle of about 60 degrees. Nuclei at each pole restitute, and following cleavage furrow formation dyads are formed instead of tetrads».

According to our point of view the sentence «nuclei at each pole restitute» is questionable since no restitution to a single nucleus takes place at all. The phenomenon is actually a fusion between two telophase non-sister nuclei or, by more exact terminology, formation of a «syntelophase nucleus» (or «telophase synkaryon»). A minor consideration is that the parallel orientation of the spindles, at MII, does not necessarily give rise to a dyad of unreduced spores (see criticism in RAMANNA, 1979).

There are also other interpretations and symbols. Many authors use the abbreviations FDR (= first division restitution) and SDR (= second division restitution) ([79]) to indicate non-reduced gametes originated from cytological anomalies which are fully independent of restitution divisions.

Since *2n* pollen (cf. *Solanum*) formed by «fused spindles» (MII) is genetically equivalent to the meiotic «first division restitution» (FDR), some authors simply write «FDR 2n gametes» (e.g. MENDIBURU & PELOQUIN, 1977).

According to this terminology the *2n* gametes of the Datura types should be qualified as «(SDR) *2n* gametes». As regards *Solanum*, STELLY & PELOQUIN (1986) write:

«Omission of the second meiotic division led to formation of second division restitution (SDR) *2n* megagametophytes». Linguistically we see a contradiction between *omission* of the second division and second division restitution megagametophytes. Further, we are equally doubtful in qualifying as «(SDR) *2n* eggs» the *2n* gametes formation described by PFEIFFER & BINGHAM (1983) in *Medicago*. In this case female meiosis usually results in the normal tetrad of gynospores. Sometimes, owing to a partial failure of cytokinesis, meiosis results in a triad, namely a chalazal 2-nucleate functional spore with two superposed 1-nucleate cells. Later on, according to PFEIFFER & BINGHAM, a nuclear fusion takes place either prior to or following the first somatogenic nuclear mitosis, (see also next pages 111-113).

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([79]) The abbreviations (FDR), i.e. «first division restitution» and (SDR), i.e. «second division restitution» have been first proposed by MENDIBURU (1971, Ph. D. Thesis, Univ. Wisconsin).

We are unable to find any qualitative difference between this case and the THOMAS' (1940) «automixis», which he hypothesized for the ES development of *Rubus nitidioides*.

We are more doubtful about the genetical reclassification on the basis of the FDR & SDR terminology of some classical embryological cases (and types) as *Hieracium, Taraxacum , Ixeris* etc. Thus, for instance, we must disagree with the following sentence by RAMANNA (1979, p. 559):

« It is well-known that stable mechanisms of 2n gamete formation are invariably associated with plants that reproduce by means of recurrent apomixis. For example, in *Hieraceum* (ROSENBERG, 1927), and *ixeris* (OKABE, 1932) 'semiheterotypic' division leads to meiotic nuclear restitution; in *Taraxacum*, *Erigeron* and *Archieraceum* (GUSTAFSSON, 1935) 'pseudo-homotypic' division leads to meiotic nuclear restitution; in *Poa* (MÜNTZING, 1940), and *Antennaria* (STEBBINS 1932) a 'mitotitized meiosis' of nuclear division leads to meiotic nuclear restitution. These cases are but a few well-known examples. In most of them there is indisputable evidence that first division restitution mechanism leads to the formation of 2n gametophytes.»

In conclusion, we emphasize here the desirability of a terminological concordance between genetical and cytological considerations.

### 3. *Semiheterotypic division, restitution nucleus and the priority over the Taraxacum type.*

JUEL (1904) is credited with the discovery of the Taraxacum type, however this priority needs a comment. SIEGFRIED SCHWERE (1896) described the occurrence of an usual mature embryo sac in *Taraxacum vulgare* and the development of the embryo following fertilization. He also claimed to have discovered in *Taraxacum* the first case of synergid fertilization (SCHWERE, 1896, Fig. 4). However in 1903 RAUNKIAER (by classic emasculation methods) established the parthenogenetic behaviour of *Taraxacum*. This statement was very soon supported by MURBECK (1904) and KIRCHNER (1904), see also a previous paper by ANDERSSON & HESSELMAN (1900). It is useful to recall that at the beginning of the century it was already well established among plant embryologists (cf. STRASBURGER & pupils) that «die Chromosomenzahl... wird durch die Befruchtung verdoppelt und durch die Tetradenteilung wieder halbiert». Is is useful also to recall that Juel, (1898, 1900) was the first to discover in *Antennaria alpina* the full suppression of the formation of the tetrad of megaspores, thus confirming the parthenogenetic behaviour claimed many years before for the same species by KERNER (1876).

Again, JUEL (1904) announced the discovery in *Taraxacum* of the case in which «Die Tetradenteilung» is reduced to a single division. Apparently no chromosome reduction occurs, although the prophase seems to be heterotypic. The result of such division is one large basal cell and one smaller apical cell. Later the basal cell grows, destroying the apical cell, and giving rise to a normal mature embryo sac.

The following year JUEL (1905) published the full report on *Taraxacum*. Comparing the reduction divisions of sexual «Cichorieen» («Hieracium umbellatum» and «Crepis tectorum») with those of «Taraxacum officinale» he notes the double chromosome thread in the prophase of the «Cichorieen» but not in *Taraxacum*; in diakinesis the «Cichorieen» show a reduced number of bivalents while *Taraxacum* has a double number of univalents. Juel also describes a new cytological feature: during diakinesis the nucleus elongates and the chromosomes split temporarily, with a behaviour regarded as a shift from heterotypic to homotypic prophase.

Several embryological investigations on the apomictic *Taraxaca* have been carried out, from 1912 to 1922, namely by SCHORBATOW (1912), OSHAWA (1913) ([80]) SEARS (1917, 1922) ([81]) and STORK (1920). They more or less confirmed JUEL's findings, again describing the occurrence of a dyad stage in place of the regular tetrad of megaspores.

Neither STORK (1920) nor SEARS (1922) mention a paper by Ro-

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([80]) OSAWA (1913, p. 460) writes: «Before entering into the spindle-formation of the first mitosis the nucleus elongates greatly and each chromosome splits into two long pieces which take the shape of X, Y or V. Fig. 70 shows one of such stages...». This is the prophase stage of the restitution nucleus, and Fig. 70 represents the first and best documentation of this peculiar atypic meiotic stage.

([81]) Sears, in his first report (1917) entitled «Amiotic Parthenogenesis in Taraxacum vulgare...» states: «in certain cases at least, it is the micropylar daughter cell which seems to function in *T. laevigatum*».

This very interesting behaviour that is the ES development from the micropylar dyad cell (a typologically important deviation from the classic Taraxacum type) is not recorded in SEARS' (1922) full report. In this report SEARS modifies the term «amiotic» into «ameiotic», and establishes four (A-D) different sequences as regards the divisions of the embryo sac mother cell. Further he describes the elongation of the nucleus presently known as restitution nucleus as an «amitotic constriction of the sequence D in E.S.M.C.». The most common sequence that is case B, is described as follows: «B, a qualitative division resulting in diads from which the functional embryo sacs arise and for which the term ameiosis is proposed».

PLATE VII

From Rosenberg (1917, p. 194, Fig. 26).

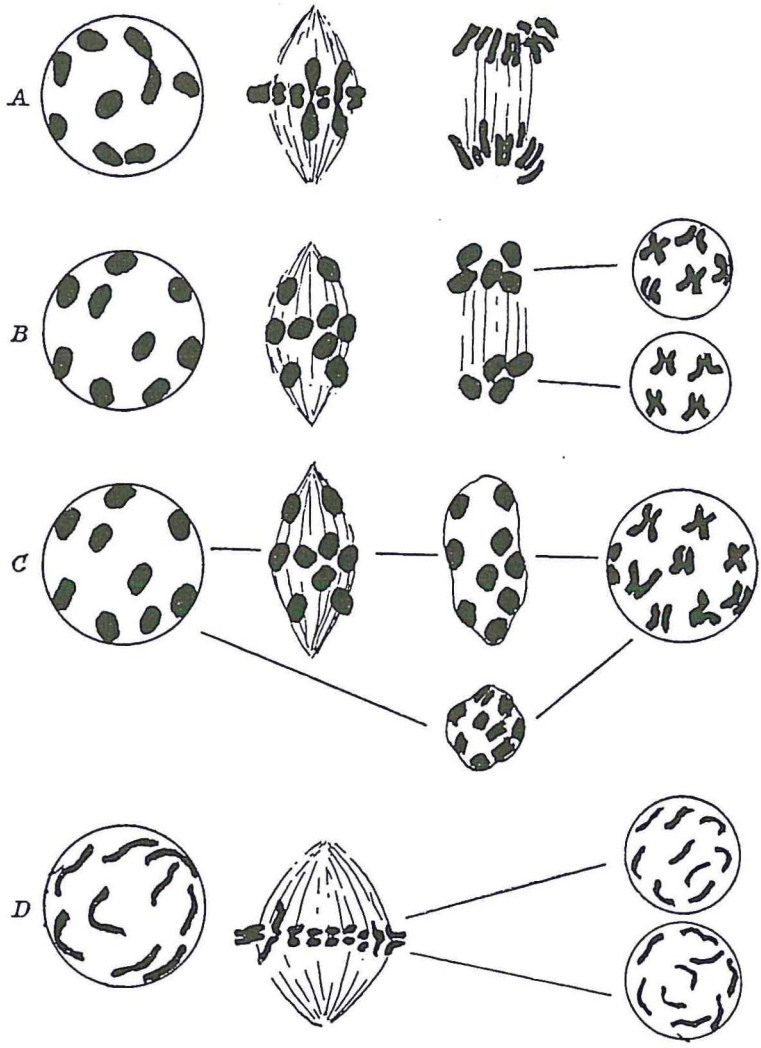


Fig. 26. Schema der in asexuellen Archieracien beobachteten P. M. Z.-Teilungen, A *H. boreale*-Typus; B, C halbheterotypische Teilung; D Äquations-teilung, diploid. Vgl. Text sid. 193.

SENBERG (1917) ([82]) from which Fig. 26 is reprinted here, see Plate VII. This summarizes the four main patterns of abnormal meiosis, found by ROSENBERG (1907... 1917) in the genus *Hieracium*. Today this scheme is self explanatory, although the following sentences should be quoted (cf. ROSENBERG, 1917, p. 193-194):

> « In B ist die halbheterotypische Teilung dargestellt. Die Chromosomen sind alle ungepaart, keine eigentliche Äquatorialplatte wird gebildet, sondern die Chromosomen sind auf der Spindelfigur zerstreut; in der Anaphase werden sie ganz willkürlich nach den Polen geführt. In dem vorliegenden Falle kommen 5 Chromosomen zu dem einen und 4 zum anderen Tochterkern. In der Interkinese werden sie längsgespalten und eine gewöhnliche homotypische Teilung folgt.
>
> In C ist die S. 188 beschriebene Modifikation dieser Teilung dargestellt. Sie kann in zwei Richtungen gehen. Entweder wird eine halbheterotypische Spindelfigur gebildet, die Chromosomen werden aber nicht an den Polen geführt, sondern die Spindelfigur wandelt sich in einen Kern um, wo die Chromosomen eine Längsspaltung beginnen, also eine Art Interkinese, um später in die homotypische Teilung zu übergehen. In anderen Fällen tritt der P. M. Z.-Kern aus der Diakenese direkt ohne Spindelbildung, durch ein Kontraktionsstadium, in die Interkinese über. In beiden Fällen ist die folgende Teilung eine Äquationsteilung mit der somatischen Chromosomenzahl.
>
> In Fig. D ist der *H. pseudoillyricum*-Typus abgebildet, wo die P. M. Z. eine typische, somatische Kernteilung zeigt. »

Last but not least, in this paper ROSENBERG (1917, p. 204) gives a very elegant reinterpretation of the abnormal meiosis in *Taraxacum* (and in other similar cases as ERIGERON etc.), namely:

> « Wenn man diese Angaben über die E. M. Z.-Entwicklung in *Taraxacum* mit den Kernverhältnissen bei der halbheterotypischen Teilung, etwa in *H. lacerum* oder *H. laevigatum*, vergleicht, so scheint es mir, als ob eine gewisse Übereinstimmung dieser Erscheinungen »

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([82]) In this famous paper ROSENBERG established his «Die halbheterotypische Teilung» (ROSENBERG, 1917, p. 186).

This division has later been simply translated into «divisione semieterotipica» by CARANO (1924, p. 151) and by CHIARUGI (1926). However, some years before, HILDUR LJUNGDAHL, (1922, p. 106), describing the occurrence of such an anomalous division in Papaver hybrids, wrote: «semiheterotyp» in place of «halbheterotypisch», and namely «...Ich habe aber auf diesen Grenzfall aufmerksam machen wollen, da wir es bei dieser Hybride mit der Modifikation der heterotypen Teilung zu tun haben, die ROSENBERG semiheterotyp bezeichnet. (Vgl. «halbheterotipische Teilung» in Sv. Bot. Tidskr. 1917, S. 202!)». It is worth mentioning that ROSENBERG himself in 1926 (and in later accounts) adopted the spelling «die semiheterotypische Teilung».

unverkennbar sei. Man braucht nicht mit SCHKORBATOW zu »parallellen Elementararten» zu greifen um die verschiedenen Kernstrukturen zu erklären. Das Vorkommen in den E. M. Z. in *Taraxacum* (und vielleicht anderen apogamen Arten) von zwei Arten der »Diakinese» lässt sich meiner Ansicht nach in folgender Weise erklären: die Prophase mit längsgespaltenen, dünnen Chromosomen ist die Fortsetzung der »dicken» Diakinese und mit der Interkinese vergleichbar. Vielleicht wird eine Spindelfigur, nach dem halbheterotypischen Schema angelegt, dieselbe wird doch direkt in einen Kern mit längsgespaltenen Chromosomen umwandelt, oder der Prophase-Kern geht direkt durch ein Kontraktionsstadium (vgl. Fig. 22 in die Interkinese über. In *Erigeron annuus*, der nach TAHARA (1915 b) apogame Embryoentwicklung zeigt, kommen Spindelfiguren vor, die sehr an eine halbheterotypische erinnern (z. B. die Figur Seite 248). Das Vorkommen in gewissen apogamen Arten von sterilen Samenknospen lässt sich dann vielleicht dadurch erklären, dass hier eine halbheterotypische Teilung vollendet wurde ohne Übergang in eine Interkinese mit längsgespaltenen Chromosomen in der somatischen Anzahl.

In 1926 CHIARUGI translated into «divisione semieterotipica» ([83]) ROSENBERG's «halbheterotypische Teilung» and ascribed to the Taraxacum type (cf. also CHIARUGI 1927, p. 100), as a specific trait, the occurrence of «una cariocinesi semieterotipica abortita, ovvero una contrazione semieterotipica del nucleo».

The following year, ROSENBERG (1927) again discussing and documenting the behaviour of the semiheterotypic division in the PMCs of *Hieracium*, coined the very appropriate term «restitution-nucleus» ([84]) and at the same time claimed its occurrence during ES

([83]) In all embryological literature the expression *hemi-heterotypic* in place of *semiheterotypic* has been adopted exclusively by B. ANZALONE (1948, pp. 8-9: Summary) in describing the occurrence of the restitution nucleus in *Taraxacum megalorrhyzon*. However, in this case, the expression *hemi-heterotypic* is nothing other than the English translation of the italian espression «divisione semieterotipica» and not a terminological change suggested by a linguistic criticism.

([84]) In two papers published one year earlier on the restitution nucleus ROSENBERG (1926 *a*, *b*) wrote: «Regressions-kern» and «Regressions kernbildung». ROSENBERG (1927 *a*, p. 321) comments and modifies his terminology: «In einer neulich erschienenen Arbeit (1926 a) habe ich den Terminus Regressionskern vorgeschlagen, aber es scheint mir, dass Restitutionskern besser der Entstehungsweise dieses Kerntypus entspricht». In the following p. 336 he summarizes: «The semiheterotypic meta- and anaphase very often are not completed, but are interrupted by a premature homotypic division, whereby *Restitution-nuclei* are formed. Round the entire spindle figure a new nuclear wall is formed, resulting in the production of a single large nucleus, the chromosomes of which divide quite in the same manner as in normal interkinesis, but with the diploid number of chromosomes».

development in the species of *Taraxacum* investigated by JUEL, OSAWA etc. ([85]).

The following year KUWADA (1928) gives the first correct and detailed microphotographic documentation of the occurrence of the Taraxacum type in *Balanophora japonica* and fully confirmed ROSENBERG's (1927) interpretation. In *Balanophora* (cf. KUWADA, 1928, p. 120) «the formation of the restitution-nucleus takes place at the heterotype metaphase or at slightly later stages. When it occurs at the metaphase, the restitution-nuclei will be spherical... Restitution-nuclei formed at later stages of the division (anaphase) were of irregular shapes, some being of the form which recall amitosis..., others being of much elongated forms... and still others being divided into two nuclei of unequal sizes».

More recent and detailed *Taraxacum* investigations (see FAGERLIND, 1947*b*; BATTAGLIA, 1948) also basically agree with KUWADA's descriptions.

From a typological point of view, since ROSENBERG's interpretation must be acknowledged, we believe that the Taraxacum type should be qualified as Taraxacum type (JUEL, 1904 - ROSENBERG, 1917).

4. *The restitution nucleus: the need for further modern reinvestigation.*

The heterotypic restitution nucleus characterizes two main types of unreduced ES development, which are the Taraxacum and the Ixeris types (see below).

We must emphasize the fact that in many cases is difficult or very questionable to prove whether this anomalous aneumeiotic pattern come from the environment or from a genetic cause or from their interaction.

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([85]) ROSENBERG (1927, p. 325) writes:

> « Ich möchte hier schon einen Vergleich dieses Prozesses mit gewissen Entwicklungsstadien der Embryosackmutterzelle parthenogenetischer *Taraxacum*-Arten anstellen. Eben der oben nachgewiesene Zusammenhang zwischen Dyadenbildung im Gonotokont mit Restitutionskernen hat mich zu dem Gedanken geführt, ob nicht die so sehr eigenartige Bildung des Embryosackes in *Taraxacum* eine Erklärung finden könnte. In *Taraxacum* haben JUEL, OSAWA u. a. gezeigt, dass die Embryosackmutterzelle einmal sich teilt, also Dyaden bildet, mit den diploiden Chromosomenzahl. Es scheint mir die Vermutung berechtigt, dass hier auch Restitutionskerne gebildet werden, und dass dadurch die merkwürdige einmalige Teilung der Embryosackmutterzelle ihre natürliche Erklärung finden könnte. »

PLATE VIII

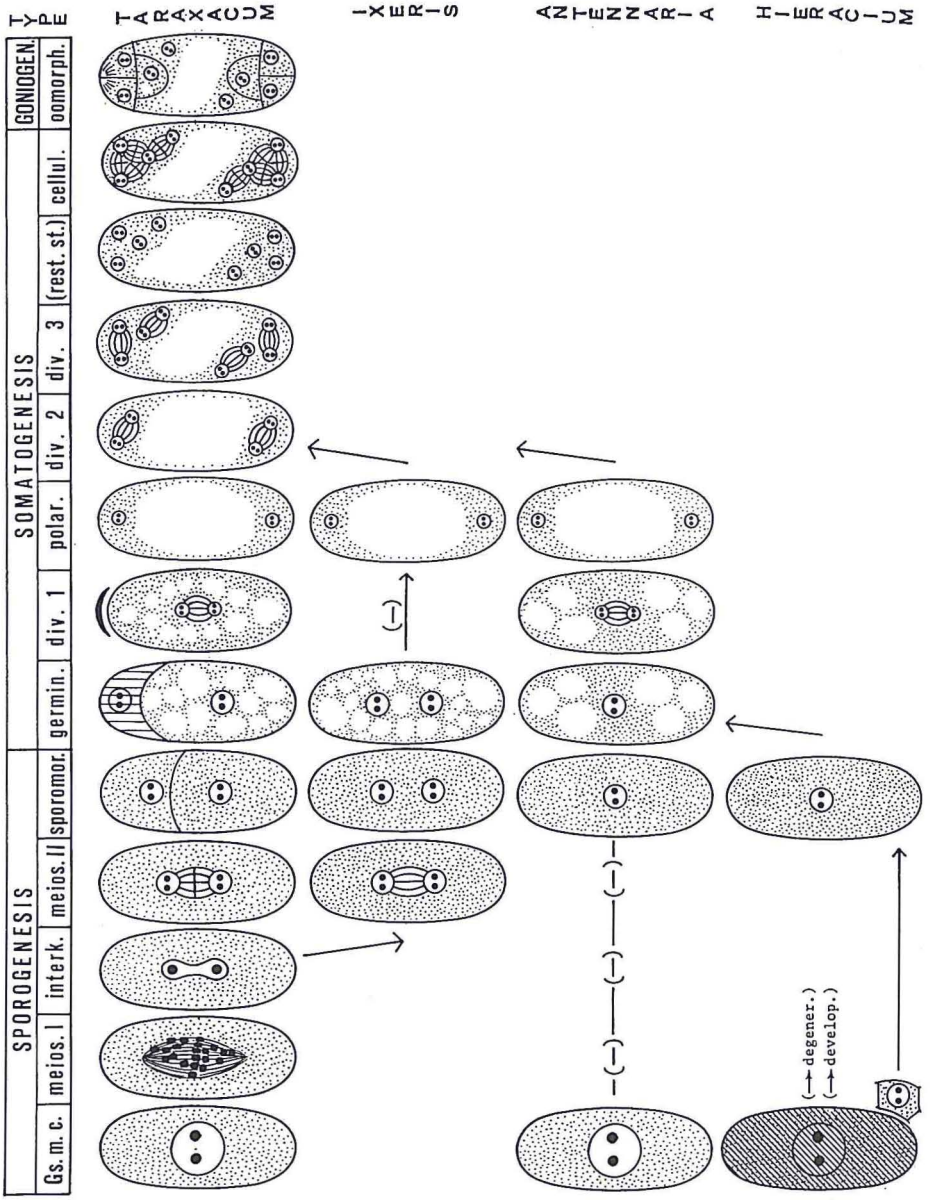

SPOROGENESIS
SOMATOGENESIS
GONIOGEN.
TYPE
Gs. m. c.
meios. I
interk.
meios. II
sporomor.
germin.
div. 1
polar.
div. 2
div. 3
(rest. st.)
cellul.
oomorph.
TARAXACUM
XERIS
ANTENNARIA
HIERACIUM
(–) degener.
(–) develop.

PLATE IX

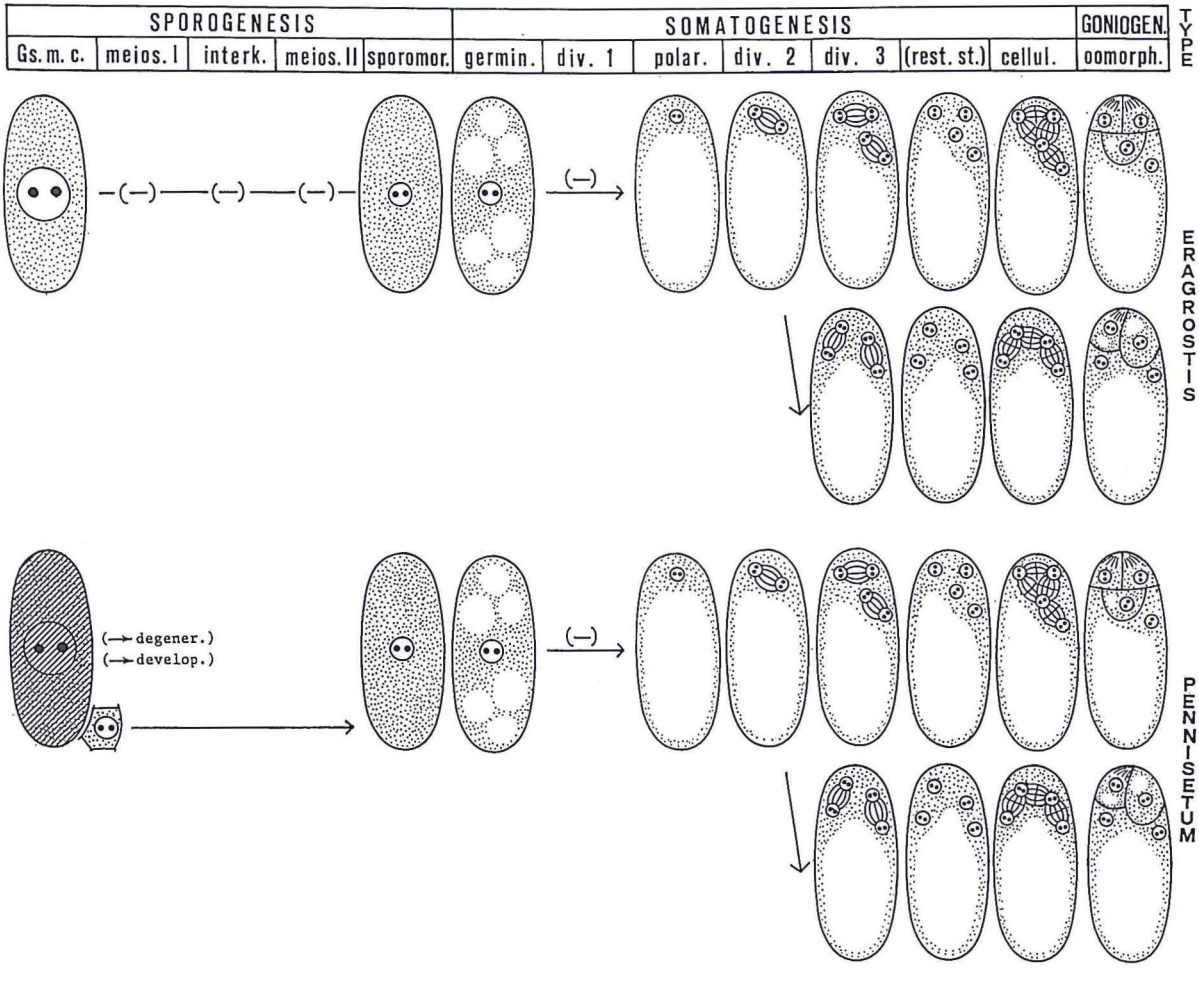

SPOROGENESIS
SOMATOGENESIS
GONIOGEN.
TYPE
Gs. m. c.
meios. I
interk.
meios. II
sporomor.
germin.
div. 1
polar.
div. 2
div. 3
(rest. st.)
cellul.
oomorph.
ERAGROSTIS
(→ degener.)
(→ develop.)
PENNISETUM

PLATE X


SPOROGENESIS
SOMATOGENESIS
GONIOGEN.
TYPE
Gs. m. c.
meios. I
interk.
meios. II
sporomor.
germin.
div. 1
polar.
div. 2
div. 3
(rest. st.)
cellul.
oomorph.
ERAGROSTIS II?
PENNISETUM II?
(→ degener.)
(→ develop.)

## PLATES VIII, IX, X

Schematic representation of the embryo sac types discussed in the Text. Synergids show the filiform apparatus. The development of the female gametophyte is divided into the following three parts:

— SPOROGENESIS period. This period has been subdivided into 5 stages, namely:
a) *Gs.M.C.* = gynospore mother cell;
b) *Meios. I* = meiosis I = heterotypic division;
c) *interk.* = interkinesis;
d) *Meios. II* = meiosis II = homoetypic division;
e) *Sporomorph.* = Sporomorphogenesis. In this stage the products of meiosi become morphologically and physiologically spores;

— SOMATOGENESIS period. During this period the part of the gametophyte, which interpretatively can be defined as somatic, develops, and consequently the nuclear divisions which occur in this period are termed somatogenic divisions. The author distinguishes in the primitive ES type of the angiosperms (the Polygonum type) three successive somatogenic divisions as *div.* 1, *div.* 2 & *div.* 3 (first, second and third somatogenic divisions). In the interpretative system of Chiarugi (1927), only div. I belongs to *Somatogenesis*, while div. 2 and div. 3 belong to *Gametogenesis* (see below).

The *Somatogenesis* period has been subdivid into 7 stages:
a) *Germin.* = spore germination = beginning of gametophyte development;
b) *Div.* 1 = first somatogenic division;
c) *Polar.* = polarization = specific arrangement of the spore nuclei, or their derivatives, within the gametophyte;
d) *Div.* 2 = second somatogenic division;
e) (*Rest. st.*) = resting stage = the regular resting stage between second and third somatogenic division. This stage has been introduced into the present graphic representations entirely for didactic or descriptive reasons, i.e to illustrate the nuclear status of the gametophyte after the 2nd somatogenic division.
f) *Div.* 3 = third somatogenic division;
g) *Cellul.* = cellularization = wall formation in Battaglia (1951);

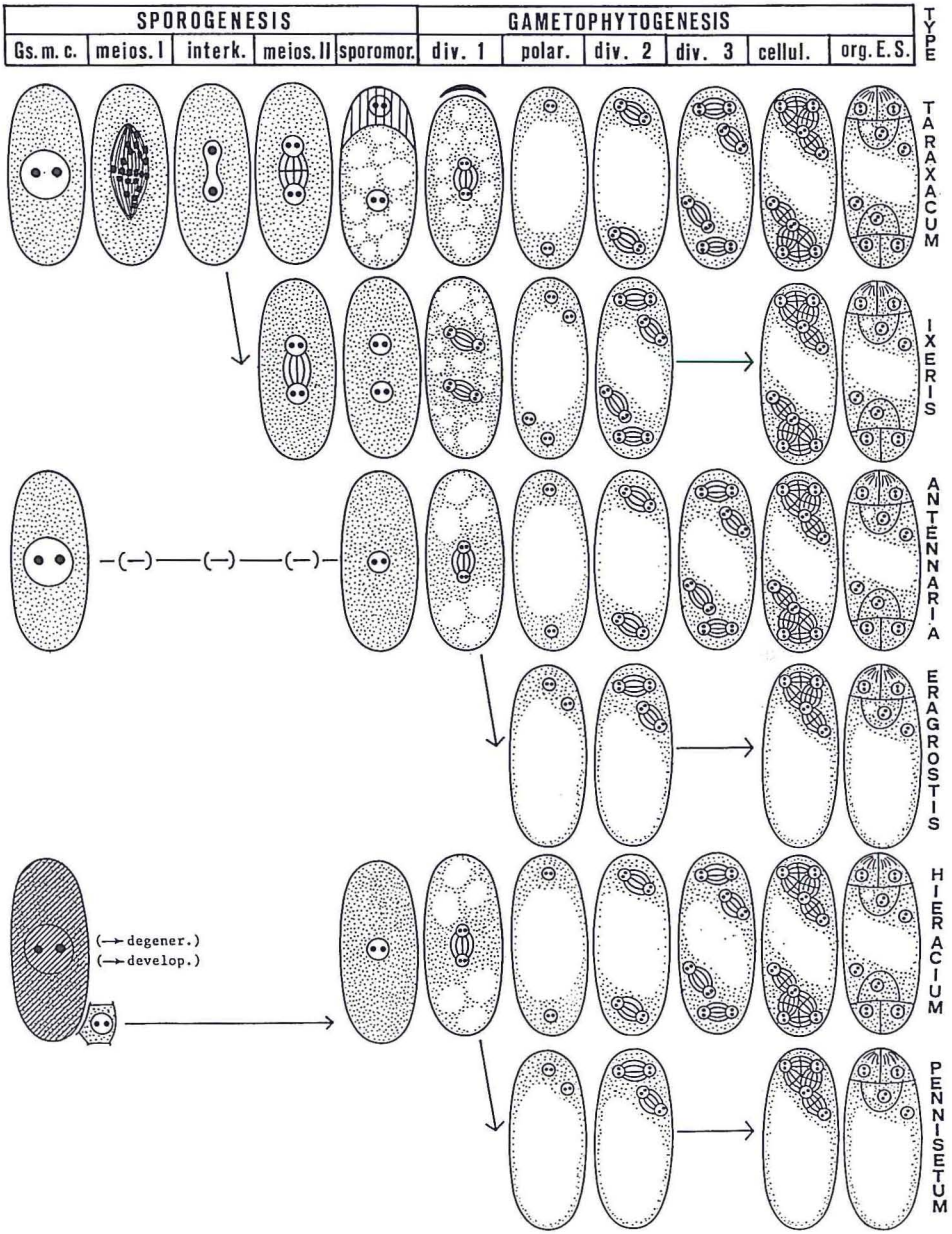
— GONIOGENESIS period. Goniogenesis (Chiarugi's Gametogenesis) is the abbreviation of *Archegoniogenesis* = *Gynogoniogenesis* (*Gynogonium* = *Archegonum* cf. Battaglia, 1982).

According to the author's view, the goniogenic divisions have been totally suppressed in the angiosperms, and *goniogenesis* is represented exclusively by the *oomorph.* (= *oomorphogenesis*) stage. During thi stage a micropylar cell of the gametophyte takes on the function and morphology of the egg cell; *org. E.S.* = organized embryo sac.

In all figures the symbol (-) signifies a suppression of division (or stage).

PLATE XI

(see the Text p. 113)



We also believe that the frequent occurrence of two remarkably different patterns of meiosis in the micro-and macrosporogenesis within the same individual plant merit much more investigation.

From a karyological point of view «the block and reversion» to restitution nucleus can occur at different stages of the heterotypic division. It is quite clear today that there is «a strong need and large space» for restitutional reinvestigations by combining old and modern methods such as TEM and fluorescence techniques.

Only such studies will result in a better knowledge of this very interesting process and at the same time establish a sound basis for a better classification of the restitutional phenomenon.

5. *Occurrence of the Taraxacum type among plants retaining apomictic embryony.*

Provided that the eventual development of the ES from the micropylar cell of the unreduced dyad deserves a more adequate attention from the embryologists (as regards future reinvestigations), the classic 8-nucleate Taraxacum type has been established in several genera such as *Antennaria, Balanophora, Chondrilla, Elatostema, Hieracium, Taraxacum, Wikstroemia,* etc. The interested reader has only to consult the most recent embryological papers and books, but there is also a strong need for an updated and adequately commented list of plants that are commonly called apomictic.

IVf. *Ixeris type (aneumeiotic ES: 8-nucleate, dikaryosporic).*

As in the Taraxacum type, here meiosis I gives rise to a restitution nucleus. At the end of meiosis II, wall formation is omitted and a single «dikaryosporic» initial of the gametophyte is formed. Two more nuclear divisions lead to the morphologically normal 8-nucleate unreduced ES. The Ixeris type, first correctly described and documented by Sakuichi Okabe (1932, see also 1963), is rare among non-amphimictic plants. It is found in species of *Erigeron, Ixeris, Rudbeckia, Statice* etc.

## V. Recurrent types of unreduced embryo sac: doubtful cases.

### Va. Gustaffson's *(1934) pseudohomotypic division (type B in* Battaglia, *1963).*

### Vb. Håkansson & Levan's *(1957) endo-duplicational meiosis (Allium nutans types I & II in Battaglia, 1963).*

1. *Allium nutans types I & II: criticism and reinterpretation.*

2. *Allium odorum type versus Allium nutans type. Proposal for a new typology: Allium I type («reduced-tetraploid» & recurrent) and Allium II type («reduced-octoploid» & non-recurrent).*

### Va. Gustaffson's *(1934) pseudohomotypic division (type B in* Battaglia, *1963).*

We consider the establishment of a second Taraxacum type to be unjustified (i.e. Taraxacum II type, cf. «type B» *in* Battaglia, 1963, based on the occurrence of a mitotic-like monokaryokinetic meiosis termed «pseudohomotypic division» ([86]) by Åke Gustaffson (1934*a*, *b*, 1935). According to this author, in the parthenogenetic species of *Taraxacum*, and as an alternative to the usual formation of the restitution nucleus, there occurs an abnormal meiosis in which the pairing is omitted and the univalents divide regularly giving rise to an unreduced dyad. The chalazal cell functions as ES initial cell and by 3 subsequent nuclear divisions the usual 8-nucleate ES is formed.

Fagerlind (1944*b*) referred to this abnormal meiotic process as

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([86]) «Pseudohomoeotypic» is linguistically better than the usual «homotypic» (cf. Wilson, 1906, p. 441: «Homoeotypical mitosis»), and in any case there are reasons for refuting the expression «pseudohomotypic division».

Apart from the consideration that such an anomalous meiosis was earlier described in animal cytology, there are conceptual reasons against the acceptance of this terminological definition, namely:

— the division is indeed homoeotypic, at least in that the centromeric division actually occurs,

— the specific trait of this division consists of the fusion of the two meiotic division into a monokaryokinetic process.

It follows that other expressions such as «monomitotic-like meiosis» or «mitotic-like monokinetic meiosis» (we do not enjoy «mitotized meiosis»), seem to us by far more correct and clear than the current «pseudohomotypic division».

«semiapospory» (87) and later on we called it «pseudomeiosi» (BATTAGLIA, 1945*b*) (88).

However, GUSTAFFSON's figures leave room for a different interpretation and both FAGERLIND (1947*b*) and BATTAGLIA (1948), reinvestigating apomictic Taraxaca, reinterpreted GUSTAFFSON's documentation as stages referable to the restitutional Taraxacum type.

Since in the last 30 years many embryologists have reinvestigated the embryology of the parthenogenetic *Taraxaca* without obtaining evidence of the «pseudohomoeotypic division» we believe that the occurrence of such type of division is very doubtful and consequently the establishment of a second Taraxacum type is not justified.

The two embryological types hypothetically characterized by the occurrence of a pseudohomoeotypic division, followed or not by cytokinesis, had respectively been distinguished as types B & C by BATTAGLIA (1963).

The occasional occurrence of the «pseudohomoeotypic division» (sometimes renamed «pseudohomotypic meiosis») has been cited in several papers without any cytological documentation. Such papers are intentionally not mentioned here since they are considered as 'undocumented doubful cases'.

## Vb. HÅKANSSON & LEVAN's *(1957) endo-duplicational meiosis (Allium nutans types I & II in* BATTAGLIA, *1963).*

### 1. *Allium nutans type I & II: criticism and reinterpretation.*

In 1958-59 we established (cf. BATTAGLIA, 1963) the Allium nutans Types I and II as follows:

> (d) *Allium nutans Type I* — This type has been recorded only in *Allium nutans* (Håkansson, 1951) and *Allium odorum* (Håkansson & Levan, 1957). As in the sexual species of *Allium* the embryo sac is bisporic, and its development apparently follows the Allium type (*see also* Battaglia, 1958b). Owing to an atypical meiosis, however, the two nuclei of the

(87) Although «hemiapospory» is linguistically better than «semiapospory», for the sake of terminological priority we retain the original Fagerlind's «semiapospory» expression. The same criticism is valid as regards the wellknown ROSENBERG's «semiheterotypische Teilung».

(88) At that time (cf. BATTAGLIA, 1945 *b*) we overlooked GREGOIRE's (1910, p. 246) priority over the terminological couplet «euméiose & pseudoméiose».

functional gynospore possess the unreduced (2*r*) chromosome number. According to Håkansson & Levan (1957, p. 198) " a premeiotic probably endomitotic doubling makes the meiotic prophase start out with the double zygoid chromosome number."

(e) *Allium nutans Type II* — Here the two nuclei of the functional gynospore (*see* Allium nutans, type I) possess the 4*r* chromosome number. It differs from the above in that two endomitotic doublings take place in the meiotic prophase leading to chromosomes with eight chromatids. This condition has been recorded only in *Allium nutans* (Håkansson & Levan, 1957, p. 192).

These two types, according to HÅKANSSON & LEVAN (1957) are characterized by the occurrence of a new meiotic pattern termed by these authors «endo-duplicational meiosis». This new cytological phenomenon would consist of «one extra division during meiotic prophase» which would take place once in type I and twice in type II.

Since, in most comprehensive reviews on apomixis (e.g. RUTISHAUSER, 1967, 1969) these two types are simply cited as Allium nutans type (= our A. nutans I type) and the HÅKANSSON & LEVAN's (1957) endo-duplicational meiosis is usually reported as a premeiotic endomitosis ([89]), the following sentences from HÅKANSSON & LEVAN (1957, p. 192) should be quoted in full:

**1. The autobivalent formation of Allium odorum**

The female meiosis of *Allium odorum* differs from the male meiosis in the following respects: (1) Only bivalents are formed, the male meiosis showing a high frequency of multivalents; (2) the bivalents are present in the zygoid number; (3) the bivalents are characterized by a strikingly uniform shape, and their chiasma frequency is high.

It should be mentioned here, in passing, that the other *Allium* apomict

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([89]) For instance CRANE (1989, p. 14) writes: «Four subcategories of altered meiosis can be recognized. The first, termed diplounivalent meiosis by BATTAGLIA (1963, op. cit.), occurs in *Allium odorum, A. nutans,* and *A. tuberosum* (HAKANSSON and LEVAN, op. cit.; GOHIL and KAUL, 1981, Chromosoma 82: 735-739), and is simply normal meiosis after two rounds of chromosome replication without the opportunity for centrometric separation.

We do not agree with this sentence because of the following considerations:

— we wrote diplounivalent *mitosis* and not *meiosis* (cf. meiosi apoomeotipica: BATTAGLIA, 1945 *b*; mitosi a diplounivalenti: BATTAGLIA, 1947 *d* and specifically we wrote: «A third type, *post-meiotic diplounivalent,* occurs in connection with an apohomotypic meiosis in which the homotypic division is replaced by a resting stage», cf. BATTAGLIA, 1963, p. 223.

— We cannot consider as normal a hypothetical meiosis characterized by «two rounds of chromosome replication». Incidentally, according to this interpretation and terminology, the Allium nutans II type would be characterized by three rounds of chromosome replication!

studied by us, *Allium nutans*, has the same type of female meiosis. It should be observed, however, in relation to point (3) that the bivalents of female *nutans* are more variable in type than in *odorum*, the typical ring-shape of *Allium* bivalents predominating. A striking deviation found in the female *nutans* meiosis is the rather frequent occurrence of two endo-duplications in meiotic prophase, leading to diplo-bivalents with eight chromatids. So, even though differences occur between the two species, there is no doubt that, generally speaking, they belong to the same type of meiotic modification, both being cases of endo-duplicational meiosis (HÅKANSSON, 1951, HÅKANSSON and LEVAN, unpublished).

The entire body of existing evidence suggests the following explanation for the data observed: each premeiotic chromosome has undergone one extra division during meiotic prophase, allowing each univalent to develop into a bivalent, here called *autobivalent*. Before the zygotene stage each univalent is subjected to an endo-duplication, which will result in the mating tendency, normally acting between the homologues, being already satisfied. Thus, the pairing takes place between the two sister halves of each univalent chromosome. This is a mode of pairing

. . . . . .

It is impossible to decide the exact moment of the extra chromosome reproduction. The exclusive formation of bivalents indicates, however, that the products of endomitosis cannot have fallen apart before the onset of zygotene, otherwise occasional multivalents would have been expected. The time limit backwards for the endomitosis is more difficult to determine. It may even be theoretically possible that the extra chromosome division appearing in the emc may be that of the last archesporial mitosis, which has reverted before its completion. In our opinion, however, an endo-duplication in the young emc nucleus is more probable. We base this opinion on the fact that we have never seen any clear evidence of restitution mitosis in the subepidermal layer of very young ovules, although the early stages have been carefully searched for such mechanisms.

. . . . . .

The embryological documentation by HÅKANSSON & LEVAN, together with the sentences cited above, suggest to us the following comments and criticism, both formal and cytological. An alternative reinterpretation of the ES development in these species of *Allium* is also proposed, as a guide for future reinvestigation of this complicated embryological development.

*a*) It is evident that the Allium nutans II type, owing to the hypothetical occurrence of «two endoduplications in meiotic prophase», would not be considered as a recurrent type and consequently listed under the non-recurrent types.

*b*) HÅKANSSON & LEVAN (1957, p. 192), emphasizing the importance

of the fact that *A. nutans* and *A. odorum* «belong to the same type of meiotic modification, both being cases of endoduplicational meiosis» cite two accounts: HÅKANSSON (1951), and HÅKANSSON & LEVAN (unpublished) the second of which has never been printed (90).

In the absence of such an account we were unable to gave a schematic representation of the Allium nutans types in our paper on apomixis (BATTAGLIA, 1963).

*c*) HÅKANSSON & LEVAN (1957, p. 192) report «the rather frequent occurrence of two endoduplications in meiotic prophase, leading to diplo-bivalents with eight chromatids».

It seem to us that these 8-chromatid structures should be called «*autoquadrivalents*» or, at least, «*diplo-autobivalents*». In any case, they should not be called *diplo-bivalent* since BARBER (1940) first coined this term to indicate a quite different *post-meiotic* 8-chromatid structure, see also «mitosi a diplobivalenti» BATTAGLIA, 1947*d*) and the Fritillaria type (male gametophyte development) in BATTAGLIA (1951*a*) (91).

However, we wish to point out that 8-chromatid structures were not documented by HÅKANSSON & LEVAN (1957).

*d*) We wish also to add a minor formal consideration as regards terminologies related to the inadequacy of the usual terms haploid, diploid, tetraploid (or reduced, unreduced etc.) when referring to polyploid biotypes. HÅKANSSON & LEVAN (1957), describing a deviating

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(90) Unfortunately Prof. ARTHUR HÅKANSSON died in 1961. Prof. ALBERT LEVAN became more and more interested in human chromosomes and in 1956 first established the correct human chromosome number (cf. TIJO & LEVAN 1956).

(91) We wrote (BATTAGLIA 1951 *a*, p. 111):

> 7. FRITILLARIA TYPE — Produced experimentally by Barber (1940) by the action of high temperature on plants of *Fritillaria meleagris*. The first meiotic division is arrested at diakinesis. There follows a long resting stage (suppression of second division), during which chromosome reproduction occurs. The bivalents, therefore, acquire the structure of *diplobivalents*. Consequently the first pollen grain division is a *diplobivalent mitosis* (cf. Battaglia, 1947g) and produces generative and vegetative (tube) nuclei which are both tetraploid.

meiotic behaviour on the male side of *A. odorum*, use the term «azygoid», «zygoid» and «double zygoid» in the place of the corresponding haploid, diploid and tetraploid (i.e. the terminology referable to the diploid biotypes). Since «hemizygoid» is cytologically more correct than «azygoid», we could suggest the equivalent terminological series «hemizygoid», «zygoid», «dizygoid» etc. However, we must also recall JÖRGENSEN's (1928) couplet «gametic & somatic». It follows that the series «hemigametic», «gametic» and «digametic» (numbers), might be a better terminological system to describe the chromosome complement of polyploids.

In any case we believe that such formal questions are matters for discussion in terminological sections of future botanical congresses.

*e*). Because the meiotic configurations (leptotene etc.) drawn by HÅKANSSON and LEVAN for both *A. nutans* and *A. odorum* are quite regular, together with the fact that meiotic 8-chromatid structures have never been documented, *we must conclude that no meiotic endoduplication takes place in the female reproduction of both A. odorum and A. nutans.*

Since, so far as we are aware, no careful karyological reinvestigation of the Allium nutans types has yet been attempted and on the contrary an Allium nutans type, characterized by one supernumerary chromosome replication, more or less clearly qualified as endomitotic, is reported in most modern embryological literature, we take the opportunity of suggesting below an alternative reinterpretation of the ES development of the two Allium nutans types.

HÅKANSSON & LEVAN themselves (1957, p. 193) have given us the key for a reinterpretation in that they write:

> In addition, endomitotic processes are very common in nucellus cells, especially in *Allium nutans*. Mitoses with diplochromosomes and quadruplochromosomes were repeatedly seen. This feature is found also on the male side of *Allium nutans*, pmc:s with doubled chromosome number being frequent.

Il follows that the E.M.Cs, before the start of the meiotic process, can have three different chromosome numbers; diploid (at the end of one premeiotic regular mitotis), tetraploid (at the end of one premeiotic diplochromosome mitosis) and octoploid (at the end of one premeiotic quadruplochromosome mitosis). It is obvious that we use the terms diploid, tetraploid, etc. for the sake of simplicity.

The diploid E.M.Cs can follow two different patterns of ES development. The first pattern develops according to our reduced, dikaryosporic (bisporic) Melica type (formerly Scilla or Allium fistulosum type).

The second pattern develops according to an apohomoeotypic type identical to that of the Datura type. This second pattern is clearly recorded by HÅKANSSON & LEVAN (1957, p. 181), in fact they write:

> However, in the normal case the emc is divided by a transversal wall into one upper small cell, the further development of which fails, and one lower cell, which forms the es. After the first meiotic division an unusually long time interval elapses before the second division. The nucleus of the dyad cell has thus not the ordinary interkinetic structure but rather the appearance of a deep resting stage. Such a delay in the division of the dyad nucleus is known in connection with the formation of non-haploid es:s, for instance, in a dyad-forming mutant of *Datura* (SATINA and BLAKESLEE, 1935) or more exceptionally in apomictic *Archieracium* (BERGMAN, 1941).

Because the normal E.M.Cs develop according to the reduced Melica type, the second pattern described above would also be recognized as the «Datura (apohomoeotypic-Melica) type», see the chapter regarding to the Datura type.

The tetraploid E.M.Cs are responsible for the formation of diakinetic stages (etc.) showing the diploid («zygoid») number of so-called «autobivalents».

Finally, the octoploid E.M.Cs are responsible for the formation of diakinetic stages (etc.) showing the tetraploid number («double zygoid») of «autobivalents».

We must now try to give answers to two obvious questions, which are:

— why are there only «autobivalent» configurations?

— is there homologous or non-homologous meiotic pairing?

Preliminarly we need to establish an adequate terminology as regards the chromatid structures which occur in both diplo- and quadruplo-chromosome mitoses.

To avoid the establishments of very different additional terminologies we retain the prefix «auto» to elaborate our terminological system.

The usual mitotic chromosome (here called monochromosome) (92) consists of two chromatids produced by the first normal

(92) Monochromosome: first proposed by WHITE (1935: MONOCHROMOSOMEN & DIPLOCHROMOSOMEN) and later by BATTAGLIA (1950*b*: Endomitosi a monocromosomi).

replication (i.e. «duplication») (93).

We call these chromatids «autochromatids of the first cycle» (first replication) or more simply «1st-autochromatids».

Owing to «one extra-replication», the diplo-chromosome consists of four «autochromatids of the second cycle», shortly four «2nd-autochromatids».

Because of the «two extra-replications», the quadruplo-chromosome consists of eight «autochromatids of the third cycle», that is, in short, eight «3rd-autochromatids» (94).

How do the poly-autochromatid structures divide at the anaphase stage?

During the prometaphase stage a diplochromosome first separates into 2 monochromosomes. These monochromosomes shortly congregate on the metaphase plane where, after normal orientation, each monochromosome divides into regular anaphase chromatids. Thus, according to the terminology mentioned above, and referring to the diplochromosome mitosis, two «2nd autochromatids» spatially very near each other, migrate to each pole, during the anaphase stage. It follows that in the case in which the meiotic process is immediately preceded by a diplochromosome mitosis, meiotic prophase pairing preferentially occurs between two (replicated) «2nd-autochromatids» without any chance for homologous pairing. (Since the leptotene chromosome is, morphologically, a single thread we propose the term «leptotene replicated chromatid» in place of the current «leptotene chromosome»).

The quadruplochromosome basically divides according to the same pattern, that is the original «8-chromatid configuration» separates gradually into two «4-chromatid structures» and then into four monochromosome («2-chromatid structures», terminologically: «3rd-autochromatids»). Finally each monochromosome divides normally at the anaphase stage. It follows that if meiosis begins at the following division, the early zygotene pairing should be recognized as a «pairing between two (replicated) 3rd-autochromatids». Natur-

(93) As regards «autoreduplication» and «autoduplication», linguistically equivalent terms, cf. BATESON & PUNNETT (1911: «reduplication») and BRIDGES (1919: «duplication»).

(94) The series of «autochromatids of first (second, third) order», that is «1st order autochromatids» (etc.) is equally proposable. However, the phrase «1st autochromatids» seems to us both shorter and equally clear.

ally in this case the diakinetic stages would show the tetraploid number of HÅKANSSON & LEVAN's «autobivalents».

In addition we also believe that in the cases in which the diplo-, or quadruplo-chromosome mitoses are rapidly followed by a normal mitosis, instead of the beginning of meiosis, the primitive spatial arrangements between «2nd-», or «3rd-autochromatids», which occur at the end of diplo- or quadruplo-chromosome mitoses, would be modified during such pre-meiotic mitosis. Thus, in these cases, when the meiotic process begins «homologous» configurations (e.g. trivalents etc.) in addition to the typical «autologous» configurations could be observed.

As a consequence of our reinterpretation as regards the pre-meiotic chromosome doubling in the female side of *A. nutans*, we would like to point out the occurrence of two genetically different patterns of «true» meiotic pairing: in addition to the usual «homologous-pairing» there is the new pattern outlined above for the A. nutans types and which might be defined «*autologous-pairing*».

2. *Allium odorum type versus Allium nutans type. Proposal for a new typology: Allium I type («reduced-tetraploid» & recurrent) and Allium II type («reduced-octoploid» & non-recurrent).*

Since the criticism outlined in the preceding pages takes into consideration only the meiotic behaviour, for the sake of simplicity we have retained our old terminology «A. nutans types I and II». However, on the basis of such critical considerations we must conclude, that the two Allium nutans types based on the HÅKANSSON and LEVAN's paper cannot be accepted. The rejection of HÅKANSSON & LEVAN's (1957) hypothesis automatically suggests reconsideration of an old embryological paper by MODILEWSKI (1931) on *Allium odorum*. HÅKANSSON & LEVAN (1957, p. 179-180) cited MODILEWSKY's embryological data as follows:

> MODILEWSKY (1931) describes meiosis in pmc:s and emc:s. In the latter case he finds, on the one hand, a normal meiosis leading up to »16 Gemini» and, on the other hand, a deviating meiosis type leading to the double number of chromosomes. Although he refers to the process involved in this chromosome doubling with the misleading term »Restitution» and the nucleus resulting, »Restitutionskern», it is quite clear from his descriptions that he does not mean an ordinary restitution mechanism. He is speaking of »eine Restitution in dem praediakinetischen Stadium» (p. 36), and in his Fig. 35 a first metaphase is represented with about 32 elements, »mittlerer Länge und Dicke im Vergleiche mit den heterotypischen und somatischen Chromosomen» (p. 45).

However, we believe that MODILEWSKY's paper deserves a larger citation and at least the following sentences can be usefully reported, cf. MODILEWSKY (1931, p. 36-37, 40):

> Der Faden dieses Knäuels scheint ziemlich dicht gedreht zu sein, als ob die Kraft, welche dieses Zusammenziehen veranlasst hat, eine sehr grosse wäre und der Faden selbst seinerseits durch eine grosse Elastizität charakterisiert würde. Aus diesem Knäuel lösen sich allmählich Teilstücke von Chromatinfaden doppelter Natur. Solche Segmente des Chromatinfadens in allen Fällen, als Gemini zu schätzen, wäre vielleicht unrichtig. Die Fig. 32 zeigt eine Zahl von Segmente, welche sich der haploiden Zahl mehr nähert und also der jungsten Diakinese wahrscheinlich entspricht. Dagegen ist es möglich auf der Fig. 33 eine Zahl von gespaltenen Chromatinsegmente zu beobachten, welche sich fast alle von dem Knäuel schon abgetrennt haben und welche ohne Voreingenommenheit auf 32 zu schätzen möglich ist.
>
> Die angeführten Beobachtungen zwingen zur Annahme, dass zweierlei Typen der Kernteilung in den Embryosackmutterzellen von *Allium odorum* vorhanden sind; eine normale Reduktionsteilung, die schliesslich 16 Gemini bildet und ein anderer Typus, bei welchem eine Restitution in dem praediakinetischen Stadium der diploiden Chromosomenzahl stattfindet. Dass solche zwei Typen der Kernteilung vorhanden sind beweisen folgende Bilder. Die Fig. 34 zeigt eine Anaphase der Reduktionsteilung in einer Embryosackmutterzelle, die etwas schief getroffen wurde und wo die haploide Zahl der Chromosomen genug deutlich hervortritt. Die Anwesenheit von haploiden Eizellen, worübernoch weiter die Rede sein wird, die Feststellung von doppelter Befruchtung, alles das lässt keinen Zweifel daran, dass die Reduktionsteilung in gewissen Fällen bis zu ihrem normalen Ende in den Embryosackmutterzellen von *Allium odorum* gebracht wird.
>
> Aber auch oft kommt die andere Art der Kernteilung in Embryosackmutterzellen vor.
>
> Die Fig. 35, stellt drei Schnitte eines Kerns in der Embryosackmutterzelle dar, in welchen die diploide Zahl der einfachen Chromosomen sehr deutlich sichtbar ist und einige von den letzteren weisen einen Spalt auf. Diese Chromosomen des Restitutionskerns sind viel schmäler, schlanker und länger, als die der echten Gemini der Diakinese, obwohl kürzer, als die Chromosomen des somatischen Kernes. Die Zahl der längeren ganzen Chromosomensegmente auf den drei Schnitten des abgebildeten Kerns gleicht 29 und die Zahl der durchgeschnittenen kürzeren Segmente, welche der Länge nach der Hälfte der ganzen Chromosomen gleichen, ist 6; also die Gesamtzahl ist ungefähr 32, was der diploiden Zahl der Chromosomen bei *Allium odorum* entspricht.
>
> . . . . . .
>
> Wenden wir uns an die Reduktionsteilung, so finden wir bei *Allium odorum* solche Verhältnisse, welche bei einigen anderen Angiospermen bekannt sind. *Allium odorum* gehört zu derjenige Gruppe der parthenogenetischen Pflanzen, bei welchen die Pollenetwicklung vollständig normal sich abspielt. Dagegen entsteht in den Kernen der Embryosackmutterzellen von *Allium odorum* teilweise normale Reduktionsteilung, teilweise aber die Restitution der somatischen Chromosomenzahl. Der Mechanismus der letzteren Erscheinung ähnelt demjenigen einiger anderen, parthenogenetischen Pflanzen und, als kritische Phase der Umwandlung ist der Übergang von dem späten Spirem zur frühesten Diakinese anzunehmen.

It seems to us that MODILEWSKY's account does not differ embryologically from that of HÅKANSSON & LEVAN (1957), and, typologycally, an A. odorum I type would be recognized as having priority over our A. nutans I type.

Because MODILEWSKY never observed E.M.Cs of *A. odorum* developing according to our A. nutans II type, nor HÅKANSSON & LEVAN the occurrence of their diplo-bivalents in *A. odorum*, our A. nutans II type should be confined to the *nutans* species alone.

Nevertheless, this conclusion cannot be accepted. Very probably both diplo-and quadruplo-chromosome pre-meiotic mitoses occur in the ovules of *Allium*- species, parthenogenetic or not, diploid or non-diploid!

Since the «dikaryosporic & reduced» Allium fistulosum type, for question of priority, should now be renamed the Melica type (cf. BATTAGLIA, 1987 d), we suggest, as a consequence, the typological solution Allium I & II types, in place of the old A. nutans types I & II (BATTAGLIA 1963).

Further, it is clear that neither of such types, recurrent and non-recurrent respectively, can be defined as «unreduced» types.

It seems to us that type I might be recognized as «reduced-tetraploid» and type II as «reduced-octoploid».

Conclusively, in the absence of an adequate embryological reinvestigation of the parthenogenetic *Allia*, we propose the following provisional typology for the old Allium nutans types:

Allium I type (reduced-tetraploid; recurrent) ([95]);

Allium II type (reduced-octoploid; non-recurrent) ([95]).

Finally the two very interesting Datura types which arise in the cases of occurrence of the apohomoeotypic Allium I or Allium II types, should not be overlooked. Indeed the «Datura (apohomoeotypic-Allium I) type» would have a tetraploid egg cell and the «Datura (apohomoeotypic-Allium II) type» an octoploid egg cell; see also page 106.

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([95]) The Allium I type cited in the most recent embryological literature as Allium nutans type, besides *A. odorum* and *A. nutans*, has been described in *A. tuberosum* (this species, commonly called Chinese chives is closely related to *A. odorum*) by GOHIL & KAUL (1981), see also GOHIL & KOUL (1983), KOJIMA & KAWAGUCHI (1989) and KOJIMA, NAGATO & HINATA (1989). The paper by GOHIL & KOUL (1983) is worth mentioning since these authors describe the occurrence, during male meiosis, of the present Allium I type. They further write: «The male sporogenous tissue of the progeny plants is chimaeric with cells having zygoid and double the zygoid number of chromosomes».

The occurrence of both the Allium I & II types has been recorded by HÅKANSSON & LEVAN (1957) only for *A. nutans*. It is obvious that the coexistence of the two types should be assumed to occur also in other parthenogenetic Allia.

## VI. A SHORT LOOK AT THE NON-RECURRENT TYPES.

VIa. *Datura type.*

VIb-VIe. *Rudbeckia I-IV types.*

VIf-g. *Antennaria carpatica I-II types.*

VIh. *Leontodon II type.*

VIi. *Istances of post-meiotic chromosome doubling or endogametophytic diploidization («Automixis», «Synkaryogenesis»).*

### VIa. *Datura type*

We briefly discuss in the chapter on non-recurrent types, the Datura type (cf. BATTAGLIA, 1951 *a*), since there is no convincing documentation of the recurrent occurrence of this ES development *in nature*, in one species, or even in one individual (see p. 7: «recurrent type»).

The Datura type was discovered, correctly interpreted and well documented by SATINA & BLAKESLEE (1935) in Datura $F_2$ plants from radium-treated pollen (See preliminary report in BLAKESLEE, 1930).

In this type the heterotypic division is regular and produces a normal dyad after which there is a long resting stage followed by degeneration of the upper cell.

In untreated plants of *Datura*, which have the reduced Polygonum type of ES development, the long period of quiescence is absent and regular homoeotypic division occurs. In the present Datura type the lower cell functions as the ES initial cell and since the second meiotic division is suppressed ([96]) its chromosomes (2-chromatid structures, uinivalents sensu lato) are duplicated before the beginning of the next division (= the first division of the ES) and thus appear as 4-chromatid structures or diplounivalents. Because of the occurrence of diplounivalents, the first division of

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([96]) See «meiosi apoomeotipica» in BATTAGLIA (1945 b); translated into «apohomotypic meiosis» in BATTAGLIA (1963) and here modified into «apohomoeotypic meiosis». As early as 1906 WILSON rightly translated into «*homoeotypic* division» WEISMANN's (1887) «*homötypische* Theilung».

the ES, mentioned above, is mitotic and is called diplounivalent mitosis ([97]).

The two unreduced nuclei arising from the diplounivalent mitosis undergo two further nuclear divisions to form the usual 8-nucleate unreduced ES.

In our opinion the Datura type has been recorded convincingly only by SATINA & BLAKESLEE (1935) in their embryological mutants of Datura. Indeed, the occasional suppression of the second meiotic division has been cited in several embryological papers without the necessary documentation as regards the occurrence of the diplounivalent mitosis. Such instances are omitted here since they are considered only as undocumented cases.

To make the typology of the Datura type, more accurate we would like to add the following consideration:

Because normal plants of *Datura* have an ES development of the reduced Polygonum type, this Datura type would be an apohomoeotypic Polygonum type. It follows that its most accurate typology is «Datura (apohomoeotypic Polygonum) type» (diploid egg cell).

By analogy the apohomoeotypic Melica type (ex Allium fistulosum type) would be recognized as the «Datura (apohomoeotypic Melica) type» (diploid egg cell) ([98]); cf. also the «Datura (apohomoeotypic Allium I) type» (tetraploid egg cell) and the «Datura (apohomoeotypic Allium II) type» (octoploid egg cell), see page 104».

VIb. *Rudbeckia I type.*

This type (cf. BATTAGLIA, 1946*c*; 1947*a*; 1951*b*; Fig. 1; 1963: Fig. 8/24, *R. laciniata*) is an occasional deviation from the Ixeris type development observed only in *Rudbeckia laciniata.* The heterotypic division ends with a restitution nucleus. The following homoeotypic division results in two nuclei with a small accessory nucleus of varying size located in the micropylar region of the ES. There follows an ES development similar to the Ixeris type, but the micropylar region, at the end of the nuclear divisions, is occupied only by 4

([97]) The diplounivalent mitosis is characterized by the occurrence of a tetrachromatid structure, the «diplounivalent» while any 2-chromatid structure which originates during meiosis is considered as «univalent», cf. BATTAGLIA (1947 d).

([98]) The Datura (apohomoeotypic Melica) type may (occasionally?) occur in *Allium nutans*, see page 100.

small nuclei derived from the accessory nucleus. After cellularization these four nuclei form the synergids, the egg (a very peculiar miniature egg apparatus) and one small upper central nucleus. The middle part of the ES contains more than one central cell. In the chalazal region of the ES, a variable number of egg-like antipodal cells are differentiated. In other cases the accessory nucleus is formed at the end of the heterotypic division, resulting in differences in the total number of nuclei produced and of their organization. Whether the mini-egg cell or the large egg-like antipodal cells can develop further or degenerate is still unknown.

We believe that experiments involving, tissue culture which utilize such very atypical embryo sacs (occurrence of a mini-egg, supernumerary central cells and both egg-like and non egglike antipodal cells) would be of very great morphological interest.

VIc. *Rudbeckia II type.*

This type (cf. BATTAGLIA, 1946*b*, *c*; 1951*b*: Fig. 1; reclassified as «Rudbeckia Type II, 8-nucleate» in BATTAGLIA, 1963: Fig. 8/24) is another occasional deviation from the Ixeris type development, observed in both *Rudbeckia laciniata* and *R. speciosa*. After the restitutional meiosis, a large and permanent vacuole occupies the greater part of the ES, including the micropylar region. There follows a nuclear polarization of the 0+2 arrangement. The final stage is 8-nucleate (0+8) and usually the mature ES shows 1 central nucleus and 7 antipodal cells, some of which are egg-like.

The further development of these egg-less embryo sacs has not yet been investigated.

VId. *Rudbeckia III type.*

This type (cf. BATTAGLIA 1946 *b*, *c*; 1951 *b*: Fig. 1; reclassified as «Rudbeckia Subtype II, 4-nucleate» in BATTAGLIA, 1963: Fig. 8/24) differs from the above in that the last division is omitted. Thus a 4-nucleate stage is produced which, after cellularization, shows 1 central cell and 3 antipodal cells, two of which are usually egg-like.

Rarely the last nuclear division is not entirely suppressed and may involve one or more nuclei. These very occasional variations have been designated «Rudbeckia II, sub-types 7-, 6-, and 5-nucleate» in BATTAGLIA (1963). As stated before, the Rudbeckia III type has been found in both *Rudbeckia laciniata* and *R. speciosa*.

VIe. *Rudbeckia IV type*

This type (cf. BATTAGLIA, 1946*b*, *c*; 1951*b*: Fig. 1; reclassified as «Rudbeckia Type III» in BATTAGLIA, 1963: Fig. 8/25) is characterized by the formation of a restitution nucleus at the end of each of the two meiotic divisions. Thus, at the end of the meiotic process, the initial cell of the ES possesses only one very large nucleus called birestitution nucleus ([99]) which has the *4r* chromosome complement ([100]).

The further development of this 1-nucleate non-reduced (4r) ES has never been observed. The birestitution nucleus has been seen very rarely in *Rudbeckia speciosa* (BATTAGLIA, 1946 *b*) *R. laciniata* (BATTAGLIA, 1946*c*) and in *Erigeron karwinskianus* var. *mucronatus* (BATTAGLIA, 1950*a*). The occurrence of the birestitutional meiosis in *Musa* (8-nucleate 4r-ES) reported by DODDS & PITTENDRIGH (1946) is very doubtful since it has not been convincingly documented.

VIf-g. *Antennaria carpatica types I & II*

These types (cf. BERGMAN, 1951; BATTAGLIA, 1956, 1963) are occasional and very doubtful anomalies, reinterpreted (BATTAGLIA, 1963) in agreement with the Taraxacum type.

VIh. *Leontodon II type.*

This type (cf. BERGMAN, 1953 *a*, 1941; BATTAGLIA, 1951 *b*: «Leontodon I type»; BATTAGLIA, 1963: «Leontodon Type II») is an occasional, very doubtful anomaly observed in one plant of *Leontodon hispidus*. A reinvestigation of the embryological behaviour of *Leontodon hispidus* is very desirable.

VIi. *Instances of post-meiotic chromosome doubling or endogametophytic diploidization («Automixis», «Synkaryogenesis»).*

Since we define as «gynospore» any initial cell of the embryo sac, the Datura type (i.e. the occurrence of apohomoeotypic meiosis)

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([99]) The birestitution nucleus has first discovered in the P.M.Cs of *Rudbeckia laciniata* (cf «nucleo di birestituzione»: BATTAGLIA, 1945 *a*).

([100]) As regards the symbols *r* = reduced (chromosome number), *2r* = unreduced, etc. cf. BATTAGLIA (1955 *a*).

is an instance of post-meiotic chromosome doubling or endogametophytic (endo-embryo sac) diploization.

As repeatedly mentioned before, we consider doubtful all embryological descriptions claiming the occurrence of apohomoeotypic meiosis, but lacking an adequate documentation of the first post-meiotic division (diplounivalent mitosis).

In addition to this case, already discussed, in the embryological literature there are many papers claiming the occurrence of endo-embryo sac diploidization by nuclear fusion. This cytological behaviour is almost unanimously described as «automixis».

We have recently presented (and discussed) documentation (BATTAGLIA, 1988) confirming the possibility of the occasional fusion of two micropylar nuclei during the ES development of species of *Tamarix* (see our Tamarix types, Plate III in BATTAGLIA, 1988).

In discussing such nuclear fusion we wrote:

«This phenomenon is usually called *automixis* (THOMAS, 1940). Because THOMAS was unaware of a former use of this therm by HARTMANN (1909, Automixis: 1. Paedogamie, 2. Autogamie, 3. Pseudogamie; see also BATTAGLIA 1985*a*), the equivalen term *synkaryogenesis* (that is diploidization by synkaryogenesis), suggested by the author in 1963, seems to be preferable».

In this connection we wish also to add the following considerations:

a) the related meaning of *endomixis*, although proposed by WOODRUFF & ERDMANN (1914), for *Paramaecium*, cannot be ignored (see also *endomixis, exomixis* and *automixis* in *Prell*, 1921, 1923; *mixis, amixis, promixis, metamixis* in ANKEL 1927; 1929; other data in BATTAGLIA 1985a);

b) the traditional concept of *mixis* implies the involvement of gametes;

c) as early as 1907, STRASBURGER coined the terms «Synhaploid (Syndiploid) Zelle» (also «Syndiploide Kernplatten», «Syndiploide Kern») for cells which posses twice the haploid (diploid) number of chromosomes owing to nuclear fusion.

Thus, we consider that the choice of the term «automixis» to indicate the occurrence of nuclear fusion within the embryo sac is unsatisfactory. The expression «Synkaryon formation» of «Synkaryogenesis», seems to us much more appropriate.

As regards the occurrence of the so-called «automixis» in angiosperm embryology, it is not the purpose of this paper to write

a review as detailed as that, for instance, recently published by MOGIE (1986). Nevertheless at least a few cytological remarks are considered necessary.

THOMAS (1940) first introduced the term «automixis» to a classification of «the various types of reproductive mechanisms» and disregarding all terminological considerations and priorities, wrote: «Automixis: fusion of immediate products of meiosis; fusion of haploid nuclei within the embryo sac». This paper mainly concerns the «Reproductive versatility in *Rubus*», and THOMAS describing the reproduction of *R. nitidioides* specified: «The embryological studies show that aposporic development is the rule...».

> « In addition to aposporic development, certain abnormalities within the sexual embryo-sac are not uncommon. The young embryo-sacs may contain two nuclei at one end and only one at the other. This is presumably due to lack of time co-ordination of nuclear divisions at the two ends, such as has been observed in *Tulipa* (Newton, 1927; La Cour, unpublished). Furthermore, evidence has been obtained that the daughter nuclei of the nucleus which divides first may fuse again. The undivided nucleus then divides, and this may be followed by a division of the fused nucleus. Although the further development of the "diploid" nuclei has not yet been traced, it evidently provides another possible mechanism of apomictic reproduction. »

THOMAS' paper lacks any documentation and, consequently, the 4-nucleate stage (two diploid micropylar nuclei and two haploid chalazal nuclei), mentioned above, and obviously never observed, is nothing other than a simple hypothesis.

There are many embryological investigations on the apomictic *Rubi* from 1950 to date. No trace of THOMAS' automixis was found by CHRISTEN (1950, 1952), EINSET (1951), PRATT & EINSET (1955), HASKELL (1960, 1966) or DOWRICK (1961, p. 681: «In the present material it was impossible to establish the method whereby doubling of haploid nuclei in the embryo sac occurred»). However, in 1966, DOWRICK again stated (1966, p. 250) «The origin of the tetraploid *laciniatus*-like progeny and the pentaploid and hexaploid seedlings is more difficult to understand. It is clear, however, that the tetraploids must have arisen by doubling of the chromosome number prior the embryo formation. This could occur in one of two ways, either by restitution at the first division of the egg cell or by automixis, i.e. fusion of nuclei within the embryo sac». Thus, once more, these cytological phenomena were simply hypothesized.

Surprisingly, in 1965, GERLACH, for *R. caesius*, described the oc-

currence of chromosome doubling at the beginning of embryo development. This author specifically wrote:

> « In the case of parthenogenetic development, chromosome-doubling in the haploid egg cell takes place by fusion of two haploid nuclei, which are produced by the division of a haploid egg nucleus. This autogamy begins only after the pollen tube has entered a synergid. Usually, the synergid does not discharge its contents into the embryo sac. But this event, if it does take place, may cause additional fertilization, even after the beginning of the autogamic process. Furthermore, an egg nucleus, having doubled its chromosome number by autogamy, seems to be able to repeat this procedure once over.
>
> On the other hand, a haploid egg cell is capable of developing into a haploid proembryo. The nuclei would then double their chromosomes by autogamy in the cells of that proembryo. If one of the cells fails to do this, the result is a haploid-diploid chimera.
>
> The division of the egg nucleus, preparing autogamy, is orientated in such a way that the two daughter nuclei are not placed in the gradient of polarity in the egg plasm. »

Apart from the consideration that this cytological behaviour cannot be qualified as endogametophytic, the documentation presented by GERLACH, as for instance, that reported here in the Plate XII (see GERLACH'S Abb. 14 *a*-14 *c*) is clearly unconvincing for experienced embryologists. The lack of any meta-anaphase stage, unequivocally documenting the true chimeric nature (haploid & diploid cells) of the proembryos compel us to qualify this case as very doubtful and awaiting reinvestigation.

To conclude our remarks on the occurrence of «automixis» in *Rubus*, we wish to add that in most recent embryological investigations on this genus, both THOMAS' «automixis» and GERLACH'S «autogamy», have been neither observed nor hypothesized, cf. PETROV & SUKHAREVA (1977); CZAPIK (1981, 1983, 1987), NYBOM (1986, 1988, 1989) etc.

At least on the basis of the available microphotographic documentation) the case reported by PFEIFFER & BINGHAM (1983) for a particular clone of *Medicago sativa*, seems to be a more acceptable instance of endo-embryo sac diploidization or ES synkaryogenesis.

PFEIFFER & BINGHAM (1983, p. 107) write:
«The cytological mechanism of $2n$ egg formation was studied in several diploid ($2n = 2x = 16$) and tetraploid ($2n = 4x = 32$) clones of cultivated alfalfa (*Medicago sativa* L.). The comparison of normal megasporogenesis with megasporogenesis that produced $2n$ eggs was made using an ovule clearing technique with methyl salicylate. Developmental sequences in the formation of $n$ and $2n$ eggs were the same through anaphase II. Following anaphase II in $2n$ egg formation cytokinesis occurred only in the micropylar diad, not in the

chalazal diad. Micropylar megaspores disintegrated leaving a functional unreduced megaspore of the second division restitution (SDR) type at the chalazal end. The two nuclei in the megaspore can fuse prior to the mitotic divisions or during the first two mitotic divisions. The SDR mechanism of $2n$ egg formation was confirmed in selected diploid clones by comparing half-tetrad analysis of $2n$ eggs with half-tetrad analysis of a known first division restitution (FDR) $2n$ pollen producer».

PLATE XII

(From Gerlach, 1965). Details in the Text.

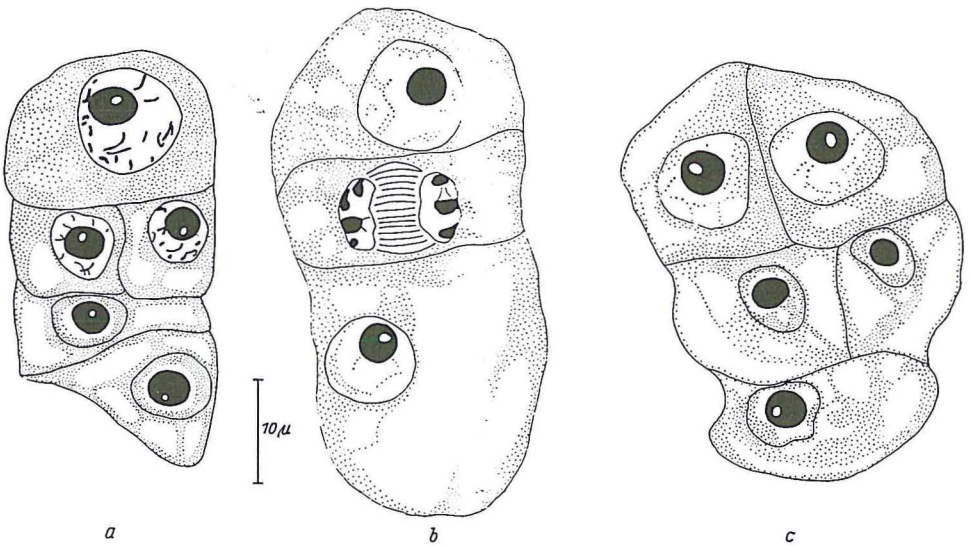


Abb. 14. a) Chimäre: Kern der obersten Zelle diploid, die restlichen Kerne haploid. b) Embryo mit diploidem Kern in der Basalzelle. c) Embryo mit haploidem Kern in der Basalzelle

As regards their documentation: Fig. 2D shows a 2-nucleate megaspore (described as: «Unreduced primary megaspore»). Fig. 2E shows a young ES with two apparently, fusing nuclei in the middle region of the ES («Nuclear fusion prior to first mitosis»); Fig. 2F shows a large vacuolized and polarized 2-nucleate ES. Each of the two nuclei shows 2 nucleoli and is larger than the normal haploid nuclei. This

stage («Nuclear fusion following second mitosis») might be interpreted as the 2-nucleate stage following the 1-nucleate stage of the fig. 2E; Figs. 2G-2H («Nuclear fusion following second mitosis. Two planes of focus») actually show a 4-nucleate stage, (2+2), with the nuclei of each pair very near or touching each other.

We cannot consider PFEIFFER & BINGHAM's documentation to be fully satisfactory and further studies of this very interesting case seem necessary.

In the embryological literature there are also other instances of «automixis» (sensu lato) indirectly inferred from genetical considerations. However, since in these papers, not mentioned here for the sake of brevity, the genetical considerations do not imply *exclusively* the occurrence of «automixis» (or «nuclear fusion») their lack of proper cytological documentation qualifies these accounts as «data awaiting confirmation».

## VII. SIMPLIFIED AND INTERPRETATIVE REPRESENTATIONS OF THE RECURRENT TYPES OF UNREDUCED EMBRYO SACS.

Usually the various types of ES development are represented in a scarcely interpretative manner, that is distinguishing only a «sporogenesis» followed by a «gametophytogenesis». Therefore the divisions are qualitatively subdivided into meiotic and post-meiotic.

Following this scheme the recurrent types of unreduced embryo sacs, discussed in the present work, have been reconstructed in Plate XI The divisions of the «gametophytogenesis» have, necessarily, an exclusively chronological value and consequently in the types Ixeris, Eragrostis and Pennisetum the third division of the normal development is suppressed. We consider this reconstruction excessively simplified and qualitatively unsatisfactory.

Therefore, starting from a pattern first suggested by CHIARUGI (1926, 1927) and modified by the present author (cf. BATTAGLIA, 1951*a*, 1963 etc.) in an «apo-archegonial sense», we have again (cf. Plates VIII-X) reconstructed the types of unreduced embryo sacs discussed in the present work.

This new reconstruction is strictly linked with the stages of development actually observed and not just implied. Consequently, because in the embryological literature results that in *Eragrostis* as well as in *Pennisetum* the first division of the ES takes place *after*

polarization (and not *before*), the correct reconstruction of these two types of development corresponds to the scheme indicated in Plate IX (and not to that of Plate X). Naturally, future embryological research should discover also the occurrence of the types indicated as «Eragrostis (Pennisetum)II? type» (see Plate X).

The reconstructions reproduced in Plates VIII and IX also allow the placing of these types of development in the evolutionary sequence recently proposed by us (BATTAGLIA, 1989) for the angiospermic female gametophyte.

When the origin of the initial of the ES («ameio» = «ameiotic; apomeio» = «apomeiotic»; «aneumeio» = «aneumeiotic» mk. = monokaryosporic, dk. = dikaryosporic), is also taken into consideration the unreduced embryo sacs reconstructed in Plates VIII, IX have the following evolutionary formulae (details in BATTAGLIA, 1989) ([101]):

*Taraxacum* type: ($P^1C^4$) aneumeio. mk.
*Ixeris* type: ($P^mC^4$) aneumeio. dk.
*Antennaria* type: ($P^1C^4$) apomeio. mk.
*Hieracium* type: ($P^1C^4$) ameio. mk.
*Eragrostis* type: ($P^{apom.}C^4$) apomeio. mk.
*Pennisetum* type: ($P^{am.}C^4$) ameio. mk.

Lastly, the above formulae indicate that the 4-nucleate Eragrostis and Pennisetum types, being characterized by «post-apomeiosis polarization», ($P^{apom.}$), or «post-ameiosis polarization», ($P^{am.}$), represent the more highly evolved pattern of ES development in the apomictic angiosperms. This cannot be extended to the «Eragrostis (Pennisetum) II?» types (Plate X), because these are characterized by the less highly evolved «post- div. 1 polarization» = ($P^1$).

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([101]) $P^m$ = «post-meiosis polarization» = polarization occurring after normal or abnormal meiosis;

$P^{apom.}$ = «post-apomeiosis polarization» = polarization occurring after apomeiosis;

$P^{am.}$ = «post-ameiosis polarization» = polarization occurring after ameiosis;

$P^1$ = «post-div. 1 polarization = polarization occuring after the first somatogenic division (= div. 1 = first post-meiotic division);

$C^4$ = «cellularization four micropylar nuclei», that is the cellarization takes place when four nuclei are present in the micropylar end of the gametophyte.

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## REFERENCES

ÅKERBERG E. (1939) - Apomictic and sexual seed formation in Poa pratensis. *Hereditas*, **25**, 359-370.

ALLEN N.S. (1983) - Cytoplasmic streaming in plant cells and its relation to the cytoskeleton. In Earnshaw & Steer eds., The application of laser light scattering. pp. 529-543, *Plenum Publ. Co.*

ALLEN N.S., ALLEN R.D. (1978) - Cytoplasmic streaming in green plants. *Ann. Rev. Biophys. Bioeng.*, **7**, 497-525.

ALLEN R.D., ALLEN N.S. (1982) - Video microscopy in the study of protoplasmic streaming and cell movement. *Protoplasma*, **109**, 201-216.

ALLEN R.D., ALLEN N.S. (1983) - Video enhanced microscopy with a computer frame memory. *J. Microsc.*, **1**, 3-17.

ALLEN N.S., SCHUMM J.H. (1990) - Endoplasmic reticulum, calciosomes and their possible roles in signal transduction. *Protoplasma*, **154**, 172-178.

ANDERSSON G., HESSELMAN H. (1900) - Bidrag till kännedom om Spetsbergens och Beeren Eilands kärlväxtflora. *Bihang till Sv. Vet.-Akad. Handl.*, **26** (3), 1-15.

ANKEL W.E. (1927) - Neuere Arbeiten z. Zytol. d. natürlichen Parthenogenese d. Tiere. *Zeitsch. f. indukt. Abstamm. u. Vererb.*, **45**, 232-370.

ANKEL W.E. (1929) - Neuere Arbeiten z. Zytol... *Zeitsch. f. indukt. Abstamm. u. Vererb.*, **52**, 318-370.

ANZALONE B. (1949) - Osservazioni citoembriologiche in Taraxacum megalorrhizon. *Ann. Bot.* (Roma), **23**, 31-34.

ASKER S. (1979) - Progress in apomixis research. *Hereditas*, **91**, 231-240.

BALFOUR I.B. (1887) - Sporophore and Sporophyte. *Ann. Bot.*, **1**, 77-80.

BARBER H.N. (1940) - The suppression of meiosis and the origin of diplochromosomes. *Proc. Roy. Soc. London*, B, **128**, 170-185.

BARY A. DE - Cf. De Bary A.

BASHAW E.C. (1953) - An investigation of the morphology, cytology and mode of reproduction of *Cenchrus setigerus* Vahl. Ph. D. dissertation, Texas A & M Univ., College Station.

BASHAW E.C. (1962) - Apomixis and sexuality in Buffel grass. *Crop. Sci.*, **2**, 412-415.

BASHAW E.C., HOLT E.C. (1958) - Megasporogenesis, embryo sac development and embryogenesis in Dallis grass, *Paspalum dilatatum Agron. J.* (U.S.A.), **50**, 753-756.

BATESON W., PUNNETT R.C. (1911) - On gametic series involving reduplication of certain terms. *J. Gen.*, **1**, 293-302.

BATTAGLIA E. (1945a) - Fenomeni citologici nuovi nella embriogenesi («semigamia») e nella microsporogenesi («doppio nucleo di restituzione») di *Rudbeckia laciniata. N. G. Bot. Ital.*, **52**, 34-38.

BATTAGLIA E. (1945b) - Sulla terminologia dei processi meiotici. *N. G. Bot. Ital.*, **52**, 42-57.

BATTAGLIA E. (1946a) - Ricerche cariologiche ed embriologiche sul genere *Rudbeckia*. 1-5. Il gametofito femminile e maschile di *R. bicolor. R. hirta. R. hirta var. meine freude. R. amplexicaule e R. purpurea (Echinacea purpurea). N. G. Bot. Ital.* **53**, 1-26.

BATTAGLIA E. (1946b) - Ricerche cariologiche ed embriologiche sul genere *Rudbeckia*. 6. Apomissia in *R. speciosa. N. G. Bot. Ital.* **53**, 27-69.

BATTAGLIA E. (1946c) - Ricerche cariologiche ed embriologiche sul genere *Rudbeckia*. 7. Apomissia in *R. laciniata*, ed amfimissia nella sua varietà a fiori doppi. *N. G. Bot. Ital.*, **53**, 437-482.

BATTAGLIA E. (1946d) - Ricerche cariologiche ed embriologiche sul genere *Rudbeckia*. S. Semigamia in *R. laciniata. N. G. Bot. Ital.*, **53**, 483-511.

BATTAGLIA E. (1947a) - Ricerche cariologiche ed embriologiche sul genere *Rudbeckia*. 9. Le anomalie del gametofito femminle cellularizzato di *R. laciniata. N. G. Bot. Ital.*, **54**, 377-405.

BATTAGLIA E. (1947b) - Ricerche cariologiche ed embriologiche sul genere *Rudbeckia*. 10. Le anomalie della meiosi durante la microsporogenesi di *R. laciniata* con particolare riguardo alla formazione del nucleo di restituzione. *N. G. Bot. Ital.*, **54**, 406-431.

BATTAGLIA E. (1947c) - Ricerche cariologiche embriologiche sul genere *Rudbeckia*. 11. Semigamia in *R. Speciosa. N. G. Bot. Ital.*, **54**, 531-559.

BATTAGLIA E. (1947d) - Sulla terminologia dei processi mitotici. *N. G. Bot. Ita.*, **54**, 596-632.

BATTAGLIA E. (1947e) - Sulla terminologia dei processi apomittici. *N. G. Bot., Ital.*, **54**, 674-696.

BATTAGLIA E. (1948) - Ricerche sulle parameiosi restituzionale nel genere Taraxacum. *Caryologia* **1**, 1-47.

BATTAGLIA E. (1949) - L'alterazione della meiosi nella riproduzione apomittica di Chondrilla juncea. *Caryologia* **2**, 23-30.

BATTAGLIA E. (1950a) - L'alterazione della meiosi nella riproduzione apomittica di Erigeron karwinskianus var. mucronatus. *Caryologia* **3**, 165-204.

BATTAGLIA E. (1950b) - Sui fenomeni endomitotici: Una precisazione terminologica. *Caryologia* **2**, 298-300.

BATTAGLIA E. (1951a) - The male and female gametophytes of angiosperms - an interpretation. *Phytomorphology* **1**, 87-116.

BATTAGLIA E. (1951b) - Development of angiosperm embryo sacs with non-haploid eggs. *Amer. J. Bot.* **38**, 718-724.

BATTAGLIA E. (1955a) - New symbols in cytology. *Phytomorphology* **5**, 171-172.

BATTAGLIA E. (1955b) - The concepts of spore, sporogenesis and apospory. *Phytomorphology* **5**, 173-177.

BATTAGLIA E. (1955c) - Unusual cytological features in the apomictic *Rudbeckia sullivanti*. *Caryologia* **8**, 1-32.

BATTAGLIA E. (1956) - Do new types of embryo sac development occur in *Antennaria carpatica*? *Phytomorphology* **6**, 119-123.

BATTAGLIA E. (1963) - *Apomixis*. In Maheshwari P. (ed.): *Recent Advances in the Embryology of Angiosperms. Delhi*, 221-264.

BATTAGLIA E. (1971) - The embryo sac of Podostemaceae - An interpretation. *Caryologia* **24**, 403-420.

BATTAGLIA E. (1980a) - Embryological questions: 1. On the occurrence of the last step of the male gametophyte evolution in Spiranthes (Orchidaceae). *Ann. Bot.* (Roma), **39**, 1-7.

BATTAGLIA E. (1980b) - Embryological questions: 2. Is the endosperm of Angiosperms sporophytic or gametophytic? *Ann. Bot.* (Roma), **39**, 9-30.

BATTAGLIA E. (1981) - Embryological questions: 3. Semigamy, Hemigamy and Gynandroembryony. *Ann. Bot.* (Roma), **39**, 173-175.

BATTAGLIA E. (1982) - Embryological questions: 4. Gynogonium versus Archegonium and the generalization of the prefixes andro- and gyno- in plant reproduction. Appendix: Bischoff T.G. (1835) «De Hepaticis...». *Ann. Bot.* (Roma), **40**, 1-48.

BATTAGLIA E. (1983) - Embryological questions: 5. Discussion of the concepts of spore, sporogenesis and apospory in relation to the female gametophyte of angiosperms. Ann. Bot. (Roma), **41**, 1-25.

BATTAGLIA E. (1985a) - Meiosis and Mitosis: a terminological criticism. *Ann. Bot. (Roma)*, **43**, 101-140.

BATTAGLIA E. (1985b) - Embryological questions: 6. Anticline versus Antigone and the priority over the Hyacinthoides (ex-Endymion) type. *Ann. Bot.* (Roma), **43**, 141-179.

BATTAGLIA E. (1986a) - Embryological questions: 7. Do new types of embryo sac occur in Schisandra? *Ann. Bot.* (Roma), **44**, 69-82.

BATTAGLIA E. (1986b) - Embryological questions: 8. Euphorbia dulcis type versus Fritillaria type. *Ann. Bot.* (Roma), **44**, 97-136.

BATTAGLIA E. (1987a) - Embryological questions: 9. Who discovered the mono- and polysiphonous pollen grains? A documentation of the role played (1760-1830) by C. Linnaeus, D. Cirillo, A. Brongniart and G.B. Amici. *Atti Soc. Tosc. Sc. Nat., Mem., Serie B*, **94**, 53-125.

BATTAGLIA E. (1987b) - Embryological questions: 10. Have the expressions 'polar nuclei' and 'secondary nucleus' been rightly established? Appendix: Hofmeister W. (1847), Untersuchungen... bei... Oenothereen. *Atti Soc. Tosc., Sci. Nat., Mem., Serie B*, **94**, 127-150.

BATTAGLIA E. (1987c) - Embryological questions: 11. Has the debated case of Podostemaceae been resoived? *Ann. Bot.* (Roma), **45**, 37-64.

BATTAGLIA E. (1987d) - Embryological questions: 12. Have the Polygonum and Allium types been rightly established? *Ann. Bot.* (Roma), **45**, 81-117.

BATTAGLIA E. (1988) - 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)? *Atti Soc. Tosc. Sci. Nat. Mem., Serie B* **95**, 69-82.

BATTAGLIA E. (1989) - The evolution of the female gametophyte of angiosperms: an interpretative key. (Embryological questions: 14). *Ann. Bot.* (Roma), **47**, 7-144.

BATTAGLIA E. (1990) - Embryological questions: 15. Does the case spore-nucleus = egg-nucleus occur in angiosperm female gametophytes? *Ann. Bot.* (Roma), **48**, 7-48.

BERGMAN B. (1935a) - Zytologische Studien über die Fortpflanzung bei den Gattungen Leontodon und Picris. *Sv. bot. Tidskr.* **29**, 155-301.

BERGMAN B. (1935a) - Zytologischen Studien über sexuelles und asexuelles Hieracium umbellatum. *Hereditas* **20**, 47-64.

BERGMAN B. (1941) - Studies on the embryo sac mother cell and its development in Hieracium subg. Archieracium. *Svensk Bot. Tidskr.* **35** (1), 1-41.

BERGMAN B. (1951) - On the formation of unreduced gametophytes in the females of Antennaria carpatica. *Hereditas* **37**, 501-518.

BHANDARI N.N., CHITRALEKHA P. (1989) - Cellularization of the female gametophyte in *Ranunculus sceleratus* Linn. *Can. J. Bot.* **67**, 1325-1330.

BHANWRA R.K. (1988) - Embryology in Relation to Systematics of Gramineae. *Ann. Botany* **62**, 215-233.

BHANWRA R.K., CHODA S.P. (1981) - Apomixis in Eremopogon foveolatus (Graminaceae). *Nordic J. Bot.* **1**, 97-101.

BHANWRA R.K., CHODA S.P. (1984) - Apomixis in the Gramineae. *Res. Bull. (Sci.) Panjab Univ.*, **35** (III-IV): 127-134.

BHANWRA R.K., CHODA S.P. (1986) - Comparative embryology of Echinochloa colonum and Echinochloa crusgalli (Poaceae). *Proc. Indian Acad. Sci. (Plant Sci.)* **96**, 71-78.

BHANWRA R.K., CHODA S.P. and KUMAR S. (1982) - Comparative embryology of some grasses. *Proc. Indian Nat. Sci. Acad.* **B48**, 152-162.

BHANWRA R.K., CHOSA S.P. and KUMAR R. (1985) - Comparative embryology of *Brachiaria ramosa* and *Poa annua*. *Res. Bull. Panjab Univ. Sci.* **36**, 245-253.

BHANWRA R.K., SONI D.V. (1986) - The mode of reproduction in *Oplismenus burmanii, O. compositus* and *Paspalum distichum*. *Proc. Indian Nat. Sci. Acad.* Cited by BHANWRA & CHODA (1986).

BILANCIONI G. (1906) - Dizionario di Botanica Generale. Hoepli (Milano).

BIRARI S.P. (1980) - Apomixis in sexuality in Themeda Forssk. at different ploidy levels (Gramineae). *Genetica* **54**, 133-139.

BIRARI S.P. (1981) - *Mechanism of apomixis in Pennisetum polystachyon Schultz.* J. Maharash. Agric. Univ. Pune, **6**, 206-212.

BLAKESKEE A.F. (1930) - (No title). Quoted in Carnegie Inst. Washington. *Yearbook* **29**, 39.

BLEIER H. (1931) - Untersuchungen über die Sterilität der Kartoffel. *Arch. Pflanzenbau* **5**, 545-560.

BOWER F.O. (1885) - On Apospory in Ferns (with special reference to Mr. Charles T. Druery's Observations). *Journ. Linnean Soc.* (Botany), **21**, 360-368 (read 18th December 1884).

BOWER F.O. (1887) - On apospory and allied Phenomena. *Trans. Linnean Soc.* (Botany), **2**, 301-326.

BOWER F.O. (1888) - On some Normal and Abnormal Developments of the Oophyte in Trichomanes. *Ann. Bot.* **1**, 269-305.

BOWER F.O. (1890) - On antithetic as distinct from homologous alternation of generations in plants. *Annals of Botany*, **4**, 347-370.

BRIDGES C.B. (1919) - Duplications. *Anat. Rec.* **15**, 357-358.

BRIX K. (1974) - Sexual Reproduction in *Eragrostis curvula* (Schrad.) Nees. *J. Plant Breeding* **71**, 25-32.

BROWN W.H. (1909) - The embryo sac of *Habenaria. Bot. Gaz.* **48**, 241-250.

BROWN W.H., SHARP L.W. (1911) - The embryo sac of *Epipactis. Bot. Gaz.* **52**, 439-452.

BROWN W.V. (1958) - Apomixis in the Gramineae: Panicoideae. *Amer. J. Bot.* **45**, 253-263.

BROWN W.V., EMERY W.H.P. (1957a) - Apomixis in the Gramineae, tribe Andropogoneae: *Themeda triandra and Bothriochloa ischaenum. Bot. Gaz.*, **118**, 246-253.

BROWN W.V., EMERY W.H.P. (1957b) - Some South African Apomictic Grasses. *J. South Afric. Botany*, **23** (IV): 123-125.

BROWN W.V., EMERY W.H.P. (1958) - Apomixis in the Gramineae: Panicoideae. *Am. J. Bot.*, **45**, 253-263.

BROWN R.C., LEMMON B.E. (1988a) - Cytokinesis occurs at boundaries of domains delimited by nuclear-based microtubules in sporocytes of Conocephalum conicum (Bryophyta). *Cell Motility and the Cytoskeleton* **11**, 139-146.

BROWN R.C., LEMMON B.E. (1988b) - Microtubules associated with simultaneous cytokinesis of coenocytic microsporocytes. *Amer. J. Bot.*, **75**, 1848-1856.

BROWN R.C., LEMMON B.E. (1989) - Minispindles and cytoplamic domains in microsporogenesis of orchids. *Protoplasma*, **148**, 26-32.

BULLER A.H.R. (1941) - The diploid cell and the diploidization process in plants and animals, with special reference to the higher fungi, I, II. *Bot. Rev.*, **7**, 335-431.

BURNETT J.H. (1956) - The mating systems of Fungi. I. *New Phytol.*, **55**, 50-90.

BURSON B.L., BENNETT H.W. (1970 a) - Cytology, method of reproduction, and fertility of Brunswickgrass, *Paspalum nicorae* Parodi. *Crop. Sci.*, **10**, 184-187.

BURSON B.L., BENNETT H.W. (1970 b) - Cytology and reproduction of three *Paspalum* species. *J. Heredity*, **61**, 129-132.

BURSON B.L., BENNETT H.W. (1971 a) - Chromosome numbers, microsporogenesis, and mode of reproduction of seven *Paspalum* species. *Crop. Sci.*, **11**, 292-294.

BURSON B.L., BENNETT H.W. (1971 b) - Meiotic and reproductive behaviour of some introduced *Paspalum* species. *J. Miss. Acad. Scl.*, **17**, 5-8.

BURTON G.W. (1948) - The method of reproduction in Common Bahiagrass *Paspalum notatum. J. Amer. Soc. Agron.*, **40**, 443-452.

BURTON G.W. (1955) - Breeding Pensacola Bahiagrass, *Paspalum notatum.* I. Method of reproduction. *Agron. J.*, **47**, 311-314.

CARANO E. (1924) - Osservazioni sul meccanismo di divisione della cellula madre del sacco embrionale nelle piante apogame. *C.R. Accad. Lincei*, Roma, **33**, 150-155.

CASS D.D., PETEYA D.J. and ROBERTSON B.L. (1985) - Megagametophyte development in *Hordeum vulgare*. 1. Early megagametogenesis and the nature of cell wall formation. *Canad. J. Bot.*, **63**, 2164-2171.

CASS D.D., PETEYA D.J. and ROBERTSON B.L. (1986) - Megagametophyte development in *Hordeum vulgare*. 2. Later stages of wall development and morphological aspects of megagametophyte cell differentiation. *Can. J. Bot.*, **64**, 2327-2336.

CELARIER R.P., HARLAN J.R. (1955) - Studies on Old World bluestems. *Oklahoma Agr. Exp. Sta. Tech. Bull.*, **T-58**, 1-31.

CELARIER R.P., HARLAN J.R. (1956) - Annual Report of progress. Sect. I Old world Bluestems. *Oklahoma Agr. Exp. Sta.*, pp. 1-43.

CELARIER R.P., HARLAN J.R. (1957) - Apomixis in *Botheriochloa, Dichantium* and *Capillipedium*. *Phytomorph.*, **7**, 93-102.

CHADEFAUD M. (1975) - L'origine «para-floridienne» des Eumicètes et l'archétype ancestral de ces champignons. *Ann. Sci. Nat. Botanique*, Ser. 12, **16**, 217-247.

CHAMBERLAIN C.J. (1905) - Alternation of generations in animals from a botanical standpoint. *Bot. Gaz.*, **39**, 139-144.

CHATTERJI A.K., TIMOTHY D.H. (1969a) - Apomixis and tetraploidy in *Pennisetum orientale* Rich. *Crop Science*, **9**, 796-799.

CHATTERJI A.K., TIMOTHY D.H. (1969b) - Microsporogenesis and embryogenesis in *Pennisetum flaccidum* Griseb. *Crop Science*, **9**, 219-222.

CHIARUGI A. (1926) - Aposporia e apogamia in *Artemisia nitida*. *N. G. Bot. Ital.*, **33**, 501-626.

CHIARUGI A. (1927) - Il gametofito femmineo delle Angiospermae nei suoi vari tipo di costruzione e di sviluppo. *N. G. Bot. Ital.*, **34**, 1-133.

CHIARUGI A., FRANCINI E. (1930) - Apomissia in *Ochna serrulata*. *N. G. Bot. Ital.*, **37**, 1-250.

CHODA S.P., BHANWRA R.K. (1977) - The mode of reproduction in *Bothriochloa odorata* (Lisboa) A. Camus and *Paspalum distichum* Linn. *Proc. Indian Natl. Sci. Acad. Part B, Biol. Sci.*, **43**, 175-183.

CHODA S.P., BHANWRA R.K. (1980) - Apomixis in *Capillipedium huegelii* (Hack.) Stapf (Gramineae). *Proc. Indian Natl. Sci. Acad. Part B, Biol. Sci.*, **46**, 572-578.

CHRISTEN H.R. (1950) - Untersuchungen über die Embryologie pseudogamer und sexueller *Rubus*-arten. *Ber. Schweiz. Bot. Ges.*, **60**, 153-198.

CHRISTEN H.R. (1952) - Die embryologie von Rubus idaeus und von bastarden zwischen Rubus caesius und Rubus idaeus. *Zeitsch. f. indukt. Abstam.-Vererb.* **84**, 454-461.

CHRISTOFF M.A., MOSKOVA R. (1972) - The apomixis and the polyembryony in *Bothriochloa ischaenum* L. (= *Andropon ischaemum* (L.) Keng.). *Genet. Sel.*, **5**, 71-86.

COOPER D.C. (1935a) - Macrosporogenesis and development of the embryo sac of *Lilium henryi*. *Bot. Gaz.* **97**, 346-355.

COOPER D.C. (1935b) - Macrosporogenesis and embryology of *Medicago*. *J. Agr. Res.*, **51**, 471-477.

COOPER D.C. (1935c) - Microsporogenesis and the development of the male gametes in *Portulaca oleracea*. *Amer. J. Bot.*, **22**, 453-459.

Cooper D.C. (1939) - Development of megagametophyte in *Erythronium albidum. Bot. Gaz.*, **100**, 862-867.

Cooper D.C. (1941) - Macrosporogenesis and the development of the seed of *Phryma leptostachya. Amer. J. Bot.*, **28**, 755-761.

Corti B. (1774) - Osservazioni microscopiche sulla *Tremella* e sulla circolazione del fluido in una pianta acquaiula. Lucca 127.

Coulter J.M. (1898) - Contribution to the life-history of *Ranunculus. Bot. Gaz.* (Chicago), **25**, 73-88.

Coulter J.M. (1908) - Relation of megaspores to embryo sacs in angiosperms. *Bot. Gaz.*, **45**, 361-366.

Crane C.F., Carman J.G. (1987) - Mechanisms of apomixis in Elymus rectisetus from eastern Australia and New Zealand. *Amer. J. Bot.*, **74**, 477-496.

Crane C.F. (1989) - A proposed classification of apomictic mechanisms in flowering plants. *Apomixis Newsletter*, **1**, 11-19.

Cresti A., Gori P., Pacini E. (1988) - Sexual reproduction in higher plants. Springer-Verlag.

Czapik R. (1981) - Elementary apomictic process in Rubus L. *Acta Soc. Botan. Polon.*, **50**, 201-204.

Czapik R. (1983) - Embryological problems in Rubus L. In Fertiliz. and Embryogen. in ovulated Plants. Veda, Bratislava, pp. 375-379.

Czapik R. (1987) - Apomixis in Rubus Bellardii Weihe. *Acta Biol. Cracov. (Bot.)*, **29**, 45-52.

Dangeard P.A. (1902) - Recherches sur Eugleniens. *Le Botaniste*, **8**, 95-357.

Darlington C.D. (1937) - Recent Advances in Cytology. *2nd. ed. Churchill Ltd. London.*

Davis B.M. (1904a) - Studies on the Plant Cell.-III. *Amer. Nat.*, **38**, 571-594.

Davis B.M. (1904b) - Studies on the Plant Cell.-IV. *Amer. Nat.*, **38**, 725-760.

Davis B.M. (1905a) - Studies on the Plant Cell.-V. Amer. nat., **39**, 217-268.

Davis B.M. (1905b) - Studies on the Plant Cell.-VI. *Amer. Nat.*, **39**, 449-499.

Davis B.M. (1905c) - Studies on the Plant Cell.-VII. *Amer. Nat.*, **39**, 555-599.

Davis G.L. (1966) - Systematic embryology of the angiosperms. John Wiley, New York.

D'Cruz R., Reddy P.S., (1971) - Inheritance of apomixis in *Dichanthium. Indian J. Genet. Plant Breed.*, **31**, 451-460.

De Bary A., Strasburger E. (1877) - *Acetabularia mediterranea. Bot. Zeit.*, **35**, 713-758 (713-736 De Bary; 737-756: Strasburger).

De Bary A. (1884) - *Vergleichende Morphologie und Biologie der Pilze, Mycetozoen und Bakterien.* Verlag W. Engelmann, Leipzig.

Dodds K.S., Pittendrigh C.S. (1946) - Genetical and cytological studies of Musa. VII. Certain aspects of polyploidy. *Jour. Genet.*, **47**, 162-177.

Dowrick G.J. (1961) - Biology of reproduction in Rubus. *Nature*, **191**, 680-682.

Dowrick G.J. (1966) - Breeding system in tetraploid Rubus species. *Genet. Res.*, **7**, 245-253.

Druery C.T. (1885a) - Observations on a singular Mode of Development in the Lady-Fern (Athyrium Filix-foemina). *Jour. Linnean Soc.* (Botany), **21**, 354-357, (read 19th June, 1884).

Druery C.T. (1885b) - Further Notes on a singular Mode of Reproduction in Athyrium

Filix-foemina, var. clarissima. *Jour. Linnean Soc.* (Botany), **21**, 358-360. (read 20th November, 1884).

DUJARDIN M., HANNA W. (1984) - Microsporogenesis, reproductive behaviour, and fertility in five Pennisetum species. *Theor. Appl. Genet.*, **67**, 197-202.

DUJARDIN M., HANNA W. (1988) - Production of 27-, 28-, and 56-chromosome apomictic hybrid derivatives between pearl millet (2n = 14) and Pennisetum squamulatum (2n = 54). *Euphytica*, **38**, 229-235.

DYER THISELTON W.T. (1884) - Apospory in Ferns. *Nature*, **31**, 151 (Dec. 18, 1884).

DYER THISELTON W.T. (1885) - Apospory in Ferns. *Nature*, **31**, 216 (Jan. 8, 1885).

EDMAN G. (1929) - Zur Entwicklungsgeschichte der Gattung *Oxyris*, nebst zytologischen, embryologischen und systematischen Bemerkungen über einige andere Polygonaceen. *Acta Hort. Berg.*, **9**, 165-291.

EDMAN G. (1931) - Apomeiosis und Apomixis bei *Atraphaxis frutescens. Acta Hort. Berg.*, **11**, 13-66.

EINSET J. (1951) - Apomixis in American polyploid blackberries. *Amer. J. Bot.*, **38**, 768-772.

EMERY W.H.P. (1957) - A study of reproduction in Setaria macrostachya and its relatives in the southwestern United States and northern Mexico. *Bull. Torrey Club*, **84**, 106-121.

EMERY W.H.P., BROWN W.V. (1958) - Apomixis in the Gramineae. Tribe Andropogoneae. *Heteropogon contortus. Madrono*, **14**, 238-246.

ERDELSKÁ O., INST. WISS. FILM (1973) - Samenanlage und frübe Endospermentwicklung von Jasione montana (Campanulaceae). Film C 1075 des IWF, Göttingen. Publikation von O. Erdelská, *Publ. Wiss. Film., Sekt. Biol., Bd.* **6**, 111-124.

ERDELSKÁ O. (1974) - Contribution to the study of fertilization in the living embryo sac. In H.F. Linskens edit. Fertilization in higher plants. *North-Holland Publ. Comp.*, Amsterdam, pp. 191-195.

ERDELSKA O. (1983) - Microcinematographical investigation of the female gametophyte, fertilization and early embryo and endosperm development. *In* Fertilization and embryogenesis in ovulated plants. *Edited by* O. Erdelska, M. Ciamporova, A. Lux, A. Pretova, and J. Tupy. Proceedings of the 7th International Cytoembryological Symposium. Veda, Bratislava, pp. 49-54.

ERDELSKÀ O. (1985) - Film C 1463/1895. Inst. f.d. wiss. Film, Gottingen.

ERNST A. (1908a) - Zur Phylogenie des Embryosackes der Angiospermen. *Ber. dtsch. bot. Ges.*, **26**, 419-438.

ERNST A. (1908b) - Ergebnisse neueren Untersuchungen uber den Embryosack der Angiospermen. *Verh. d. Schweiz. Naturforsch. Ges.*, **91** (1), 230-263.

EVANS L.T., KNOX R.B. (1969) - Environmental control of reproduction in *Themeda australis. Aust. J. Bot.*, **17**, 375-389.

EYMÉ J. (1961) - Recherches cytologiques sur le gamétophyte femelle de Helleborus foetidus L. et Helleborus niger L. *Le Botaniste*, **44**, 255-289.

EYMÉ J. (1965) - Observations cytologiques sur l'archéspore et le sac embryonnaire de Tulipa oculus-solis St. Am. et Tulipa silvestris L. *Le Botaniste*, **49**, 109-155.

FAGERLIND F. (1940) - Die Terminologie der Apomixis Prozesse. *Hereditas*, **26**, 1-22.

FAGERLIND F. (1944a) - Die Samenbildung und die Zytologie bei agamospermischen und sexuellen Arten von *Elatostema* und einigen nehestehenden Gattungen nebst

Beleuchtung einiger damit zusammenhangender Probleme. *Kgl. Svensk. Vet.-Akad. Handl.*, (3) **21**, 1-130.

FAGERLIND F. (1944b) - Is my terminology of the apomictic phenomena of 1940 incorrect and inappropriate? Hereditas **30**, 590-596.

FAGERLIND F. (1944c) - Der tetrasporische Angiospermen-Embryosack und dessen Bedeutung für das Verhältnis der Entwicklungsmeckanik und Phylogenie des Embryosackes. *Arkiv. f. Bot.*, **31A**, 1-71.

FAGERLING F. (1947a) - Die Restitutions- und Kontraktionskerne der *Hieracium*-Mikrosporogenese. *Svensk bot. Tidskr.*, **41**, 365-390.

FAGERLIND F. (1947b) - Macrosporogenesis und Embryosackbildung bei agamospermischen *Taraxacum*-Biotypen. *Svensk bot. Tidskr.*, **41**, 365-390.

FARMER J.B., MOORE J.E.S. (1905) - On the Maiotic Phase (Reduction Divisions) in Animals and Plants. *Quart. Journ. Microsc. Sci.*, **48** (4), 489-557.

FARQUHARSON L.I. (1955) - Apomixis and polyembryony in *Tripsacum dactyloides. Amer. Jour. Bot.*, **42**, 737-743, 1955.

FARUOI S.A., AFRIDI S., USMANI S.M.H. (1975) - Apomixis and Polyembryony in some Andropogoneae from Pakistan. *Pak. J. Bot.*, **7**, 135-138.

FISHER W.D. (1953) - A study of the morphology, cytology and breeding behavior of *Pennisetum ciliare*. Ph. D. dissertation, Texas A & M Univ., College Station.

FISHER W.D., BASHAW E.C. & HOLT E.C. (1954) - Evidence for apomixis in *Pennisetum ciliare* and *Cenchrus setigerus*. *Agron. J.*, **46**, 401-404.

FOCKE W.O. (1881) - Die Pflanzenmischlinge, ein Beitrag zur Biologie der Gewächse. Berlin (Borntraeger).

FUKUDA Y. (1927) - Cytological studies on the development of the pollen-grain in different races of Solanum tuberosum L., with special reference to sterility. *Bot. Mag.* (Tokyo), **41**, 459-474.

GERASSIMOVA-NAVASHINA H., (1954a) - The development of the embryo sac and the origin of Angiosperms. *Bot. Zhur.*, Dokl. Acad. Nauk SSSR **95**, 877-880.

GERASSIMOVA-NAVASHINA H. (1954b) - *Development of the embryo sac, double fertilization and the origin of Angiosperms. Bot. Zhur.* **39**, 655-680.

GERASSIMOVA-NAVASHINA H. (1958) - The gametophyte of the angiosperms and the fundamental features of the development and functioning of their reproductive elements. (In Russian with English Summary). *Problemy Bot.*, **3**, 125-167.

GERASSIMOVA-NAVASHINA H. (1961) - Fertilization and events leading up to fertilization and their bearing on the origin of Angiosperms. *Phytomorphology*, **11**, 139-146.

GERLACH D. (1965) - Befruchtung und Autogamie bei Rubus caesius. *Biol. Zentralbl.*, **84**, 611-633.

GILDENHUYS P.J., BRIX K. (1958). Cytological abnormalities in *Pennisetum dubium*. *Heredity*, **12**, 441-452.

GILDENHUYS P.J., BRIX K. (1959) - Apomixis in *Pennisetum dubium*. *S. Afr. J. agric. Sci.*, **2**, 231-45.

GOHIL R.N., KAUL R. (1981) - Studies on male and female meiosis in Indian Allium. *Chromosoma* (Berl.), **82**, 735-739.

GOHIL R.N., KOUL A.K. (1983) - Seed progeny studies in Alliums. II. Male meiosis in the progeny plants of tetraploid Allium tuberosum Rottl. ex Spreng. *Cytologia*, **48**, 119-130.

GREGOIRE V. (1910) - Les Cinèses de maturation dans les deux règnes. *La Cellule*, **26**, 223-422.

GUIGNARD L. (1882) - Recherches sur le sac embryonnaire des phanerogames angiosperms. *Ann. Sci. nat. Bot.* (6) **13**, 136-199.

GUIGNARD L. (1884) - Recherches sur la structure et la division du noyau cellulaire chex les végétaux. *Ann. Sci. nat. Bot.* (6) **17**, 5-59.

GUIGNARD L. (1885) - Nouvelles recherches sur le novau cellulaire. *Ann. Sci. Nat. Bot.* (Paris) (6), **20**, 310-372.

GUIGNARD L. (1889) - Études sur les phenomenes morphologiques de la fécondation. *Bull. Soc. bot. France*, **36**, 100-146.

GUIGNARD L. (1890a) - Sur la formation et la différenciation des éléments sexuels qui interviennent dans la fécondation. *C.R. Acad. Sci. Paris*, **110**, 590-592.

GUIGNARD L. (1890b) - Sur la mode d'union des novaux sexuels dans l'acte de la fécondation. *C.R. Acad. Sci. Paris*, **110**, 726-728.

GUIGNARD L. (1891) - Nouvelles études sur la fécondation. *Ann. Sci. nat. Bot.* (7), **14**, 163-296.

GUIGNARD L. (1898) - Les centres cinétiques chez les végétaux. *Ann. Sci. nat. Bot.*, (8) **6**, 177-220.

GUIGNARD L. (1900a) - L'appareil sexuel et la double fécondation dans les Tulipes. *Ann. Sci. nat. Bot.*, (7) **11**, 365-387.

GUIGNARD L. (1900b) - Nouvelles recherches sur la double fécondation chez les végétaux angiospermes. *C.R. Acad. Sci. Paris*, **131**, 153-160.

GUPTA P.K. (1968) - Observation on the degree of apospory in three members of Andropogoneae. *Curr. scl.* (Bangalore), **37**, 295-296.

GUPTA P.K. (1969) - Apomixis in *Bothriochloa pertusa* (L.) A. Camus. *Port. Acta Biol. Ser. A*, **11**, 279-287.

GUPTA P.K., YASHVIR (1971) - Apomixis in *Cenchrus ciliaris*: A preliminary study. *Curr. Sci.* (Bangalore), **40**, 444-446.

GUSTAFSSON Å. (1934a) - Entwicklungswege der parthenogenetischen Embryosackmutterzelle. *Bot. Notiser*, 333-338.

GUSTAFSSON Å. (1934b) - Die Formenbildung der Totalapomikten. *Hereditas*, **19**, 259-283.

GUSTAFSSON Å. (1935) - Studies on the mechanism of parthenogenesis. *Hereditas*, **21**, 1-112.

GUSTAFSSON Å. (1946-47) - Apomixis in higher plants. Parts I, II, III. Lunds Univ. Arsskr. N.F. Avid. II: **43** (3), 1-69. 1946; **43** (2), 71-182. 1947; **44** (2), 183-370.

HAACKE W. (1893a) - Gestaltung und Vererbung. Eine Entwicklungsmechanik der Organismen. *Leipzig*.

HAACKE W. (1893b) - Die Träger der Vererbung. *Biol. Centralblatt*, **13**, 525-542.

HAIR J.B. (1956) - Subsexual reproduction in *Agropyron*. *Heredity*, **10**, 129-160.

HÅKANSSON A. (1951) - Parthenogenesis in *Allium*. *Bot. Not.* 1951, 143-179.

HÅKANSSON A., LEVAN A. (1957) - Endo-duplicational meiosis in Allium odorum. *Hereditas*, **43**, 179-200.

HARLAN J.R., CELARIER R.P., RICHARDSON W.L., BROOKS M.H., MEHRA K.L. (1958) - Studies on Old World Bluestems II. *Okla. Agri. Exp. Sta. Tech. Bull.*, T-72, 3-23.

HARLAN J.R., BROOKS H.M., BORGAONKAR D.S. and DE WET J.M.J. (1964) - Nature and inheritance of apomixis in *Bothriochloa* and *Dichanthium*. *Bot. Gaz.*, **125**, 41-46.

HARTMANN M. (1909) - Autogamie bei Protisten und ihre Bedeutung für das Befruchtungsproblem. *Arch. f. Protist.*, **14**, 264-334.

HARTOG M. (1904) - Some Problems of Reproduction. II. *Quart. Journ. Micr. Sci.*, 47 (4), 583-608.

HASKELL G. (1960) - Role of the male parent in apomictic Rubus species. *Heredity*, **14**, 101-113.

HASKELL G. (1966) - The history, taxonomy and breeding system of apomictic british Rubi. In Hawkes J.G. (ed.) «Reproductive Biology and taxonomy of vascular plants. *Pergamon Press*, Oxford, pp. 141-151.

HENDERSON I.F., HENDERSON W.D. (1953) - A Dictionary of Scientific Terms. Fifth ed. by Kenneth J.H., Van Nostrand Co. New York.

HERR J.M. (1971) - A new clearing squash tecnique for the study of ovule development in angiosperms. *Amer. J. Bot.*, **58**, 785-790.

HERR J.M., Jr. (1982) - An analysis of methods for permanently mounting ovules cleared in four - and-a - half type clearing fluids. *Stain Tech*, **57**, 161-169.

HERR J.M. (1985) - The removal of phlobaphenes for improved clearing of sections and whole structures. *Amer. J. Bot.*, **72**, 817.

HOWE T.D. (1975) - The female gametophyte of three species of *Grindelia* and of *Prionopsis ciliata* (Compositae). *Am. J. Bot.*, **62**, 273-279.

ISLAM A.S., DASS A. (1970) - Apomixis in *Cenchurus pennisetiformis* Hochst. *Proc. 21-22 Pak. Sci. Conf. Rajshahi* Part. III.

JACKSON B.D. (1928) - A glossary of botanical terms. G. Duckworth Co. London. (Fourth. ed.).

JANET CH. (1912) - Le sporophyte et la gametophyte du végétal. Le soma et le germen de l'insecte. Limoges.

JÖRGENSEN C.A. (1928) - The experimental formation of heteroploid plants in the genus Solanum. *Jour. Genet.*, **19**, 133-211.

JOHANSEN D.A. (1929) - Studies in the morphology of the Onagraceae. 1. *Hartmannia tetraptera. Bull Torrey Bot. Cl.*, **56**, 285-298.

JOHRI B.M. (1984) - Embryology of angiosperms. Springer-Verlag. Berlin, Heidelberg, New York, Tokyo.

JUEL H.O. (1898) - Parthenogenesis bei *Antennaria alpina. Beih. Bot. Ztbl.*, **74**, 369-372.

JUEL H.O. (1900) - Vergleichende Untersuchungen über typische und parthenogenetische Fortpflanzung bei der Gattung *Antennaria. Kgl. Svensk. Vet-Akad. Handl.* **33**, 1-59.

JUEL H.O. (1904) - Die Tetradenteilung in der Samenanlagen von *Taraxacum. Arkiv. f. Bot.*, **2**, 1-9.

JUEL H.O. (1905) - Die Tetradenteilung bei *Taraxacum* und anderen Cichoraceen. *Kgl. Svensk. Vet.-Akad. Handl.*, **39**, 1-21.

KAMIYA N. (1959) - Protoplasmic streaming. *Protoplasmatologia*, **8**, 3 a. Vienna: Springer, 199 pp.

KAMIYA N. (1981) - Physical and chemical basis of cytoplasmic streaming. *Ann. Rev. Plant. Physiol.*, **32**, 205-236.

KERNER A. (1874) - Vorläufige Mittheilungen über die Bedeutung der Asyngamie für die Entstehung neuer Arten. Ber. d. naturwiss. - med. Vereins Innsbruck.: 1-10 (as reprint).

KERNER A. (1876) - Parthenogenesis bei einer angiospermen Pflanze. *Sitzb. Math. Nat, Classe Akad. Wiss. Wien*, Abt. I, **74**, 469.

KHOKHLOV S.S. (1970) - cf. Khohlov S.S. (1976).

KHOKHLOV S.S. (1976) - Evolutionary genetic problems of apomixis in Angiosperms. In Khlokhlov S.S. ed. «Problems of Evolution, Genetics, and breeding of apomictic plants», pp. 3-17. Amerind Publ. Co. New Delhi.

KNIEP H. (1928) - Die Sexualität der niederen Pflanzen. G. Fischer, Jena.

KNOX R.B., HESLOP-HARRISON J. (1963) - Experimental control of aposporous apomixis in a grass of the Andropogoneae. *Bot. Notiser*, **116**, 127-141.

KOERNICKE M. (1905) - Die nueren Arbeiten über die Chromosomenreduktion im Pflanzenreich und daran anschliessende Karyokinetische Probleme. II. Bericht. *Bot. Zeit.*, **63**, 289-307.

KOJIMA A., KAWAGUCHI T. (1988) - Dihaploids derived from unpollinated ovule culture of Chinese chives. *Proc. Eucarpia 4th Allium Symp.*: 212-217.

KOJIMA A., NAGATO Y., HINATA K. (1989) - Proc. 6th intern. Congr. SABRAO.

KUWADA Y. (1928) - On the occurrence of restitution nuclei in the formation of the embryo sac of *Balanophora japonica*. *Bot. Mag.* (Tokyo), **42**, 117-129.

LIEBENBERG H. (1961) - *Apomiksie by* Eragrostis *en* Themeda. Ongepubliseerde M.Sc. verhandeling, Universiteit van Stellenbosch.

LIEBENBERG H., PIENAAR R. DE V. (1962) - Apomiksie by *Eragrostis* en *Themeda*. Verrigtinge van die 2de Kongres van die Suid-Afrikaanse Genetiese Vereniging. 150-153.

LIEBENBERG H. (1990) - Cytotaxonomic studies in Themeda triandra Forssk.: Part III: Sexual and apomictic embryo sac development in 53 collections. *South Afr. J. Bot.*, **56**, 554-559.

LJUNGDAHL H. (1922) - Zur Zytologie der Gattung *Papaver*. *Svensk bot. Tidskr.*, **16**, 103-114.

LOVE A., LOVE D. (1975) - Plant Chromosomes. J. Cramer.

LOVE A., CONNOR H.E. (1982) - Relationships and taxonomy of New Zealand wheat grasses. *New Zealand Jour. Bot.*, **20**, 169-186.

MAHESHWARI P. (1941) - Recent work on the types of embryo sacs in Angiosperms. *J. Indian Bot. Soc.*, **20**, 229-261.

MAHESHWARI P. (1947) - Tetranucleate embryo sacs in Angiosperms. Lloydia **10**, 1-18.

MAHESHWARI P. (1948) - The angiosperm embryo sac. *Bot. Rev.*, **14**, 1-56.

MAHESHWARI P. (1950) - An introduction to the embryology of angiosperms. McGraw-Hill Book Co., Inc., New York and London.

MAHESHWARI P. (ed.) (1963) - Recent Advances in the Embryology of Angiosperms. Delhi.

MAIRE R. (1900a) - L'évolution nucleaire chez les Endophyllum. *Journ. Bot.*, 14, 80-97, 369-382.

MAIRE R. (1900b) - L'évolution nucleaire chez les Uredinées. Compt. Rendus Congrès intern. *Botanique Expos. Univ.* Paris, 135-150 (1901).

MCWILLIAM J.R., SHANKER K., KNOX R.B. (1970) - Effects of temperature and photoperiod on growth and reproductive development in *Hyparrhenia hirta*. *Australian Jour-*

*nal of Agricultural Research*, **21**, 557-69.

MENDIBURU A.O. (1971) - The significance of 2n gametes in potato breeding and genetics. Ph. D. Dissertation. University of Wisconsin.

MENDIBURU A.O., PELOQUIN S.J. and MOK D.W.S. (1974) - Potato breeding with haploids and 2*n* gametes. *In* Haploids in higher plants. *Edited by* K. Kashs. University of Guelph, Guelph, Ont. pp. 249-258.

MENDIBURU A.O. & PELOQUIN S.J. (1977) - Bilateral sexual polyploidization in potatoes. *Euphytica*, **26**, 573-583.

MERRIAM-WEBSTER A. (1976) - Webster's Third New Intern. Dictionary. G. & C. Merriam Co., Springfield, Mass. U.S.A.

MEURMAN O., RANKEN G. (1932) - Untersuchungen über die Chromosomenverhältmisse bei kultivierten Kartoffelsorten. Soc. Scientiarum Fenica Connectatione. *Biologiae*, **3**, 1-27.

MODILEWSKI J. (1930) - Neue Beiträge zur Polyembryonie von *Allium odorum*. *Ber. Deut. Bot. Ges.*, **48**, 285-294.

MOGIE M. (1986) - Automixis: its distribution and status. *Biol J. Linn. Soc.*, **35**, 321-329.

MOK D.W.S., PELOQUIN S.J. (1975a) - Three mechanism of 2n pollen formation in diploid potatoes. *Can. J. Genet. Cytol*, **17**, 217-225.

MOK D.W.S., PELOQUIN S.J. (1975b) - The inheritance of three mechanisms of diplandroid (2n pollen) formation in diploid potatoes. *Heredity*, **35**, 295-302.

MOTTIER D.M. (1897) - Über das Verhalten der Kerne bei der Entwicklung des Embryosackes und die Vorgänge bei der Befruchtung. *Jahrb. f. wiss. Bot.*, **31**, 125-158.

MOSKOVA R.D., YAKOLEV M.S. (1974) - Apomixis of *Bothriochloa ischaemum* L. Flowering, pollination, fertilisation. In *Fertilisation in Higher Plants* Ed. H.F. Linskens, pp. 341-349, North Holland Publishing Co., Amsterdam.

MUNIYAMMA M. (1978) - Variation in microsporogenesis and the development of embryo sac in *Echinochloa stagnina* (Retz.) P. Beauv. (Gramineae); *Bot. Gaz.*, **130**, 87-94.

MÜNTZING A. (1933) - Apomictic and sexual seed formation in *Poa. Hereditas*, **17**, 131-154.

MÜNTZING A. (1940) - Further studies on apomixis anf sexuality in *Poa. Hereditas*, **26**, 115-190.

MURBECK S. (1904) - Parthenogenese bei den Gattungen *Taraxacum* und *Hieracium*. *Bot. Notiser*, 285-296.

MURTHY U.R. (1973) - Polyploidy and apomixis in *Apluda mutica* L. var. *aristata* (L.) Pilger. *Cytologia* (Tokio), *38*, 347-356.

NAGENDRAN C.R., DINESH M.S. (1989) - The Embryology of Angiosperms: a classified bibliography. *Indira Publ. House Michigan*, USA.

NAKAGAWA H. (1990) - Embryo Sac Analysis and Crossing Procedure for Breeding Apomictic Guineagrass (Panicum maximum Jacq.). *Jarq*, **24**, 163-168.

NARAYAN K.N. (1951) - Cytogenetic studies of apomixis in *Pennisetum*. Ph. D. dissertation, Univ. of Calif. Berkeley.

NARAYAN K.N. (1955a) - Cytogenetic studies of apomixis in *Pennisetum-I. Pennisetum clandestinum*, Hochst. *Proc. Indian Acad. Sci.*, **41B**, 195-208.

NARAYAN K.N. (1955b) - Cytogenetic studies of apomixis in *Pennisetum - II Pennisetum latifolium Spreng. J. Mysore Univ.*, **14B**, 33-42.

NARAYAN K.N. (1962) - Apomixis in some species of *Pennisetum* and in *Panicum anditotale*. In Plant Embryology Ed. P. Maheswari, pp. 55-61, CSIR, New Delhi.

NARAYANASWAMI S. (1953) - The structure and development of caryopsis in some Indian millets. 1. *Pennisetum thyphoideum*. *Phytomorphology*, **3**, 98-112.

NARAYANASWAMI S. (1954) - The structure and development of caryopsis in some Indian millets. 2. *Paspalum scrobiculatum*. *Bull. Torrey Bot. Club*, **81**, 288-299.

NARAYANASWAMI S. (1955a) - The structure and development of caryopsis in some Indian millets. 3. *Panicum miliare* and *P. miliaceum*. *Lloydia*, **18**, 61-73.

NARAYANASWAMI S. (1955b) - The structure and development of caryopsis in some Indian millets. 4. *Echinochloa frumentacea*. *Phytomorphology*, **5**, 161-171.

NARAYANASWAMI S. (1956) - The structure and development of caryopsis in some Indian millets. 6. *Setaria italica*. *Bot. Gaz.*, **118**, 112-122.

NEWCOMB W. (1973a) - The development of the embryo sac of sunflower *Helianthus annuus* before fertilization. *Can. J. Bot.*, **51**, 863-878.

NEWCOMB W. (1973b) - The development of the embryo sac of sunflower Helianthus annuus after fertilization. *Canad. J. Bot.*, **51**, 879-890.

NOGLER G.A. (1984) - Gametophytic Apomixis, in B.M. Johri, Embryology of Angiosperms, pags. 475-519. Springer-Verlag Berlin Heidelberg.

NYBOM H. (1986) - Chromosome numbers and reproduction in Rubus subg. Malachobatus. *Pl. Syst. Evol.*, **152**, 211-218.

NYBOM H. (1988) - Apomixis versus sexuality in blackberries (Rubus subgen. Rubus, Rosaceae). *Pl. Syst. Evol.*, **160**, 207-218.

NYBOM H. (1989) - Temporal and spatial patterns in the production of pollen, ovules and seeds in pseudogamous blackberries (Rubus subgenus Rubus). *Holoarctic Ecology*, **12**, 120-129.

NYGREN A. (1954) - Apomixis in the angiosperms II. *Bot. Rev.*, *20*, 577-649.

NYGREN A. (1967) - Apomixis in Angiosperms. *Encycl. Pl. Physiol.*, **18**, 551-596.

OKABE S. (1932) - Parthenogenesis in Ixeris dentata. *Bot. Mag.* (Tokyo), **46**, 518-523.

OKABE S. (1963) - Cytological and Embryological Studies of the Ixeris dentata Group. *Bull. Hiroshima Women's Junior College*, **14**, 34-41.

OSAWA J. (1913) - Studies on the cytology of some species of Taraxacum. *Arch. f. Zellf.*, **10**, 450-469.

PEARSON H. (1909) - Further observations on *Welwitschia*. *Philos. Trans. Roy Soc. London, B*, **200**, 331-402.

PERNES J., CHAUME R., RENE J., SAVIDAN Y. (1975) - Schema d'amélioration génétique des complexes agamiques du type *Panicum*. «Cah. ORSTOM», *sér. Biol.*, **10** (2), 67-75.

PETROV D.F., SUKHAREVA N.B. (1977) - Some cytoembryological characters of facultatively apomictic raspberries (Rubus idaeus L.). In Petrov F.D. (ed.), Cytogenetic basis of plant breeding. Nauka Siberian Branch (Novosibirsk).

PFEIFFER T.W., BINGHAM E.T. (1983) - Abnormal meiosis in alfalfa, Medicago sativa: cytology of 2N egg and 4N pollen formation. *Can. J. Genet. Cytol.*, **25**, 107-112.

PORTER T.R. (1936) - Development of the megagametophyte and embryo of *Allium mutabile*. *Bot. Gaz.*, **98**, 317-327.

PRATT C., EINSET I. (1955) - Development of the embryo sac in some American blackberries. *Amer. J. Bot.*, **42**, 637-645.

PRELL H. (1921) - Anisogametie, Heterogametie und Aëthogametie als biologische Wege zur Förderung der Amphimixis. *Arch. f. Entw. Mech.*, **49**, 463-490.

PRELL H. (1923) - Der Vererbungstheoretische Character der Parthenogenese. *Genetica*, **5**, 191-208.

PRITCHARD A.J. (1967) - Apomixis in *Brachiaria decumbens*. *J. Aust. Inst. agric. Sci.*, **33**, 264-265.

PRITCHARD A.J. (1970) - Meiosis and embryo sac development in *Urochloa mosambicensis* and three *Paspalum* species. *Austr. J. Agric. Res.*, **21**, 648-652.

RABAU T., LONGLY B., LOUANT B.P. (1986) - Ontogenèse des sacs embryonnaires non réduits chez Eragrostis curvula. *Can. J. Bot.*, **64**, 1778-1785.

RAMANNA M.S. (1979) - A re-examination of the mechanisms of 2*n* gamete formation in potato and its implications for breeding. *Euphytica*, **28**, 537-561.

RAMANNA M.S. (1983) - First division restitution gametes through fertile desynaptic mutants of potato. *Euphytica*, **32**, 337-350.

RAUNKIAER C. (1903) - Kimdanelse uden Befrugtning hos Mälkebötter. *Bot. Tidskr.*, **25**, 110-140 (1903).

REDDY P.S., D' CRUZ R. (1969) - Mechanism of apomixis in *Dichanthium annulatum*. *Bot. Gaz.*, **130**, 71-79.

REES-LEONARD O.L. (1935) - Macrosporogenesis and development of the macrogametophyte of *Solanum tuberosum*. *Bot. Gaz.*, **96**, 734-750.

REGNARD E. (1914a) - Action d'une gregarine (Metamera Schunbergi Duke) sur l'épithélium de son hôte (Glossosiphonia compianata L.). *C.R. Soc. Biol.* (Paris) **66** (1), 124-126.

REGNARD E. (1914b) - Quelques particularités de la Metamera Schubergi Duke, et son action sur l'épithèlium intestinal de Glossosiphonia complanata (L.). *Arch. Zool. Exper. Gen.*, **54**, 1-13.

RENNER O. (1916) - Zur Terminologie des pflanzlichen Generationwechsels. *Biol. Ztbl.*, **36**, 337-374.

ROSENBERG O. (1906) - Über die Embryobildung in der Gattung *Hieracium*. *Ber. dtsch. bot. Ges.* **24**, 157-161.

ROSENBERG O. (1907) - Experimental and cytological studies in the *Hieracia*. 2. Cytological studies on the apogamy in *Hieracium*. *Bot. Tidssk.*, **25**, 143-170.

ROSENBERG O. (1917) - Die Reduktionsteilung und ihre Degeneration in *Hieracium*. *Svensk. Bot. Tidsk.*, **11**, 145-206.

ROSENBERG O. (1926a) - Zur Mechanismus der diploiden Kernteilung in Pollenmutterzellen. *Arkiv f. Botanik*, **20**, 1-5.

ROSENBERG O. (1926b) - Uber die Verdoppelung der Chromosomenzahl nach Bastardierung. *Ber. d. deutsch. Bot. Gesellsch.*, **44**, 455-460.

ROSENBERG O. (1927a) - Die Semiheterotypische Teilung und ihre Bedeutung fur die Entstehung verdoppelter Chromosomenzahlen. *Hereditas*, **8**, 305-338.

ROSENBERG O. (1927b) - Homoeotypic division in uninucleate Pollen mother cells. *Hereditas*, **9**, 285-288.

ROSENBERG O. (1930) - Apogamie und Parthenogenesis bei Pflanzen. *In* Baur E. and M. Hartman, Berlin: Handbuch der Vererbungswissenchaft **12**, 1-66.

RUTGERS F.L. (1923) - The female gametophyte of angiosperms. *Ann. Jard bot. Buitenz*, **33**, 1-5.

RUTISHAUSER A. (1967) - Fortpflanzungmodus und meiose apomiktischer Blütenpflanzen. *Protoplasmatologia*, **6** (3). Springer-Verlag. Wien-New York.

RUTISHAUSER A. (1969) - Embryologie und Fortpflanzungsbiologie der Angiospermen. Springer-Verlag. Wien-New York.

SARAN S., DE WET J.M.J. (1969) - A structural peculiarity observed in the sexual embryo sacs of *Dichantium intermedium*. *Can. J. Bot.*, **47**, 1205-1206.

SARAN S., DE WET J.M.J. (1976) - Environmental control of reproduction in *Dichanthium intermedium* (Gramineae). *Bull. Torrey Bot. Club*, **97**, 6-13.

SATINA S., BLAKESLEE A.F. (1935) - Cytological effects of a gene in *Datura* which caused dyad formation in sporogenesis. *Bot. Gaz.*, **96**, 521-532.

SATYAMURTHY T.V. CH., SESHAVATARAM V. (1983) - Apospory in *Eremopogon foveolatus* (Del.) Stazpf. *Curr. Sci.*, (Bangalore) **52**, 1072-1073.

SAVIDAN Y. (1975) - Contribution a l'étude de l'hérédité de l'apomixie chez *Panicum maximum* Jacq. (analyse des sacs embryonnaires). «Cah. Orstom», ser. Biol., **10**, 91-95.

SAVIDAN Y. (1978) - Gametophytic apomixis in the Gramineae and its use in plant breeding. *Ann. Amelior. Plant.* (Paris), **28**, 1-9.

SAVIDAN Y. (1980) - Chromosomal and embryological analyses in sexual X apomictic hybrids of *Panicum maximum* Jacq. *Theor. Appl. Genet.*, **57**, 153-156.

SAVIDAN Y. (1982) - Embryological analysis of facultative apomixis in *Panicum maximum*. *Crop. Sci.*, **22**, 467-469.

SAVIDAN Y.H., CRANE C.F. eds. (1989, 1990) - Apomixis Newsletter 1 & 2. ORSTOM & Dept. Soil, Crop Sci. Texas A & M Univ. College Station, USA.

SCHAFFNER J.A. (1901) - A contribution to the life history and cytology of *Eryhronium*. *Bot. Gaz.*, **31**, 369-387.

SCHMIT A.C., LAMBERT A.M. (1990) - Microinjected fluorescent phalloidin in vivo reveals the F-actin dinamics and assembly in higher plants mitotic cells. *Plant Cell*, **2**, 129-138.

SCHNARF K. (1936) - Contemporary understanding of embryo sac development among angiosperms. *Bot. Rev.*, **2**, 565-585.

SCHNIEWIND-THIES J. (1901) - Die Reduktion der Chromosomenzahl und die folgenden Kernteilungen in den Embryosackmutterzellen der Angiospermen. Thesis, Jena.

SCHORBATOW L. (1912) - Parthenogenese und apogame Entwicklung bei den Blütenpflanzen. Entwicklungsgeschichtliche Studien an *Taraxacum officinale*. *Trav. Soc. nat. Univ. imp. Kharkhow*, **45**, 15-55.

SCHULTZ K.H. (1822) - Ueber den Kreislauf des Saftes im Schöllkraute und in mehren andern Pflanzen und über die Assimilation des rohen Nahrungsstoffes in den Pflanzen überhaupt. Mikroskopische Beobachtungen und Entdeckungen. Mit einer Vorrede *Links*. Berlin, Dümmler. (1822), 8. XIV, 66 p., 1 tab.

SCHULTZ K.H. (1824) - Ueber den Kreislauf des Saftes in den Pflanzen. Erläuternde Bemerkungen. Berlin, Reimer. (1824), 8. 64 p.

SCHULTZ K.H. (1823-1828) - Die Natur der lebendigen Pflanze. Erweiterung und Bereicherung der Entdeckungen des Kreislaufs im Zusammenhange mit dem ganzen Pflanzenleben nach einer neun Methode dargestellt. (1823-28), 2 Theile. 8 - I: (etiam inscribitur: Die Pflanze und das Pflanzenreich.) Berlin, Reimer. (1823), LII, 693 p., 4 tab. - II: (etiam inscribitur: Die Fortpflanzung und Ernährung der Pflanzen.) Stuttgart, Cotta. (1828), XVI, 624 p., 3 tab.

SCHULTZ H. CH. (1831) - Lettre sur la Circulation des fluides dans les Végétaux, adressée à l'Académie des Sciences de Paris, le 6 septembre 1829. *Ann. Sci. Natur.* (Paris) **22**, 75-79.

SCHULTZ K.H. (1832) - Natürliches System des Pflanzenreichs nach seiner innern Organisation, nebst einer vergleichenden Darstellung der wichtigsten aller früheren künstlichen und natürlichen Pflanzensysteme. Berlin, Hirschwald. (1832), 8. XXVIII, 586 p., 1 tab.

SCHULTZ K.H. (1839) - Sur la circulation et sur les vaisseaux lactifères dans les plantes. Mémoire qui a remporté le grand prix pour 1833. Paris et Berlin, Hirschwald. (1839), 4. 110 p., 23 tab.

SCHULTZ K.H. (1841) - Die Cyklose des Lebenssaftes in den Pflanzen. Herausgegeben von der Kaiserl. Leop. Carol. Akademie der Naturforscher. Breslau und Bonn (1841), 4. XII, 355 p., 31 tab. nigr., 2 tab. col. (cf. Nov. Acta Acad. caes. Leop. Carol. Nat. Cur. vol. XVIII. Supplementum II).

SCHWERE S. (1896) - Zur Entwickelungsgeschichte der Frucht von Taraxacum officinale Web. Ein Beitrag zur Embryologie der Compositen. *Flora*, **82**, 32-66.

SEARS P.B. (1917) - Apomictic parthenogenesis in Taraxacum vulgare and T. laevigatum. *Ohio J. Sci.*, **27**, 97-100.

SEARS P.B. (1922) - Variation in cytology and gross morphology of Taraxacum. *Bot. Gaz.*, **73**, 308-325.

SEIFRIZ W. (1943) - Protoplasmic streaming. *Bot. Rev.*, **9** (2), 50-123.

SESHAVATARAM V. (1977) - The mechanism of apomixis in some forage grasses. In: Recent Trends and Contacts between Cytogenetics, Embryology and Morphology (Ed. V R Dnyansager et al) pp. 323-330, Today & Tomorrow's Printers and Publishers, New Delhi.

SESHAVATHARAM V. (1978-1983) - Embryological Studies on Apomixis in Some Forage Grasses. Indian Council Agric. Res. (Project Report) Andra University, Waltair (India).

SHANTHAMMA C. (1979) - Reproductive behaviour of *Pennisetum macrostachyum* Benth., and a new basic chromosome number in the genus *Pennisetum*. *Bull Torrey Bot. Club*, **106**, 73-78.

SHANTHAMMA C. (1982) - Apomixis in *Cenchrus glaucus* Mudaliar et Sundaraj. *Proc. Indian Acad. Sci. B Part II (Plant Sci)*, **91**, 25-35.

SHANTHAMMA C., NARAYAN K.N. (1977) - Formation of nucellar embryos with total absence of embryo sacs in two species of Gramineae. *Ann. Bot.*, **41**, 469-470.

SHARP L.W. (1921) - An Introduction to Cytology. (1st ed.). Mc-Grow-Hill Book Co. New.

SHARP L.W. (1926) - An Introduction... (2nd ed.). McGrow-Hill Book Co. New York.

SHARP L.W. (1943) - Fundamentals of Cytology. McGrow-Hill Book Co. New York.

SIMPSON C.E., BASHAW E.C. (1969) - Cytology and reproductive characteristics in Pennisetum setaceum. *Am. J. Bot.*, **56**, 31-36.

SINDHE A.N.R. (1976) - Reproductive behaviour in *Pennisetum squamulatum*; Indo-Soviet Symp. on the embryology of crop plants. New Delhi, India. Abst. pp. 41.

SMITH F.H. (1942) - Development of the gametophytes and fertilization in *Camassia*. *Am. J. Bot.*, **29**, 657-663.

SMITH F.H. (1943) - Megagametophyte of *Clintonia*. *Bot. Gaz.*, **105**, 263-267.

SNYDER L.A., HERNANDEZ A.R. & WARMKE H.E. (1955) - The mechanism of apomixis in *Pennisetum ciliare*. *Bot. Gaz.*, **116**, 209-221.

SNYDER L.A. (1957) - Apomixis in *Paspalum secans*. *Am. J. Bot.*, **44**, 318-324.

SODERSTROM T.R., HILU K.W., CAMPBELL C.S., BARKWORTH ed. (1986) - Grass Systematics and Evolution. Smithsonian Inst. Press; Washington D.C.

SOLNTSEVA M.P. (1989) - Classification of the embryo sacs of apomictic plants, including the structural basis of heterogeneity among embryo-sac nuclei. *Apomixis Newsletter*, **1**, 4-10.

STEBBINS G.L. (1932) - Cytology of Antennaria. 2. Parthenogenetic species. *Bot. Gaz.*, **94**, 322-344.

STEBBINS G.L. (1941) - Apomixis in the angiosperms. *Bot. Rev.*, **7**, 507-542.

STEBBINS G.L. (1950) - Variation and evolution in plants. Columbia Univ. Press, New York.

STELLY D.M., PELOQUIN S.J., PALMER R.G., CRANE C.F. (1984) - Mayer's hemalum-methyl salicylate: a stain-clearing technique for observations within whole ovules. *Stain Technol.*, **59**, 155-161.

STELLY D.M., PELOQUIN S.J. (1986) - Formation of 2*n*-mega-gametophytes in diploid tuber-bearing *Solanums*. *Am. J. Bot.*, **73**, *1351-1363.*

STORK H.E., (1920) - Studies in the genus Taraxacum. *Bull. Torrey Bot. Club*, **47**, 199-210.

STOSCH H.A. VON (1972) - La signification cytologique de la «cyclose nucleaire» dans le cycle de vie des Dinoflagellés. *Soc. Bot. Franc. Memoires*, pp. 201-212.

STOVER E.L. (1937) - The embryo-sac of *Eragrostis cilianencis* Link. A new type of embryo-sac and a summary of grass embryo-sac investigation. *Ohio Jour. Sci.*, **37**, 172-181.

STRASBURGER E. (1877) - Über Befruchtung und Zelltheilung. *Jenaische Ztschr. f. Naturw.*, **11**, 435-536.

STRASBURGER E. (1878) - Über Befruchtung und Zelltheilung. Jena: Dabis.

STRASBURGER E. (1884) - Neuere Untersuchungen über den Befruchtungsvorgang bei den Phanerogamen als Grundlage für eine Theorie der Zeugung. Jena.

STRASBURGER E. (1905) - Die Apogamie der Eualchemillen und allgemeinne Gesichtspunkte, die sich aus ihr ergeben. *Jahrb. f. wiss. Bot.*, **41**, 88-164.

STRASBURGER E. (1907) - Die Ontogenie der Zelle seit 1875. *Progressus Rei Botanicae.*, *1*, 1-138.

STREETMAN L.J. (1963a) - Reproduction of the lovegrasses, the genus *Eragrostis*. I. *Wrightia*, **3**, 41-51.

STREETMAN L.J. (1963b) - Reproduction of the lovegrasses, the genus *Eragrostis*. II. *Wrightia*, **3**, 52-60.

SWAMY B.G.L. (1944) - A reinvestigation of the embryo-sac of *Eragrostis cilianencis* Link. *Curr. Sci.*, **13**, 103-104.

TALIAFERRO C.M., BASHAW E.C., (1966) - Inheritance and control of obligate apomixis in breeding buffelgrass, *Pennisetum ciliare. Crop Sci.*, **6**, 473-476.

THISELTON DYER W.T.: cf. Dyer Thiselton W.T.

THOMAS P.T. (1940) - Reproductive versatility in Rubus II. The chromosomes and development. *Journ. Gen.*, **40**, 119-128.

TIKHOMIROV V.N. et al. (ed.) (1990) - *Abstracts XI Intern. Symp. Embryol. Seed Reproduction. Nauka, Leningrad.*

TJIO J.H. et LEVAN A. (1956) - The chromosome number of man. *Hereditas*, **42**, 1-6.

TOTHILL J.C. (1968) - Variation and apomixis in *Heteropogon contortus*, Gramineae. *Bol. Soc. Argent. Bot.*, **12**, 188-201.

TOTHILL J.C., KNOX R.B. (1968) - Reproduction in *Heteropogon contortus*. I. Photoperiodic effects on flowering and sex expression. *Aust. J. agric. Res.*, **19**, 869-78.

TUCKER E.B., ALLEN N.S. (1986) - Intracellular particle motions (cytoplasmic streaming) in staminal hairs of Setcreasea purpurea: effect of azide and low temperature. *Cell Motility and Cytoskeleton*, **6**, 305-313.

VAN LAMMEREN A.A.M., KREIJZER C.I., WILLEMSE M.T.M., KIEFT H. (1985) - Structure and function of the microtubular cytoskeleton during pollen development in Gasteria verrucosa (Mill.). *H. Duval. Planta*, **165**, 1-11.

VAN LAMMEREN A.A.M. (1988) - Structure and function of the microtubular cytoskeleton during endosperm development in wheat: an immunofluorescence study. *Protoplasma*, **146**, 18-27.

VINES S.H.H. (1878) - The «Pro-Embryo» of Chara: An Essay in Morphology. *Journ. of Botany, n.s.*, **7**, 355-363.

VOIGHT P.W. (1971) - Discovery of sexuality in *Eragrostis curvula* (Schrad.) Nees. *Crop. Sci.*, **13**, 424-425.

VOIGHT P.W. & BASHAW E.C. (1972) - Apomixis and sexuality in *Eragrostis curvula. Crop. Sci.*, **12**, 843-847.

VOIGHT P.W., BASHAW E.C. (1976) - Facultative apomixis in *Eragrostis curvula. Crop. Sci.*, **16**, 803-806.

VORSTER T.B., LIEDENBERG H. (1977) - Cytogenetic studies in the *Eragrostis curvula* complex. *Bothalia*, **12** (2) 215-221.

VORSTER T.B., LIEBENBERG H. (1984) - Classification of embryo sacs in Eragrostis curvula Complex. *Bothalia*, **15**, 167-174.

WADA B. (1981) - Mitotic Cell Studies on in vivo Observations XI. Various causes which prevent an elucidation of mitosis. *Cytologia*, **46**, 599-621.

WALKER T.G. (1979) - The Cytogenetics of Ferns. In Dyer A.F., The Experimental Biology of Ferns, pp. 87-131. Academic Press London & New York.

WARMKE H.E. (1952) - Apomixis in grasses, with special reference to *Panicum maximum. Proc. 6th Int. Grassland Cong.*, 209-215.

WARMKE H.E. (1954) - Apomixis in Panicum maximum. *Amer. Jour. Bot.*, **41**, 5-11.

WEBB M.C., GUNNING B.E.S. (1990) - Megasporogenesis in Arabidopsis thaliana, including the microtubular cytoskeleton. XI Inter. Symp. Embryol. Seed Reproduction, p. 211. Nauka, Leningrad.

WEISMANN A. (1872) - Ueber den Einfluss der Isolirung auf die Artbildung. W. Engelmann, Leipzig.

WEISMANN A. (1883) - Ueber die Vererbung. Fischer, Jena.

WEISMANN A. (1885) - Die Continuität des Keimplasma's als Grundlage einer Theorie der Vererbung. Fischer, Jena.

WEISMANN A. (1886) - Über die Bedeutung der Sexuellen Fortpflanzung für die Selectionstheorie. Jena.

WEISMANN A. (1887) - Ueber die Zahl der Richtungskörper und über ihre Bedeutung für die Vererbung. Fischer, Jena.

WEISMANN A. (1889) - Essays upon Heredity and kindred Biological Problems (authorized translation). Clarendon Press, Oxford.

WEISMANN A. (1891) - Amphimixis oder die Vermischung der Individuen. Fisher, Jena.

WEISMANN A. (1892) - Das Keimplasma. Eine Theorie von der Vererbung. Fisher, Jena.

WHITE M.J.D. (1935) - Eine Neue Form von Tetraploidie nach Röntgenbestrahlung. *Naturwissenschaften*, **24**, 390-391.

WILLEMSE M.T.M., VAN WENT J.L. (1984) - The female gametophyte. In: Embryology of angiosperms. *Ed.* B.M. Johri. Springer-Verlag, New York, pp. 159-196.

WILLEMSE M.T.M., VAN VENT J.L. eds (1985) - Sexual reproduction in seed plants, ferns and mosses. Wageningen: Pudoc.

WILMS H.J. (1981) - Ultrastructure of the developing embryo sac of spinach. *Acta Bot. Neerl.*, **30**, 75-99.

WILSON E.B. (1906) - The Cell in Development and Inheritance. Macmillan Co. New York, London (2nd ed.).

WINKLER H. (1904) - Über Parthenogenesis bei Wikstroemia indica (L.) C. A. Mey. *Ber. d. deutsch. Bot. Gesell.*, **22**, 573-580.

WINKLER H. (1906) - Ueber Parthenogenesis bei Wikstroemia indica (L.) C.A. Mey. *Ann. Jard. Bot. Buitenzorg, Ser. 2*, **5**, 208-274.

WINKLER H. (1908) - Über Parthenogenesis und Apogamie in Pflanzenreich. *Prog. Rei. Bot. Jena*, **2**, 293-454.

WINKLER H. (1920) - Verbreitung und Ursache der Parthenogenesis im Pflanzenreiche. Jena.

WINKLER H. (1934) - Fortpflanzung der Gewächse. In Dittler et al. ed. Handwörterbuch der Natur wissenschaften, 2, Aufl., 451-461.

WINKLER H. (1942) - Über den Biontenwechsel und die Abweichungen von seinen normalen verlauf. *Planta*, **33**, 1-90.

WOODFRUFF L.L., ERDMANN R. (1914) - A normal periódic reorganization process without cell fusion in Paramaecium. *Journ. Exper. Zool.*, **17**, 425-518.

YOUNG B.A., SCHULZ-SCHAEFFER J. & CARROL T.W. (1979) - Anther and pollen development in male-sterile intermediate wheat grass plants derived from wheat X wheat grass hybrids. *Can. J. Bot.*, **57**, 602-618.

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