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Caryoneme alternative to chromosome and a new caryological nomenclature

Battaglia Emilio

Dipartimento di Scienze Botaniche, Università di Pisa, via L. Ghini 5, 56126 Pisa, Italy.

Dedicated to the memory of Prof. Charles Berger S. J. (1901-1966)

Abstract — The author has been disappointed by the illogicality of the present chromatin –chromosome terminology based on two terms both inappropriately ascribed to a non-coloured state. Since such terms belong to the caryological terminology this consideration suggests the choice of the prefix caryo in the place of the chromo – chromato prefixes.
As regards the question of a term alternative to chromatin, since the author has already coined the term *caryoneme* (cf. Battaglia 1993, p. 89) as a term strictly pertinent to the chromosome morphology, analogously he also proposes caryonematin as an alternative to the present chromatin. However, the author considers caryonematin nothing else than a provisional term waiting for a general re-evaluation of the chromo – chromatin terminology.
Since the choice of the prefix caryo suggests the synonymy caryosome = chromosome, the author does not support a modern re-use or re-definition of caryosome. On the contrary the author supports a wide terminological system based on caryoneme and related compound terms. Thus, for instance, given that the chromatid is the unit of the chromosome organization, reproduction, rearrangement (crossing-over) and redistribution, the author proposes caryoneme as an alternative to chromatid.
Consequently, since the mitotic prophase chromosome is a di-chromatid structure, the author in this case proposes the term caryodineme. Once established the interpretation of caryodineme, the chromosome strandedness should be consequently redefined in agreement with the classic series of the prefixes mono-, di-, tetra-, octa-… poly- as follows:
caryomononeme = chromatid = mitotic anaphase chromosome,
caryodineme = mitotic prophase chromosome,
caryotetraneme = diplochromosome,
caryooctaneme = quadruplochromosome,
caryopolyneme = polychromosome.
Furthermore, for the sake of duly documentation of the terminological priorities is included in the present paper a detailed list (cf. Tabs. 1-10) of chromatin – chromosome compound or derivative terms, together with obsolete synonyms, thus avoiding their future re-coining by unaware modern researchers.
Further, owing to their historical value and cytological interest, many terms such as mitosis (wide sense), polyploidy, polyteny, polysomaty have been critically discussed.
Lastly, a caryological presentation of the finest morphological details of the di-, tetra- and caryooctaneme divisions closes this terminological and documentary account.

Key words: amitosis, caryokinesis, caryoneme, caryomononeme, caryodineme, caryotetraneme, caryooctaneme, caryopolyneme, caryonematin, caryotin, chromatin, chromonema, chromosome, endomitosis, hemiosis, meiosis, mitosis, mono-, diplo-, auto- allosomes, polyneme, polyploidy, polysomaty, polyteny.

INTRODUCTION

In earlier terminological papers the author has already pointed out to the cytological community that many of the most familiar terms are inadequate or illogical or, in some cases, etymologically incorrect so that they should be replaced by more adequate alternatives suggested by the present scientific progress.

The author has been particularly disappointed by the illogicality of the present chromosomal (chromatin-chromosome) terminology based on, or inferred by, two terms, Chromatin (Flemming 1880a) and Chromosom (Waldeyer 1888), both inappropriately ascribed to a basically non coloured state.

An additional consideration highlights the purpose of the present critical analysis of such an inadequacy. There is no doubt that the classic cytological terminology (see Tab. 1), as advanced in the years 1874-1899 and greatly increased in the first half of the last century, today does not fit at all features, morphologies and structures acquired by the modern biochemical progress.

Obviously, the present author realizes that a detailed analysis of all chromosomal terminology and the proposal of an alternative system is a complex task which cannot be confined to a single account nor supported only by individual considerations. Therefore the present account is nothing else than a preliminary approach in need of further discussion in future congresses on cytogenetic terminology.

Last but not least, it has been considered useful to include in the present account a list (cf. Tabs. 1-10) of main cytogenetic terms, synonyms and obsolete definitions with the purpose of avoiding their future re-coining or proposal by unaware modern researchers.

Cytological questions analyzed and documented.

A[1]. The choice of the prefix caryo- alternative to the present chromo-, chromato- prefixes.

A[2]. The classic chromatin – chromosome terminology from 1880 to 1894: Flemming (1880), Strasburger (1882), Pfitzner (1881; 1883; 1886), Waldeyer (1888), Heidenhain (1894).

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A[5]. Chromatin and heterochromatin criticized by Barber and Callan (1950).

A[6]. Karyotin (Lundegårdh 1910; 1912) and caryonematin.

A[7]. Karyosom (-en): Ogata (1883) and Platner (1886c;d).

A[8]. Karyomiten (Schiefferdecker in Schiefferdecker and Kossel 1891).

B[1]. Criticism of Flemming's (1878-1882) mitotic terminology. a) Mitom, Karyomitom, Cytomitom, Karyomitosis …amitotische Theilung… mitosen.

B[2]. Amitose (Lowit 1890).

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c) Duplication: Bridges (1919).
d) Endo-duplication and exo-duplication: Jorgensen (1928).
e) Endoreduplication: Levan and Hauschka (1953).

F[1]. Centromere, kinetocentre and kinetochore. A linguistic comment.

F[2]. Chromosome reduplication, segregation and cell cycle. Some data on the present terminologies.

The kinetics of chromosome reduplication and segregation have been widely investigated by cytologists. The main data on this field deserves a short discussion restricted here to the priorities and to the linguistic criticism. Historical considerations also suggest subdividing the terminological discussion into two separate groups:

F[2]**-a**. The classic kinase, kinetin and kinesin terminologies:
Kinase: Pawlow 1898.
Kinetin: Miller, Skoog, von Saltza and Strong 1955.
Kinesin: Vale, Reese and Sheetz 1985.

F[2]**-b.** *The new terms proposed by the modern literature.*
Chromokinesin: Wang & Adler 1995.
Clathrin: Pearse 1975.

Kleisin: GRUBER *et al*. 2003.
Monopolin: TOTH *et al*. 2000.
Securin: TOTH *et al*. 1999.
Separase: ÖSTERGREN & ANDERSON 1973; UHLMANN *et al*. 2000.
Separin: CIOSK *et al*. 1998.
Shugoshin: KITAJIMA, KAWASHIMA, WATANABE 2004.

Condensin and cohesin:

Borealin: GASSMANN *et al*. 2004.
Bromodomain: TAMKUN *et al*. 1992.
Calcineurin: KLEE, CROUCH, KRINKS 1979.
Calcitonin: COPP, DAVIDSON, CHENEY 1961.
Calmodulin: CHEUNG, LYNCH, WALLACE 1978.
Calpain: MURACHI *et al*. 1980.
Cohesin: MICHAELIS *et al*. october 1997: "Cohesins: chromosomal proteins that prevent premature separation of sister chromatids".
Chromodomain and Chromo box: PARO & HOGNESS 1991 (chromo = chr + o + mo = chromatin organization modifier).
Condensin: HIRANO *et al*. may 1997: "Condensin, Chromosome Condensation, Protein Complexes Containing XCAP-C, XCAP-E and a *Xenopus* Homolog of the *Drosophila* Barren Protein".
Cyclomere 1972, Cyclin 1983 and Cyclosome 1995:
Cyclomere: ENGELHARDT & PUSA 1972.
Cyclin: EVANS *et al*. 1983.
Cyclosome: SADAKIN *et al*. 1995.
Izumo: INOUE *et al*. 2005.
Nesprin: ZHANG *et al.* 2001.
Nestin: LENDAHL, ZIMMERMAN, MCKAY 1990.
Netrins: SERAFINI & KENNEDY 1994; KENNEDY *et al*. 1994.
Plectin: WICHE *et al*. 1982.
Pontin: BAUER, HUBER, KEMLER 1998.
Reptin: BAUER *et al*. 2000.
Selectin: BEVILACQUA *et al*. 1991.
Syntaxin: BENNETT, CALAKOS, SCHELLER 1992.
The eph gene, eph protein: HIRAI *et al*. 1987 and the Ephrins: Eph Nomenclature Committee, cf. CELL, 1997.
Tubulin: MOHRI 1968.

F[3]. The mono- polychromosome terminology. Older historical data:
a) Monochromosomic and polychromosomic: GREGOIRE and WYGAERTS (1910). CHODAT (1925).
b) Monochromosome (WINGE 1917).
c) Haplochromosome: MORGAN (1924), CHODAT (1925).
d) Diplochromosome: MORGAN (1924); diplochromosome and monochromosome of WHITE (1935a; b), polychromosome and diplobivalent of BARBER (1940).
e) Tetradi somatiche: DELLA VALLE (1907)
f) Tetrachromosome: BERGER and WITKUS (1946)
g) Quadruplochromosome: BIESELE, POYNER and PAINTER (1942).

G. Soma terms in cytology
a) Historical old terms (1888-1899).
b) Soma compound terms pertinent to the classic chromosome terminology: MONTGOMERY (1904; 1905).
c) The mono, di, tri, … endekasome and the simplex, duplex (etc.) system of BLAKESLEE (1921).

H. Endomitosis: history and terminology.
a) Historical priority (HEIDENHAIN 1919: endomitose, endoamitose) and compound derivatives.
b) The endomitosis of GEITLER (1939).
c) Cytological literature from 1939 to 1945:

- Pfuhl (1939: Die mitotischen Teilungen der Leberzellen im zusammenhang mit den allgemeinen Fragen über Mitose und Amitose).
- Painter and Reindorp (1939: Endomitosis in the nurse cells of the ovary of Drosophila melanogaster).
- D'Ancona (1939: Grandezze nuclear e poliploidismo nelle cellule somatiche).
- Huskins (1942: Structural differentiation of the nucleus).
- Biesele, Poyner and Painter (1942: Nuclear phenomena in cancer).
- White (1942: Nucleus, chromosomes and genes), in Bourne, G. Cytology and Cell biology, Chapter V, 1942. Oxford.
- Painter (1943: Cell growth and nucleic acids in the pollen of *Rhoeo discolor*).
- Favarger (1944: Sur quelques phénomènes de pseudo- appariement des chromosomes dans les tissues somatiques; 1946: Recherches caryologiques sur la sous-famille de Silénoïdées).
- Witkus (1945: Endomitotic tapetal cell divisions in *Spinacia*).
- Re-evaluation of the papers of Winge (1914: The pollination and fertilization processes in *Humulus lupulus* L and *H. japonicas* Sieb. Et Zucc.; 1917: The Chromosomes, their number and general importance).
- Criticism of endomitosis (Geitler) and alternative terminology: endocaryopseudomitosis, endocaryopseudoprophase (etc.), endocaryorestitution cycle, see also nucleo di endorestituzione (Battaglia 1945).
- Endomitose and exomitose: Resende (1956), Levan and Müntzing (1963), Resende (1964).

I. Polyploidy.

a) Strasburger's priorities (1905-1910).
b) Earlier historical data (Delpino 1875-1903).
c) Synhaploid and syndiploid (Strasburger 1907).
d) Octoploid (Strasburger 1910) and octaploid.
e) The terminology of Nemec (1910).
f) The terminology of Langlet (1927a;b).
g) Further historical data.

J. Polysomaty: Langlet (1927a,b).

K. Aneusomaty: Allen in Duncan (1945).

L. Endopolyploidy: White (1942; 1945).

M. Ploidy, taxoploidy and somatoploidy.

N. Polytene: Koller (1935), polyneme, syn- polyneme, caryopolynemy, genopolynemy.

O. Documentation. Caryodineme (monochromosomes), caryotetradineme (diplochromosome), caryooctaneme (quadruplochromosome) divisions (kineses) in the root-tips of *Scilla peruviana* L. (Liliaceae).

Cytological questions analyzed and documented

A[1]. *The choice of the prefix caryo- alternative to the present chromo- and chromato- prefixes* - From this point of view the author believes that there exists a logical alternative alone namely: the chromosome is morphologically the main nuclear body and this consideration clearly suggests the choice of the prefix caryo- in place of the current chromo- and chromato- prefixes. For the sake of historical accuracy a detailed analysis of the main chromosome terminology will be presented in the following chapters together with an adequate documentation today still lacking, or misquoted by the cytological literature.

A[2]. *The classic chromatin – chromosome terminology from 1880 to 1894: Flemming (1880), Strasburger (1882), Pfitzner (1881; 1883; 1886), Waldeyer (1888), Heidenhain (1894)* - As early as 1880 Walter Flemming initiated the chromatin terminology by proposing Chromatin and Achromatin[1].

[1] Flemming (1880a, pp. 1576-1580) proposed Chromatin… für die tingirbare Substanz des Kerns and Achromatin… für die nicht farbbare Substanz des Kerns.

FLEMMING (1880) was shortly followed by PFITZNER who coined Parachromatin (1883), Prochromatin (1883) and Pseudochromatin (1886). A few years later HEIDENHAIN (1894) increased the chromatin series coining Basichromatin and Oxychromatin.
The chromosome terminology started with the term Chromosomata coined by STRASBURGER (1882) and shortened to Chromosom(en) by WALDEYER (1888). WALDEYER also coined Chromosoma = Chromatinkugeln.

A³. *The chromatin and the chromato – chromo terminology criticized by FOL (1891a: La chromolâtrie s'était si bien emparée des esprits…) and the new term Chromomere* - The abuse and misuse of the chromatin terminology did not escape the firm disapproval of FOL. His criticism is worthy of quotation because FOL, incidentally and let me say unexpectedly, also coined Chromomere, namely, cf. FOL 1891a, pp. 396-397:
"A force d'employer des colorations de plus en plus électives, à force d'eclaircir les tissues en les imprégnant de résines, on en est venu à ne plus voir que la chromatine, à lui attribuer toutes les fonctions et toutes le vertus et à considrer tout le reste comme un accessoire insignifiant. Pfitzner[1] est l'auteur qui personnifie en quelque sorte l'apogèe de cette aberration, contre la quelle j'ai déja protesté[2] et dont on est en train de revenir. Pour cet auteur, les corps ronds ou filiformes qui portent la sustance chromatique, les chromoméres en un mot, sont la quintescence de la vie cellulaire et le *primum movens* des phénomènes de division. Ils se meuvent et se scindent spontanément et l'amphiaster n'est qu'un phénomène accessoire et méme contestable; car comment attribuer une importance quelconque a des structures qui ne retiennent pas les couleurs d'aniline et qui pàlissent dans le baume de Canada? Ce courant d'idées peut se résumer en un mot: c'est la *théorie chromocinétique*.
Cette théorie a régné pendant longtemps et à tel point que, quand des auteurs plus récents sont revenue à la théorie centrocinétique, ils ont cru faire une grande découverte. La chromolàtrie s'était si bien emparée des esprits que la nomenclature qui répond à l'idée de la centrocinése a pu étre considérée comme tombée en désuétude et ses mots comme devenus disponibles. Je ne pourrais pas m'expliquer autrement comment FLEMMING a po prendre le terme d'aster qui avait trouvé son emploi en quelque sorte indiqué d'avance, pour essayer de l'adapter à une structure toute différente à laquelle il ne convient nullement[3]. Ce procédé n'a guére trouvé d'approbateurs.

[1] Pfitzner W. Beitraege, etc. Archiv. f. mikr. Anat. Tome 22 p. 616. 1883.
[2] H. Fol. Actualités histogéniques. Revue médic. Suisse romande, Annéa 4, n. 2, 15 février 1884.
[3] Il n'est pas d'usage entre gens civilisés de prendre un terme scientifique accepté dans un certain gens, pour l'appliquer à une chose toute différente – à moins d'avoir démontré 1° qu'il ne convenait pas à son usage primitif et, 2° qu'il convient au contraire à un usage nouveau. C'est tout le contraire qu'à fait Flemming. Il n'a pas démontré que le mot d'"aster" ne convenait pas pour désigner cette partie de la figure cinétique, il n'y aurait pas réussi. Mais il l'a emplyé pour désigner une autre chose déjà nommée"

A⁴. *Euchromatin and heterochromatin of HEITZ (1928)* - The chromatin terminology began a revival in the year 1928 when Emil Heitz proposed the historical terms euchromatin and heterochromatin. HEITZ's morphological distinction between euchromatin and heterochromatin, although anticipated by the concept of heteropyknotisch of GUTHERZ (1907), was accepted by all cytologists. In modern times, an additional series of chromatin compounds was coined, e.g. olisterochromatin (RESENDE 1945), centrochromatin (LINDEGREN 1949), fisiocromatina (GEROLA 1950), plasmochromatin (SCHRADER and LEUCHTENBERGER 1950), orthochromatin (BRINK 1960), etc., cf. Tab. 4.

A⁵. *Chromatin and heterochromatin criticized by Barber and Callan (1950)* - Sixty years after Fol's criticisms a second neat refusal of the couplet chromatin-heterochromatin appeared in a joint account of BARBER and CALLAN (1950), and namely, cf. BARBER and CALLAN (1950, pp. 174-175):
" The purpose of this letter is to suggest that the use of the word "heterochromatin" in cytological and genetical literature is undesirable.
The ending in "-in" suggests strongly that the name applies to a single chemical substance or to a a group of closely allied substances (for example, adrenalin, mucin, chitin).
The word "chromatin" is subject to nearly the same criticism as heterochromatin; but it was introduced long ago, at a time when the invention of such words may have been helpful. It is commonly used

nowadays in the sense of a substance containing, consisting of, or showing the staining and other reactions of deoxypentose nucleic acid. In the present state of biochemical and genetical knowledge, it seems doubtful whether it continues to serve as a useful purpose."

As a matter of fact, BARBER & CALLAN's criticism was fully overlooked by the following scientific literature and this, likely, owing to the difficulty of finding a convincing system alternative to a terminological state of affairs so much intricate and unanimously accepted by the biological community mainly for historical reasons.

Furthermore, in modern years, what the author considers the chromatin-chromosome terminological chaos, has been once more complicated by the establishment of a parallel terminology arisen by the abuse and (or) misuse of the two equivalent prefixes nucleo- (the combining form of nucle-o, from the Latin *nucleus*) and karyo- or caryo- (the corresponding combining form from the Greek *karyon*). These two prefixes, followed by, for instance, the word *soma* (body) allow to coin the compound terms nucleosoma and caryosoma. Since they are, respectively, the hybrid (Latin-Greek) and the pure form (Greek-Greek) of the same term, they should, logically, carry the same meaning that is "nuclear body".

On the contrary and very disappointingly, because it occurs in the modern biological literature, to the terms nucleosome and karyosome have been ascribed two quite different meanings (see criticism in BATTAGLIA 2000).

A[6]. *Karyotin (LUNDEGÅRD 1910; 1912) and caryonematin* - As early as 1910 LUNDEGÅRD proposed Karyotin (caryotin in LUNDEGÅRD 1912) as a synonym for the usual chromatin.

The author refuses this term because it refers to the nucleus and not to the chromosome as such. As regards the choice of an alternative term, since the author already coined Karyoneme (BATTAGLIA 1993), almost automatically he also proposes caryonematin. However, the author considers caryonematin nothing else than a provisional term waiting for a general re-evaluation of the chromo-chromatin terminology together with a contemporaneous analysis of the most modern terms (cf. Cohesin, condensin etc.) coined in relation to the kinetics of the chromosome segregation (see chapter G[2]).

A[7]. *Karyosome(en)*: OGATA (1883) and PLATNER (1886c; d) - The classic term Karyosome(en) has been coined by OGATA (1883) who distinguished in the nucleus the Kernkörperchen which stain with Haematoxylin; or Karyosomen and the Kernkörperchen which stain with Eosin, or Plasmosomen.

Three years later PLATNER (1886c, p. 53; 1886d, p. 354) re-described "Die Karyosomen" as follows, cf. PLATNER 1886c, p. 53:

"Der Kopf der Spermatosoms, um welchen sich, wie erwähnt, ein heller Hof, umgeben von einer Strahlenfigur gebildet hatte, nährt sich dem Elkern immer mehr, wobei ihm der Schwanz nachfolgt, also mit einem immer grössern Theil seiner Länge innerhalb des Dotters zu liegen kommt. In dem Elkern sind inzwischen einige Veränderungen vor sich gegangen, indem die in demselben befindlichen Kernelemente ihre gleichmässige Färbung verloren haben und völlig rund geworden sind. Es sei mir verstattet sie Karyosomen zu nennen."

cf. PLATNER 1886d, p. 354:

"Es bilden diese sphärischen Körper "Karyosomen", wie ich sie früher genannt habe, jetzt die einzigen geformten Bestandteils des Kernes. Ich konnte mich wenigstens, trotz der sorgfältigsten Nachforschungen, nicht von der Gegenwart des "reticulum plastinien", aus welchem Carnoy die Spindelfasern hervorgehen lässt, überzeugen."

In a short time, caryosome became widely known in Cytology, although different meanings were ascribed to it. In this context, the entry Karyosome quoted by the first edition (1896) of WILSON's The Cell, deserves citation:

"Ka'ryosome (καρυου, nut, nucleus; σωμα, body). 1. Nucleoli of he "net-knot" type, staining with nuclear dyes, as opposed to plasmosomes or true nucleoli. (OGATA 1883). 2. The same as chromosome., (PLATNER 1886). 3. Caryosome. The cell-nucleus. (WATASE 1894)."

After 1896, the term *karyosom* (also spelled karyosome and karyosoma) became a widely accepted term also in Protist cytology since LABBÉ (1896), shortly followed by SCHAUDINN and SIEDLECKI (cf. SCHAUDINN and SIEDLECKI 1897; SIEDLECKI 1898; 1899; SCHAUDINN 1900) who chose the term *karyosom* (*karyosome* in LABBÉ's paper), giving it the nucleolar meaning previously assigned to

the *Binnenkörper* of RHUMBLER (1893, p. 329) and to the *Nucleolo-Centrosoma* (also Nucleolo-Centrosom) of KEUTEN (1895, p. 219). With such a meaning, *karyosom* can be found in most of the cytological papers of the protistologists in the years from 1897 to 1905.

After 1905, the term *karyosom*, still retaining a nucleolar meaning, became frequently spelled as *caryosom* or *caryosome*. Thus *Caryosom* (*Nucleolocentrosom*) can be found in HARTMANN and PROWAZEK (1907), *grains caryosomiens* in LÉGER (1907), *caryosommitose* in ROSENBUSCH (1909), *caryosome* in CHATTON (1910), *Pseudocaryosomkerne* in HARTMANN (1911), *caryosompromitose* in BĚLAR (1915) etc.

As regards the different meanings given to the term *karyosome* in more recent years the following entries occur in some of most well-known dictionaries, namely:

"Cf. HENDERSON & HENDERSON (1953, p. 235): Karyosome (kàr'iòsòm) n. [Gk. *Karyon*, nucleus; *soma*, body.] A nucleolus of the 'net-knot' type; a chromosome; a special aggregation of chromatin in resting nucleus; the cell nucleus itself; cf. plasmosome.

Cf. KING & STANSFIELD (1990, p. 173): Karyosome a Feulgen-positive body seen in the nucleus of the Drosophila oocyte during stages 3-13. During stages 3-5, it contains synaptonemal complexes.

Cf. DORLAND's Ill. Med. Dictionary (2000, p. 875): karyo·somo … [karyo- + some] any of the condensed irregular clumps of chromatin dispersed in the chromatin network of a cell; called also *false nucleolus*, *chromatin nucleolus*, *chromatin reservoir* and *chromocenter*."

Conclusively: since caryosome etymologically means nuclear body, this term might be chosen only to indicate nuclear bodies in wide sense.

A[8]. *Karyomiten: Schiefferdecker* (in SCHIEFFERDECKER and KOSSEL 1891) - SCHIEFFERDECKER (in SCHIEFFERDECKER and KOSSEL 1891, p. 20) proposed Karyomiten in the place of the current German terms Chromosomen Schleifen, Fäden etc.

Unexpectedly, this term escaped the attention of biologists and was not adopted. For instance the first edition of the well-known text-book by E.B. WILSON (1896, p. 337) quotes Karyomite, the same as chromosome [? SCHIEFFERDECKER], but this term was not recorded in the later editions of this classic text-book. Today caryomite cannot be found in any cytological text-book or dictionary.

B[1]. *Criticism of FLEMMING's (1878-1882) mitotic terminology* - FLEMMING, in 1878-79 stated the concept of direct and indirect cell division (directe, indirecte Kernvermehrung in 1878; directe, indirect Kerntheilung in 1879) and few years later in his famous book "Zellsubstanz, Kern und Zelltheilung" (FLEMMING 1882) proposed Karyomitosis and mitosen together with other terms which represent the basis of the classic mitotic terminology.

Many terms and definitions owing to high historic interest require a comment and are summarized as follows.

a) *Mitom, Karyomitom, Cytomiton, Karyomitosis, amitotische Theilung Mitosen* - These terms were proposed on the basis of the presumed fibrillary nature of the "differenten substanzen in der Zelle". *Mitom* is the fibrillar material and is further more specified as *Karyomitom*, if relative to the nucleus, and *Cytomitom*, if relative to the Cytoplasma. The terms Kariomitosis, amitotische Theilung, Mitosen, because never fully mentioned by the cytological literature deserve large quotation, cf. FLEMMING (1882, pp. 375-376).

"Durch die von mir selbst empfohlenen Namen "indirecte und directe Kerntheilung" bin ich überhaupt nicht sehr befriedigt, da sie lang sind und über das Wesen der Theilung wenig aussagen. Einstweilen thun sie ihren Dienst, wie der Anschluss anderer Forscher zeigt. Dasselbe gilt für den Ausdruck Karyokinesis (SCHLEICHER) für die indirecte Kerntheilungen oder für die Metamorphose dabei. Er ist schon so weit in Gebrauch, dass ich ihn hier dem Verständnis zu Liebe viel angewendet habe. Aber er ist der Verbesserung fähig, denn einmal bezeichnet er ja nur "Bewegung im oder am Kern", und eine solche findet auch bei der directen Kerntheilung statt; sodann sagt er über die nähere Form der Bewegungen und bewegten Theile nicht aus.

Ich würde deshalb vorschlagen, ihn durch Karyomitosis zu ersetzen, welches kurz aus drückt: "Fadenmetamorphose im Kern."

Die indirecte Kerntheilung (resp. Zelltheilung) könnte dann kurz Mitoschisis, die directe etwa Holoschisis heissen, oder, wo man besonders ausdrücken will, dass hier Fadenmetamorphose im Kern fehlt, amitotische Theilung.

Man würde dann statt des langen Wortes "Kerntheilungfiguren" ferner kurz "Mitosen" brauchen können.
Historisch verdient übrigens den Vorrang der Vorschlag MAYZEL's: "typische Kerntheilung" für das, was in diesem Buch indirecte genannt ist. - Ich würde den Name Mitosis nur deshalb vorziehen, weil "typische Kerntheilung" nichts weiter über das Wesen des Processes aussagt, während "Karyomitosis" doch schon ausdrückt, dass dabei ein besonderer Vorgang am Fadenwerk des Kerns erfolgt."

B². *Amitose* (Lowit 1890) - The term amitose (in place of amitotische Theilung, FLEMMING 1882) can be found in LOWIT (1890) shortly followed by FLEMMING himself (1891).

B³. *Terms alternative to mitosis and amitosis. Caryokinesis and caryoneme kinesis* - It is necessary to recall that the term karyokinesis of SCHLEICHER (1878) was a few years later followed by other alternative terms proposed by CARNOY (1885) and by WHITMAN (1887). CARNOY (1885) proposed the following system:
- Cytodiérèse (HENNEGUY 1882): caryodiérèese + plasmodiérèse;
- Division cinétique = cinèse;
- Division acinétique: sténose (etranglement);
- Caryodiérèse = caryocinèse and caryosténose;
- Plasmodiérèse = plasmocinèse and plasmosténose;

Last but not least, WHITMAN (1887) coined the term cytokinesis, to indicate the normal cell division. The author here proposes an alternative terminology, that is the couplet caryoneme kinesis[1] and caryodieresis justified as follows:
Given that caryokinesis etymologically means nuclear movement, this term is questionably ascribed to mitosis which is a cytological feature consisting of a complex chromosome kinesis (reduplication, condensation and division of the chromosomes).
Therefore the author proposes caryoneme kinesis as a term alternative to the FLEMMING's mitosis. A real nuclear movement, indeed, occurs in the case of FLEMMING's amitosis, which was more adequately qualified caryodiérèse by CARNOY (1885). Thus the author considers caryodieresis as an adequate alternative to the FLEMMING's amitosis.
In any case to caryokinesis and on etymological basis, should be ascribed the meaning of nuclear kinetics, in wide sense. Thus, this term could include all forms of regular kinesis (eucaryokinesis) and all forms of irregular kinesis (aneucaryokinesis).

C. *The nema and tene terminologies. Historical data* - As early as 1896, F. ROSEN coined the term dolichonema describing the division of the spore mother cell of *Psilotum triquetrum*. Since this term has been widely ignored by the cytological literature, it deserves documentation: ROSEN (1896, p. 296): "Wenn aber die Bildung der beschriebene langen Kernfäden keinem Spiremstadum darstellt, überhaupt in den Lauf einer normalen Karyokinese nicht hineingehört, so wird es nöthig sein, einen neuen Ausdruck einzuführen, der dieses Stadium des Kerns bezeichnet. Da fragliche Fäden sich von der gewöhnlichen Kernfäden vor allen Dingen durch ihre bedeutendere Länge auszeichnen, so scheint mir der Ausdruck "Dolichonema-Stadium" passend."
Contemporaneously HENRY DIXON (1895) published a first paper entitled "On the chromosomes of *Lilium longiflorum*" and completed the cytological investigation of this matter publishing in 1901 a second account entitled "On the first mitosis of the spore mother cells of *Lilium*". The first paper (1895) is without any terminological interest but the second one is of highest historical and terminological value because here DIXON redefined dolichonema and contemporaneously proposed the new term strepsinema: DIXON (1901, pp. 129-130): "The stages of the process of mitosis in the spore-mother cells acknowledged by all observers, may be briefly summarized as follows:-
1 - The "dolichonema" stage, Plate VII, fig. 1,- The large nucleus of the spore-mother- cells is occupied by an enormously long and attenuate thread, consisting of a single series of chromatin granules (the chromomeres) imbedded, in the lignin matrix. This thread presents few or no anastomoses.
2 - In the next stage (fig. 2) the nucleus is in what I would suggest to call the "strepsinema" condi-

[1] Karyonema as a term pertinent to the chromosomal structure has been proposed by the author (BATTAGLIA 1993).

tion. The chromatin appears in much the same condition as in the preceding stage, except that in many places it may be seen that two portions of the thread are more or less loosely twisted together. The later this stage is observed, the thicker the chromatin thread appears, and the greater the amount of the thread so twisted."

About at that time, HANS VON WINIWARTER (1900, investigating the chromosome morphology of the "heterotypic division" coined several historical terms, that is:

diplotene cf. WINIWARTER 1900, p. 70
leptotene cf. WINIWARTER 1900, p. 55
pachytene cf.WINIWARTER 1900, p. 63
synaptene cf. WINIWARTER 1900, p. 54

There are many excellent cytological papers regarding this matter, published from 1903 to 1910. At least the following accounts are worthy of quotation.

BERGHS (1904 a; b). This author recorded and commented the couplet dolichonema and strepsinema.

BERGHS (1904 a, pp. 175-176):

"DIXON, o1, reprend plus longuement l'étude des cinèses polliniques de *Lilium longiflorum*. Elle lui fait adopter le schéma suivant:

1° Le dolichonema se dégage du réseau remplissant le noyau du microsporocyte. C'est un filament mince, énormément long, portant sur un substratum lininien une série unique de chromomères.

2° Sans changer de nature, il se dispose en *strepsinema.* DIXON désigne par là la disposition de l'élément chromatique consistant en ce que celui-ci est formé de filaments appairés et entrelacés. D'après l'auteur, le dolichonema se replierait sur lui-même en différents endroits; les portions ainsi rapprochées s'accoleraient deux par deux et s'entrelaceraient. C'est par ce moyen que se formerait le *strepsinema*.

3° La segmentation trasversale découpe ensuite le nombre réduit de chromosomes. Ceux-ci ont la forme d'anses ou de boucles, dont chaque branche représente une partie du dolichonema. »

BERGHS (1904 a, p. 181):

« Pour DIXON, d'abord, le passage du dolichonema au strepsinema se fait, ainsi que nous l'avons rappelé, par recourbement et rapprochement et non pas par division longitudinale.

Avant d'entamer la discussion, il convient de faire une remarque concernant le sens et l'emploi du mot dolichonema. Employé par DIXON et par d'autres auteurs, il ne désigne pas absolument le même stade. En effect, DIXON fait intervenir le synapsis vers la fin du stade dolichonema, alors que précisément d'autres nomment dolichonema le filament qui sort de synapsis (*). Or, vu la longue durée de ce stade de contraction et l'épaississement que le filament y subit,- épaississement dont le mécanisme n'est pas connu, - on pourrait se demander si le dolichonema que DIXON déclare se recourber est bien celui que d'autres auteurs disent se cliver.

BERGHS (1904 b, p. 389): «Si on examine successivement les différents noyaux de la loge, on assiste au déroulement progressif du filament contracté: les anses s'écartent de nouveau, envahissent tout le noyau, et bientôt présentent l'aspect si caractéristique du spirème, FIG. 18. C'est le "noyau pachytène" décrit par VON WINIWARTER.

Ce spirème subit ensuite les transformation que nous avons décrites dans notre premier mémoire. Il se "dédouble longitudinalement" donnant naissance ainsi au strepsinema (noyaux diplotènes de VON WINIWARTER), FIG. 20 et 21. Les "moitiés longitudinales" sont les chromosomes-filles de la cinèse hétérotypique. »

JANSSENS (1905). This author proposed three new terms that is auxospireme, amphitene and prostrepsinema.

JANSSENS (1905, p. 382):

« 3° Résolution des blocs chromatiques du stade de repos et apparition de filaments minces donnant au noyau un *aspect spirématique* caractéristique. C'est un stade analogue au *leptotene* de VON WINIWARTER, mais le filament spirématique est moins dégagé. Nous l'appellerons stade du spirème des auxocytes ou *auxospirème*, PHOTOGR. 1.

5° Stade de la première formation des filaments épais. A ce stade, on trouve des filaments épais du côté de la sphère,que nous appellerons le pole proximal du noyau. On continue à observer des filaments minces de l'autre coté ou pole distal. Nous l'appelons le stade du bouquet *amphitène,* PHOTOGR. 3 et 4 en partie.»

Janssens (1905, p. 383):
« III.Après cela, le bouquet se déforme.
1° On voit apparaitre d'abord au pole distal du noyau un clivage longitudinal des anses. Ce stade dure quelche temps et s'achemine lentement vers la séparation complète des anses en deux moitiés longitudinales. Nous le désignons par le nom de *prostrepsinema*, Photogr. 13 et 14.
2° Nous réservons le nom de *strepsinema*, adopté déja par les botanistes, au stade où cette division est complète. Ce dernier correspond au stade des noyaux *diplotènes* de von Winiwarter, Photogr. 15, 16 et la moitié de 17. »
Gregoire (1907). This paper entitled "La Formation des gemini hétérotypiques dans les Vegetaux" is very noticeable from the terminological point of view.
First, Gregoire, quoting the term Zygomit of Strasburger (cf. Strasburger 1905, p. 40), suggested the equivalent new term zygotene.
Secondly, he also proposed a joint and differential use of the suffixes-tene and -nema to indicate respectively a particolar, nuclear morphology and the corresponding stage as documented below:
Gregoire (1907, p. 370); pachynema and noyaux pachytènes.
« Nous conserverons le nom de *spirème épais* on *pachynema* parce que, dans les végétaux, nous ne connaissons pas de cas où l'orientation des anses soit assez caractéristique pour mériter le nom de bouquet. Pour désigner les noyaux eux-mêmes qui sont a ce stade,adopterons le nom de Winiwarter: *noyaux pachytènes*.
La prophase se divise, d'après cela,tout naturellement, ainsi que nous l'avons fait en 1904, en *stades préspirématiques* et *stades postspirématiques*. »
Gregoire (1907, p. 371*): leptonema and noyaux leptotènes.*
I - *Stades préspirématiques.*
1 - Nous verrons bientôt que le premier stade prophasique consiste dans la transformation du réseau nucléaire en un ensemble de filaments chromatiques minces, se dégageant peu à de toute anastomose, Fig. 7, 8, 38-44. Nous désignerons ce stade de transformation, ce stade de "filamentation", sous le nom de *noyaux leptotènes* (Winiwarter) et l'ensemble des filaments eux-mêmes sous le nom de *leptonema.*
Gregoire *(1907, p. 371): zygonema and noyaux zygotènes.*
2 - Les filaments minces s'associent ensuite, nous le montrerons à nouveau, deux par deux, de manière à donner le spirème épais ou pachynema. Le stade où cette association s'accomplit mérite un nom. Strasburger a appelé les filaments qui se conjuguent du nom de gamomites et les paires de filaments conjugués du nom de zygomites. Nous proposons, pour désigner les noyaux à ce stade, un nom en harmonie avec les désignations de pachytènes et de leptotènes et nous dirons: *noyaux zygotènes*. Pour les filaments eux-mêmes, nous conserverons les noms de Strasburger, ou bien nous pourrions dire: *zygonema*.
Gregoire (1907, p. 372*): strepsinema and noyaux strepsitènes.*
II - *Stades postspirématique.*
Au stade de spirème épais – qui dure longtemps – fait suite le phénomène qu'on appelle généralement "division longitudinale", - qui est de fait considéré par plusieurs auteurs comme une vraie division longitudinale – et que nous avons proposé (04) d'appeler "*dédoublement longitudinal*". Il est caractérisé par le fait que les filaments associés se disjoignent fort nettement l'un de l'autre, donnant ainsi des troncons *nettement* et *clairement* doubles; c'est la disposition que Winiwarter a appelée: noyaux diplotènes. Ce nom pourrait suffire. Cependant dans la plupart des objets, les deux filaments qui apparaissent ainsi clairement dans les troncons spirématiques ne tardent pas à montrer des écartements plus ou moins considérables, parfois très considérables et, en outre, ils sont plus ou moins notablement entrelacés l'un autour de l'autre. Ces entrelacements sont absolument caractéristiques de la prophase hété. C'est pourquoi, étant donné que le nom de noyaux diplotènes pourrait aussi bien s'appliquer à la prophase somatique, nous préférons employer, comme par le passé, un nom qui a été créé par Dixon et qui rappelle l'entrelacement des filaments associés. Avec Dixon, nous désignons ces filaments sous le nom de *strepsinema*. Nous proposons en outre le nom de *noyaux strepsitènes* pour faire pendant aux noms précédemment définis.
Gregoire (1907, p. 373*); leptonema, zygonema, pachynema, strepsinema and diplonema.*
III - *En résumé*:

1 - Stades préspirématiques:
a) noyaux réticulés;
b) noyaux leptotènes = leptonema;
c) noyaux zygotènes = zygonema ou zygomites;
2 - Spirème épais:
d) noyaux pachytènes = pachynema;
3 - Stades postspirématiques:
e) dédoublement longitudinal;
f) noyaux strepsitènes = strepsinema,ou: noyaux; diploténes = diplonema;
g) diacinèse = gemini définitifs.

In the year 1912 the nema terminology became enriched by its most popular term, that is chromonema, proposed by WEJDOWSKY (1912)[1].
Since chromonema has been a term accepted by all cytologist, although variably reinterpreted, it deserves a separate discussion, see next chapter "Chromonema and chromatid".
There has been a further interest towards the nema-tene terminology from 1925 to modern times. Thus, for instance, the term synaptene (WINIWARTER 1900); is very questionable from the linguistical point of view. Here, since the etymological root is synapt-, the right compound term is synapt-o-tene. Surprisingly, the term synaptotene can be found only in the well-known text-book of E. B. WILSON (1925, p. 537).Cf. Also "Synaptocyten" in VEJDOWSKY (1907, pp. 66,72).
The present terminology in this matter is summarized in Tab. 2.

Chromonema (1912) and chromatid (1900) - VEJDOWSKY (1912) coined the term chromonema, for denoting "die chromatische spirale" of the chromosomes. The following two sentences deserves quotation:

VEJDOWSKY (1912, p. 12):
"Aus dem ganzen bisher behandelten Differenzierungsprozess ergiebt sich also ganz liberzeugend die festgestellte Tatsache, dass die weiblichen und mänulichen Chromosomen in dem gereiften Ei aus zweikomponenten bestehen, einem weniger farbberen homogenen Substrate, auf dessen Oberflache der dunkel sich farbende Spiralfaden oder das Chromonema verlauft. Die mit EH. Graufarbbare Substanz ist nach dem dargestellten Sachverhalte quellbar, und diese Eigentumlichkeit veranlasst auch, dass die chromatische Spirale auf der blasseren Grundlage deutlich zum Vorschein kommt."
VEJDOWSKY (1912, p. 128):
"Wir können kurzum in der Kernbildung aus den Chromosomen zweierlei Anlagen sicherstellen;
1. Die achsiale Lininsubstanz verandert sich durch das machtige Aufquellen zur Enchylemanlage.
2. Das darduch freigewordene Chromonema entfaltet sich zum sogenannten Kerngeruste, als Anlage der Chromosomen der nachsten Generation. »
In the following cytological literature, the term chromonema (plural chromonemata) became widely accepted, however variably interpreted and frequently also synonymized to the classic term chromatid proposed as early as 1900 by MCCLUNG as follows:
"The term "chromosome" being, then, restricted to the units of the division figures, there remains no name for the parts composing these when they are compound, as in the tetrads and diads. This is the want which I believe has led to confusing the meaning of the word "chromosome". I find it very difficult to express myself clearly and succinctly regarding the compound elements without having some designation for the component parts. I should like, therefore, to propose the term "*chromatid*" for each of these, so that we might speak of the chromosomes of the first spermatocyte in the tetrad condition as being composed of four "chromatids", while those of the second spermatocyte would contain two. So far as I know, there has been no such word compounded from the familiar etymological materials of cytological nomenclature. I therefore feel free to make use of the term as being both suggestive and convenient".

[1] In the scientific literature the paternity over chromonema has been several times wrongly ascribed to F. B. WILSON, see SHARP (1934), DARLINGTON (1937), RIEGER, MICHAELIS and GREEN (1991).

As regards the terminological confusion between chromonema and chromatid, this question can be clearly documented by the entries chromatid-chromonema from the text-books by WILSON (1925) and DARLINGTON (1937) respectively:

WILSON (1925, p. 1128):

"Chromatid, each of the four parts (univalent chromosomes) of which a meiotic tetrad is composed. (MCCLUNG 1900)".

"Chromonema (*chroma,* color; *nema,* thread), a fine basichromatic thread from which arises the spireme-thread. (VEJDOVSKY 1912)".

DARLINGTON (1937, p. 574):

"Chromatid, a half chromosome between early prophase and metaphase of mitosis and between diplotene and the second metaphase in meiosis-after which stages, *I.e.*, during an anaphase, it is known as a daughter-chromosome. The separating chromosomes at the first anaphase are known as daughter-bivalents, or, if single chromatids derived from the division of univalents, daughter-univalents (MCCLUNG 1900).

"[Chromonema; -ta], the chromosome thread, q.v. (similarly leptonema, pachynema, etc., the chromosome threads at leptotene, pachytene, etc.) (WILSON 1896)".

D[1]. *Caryoneme* (1993) *and genoneme* (1934) - The author coined the term caryoneme (BATTAGLIA 1993: Karyonema) commenting a well known paper by KOLTZOFF (1934).

This author, as regards the organization of the chromosomes of the salivary glands of Drosophila proposed the new term genoneme as follows; KOLTZOFF (1934, p. 313):

"I think that the size of the chromosomes in the salivary glands is determined through the multiplication of genonemes. By this term I designate the axial thread of the chromosome, in which the geneticists locate the linear combination of genes; the cytologists call it the "axoneme" or "chromonema". In stained preparations the genoneme remains almost colorless, but at certain points small masses of chromatin-the chromomeres-are attached to it. In the normal chromosome there is usually only one genoneme; before cell-division this genoneme has become divided into two threads. I postulate that in the cells of the salivary gland, which have lost the ability of reproduction by mitosis, the genonemes have become divided four times, whereas the chromosome has remained undivided but has grown correspondingly".

The author, commenting this particular paper wrote (BATTAGLIA 1993, p. 89):

"Obviously, we disagree with KOLTZOFF's interpretation, at least in that he synonymizes genoneme to chromonema. Incidentally, according to our terminological point of view, the usual term *chromonema* (VEJDOVSKY 1912; we also accept the spelling *chromoneme*) is a very questionable term, since it refers to a *non-colored nema*. We believe the neoterm *karyonema* to be an alternative to *chromonema*, but we do not give to *karyonema,* the meaning generally ascribed to *chromonema*. Since *karyonema*, linguistically merely means "nuclear thread", its definition should be included and harmonized within the whole terminology suggested, so as to indicated at the same time the morphological and structural subdivision of the chromosome. To complete our account we should like to submit several other considerations.

We also cannot overlook the fact that the establishment of the concept of genoneme necessarily influences the meaning to be assigned to related terms such as, for instance, *genophore* (Ris 1961), *genomere* (P. W. WHITING in EYSTER 1928) and *genosome* (see the entries genomere and genosome in HENDERSON and HENDERSON 1953; RIEGER *et al.* 1991; MERRIAM-WEBSTER 1976), etc.

Although a modern redefinition of these terms is again a matter for a panel discussion, we wish to point out that such terms should be referred to the *genoneme* and not to the *karyoneme* (chromosomal structure).

Conclusively, the author would like to emphasize here once more that for the sake of etymological accuracy, all geno (gen-e-) compound terms should be referred only to the genetic field and to the DNA terminological system (see chapter E[3]). The meaning which the author assigns to caryoneme is discussed in the next chapter.

D². *Caryoneme alternative to chromosome and related standedness: caryodineme… caryopolyneme* - Once given that caryonema means by its own etymology nuclear thread, the author proposes caryoneme alternative to the present chromosome (wide sense). Since the caryoneme at the normal mitotic prophase is a structure consisting of two caryonemes, it should be appropriately defined as a caryodineme.

Furthermore, because at the onset of the anaphase the caryodineme divides into sister units it is also linguistically justified to write that the caryodineme has been divided into two caryomononemes. Clearly the caryomononeme corresponds to the chromatid of the classic terminology. There is a large caryological literature on the strandedness of the chromatids and terms such as hemichromatid have also been coined (cf. RHOADES 1961).

However, the author, as regards this question, considers to be adequate the general term caryosubneme to indicated (denote, define, qualify) the subunits of the caryomononemes. Once established the definition of the caryomononeme, the correspondence between author's series caryomononemes… caryopolynemes and the traditional series monochromosome… polychromosome is quite (fully) evident.

For the sake of historical accuracy, I must quote the terms pericaryo-neme and perineme coined and described as follows by RENAUT and DUBREIL (1906:

"Cellules connectives de la ligne rhagiocrine", p. 241): "Enfin, toutes présentent un caractère spécifique majeur qui leur est particulier, landis que; dans les mémes conditions, il manque a tous les leucocytes occupant avec elles le meme habitat: c'est l'existence costante, au sein de leur trophoplasma, d'un dispositif spécial et filaire de protoplasma supérieur, extérieur au novau, mais ordonné par rapport à sa surface. Nous donnerons à cette formation le nom de *péricaryonéme* ou plus simplement de *périnéme* pour la désigner dorénavant dans son ensemble et par un seul mot ».

D³. *Geno compound terms and DNA strandedness* - First, the author believes to be essential to summarize in Tab. 3 the main classic geno compound terms because (since) they have been many times wrongly quoted as regards their terminological paternity and interpretation. Thus, for instance, genotype should be ascribed to SCHUCHERT (1897) and not to JOHANSSENS (1909), as recorded by the cytological literature. Analogously genomere (cf. "Genomeren-Hypothese, EYSTER 1924", in RIEGER and MICHAELIS 1958) should be recorded as "WHITING in EYSTER (1928)".

A critical analysis of the terms assembled in Tab. 3 is beyond the purpose of this paper and is indeed matter for a specialized panel discussion on this complex terminological field. Nevertheless, and based on the accaptance of the author's reinterpretation of genoneme (BATTAGLIA 1993) the following definitions and sigla are presented to the attention of readers:

D=DNA,
R=RNA,
sG=single genomene strand=genomononeme=each strand of the double helix=DNA simplex,
dG=double genomene=genodineme=DNA duplex (dD),
tG=quadruple genomene=genotetraneme=DNA quadruplex (qD).

E. *The classic cytogenetical terms replication,reduplication (BATESON and PUNNET 1911,) duplication (BRIDGES 1919), endo- and exo- duplication (JORGENSEN 1928) and endoreduplication (LEVAN and HAUSCHKA 1953). Etymology and documentation* -

a) *Etymology* - For the sake of terminological completeness and unambiguity, the author believes that the modern term replication should be reserved to questions concerning the DNA molecule, while duplication should be employed in discussions concerning the chromosome terminology.

As regards etymology, the Latin term duplicatio means doubling in number, amount, etc., whilst replicatio shares several different meanings and only a few Latin classic authors ascribe to replicatus the meaning of doubled, see, e.g., DURANDO's Lexicon (1899).

The relation between the cytological duplication terms and the corresponding Latin words can be summarized as follows:

Present terms	*Latin terms*
Duplication, duple	duplicatio, duplicatus, duplus, duplex;
Quadruplication, quadruple	quadruplicatio, quadruplicatus, quadruplus, quadruplex;
Multiplication, multiple	multiplication, multiplicatus, multiplus, multiplex.

b) *Reduplication:* BATESON and PUNNET (1911) - This is the oldest term of the series. BATESON and PUNNET (1911, pp. 301-302) introduced this term in Genetics, as follows:

"TERMINOLOGY. Lastly, in view of what we now know, it is obvious that the terms "coupling" and "repulsion" are misnomers. "Coupling" was first introduced to denote the association of special factors, while "repulsion" was used to describe dissociation of special factors. Now that both phenomena are seen to be caused not by any association or dissociatio, but by the development of certain cells in excess, those expressions must lapse. It is likely that terms indicative of differential multiplication or proliferation will be most appropriate. At the present stage of the inquiry we hesitate to suggest such terms, but the various systems may conveniently be referred to as examples of *reduplication*, by whatever means the numerical composition of the gametic series may be produced."

c) *Duplication:* BRIDGES (1919) - Since litererally this term means "to be duplicated", BRIDGES (1919) rightly employed it in Genetics.

d) *Endo-duplication and exo-duplication: Jorgensen (1928)* - Endo-duplication was proposed by JORGENSEN in 1928. This proposal is another glaring example of a certain lack of linguistic ability by an outstanding scientist. Regarding the cytological meaning to be given to endo-duplication, JORGENSEN (1928, pp. 142, 155) stated:

"I suppose the diploid condition to be brought about by the process described later (p. 165) under the name of "endo-duplication", which is simply a nuclear division without cell-wall formation, followed by a fusion of the spindles in the next mitosis. Diploid daughter nuclei then result. For this there is however no direct evidence at hand yet " … " The process has a certain definite character and I shall propose for it the term "*endo-duplication*". It is characteristic of it that the whole procedure is performed within one cell."

JORGENSEN also introduced exo-duplication (the antonym of endoduplication), interpreted as follows (cf. JORGENSEN 1928, p. 155)

"At fertilisation, by which the chromosome doubling is usually brought about, the nucleus of another cell enters the egg cell, so that we might speak of "*exo-duplication*" in this case."

e) *Endoreduplication* (LEVAN and HAUSCHKA 1953) - In view of its general acceptance, the proposal of this term by LEVAN & HAUSCHKA (1953, pp. 2-3) deserves full quotation:

"The endomitosis encountered in the present material constitutes a complex series of mechanisms falling into two main categories:

1) Endomitosis with conspicuous activity inside the nuclear membrane: chromosome contraction leading to an endometaphase and back again to a despiralized stage. This is a constant feature in some tumors, and was found occasionally in all the neoplasms surveyed. It corresponds closely to the phenomenon for which GEITLER (9) coined the term "endomitosis".

2) An endomitosis in which the additional chromosome reproduction is as concealed as normal chromosome reproduction during mitosis, since it takes place during the despiralized phase. Its completion can only be recognized if a mitosis follows. As the chromosomes then contract during prophase, they have become diplochromosomes or quadruple chromosomes, each centromere being in charge of 4 or 8 chromatids. Such pictures are occasionally seen in both plant and animal material. If old specialized cells re-enter mitosis, the chromosomes often turn out to have undergone double (or even multiple) reproduction. This type is also usually referred to in the literature as "endomitosis". Since both types are to be discussed here, and since they are readily distinguishable, they will be referred to as *endomitosis* and *endoreduplication* respectively. Quite possibly, transitions between them exist; one cannot distinguish between a metaphase after a true endoreduplication and a metaphase following an endomitosis in which the centromeres have failed to divide."

There are several considerations which would suggest the refusal of the term endoreduplication. First: linguistically endoduplication and endoreduplication are almost identical terms. Second: endoreduplication (LEVAN and HAUSCHKA 1953) is a short for endocaryo repeated chromosome duplication. Again in the modern literature, endoreduplication conveys the meaning of repeated duplicatio of the DNA content as well as the chromosomes. Third: the author refuses the choice of the prefix endo (traditionally associated to GEITLER's endomitosis) but at the same time accepts re-duplication for indicating any repeated duplication (wide sense).

F[1]. *Centromere, kinetocentre and kinetochore. A linguistic comment* - A recent issue of Chromosome

Research (2004) features a collection of reviews focusing on centromere and kinetochore biology, together with the main question of chromosome segregation.

Commenting this special issue, CHRISTINE FARR (cf. Chromosome Research, 2004, vol. 12, pp. 517-520), defines centromere and kinetochore as follows:

"The centromere has long been recognized as an essential structural component of the eukaryotic chromosome required for faithful segregation in mitosis and meiosis. The term 'centromere' is used generally to refer to the chromatin upon which the complex and dynamic structure known as the kinetochore assembles. The kinetochore is positioned on the outward face of the chromosome surface and on opposite sides of the chromosome's primary constriction."

As regards this matter, the author has already analysed (cf. BATTAGLIA 2003) the history and the etymology of the couplet kinetochore (priority: J. A. MOORE in SHARP 1934) – centromere (priority: Centromer, WALDEYER 1903), recommending the acceptance of kinetochore and, at the same time, proposing kinetocentre (together with mono…polykinetocentric) as a synonym of the current centromere. Here the term kinetocentre is a reinterpretation of the old kinetisches centrum of PFITZNER (1883, p. 644), see also kinocentrum of ZIMMERMANN (1898, p. 697) and kinetocentre of GRUNDMANN (1964; 1966).

Other terms etymologically related to the couplet kinetochore-kinetocentre were also recommented by the author (BATTAGLIA 2003), as for instance, kinetomere (cf. MATTHEWS in COWDRY 1924) and kinomere (cf. SHARP 1943, p. 85; cited by HUSKINS 1943, p. 82).

The agreement as regards kinetochore and the reinterpretation of kinetocentre were supporte by several etymological considerations pertinent to the prefixes kino and kineto, summarized as follows, cf. BATTAGLIA (2003):

"As a basic evaluation, not invalidated by the occurrence of a few exceptions, the linguistic difference between the combining forms kin-o and their corresponding couplet of prefixes kino- and kineto-, can be summarized as follows:

kino- versus kineto- = transitive versus intransitive = active (causing) versus passive = motile versus movable. It is not superfluous to recalle that kino- is a combining form which derives from the Greek, χίνέω,to set in motion (namely the stem kin- and the connecting vowel-o). Also kineto- is a combining form of the Greek χιητος, movable (kinet- and -o)."

The linguistic difference mentioned above, has never been emphasized or clearly pointed out by scientific literature with the result that, today, the meaning ascribed to the two members of the kino- and kineto- couplet appears to be rather a matter of individual preference than a choice due to a proper linguistic evaluation.

Consequently, the prefix kineto- should be chosen to indicate the occurrence of passive movement, ascertained or presumable. Necessarily, the prefix kino- should be utilized for all remaining cases, which are mainly cases of active movement or induction of movement. Following this point of view, the author considers the term kinetochore as the right choice to indicate the classic chromosome primary constriction. By contrast, he refuses the present use of the term centromere and proposes kinetocentre as an alternative terminological solution. The acknowledgement of this last term makes it possible to save the usual series "mono… polycentric chromosomes" by the simple change to "mono… polykinetocentric chromosomes".

Further, in accordance with these considerations all instances referable to the occurrence of active movement should be re- qualified by the choice of the prefix kino-. Thus, the current microtubules should be termed kinotubules, the aster as kinaster, the mitotic poles as kinopoles, and so on.

F². *Chromosome reduplication, segregation and cell cycle. Some data on the present terminologies* – The kinetics of chromosome reduplication and segregation have been widely investigated by cytologists. The main data on this field deserves a short discussion restricted here to the priorities and to the linguistic criticism. Historical considerations also suggest subdividing the terminological discussion into two separate groups:

F²-a. *The classic kinase, kinetin and kinesin terminologies.*

Kinase: PAWLOW 1898.

Kinesin: VALE, REESE and SHEETZ 1985.

Kinetin: MILLER, SKOOG, VON SALTZA and STRONG 1955.

F²-b. *The new terms proposed by the modern literature.*
Chromokinesin: Wang & Adler 1995.
Clathrin: Pearse 1975.
Kleisin: Gruber *et al.* 2003.
Monopolin: Toth *et al.* 2000.
Securin: Toth *et al.* 1999.
Separase: Östergren & Anderson 1973; Uhlmann *et al.* 2000.
Separin: Ciosk *et al.* 1998.
Shugoshin: Kitajima, Kawashima, Watanabe 2004.

Condensin and cohesin:

Borealin: Gassmann *et al.* 2004.
Bromodomain: Tamkun *et al.* 1992.
Calcineurin: Klee, Crouch, Krinks 1979.
Calcitonin: Copp, Davidson, Cheney 1961.
Calmodulin: Cheung, Lynch, Wallace 1978.
Calpain: Murachi *et al.* 1980.
Cohesin: Michaelis *et al.* october 1997: Cohesins: chromosomal proteins that prevent premature separation of sister chromatids".
Chromodomain and Chromo box: Paro & Hogness 1991 (chromo = chr + o + mo = chromatin organization modifier).
Condensin: Hirano *et al.* may 1997: "Condensin, Chromosome Condensation, Protein Complexes Containing XCAP-C, XCAP-E and a *Xenopus* Homolog of the *Drosophila* Barren Protein".
Cyclomere 1972, Cyclin 1983 and Cyclosome 1995:
Cyclomere: Engelhardt & Pusa 1972.
Cyclin: Evans *et al.* 1983.
Cyclosome: Sadakin *et al.* 1995.
Izumo: Inoue *et al.* 2005.
Nesprin: Zhang *et al.* 2001.
Nestin: Lendahl, Zimmerman, McKay 1990.
Netrins: Serafini & Kennedy 1994; Kennedy *et al.* 1994.
Plectin: Wiche *et al.* 1982.
Pontin: Bauer, Huber, Kemler 1998.
Reptin: Bauer *et al.* 2000.
Selectin: Bevilacqua *et al.* 1991.
Syntaxin: Bennett, Calakos, Scheller 1992.
The eph gene, eph protein: Hirai *et al.* 1987 and the Ephrins: Eph Nomenclature Committee, cf. CELL, 1997.
Tubulin: Mohri 1968.

F²-a. *The classic kinase, kinetin and kinesin terminologies* – First the distinction between the two prefixes kino- and kineto- deserves quotqtion. The prefix kino- derives from the Greek κινεω (to set in motion) whilst kineto- derives from κινετοσ (movable), cf. the old classic term kinetogenesis (Cope 1884; 1887), so that we can write: kino- versus kineto- = transitive versus intransitive or motile versus movable.
Kinase: Pawlow 1898 – As early as 1898 Pawlow coined the term kinase, almost immediately accepted and widely quoted by the sicntific literature, cf. e. g. Oppenheimer (1909).
There are many modern data on this matter documenting, for instance, the large implication of the protein kinases in the chromosome kinetics.
Thus, to ensure a regular chromosome segregation the microtubules fibers must attach the sister kinetochores (author's kinetocentres) to the opposite poles of the spindle (bi-orientation). The Aurtora kinases (cf. Lampson *et al.* 2004; Biggins 2004) are widely implicated in this process and can also destabilize abnormally attached microtubules.
For the purpose of the present account, the author believes to be adequate only the quotation of the following main literature, namely Dirick *et al.* (1998), Clyne *et al.* (2003), Jackman *et al.* (2003), Lee & Amon (2003), Chirolie *et al.* (2003), Lampson (2004), Biggins (2004), Lampson &

KAPOOR (2005), MICHELL (2005), KISHIMOTO (2005).

Kinetin: MILLER, SKOOG, VON SALTZA and STRONG 1955 - These authors published (1955) a paper entitled "Kinetin, a cell division factor from deoxyribonucleic acid", cf. op. cit. p. 1392:

"HABERLANDT's early concept of a specific cell division hormone (wound hormone) in plants has been strengthened gradually by evidence both for the specific need and for its satisfaction by extracts or substances of natural origin. For example, a factor required for cell division is practically lacking in pith but is present in limited amounts in vascular stem tissue and leaves of tobacco and in various plant products.[2] Yeast is a rich source, the further exploration of which now has led to deoxyriponucleic acid (DNA) as the starting material[3] for the isolation of a physiologically highly active chemical.The name *kinetin* is suggested for this substance."

Unexpectedly the term kinetin was proposed without any linguistic comment nor discussion as regards the biochemical relations to the other kinases.

Kinesin: VALE, REESE and SHEETZ 1985 - These authors published a paper entitled "Identification of a novel force -generating protein, kinesin, involved in microtibule-base motility". This novel class of kinetic proteins is described and termed as follows (cf. op. cit. p. 39):

"We describe the purification, from squid axoplasm and optic lobes, of a translocator protein that induces movement of microtubules on glass and movement of beads along microtubules. We also have identified a homologous protein in bovine brain. The characteristics of these proteins are distinct from myosin and dynein and appear to define a novel class of force-generating molecules.

This protein is distinct in molecular weight and enzymatic behavior from myosin or dynein, which suggests that it belongs to a novel class of force-generating molecules, for which we propose the term kinesin."

Although kinesin is etymologically identical to kinetin, these authors fully overlooked the earlier paper of MILLER & coll. (1955).

F²-b. *The uncoordinated new terms proposed by the modern literature*

Chromokinesin: WANG & ADLER (1995) - Chromokinesin has been coined by WANG & ADLER (1995) and described as follows (op. cit. p. 761):

"In this paper we report the characterization of Chromokinesin, a hitherto undescribed member of the kinesin-like family that contains both a kinesin motor-like domain and an unusual basic-leucine zipper DNA-binding domain. Its capacity to bind DNA was verified by South-Western analysis. In situ hibrydization and immunocytochemical evidence showed its abundance in proliferating cells and its association with mitotic chromosomes. We postulate that Chromokinesin may link chromosomal DNA to spindle microtubules, and could function as a mitotic motor."

The finction of chromokinesin and its relation to other kinases have been widely investigated from 1995 to day, see e. g., references in ZWICK *et al*. 1999; FUNABIKI & MURRAY 2000; ANTONIO *et al*. 2000.

As regards chromokinesin the author limits himself to the following linguistic comment.

Since the prefix chromo implies the occurrence of a coloured state, the compound term chromokinesin only means "coloured kinesin"!

Clathrin: PEARSE 1975 - The term clathrin has been coined by BARBARA PEARSE and quoted as follows: PEARSE (1975, p. 98):

"Coated vesicles of brain are believed to be derived by micropinocytosis of synaptic membrana (HEUSER & REESE 1973). Whether the same protein is associated with the coated vesicles described in other tissues is unknown. In any event, the 180,000 molecular weight protein is likely to be an important example of a class of proteins involved in membrane movement, and I propose that it be called "clathrin". "Clathrin" itself may be able to pinch off a vesicle through interactions between its subunits and the membrane phospholipids."

See also PEARSE 1976, p. 1255: "I named the protein "clathrin" to indicate the lattice-like structures which it forms."

A few years later UNGEWICKELL & BRANTON (1981) published noticeable biochemical data on the relation between the clathrin and the coated vesicles of the brain. They write, cf. UNGEWICKELL & BRANTON (1981, p. 420):

"Clathrin, a polypeptide of molecolar weight (MW) 180,000, is the main constituent of the polygonal

network that forms the coat of coated pits and vesicles; these vesicles play a part in intracellular transport between membranous organelles[23]. This function involves specific recognition of target membranes as well as fusion and fission events that must be coordinated with the assembly, partial disassembly or reorganization of the clathrin coats. Here we show that purified clathrin coats dissociate reversibly into triskelions, structures composed of three usually bent, rather flexible legs radiating from a centre. We have determined the molecular weight of these triskelions and conclude that they contain trimers of clathrin together with about three light molecular weight polypeptide chains."

There are many scientific terms derived from the Latin term clatri-clatrorum, also clathra-clathrorum, meaning lattices, see the Oxford Latin Dictionary (Clare editor, Oxford, 1996). Thus e.g. the Webster's Third, New Intern. Dictionary (1986) records: clathrate = shaped like a lattice; the family Clathraceae, the genera Clathraria, Clathrina, etc.

Modern biochemical researches on this protein (cf. Fotin *et al.* 2004; Damm *et al.* 2005; Pfeffer 2005; Haas *et al.* 2005; Veiga & Cossart 2005; Sato *et al.* 2005; van der Blieck 2005) document the noticeable cytological function of this protein, just as clearly summarized by Royle, Bright & Lagnado (2005, p. 1152) and namely:

"Clathrin has an established function in the generation of vesicles that transfer membrane and proteins around the cell[1-4]. The formation of clathrin-coated vesicles occurs continuously in nondividing cells5, but is shut down during mitosis6, when clathrin concentrates at the spindle apparatus7,8. Here, we show that clathrin stabilizes fibres of the mitotic spindle to aid congression of chromosomes. Clathrin bound to the spindle directly by the amino-terminal domain of clathrin heavy chain."

As regards this matter the author confines himself only to the following terminologica criticism.

The choice of the term clathrin is linguistically very questionable. Indeed, given that the suffix-in of clathr-in stands for protein, the only right meaning ascribable to clathrin is "protein of the lattice" without any conformational implication.

Kleisin: Gruber et al. 2003 - Term kleisin can first be found in a paper of Gruber, Haering, Nasmyth (2003), shortly followed by other two analogous experimental accounts (Schleiffer *et al.* 2003); Haering and Nasmyth (2003), on the same topic, i.e. the biochemistry of chromosome meiotic-mitotic segregation.

These papers are of higher interest from both the experimental and the historical points of view and require a joint discussion.

For the purpose of the present account the author believes to be sufficient as well as adequate to quote the following data together with the definition of the "kleisin superfamily", concluding this matter with the linguistic comments suggested to the author by the reading of these very valuable investigations:

Gruber, Haering, Nasmyth (2003 p. 773). The term kleisin is first recorded as follows:

"We show here that the preferential association of Scc1's N-terminal fragment with Smc3's head ant its C-terminal one with that of Smc1 is conserved in its meiotic counterpart Rec8. Scc1 and Rec8 share very little sequence homology except within their first and last 100 amino acids, which are generally conserved amongst Scc1 and Rec8 homologs from a wide variety of eukaryotes. These conserved terminal sequences must contain the SMC head interaction domains because fragments containing the first 115 amino or the last 115 amino acids of Scc1's Smc3 binding N-terminal ones. This asymmetry presumably corresponds to an asymmetry of the Smc1/3 heterodimer's two heads, to which these sequences bind. The recent finding that these N- and C- terminal domains of Scc1 and Rec8 are homologous to those of ScpA proteins may be connected in a similar manner. It is for this reason that we suggest that members of this family are called kleisins (from the Greek word for closure: kleisimo). Cohesin's asymmetry is presumably shared by condensin, which contains an Smc2/Smc4 heterodimer but contrasts with the symmetry of bacterial SMC proteins. If the latter bind the ScpA, as is currently suspected, then the molecular symmetry of the SMC dimer would predict that they bind at least two molecules of ScpA in a symmetric fashion."

Schleiffer *et al.* (2003 p. 571). "We describe a superfamily of eukaryotic and prokaryotic proteins (kleisins) that includes ScpA, Scc1, Rec8, and Barren. Scc1 interacts with SMC proteins through N- and C-terminal domains to form a ring-like structure. Since these are the only domains conserved among kleisins, we suggest that ring formation with SMC proteins may define this family."

Haering and Nasmyth (2003 p. 1178). The proposal of a new protein-superfamily, qualified de-

serves the following documentation:
"Chromosome segregation depends on another SMC protein complex called condensin, whici is composed of a heterodimer of Smc2 and Smc4 associated with three additional proteins called Brn1 (Barren, CAP-H), Ycg1 (Cnd3, CAP-G) and Ycs4 (Cnd2, CAP-D2), reviewed by Losada and Hirano[33]. Might condensin also possess a ring-like architecture? The finding that the amino- and carboxy-terminal aminoacid sequences of condensin's Brn1 subunit have homology to the conserved SMC-binding domains at the termini of Scc1 and Rec8 proteins[34] suggests that Brn1 homologs might associate with the head domains of Smc2-Smc4 heterodimers in a manner that resembles Scc1's association with Smc1 and Smc3 (Fig. 2). In which case, it is conceivable that Brn1 connects the heads of Smc2 and Smc4. Scc1, Rec8 and Brn1 homologs belong to a new protein superfamily called 'kleisins' (from the Greek word for 'closure'). Besides Scc1-Rec8 (kleisin α) and Brn1 (kleisin γ), most animal and plant genomes (but not fungal ones) encode a third type of kleisin protein (kleisin β). In *C. elegans*, which lacks kleisin γ, RNAI-mediated knockdown of kleisin β (KLEE-2) produces a chromosomal prenotype similar if not indistinguishable to that of Smc2 or Smc4. The funciotn of condensin in *C.elegans* is presumably mediated by a complex containing Smc2, Smc4, and kleisin β. Vertebrate genomes encode both kleisin β and γ proteins and most animal cells may therefore possess two different types of condensin complex.[34] A third SMC protein complex composed of Smc5 (Spr18) and Smc6 (Rad18) proteins is involved in DNA demage repair. [35,36] Besides the finding that it associates with a novel protein of unknown function called Nse1 in budding yeast, [37] the Smc5-Smc6 complex awaits further characterization.
Prokaryotic genomes encode only a single SMC protein or an SMC-related protein of the MukB family. Mutations in SMC or MukB cause chromosome partitioning defects and a failure to compact nucleoids in *B. subtilis* and *E. coli*, respectively, [38,40] which leads to the formation of anucleate cells. Bacterial SMC complexes presumably act in a similar manner to their eukaryotic counterparts in organizing chromosomes, reviewed by Graumann. [41] Unlike eukaryotic SMCs, prokaryotic ones form homodimers. In *B. subtilis*, the binding of ScpA and ScpB proteins to the SMC dimer appears to augment or promote SMC function. [42] The MukE and MukF proteins do so for the SMC-like MukB protein in *E. coli.* [43] Interestingly, ScpA and its homologs also belong to the kleisin protein superfamily,[34] suggesting that ScpA might bind to the head domains of its associated SMC homodimer (Fig. 2A). SMC-kleisin complexes appear therefore to be extremely ancient chromosomal constituents."
The reading of papers mentioned above suggests to the author these linguistic considerations. First, some classic Greek terms cannot be overlooked, just as κλεισ, κλειδοσ = key: κλεισιο, κλεισεωσ = closing, closure (The term κλεισμοσ does not belong to classic Greek).
As regards the related compound terms, here the linguistic root is cleid- (cleid-o the combining form), cf. e.g. the classic Greek κλειδο-φοροσ and some modern terms such as cleidagra (clavicular), cleidoscapular, cleidomancy (recorded by the Webster's dictionary 1986). Thus, the "kleisins" could be properly called cleidoproteins.
Furthermore, for linguistic coordination with analogous terms such as cohesin, condensin, etc., the compound term cleid-o-protein could be shortened to cleidin.
However, the author does not propose cleidin in the place of cleisin. The author's criticism is made here only to provide a basis for a general revision of the terminology referable to the chromosome replication and segregation.

Monopolin: Toth et al. 2000 – The term monopolin has been coined by Toth *et al.* 2000. The chromosome segregation during mitosis is dependent on sister chromatid cohesion which is established during DNA replication, at S phase through G2 until the M phase.
Such cohesion allows a regular attachment of sister kinetochores (author's kinetocentres) to the microtubules that extend to the opposite poles. This last behaviour is termed bipolar attachment.
A quite different pattern of chromosome segregation occurs during meiosis (Meiosis I and Meiosis II; meiosis=author's hemiosis). In this case two rounds of chromosome segregation follow a single round of DNA replication.
During meiosis I the crossovers between paternal and maternal sister chromatids allow that sister chromatid cohesion now holds not just sister chromatids together but also homologous chromosomes. At the same time the sister kinetochores are attached to the microtubules from the same pole.

As regards this meiotic feature Toth and collaborators (2000), investigating the finest details of meiosis in *Saccharomyces cerevisiae* wrote: "Second, sister kinetochores always attach to microtubules from the same pole, which is known as monopolar attachment".
These authors also wrote that this type of "monopolar attachment" requires at least one meiosis-specific protein which they called monopolin (Toth *et al.* 2000, p. 1166). At the same time they also write that "the meiosis-specific cohesin (sigla Rec8), already known as a protein essential for maintaining cohesion between sister kinetochores, is not implicated in the process of monopolar attachment".
To monopolin is ascribed the the abbreviation Mam 1 (Monopolar attachment to microtubule). The term monopolin suggests to the author the following linguistic considerations. The numerical prefix mono is criticisable if ascribed to this protein! Clearly the term polokinesin is the most proper alternative. Furthermore, in this context, the fission yeast polo-kinase (abbreviation Plo1) described in *Saccharomices pombe* by Petersen & Hagan (2005) deserves citation.

Securin: Toth et al. 1999 - The term securin has been first quoted by Toth *et al.* (1999) as follows:
"Recent work has shown that sister separation depends on the destruction, by ubiquitin-mediated proteolysis, of anaphase inhibitors like budding yeast Pds1p and fission yeast Cut2p (Securins), which bind to and inhibit the Esp1/Cut1 class of sister separating proteins (Separins) (Funabiki *et al.* 1996; Ciosk *et al.* 1998)."
Almost contemporaneously Zou *et al.* (1999) mention again the term and namely:
"cause of their similar cell cycle functions, Pds1p and Cut2p are also called anaphase inhibitors or securins[1].
Looking for the terminological paternity over securin, dr. Frank Uhlmann (Chromosome Segregation Lab., Cancer Research UK, London) gave to the author the following data:
"regarding your search for the origin and linguistic explanation of the term "securin" I can report the following events. Marc Kirschner's laboratory (Zou *et al.* 1999) has identified the human orthologue of the yast Pds1/Cut2 and *Drosophila* 'pimples' proteins. This was an achievement because these orthologues are not easily recognised at the primary sequence level. Because the names for these proteins (Pds1, Cut2, pimples) were so diverse, Marc suggested to call all these proteins 'Securin'. The name stems from thefact that securin inhibits separin (now called 'separase'), i.e. securin secures separin from triggering anaphase prematurely. The idea of the name 'securin' was communicated in an informal way to Kim Nasmyth's laboratory, who accepted the idea and used the term 'securin' in the publication Toth *et al.* 1999."

Separase: Östergren & Anderson 1973, Uhlmann et al. 2000 - The term separase has been coined by Östergren & Anderson (1973: "chromatid separase") and reintroduced in the modern biochemistry by Uhlmann *et al.* (2000), and namely: Östergren & Anderson 1973:
"We may imagine that the chromatic separation could result from an enzyme being suddenly put into action to restore the original strand pairing at these points of association and might call this enzyme *chromatid separase*."
Uhlmann *et al.* 2000:
"There are good reasons to believe that proteolytic cleavage of cohesins by separin might trigger anaphase in all eukaryotic organisms. The catalytic site of yeast Esp1 is conserved in all known separins. Furthermore, an immunopurified Esp1 fraction from human cells possesses Scc1 cleavage activity and Scc1 is both cleaved and disappears from centromeres at the metaphase to anaphase transition in human cells (Walzenegger *et al.* 2000 [this issue of Cell]). Given their conservation and similarity to caspases, we suggest that separins might be better known as "chromatid separases" (Östergren and Anderson 1973), or simply "separases"."

Separin: Ciosk, Zachariae, Michaelis, Svevchenko, Mann, Nasmyth 1998 - The authors published a paper entitled "An ESP1/PDS1 Complex Regulates Loss of Sister Chromatid Cohesion at the Metaphase to Anaphase Transition in Yeast" and proposed the term separin, justified as follows:

[1] A. Toth *et al.*, Genes Dev. 13, 320 (1999)

"The properties of a cohesin called Scc1p or Mcd1p in *Saccharomyces cerevisiae* suggest how cohesion might be lost. Scc1p binds to chromosomes during S phase, it prevents premature separation of sister chromatids during G2/M, and disappears from chromosomes at the metaphase to anaphase transition (MICHAELIS *et al.* 1997). Thus, Scc1p's disappearance from chromosomes could be responsible for the separation of sister chromatids during anaphase. A key question is what causes the sudden disappearance of Scc1p and the loss of sister chromatid cohesion."
"Results described here and by YAMAMOTO *et al.* (1996b) imply that the APC promotes sister separation and dissociation of Scc1p solely through destruction of Pds1p. We purified Pds1p and found it tightly associated with a 180 kDa protein which was identified by mass spectrometric sequencing as the product of the ESP1 gene (MCGREW *et al.* 1992). We show that Esp1p is essential for the separation of sister chromatids and for the dissociation of Scc1p from all regions of chromosomes. Our data imply that the APC mediates sister chromatid separation not by degrading cohesins but by liberating the "sister-separating" Esp1 protein from an inhibitory embrace by its guardian Pds1p. Esp1p is related to fission yeast Cut1p, which is required for chromosome segregation, and associates with a protein destroyed by the APC called Cut2p (UZAWA *et al.* 1990; FUNABIKI *et al.* 1993; 1996a; 1996b). These parallels suggest that sister separation may be triggered by a similar mechanism in all eukaryotic cells."
"Esp1p is homologous to Cut1p from *Schizosaccharomyces pombe* (UZAWA *et al.* 1990) and to BimB in *Aspergillus nidulans* (MAYA *et al.* 1992), both of which are also required for nuclear division but not for reentry into the next cell cycle. The homology between these proteins is largely confined to their C-terminal 300 amino acids, which are similarly conserved in potential homologs from humans and *Caenorhabditis elegans*. cut1 mutants manage to separate chromatids at centromeric regions but do not segregate sister chromatids fully from each other (FUNABIKI *et al.* 1993). We suggest that these cut1 alleles are "leaky" and that Cut1p is not merely needed for the proper segregation of chromatids but is required like Esp1p to initiate sister chromatid separation. Thus, the Esp1/Cut1 class of sister-separating proteins might be called "separins."
Cut1p binds to Cut2p, a protein with Pds1-like properties, and is associated with mitotic spindles (UZAWA *et al.* 1990; FUNABIKI *et al.* 1993; 1996a). Though Cut1p and Esp1p are clearly related proteins with similar functions, there is little obvious sequence similarity between Pds1p and Cut2p. Furthermore, cut2^{+}, unlike PDS1, is an essential gene and is necessary for chromosome segregation (FUNABIKI *et al.* 1996a). Despite these differences, we suspect that Cut1p and Cut2p in *S. pombe* perform similar functions to Esp1p and Pds1p in *S. cerevisiae*."

Shugoshin: KITAJIMA, KAWASHIMA, WATANABE 2004 – KITAJIMA, KAWASHIMA and WATANABE investigating the meiotic divisions in fission yeast coined and interpreted the term shugoshin on the basis of the following considewrations, cf. op. cit. p. 510:
"There are clues to the molecular nature of sister chromatid cohesion and the mechanism by which it is released at the onset of anaphase[1-5]. In various eukaryotes, sister chromatid cohesion depends on a multisubunits cohesin complex including Scc1 (Rad21 in the fission yeast *Schizosaccharomyces pombe*). Anaphase-promoting complex (APC)-dependent degradation of the securin Pds1 (Cut2 in *S. pombe*) allows release of the Esp1 (Cut1 in *S. pombe*) endopeptidase (separase), which in turn cleaves Scc1, releasing sister chromatid cohesion. During meiosis, the cohesin subunit Scc1 is replaced by a meiotic counterpart, Rec8 (refs 6-10). As Rec8 complexes reside only at centromeres after after meiosis I and depletion of Rec8 disrupts centromeric cohesion, its presence at centromeres has been thought to confer the persistence of cohesion throughout meiosis I (ref. 11). Several lines of evidence[12,13] suggest that Rec8 along chromosome arms is cleaved by separase at anaphase I, whereas centromeric Rec8 (refs 14, 15), but Spo13 is not centromeric and may function indirectly.
Despite the completion of genome sequencing projects in several organisms, no homologues of Spo13 or MEI-S332 have emerged, preventing the formulation of a generalized view of protection, Concurrently studies in fission yeast18 have illuminated the importance of pericentromeric heterochromatin for recruiting centromeric Rec8 complexes and ensuring centromeric cohesion during meiosis I. However, preicventromeric heterochromatin cannot alone confer the specific protection of Rec8 at meiosis I compared with meiosis II. We now identify a meiosis-specific protein, Sgo1 (shugoshin, Japanese for 'guardian spirit'), that protects centromeric Rec8 from degradation during meiosis I."

Clearly shugoshin is not a scientific term and there is the need of proposing an alternative term. Since shugoshin belongs to the family of kinocentric proteins (currently "centromeric or kinetochore proteins") an alternative term can be suggested only within a general terminological revision and coordination of the kinocentric proteins implicated in chromosome segregation.

Condensin and cohesin - In the eucaryotes there are two classes of proteins referred to the structural maintenance of chromosomes (sigla SMC), termed condensins and cohesins according to their role in chromosome condensation and sister-chromatid cohesion respectively.
Likely a basic scheme of SMC-mediated chromosome mechanics occurs from bacteria to vertebrates.
The eukaryotes have multiple SMC proteins, classified in sub-types Smc1…Smc6, see, e.g. Torres-Rosell *et al.* (2005), Yanagida (2005).

Borealin: Gassmann et al. (2004) - Gassmann *et al.* published a paper entitled "Borealin: a novel chromosomal passenger required for stability of the bipolar mitotic spindle" and coined the term Borealin, as quoted below:
"The chromosomal passenger complex of Aurora B kinase, INCENP, and Survivin has essential regulatory roles at centromeres and the central spindle in mitosis. Here, we describe Borealin, a novel member of the complex. Approximately half of Aurora B in mitotic cells is complexed with INCENP, Borealin, and Survivin; and Borealin binds Survivin and INCENP in vitro. A second complex contains Aurora B and INCENP, but no Borealin or Survivin. Depletion of Borealin by RNA interference delays mitotic progression and results in kinetochore-spindle misattachments and an increase in bipolar spindles associated with ectopic asters. The extra poles, which apparently from after chromosomes achieve a bipolar orientation, severly dirsupt the partitioning of chromosomes in anaphase. Borealin depletion has little effect on histone H3 serine[10] phosphorylation. These results implicate the chromosomal passenger holocomplex in the maintenance of spindle integrity and suggest that histone H3 serine[10] phosphorylation is performed by an Aurora B-INENP subcomplex."
Clearly such protein was named Borealin because it is acomplex compound with Aurora B Kinases.
Almost contemporaneously Sampath *et al.* (2004), investigating the same biochemical matter, the so-called "Chromosome Passenger Complex", discovered two new components of this complex, that is Dasra A and B, following an already established terminology proposed for the chromosomal passenger complex. Sampath *et al.* (2004, p. 187) wrote:
"In cells lacking centrosomes, such as those found in female meiosis, chromosomes must nucleate and stabilize microtubules in order to form a bipolar spindle. Here we report the identification of Dasra A and Dasra B, two new components of the vertebrate chromosomal passenger complex containing Incenp, Survivin, and the Kinase Aurora B, and demonstrate that this complex is required for chromatin-induced microtubule stabilization and spindle formation."
These biochemical data are here reported because Dasra B is identical to the Borealin of Gassmann *et al.* (2004).

Bromodomain: Tamkun et al. 1992 - John W. Tamkun together with several other researchers published a joint paper entitled "brahma. A Regulator of Drosophila Homeotic Genes Structurally Related to the Yeast Transcriptional Activator SNF2/SWI2".
These very important biochemical data and the new term bromodomain have been quoted as follows (cf. op. cit. p. 566):
"The brahma (brm) gene is required for the activation of multiple homeotic genes in Drosophila. Loss of function brm mutations suppress mutations in Polycomb, a repressor of hoemotic genes, and cause developmental defects similar to those arising from insufficient expression of the homeotic genes of the Annennapedia and Bithorax complexes. The brm gene encodes a 1638 residue protein that is similar to SNF2/SWI2, a protein involved in transcriptional activation in yeast, suggesting possible models for the role of brm in the transcriptional activation of homeotic genes. In addition, both brm and SNF2 contain a 77 amino acid motif that is found in other Drosophila, yeast, and human regulatory proteins and may be characteristic of a new family of regulatory proteins.
The structural motif common to the brm, fsh, SNF2, SPT7, and CCG1 proteins – which we refer to as the "bromodomain" – may be characteristic of a new family of regulatory proteins. The motif (Figure 6) occurs twice in both fsh and CCG1 and once in the other proteins."

The term bromodomain became quickly and acritically accepted by the biochemical literature; f.i. HAYNES *et al*. (1992, p. 2603) wrote:
"Identification of conserved domains or motifs in proteins may aid in the localization and analysis of important structural and functional regions. We report here a protein sequence motif, called the bromodomain (1), that has been found in six genes from humans (CCG1 and RING3), *Drosophila* (fsh and brm), and yeast (SPT7 and SNF2). The *fsh* and *brm* genes are required maternally for proper expression of certain homeotic genes (TAMKUN *et al*. 1992; HUANG & DAVID 1990).
"In the following literature, the concept and the meaning given to bromodomain has been variously modified or reinterpreted, cf. e.g. DHALLUIN *et al*. (1999: "single bromodomain" JACOBSON *et al*. (2000. "Double Bromodomain Module").
At least apparently as well TAMKUN *et. al*. (1992) as all following authors accepting the term bromodomain, avoid to mention an earlier coining of the acronym bromo in the field of Virology. Indeed, as early as 1977 BANCROFT & HORNE coined the term "Bromovirus (brome mosaic virus)" based on the composition bro + mo + virus. Actually the coining of such bromo prefix, here mentioned only for its historical priority is criticizable because it is ambiguous and superfluous.
Indeed the bromovirus effects the graminaceous plant brome (genus *Bromus*) and consequent bromovirus is interpretable as brom + o (connecting wevel) + virus.

Calcineurin: KLEE, CROUCH, KRINKS 1979 - The "calcineurin", is a protein discovered by KLEE, CROUCH and KRINKS (1979) and termed calcineurin for its specificity for the nervous system. These authors write (op. cit., abstact):
"Abstract - The inhibitory protein that binds calmodulin and thus prevents activation of several Ca^{2+} dependent enzymes by calmodulin is shown to also bind four Ca^{2+} per mol of protein with high affinity ($Kd <= 10^{-6}$ M). On the basis of its Ca^{2+} binding properties an its localization to nervous tissue, the inhibitory protein is now called "calcineurin." Calcineurin is composed of two subunits: calcineurin A (61,000 M_r) which interacts with calmodulin in a Ca^{2+} dependent fashion, and calcineurin B (15,000 M_r) which binds Ca^{2+}. The interaction of calcineurin A with calcineurin B is independent of Ca^{2+} or Mg^{2+}. The dual interaction of calcineurin A with two different Ca^{2+} binding components and the high affinity of calcineurin for Ca^{2+} suggest a possible role for calcineurin in the regulation of free Ca^{2+} concentrations in the nervous system. Calcineurin may thereby modulate the release and action of neurotransmitters."
Calcineurin is a fitting term at least from the linguistic point of view.

Calcitonin: COPP, DAVIDSON, CHENEY 1961 - The "calcitonin" has been discovered by COPP, DAVIDSON, CHENEY (1961), see also COPP and CAMERON (1961), COPP, CAMERON, CHENEY, DAVIDSON, HENZE (1962) and named calcitonin by COPP, DAVIDSON and CHENEY (1961) and namely:
"Evidence for a new parathyroid hormone which lowers blood calcium. The name "calcitonin" is suggested for this humoral substance to distinguish it from the regular parathyroid hormone."
See also COPP *et al*. (1962, p. 639: "We have proposed that this new ormone be named "calcitonin" since it is involved in the regulation of the normal calcium level or "tone" in the body fluids").
A few years later, HIRSCH, VOELKEL and MUNSON (1964) proposed Thyrocalcitonin and namely, cf. op. cit., note 1: "Adapted from "calcitonin", the name coined by COPP *et al*. (1961) for a hypocalcinemic factor attributed to the parathyroid gland".
Both calcitonin and thyrocalcitonin are fitting terms, at least from the linguistic point of view.

Calmodulin: CHEUNG, LYNCH, WALLACE 1978 - The term calmodulin can be found in an article by W.Y. CHEUNG, T.J. LYNCH and R.W. WALLACE entitled "An Endogenous Ca^{2+} -Dependent Activator Protein of Brain Adenilate Cyclase and Cyclic Nucleotide Phoshodiesterase", published in Advances in Cyclin Nucleotide Research vol. 9, pp. 233-251, GEORGE W.J. and IGNARRO L.J. eds. 1978, Raven Press, New York, U.S.A.. The inclusion of this paper (op. cit. p. 249) deserves quotation, namely:
"The discover of an inhibitor protein of adenylate cyclase and phosphodiesterase and its Ca^{2+} -dependent complex formation with the activator is of potential interest not only to the regulation of cAMP metabolism but also to the mechanism of action of Ca^{2+} in cellular reactions or processes. As stated earlier, the inhibitor protein may be another enzyme, the activity of which is regulated by the activator in response to the cellular flux of Ca^{2+}. This could constitute a concerted regulatory system in which Ca^{2+} exerts its effects on multiple enzymes through a common effector. Within this context, the activator may serve as Ca^{2+} mediator, or as a Ca^{2+} -dependent modulator. In view of the potential

multiple and diverse functions, the activator protein may be designated calmodulin."
The author fully disagrees as regards the choice of the prefix "cal" in coining the term calmodulin. In Biochemistry, the prefix referred to the calcium is "calci", see e.g. calcipenia and calcinosis, consequently the author believes that the present calmodulin should be modified to calcimodulin.
However, the sigla CaM is rightly ascribable to the term calcimodulin, see e.g. Abzhanov et al. 2006, p. 563: "We show that calmodulin (CaM), a molecule involved mediating Ca^{2+} …", since Ca is the symbol of calcium.

Calpain and calpastatin: Murachi, Tanaka, Hatanaka, Murakami 1980 - The term calpain has been coined by these authors and justified as follows:
"Terminology - A group of proteases ‡ which requires Ca^{2+} and SH-reducing agent for its full activity is called *calpain*. The proposal is based on an implication that *cal* stands for calcium as calcitonin, calmodulin, etc., while the ending *-pain* conforms to well-known thiol proteases including papain (EC 3.4.22.2) clostripain (EC3.4.22.8), bromelain (EC 3.4.22.4), etc. Accordingly, the newly found high-molecular-weight endogenous inhibitor of calpain is called *calpastatin*. Calpain has been known to occur in various tissues under different names (see below, Table 4). There are at least two types of the enzyme, to be called *calpain* I and *calpain* II, which are eluted in this order from a DEAE-cellulose column at pH 7.5 and show higher and lower sensitivities, respectively, to Ca^{2+} concentration (see below, Table 2)."
The author disagrees once more as regards the choice of the prefix cal and consequently proposes calciase short for calciprotease and calcistatin, short for calciproteostatin. The term calpain is currently quoted in the biochemical papers, without any linguistic criticism, cf. e.g. Yousefi *et al.* (2006).

Cohesin: Michaelis, Ciosk, Nasmyth, october 1997, "Cohesins: chromosomal proteins that prevent premature separation of sister chromatids" - The term cohesin has been proposed by Michaelis, Ciosk, Nasmyth (1997 pag. 41). This paper is very remarkable for biochemical and terminological data and consequently deserves adequate quotation. Cf. op. cit. p. 35-36:
"We describe three chromosmal proteins that prevent premature separation of sister chromatids in yeast. Two Smc1p and Smc3p, are members of the SMC family, which are putative ATPases with coiled-coil domains. A third protein, which we call Scc1p, binds to chromosomes during S phase, dissociates from them at the metaphase-to-anaphase transition, and is degrades by the anaphase promoting complex. Association of Scc1p with chromatin depends on Smc1p. Proteins homologous to Scc1p exist in a variety of eukaryotic organisms including humans. A common cohesion apparatus might be used by all eukaryotic cells during both mitosis and meiosis.
To identify proteins needed for sister chromatid cohesion that might be substrates of the APC, we set out to isolate mutants that lose chromosomes at a high frequency and are capable of separating sister chromatids in the absence of APC function. By this means, we identified four genes (SCC1, SCC2, SMC1 and SMC3) involved in sister chromatid cohesion. Scc1p (sister chromatid cohesion) binds to chromosomes during S phase, dissociates from them at the metaphase-to-anaphase transition, is at this stage degraded by the APC, and is essential for preventing premature sister chromatid separation. Smc1p and Smc3p are also chromosomal proteins. They belong to a family of proteins, members of which are important for chromosome condensation and form part of the longitudinal axis of mitotic chromosomes in vertebrates (Hirano *et al.* 1995; Koshland and Strunnikov 1996). The association of Scc1p with chromatin depends on Smc1p. Proteins similar to Scc1p exist in fission yeast (Birkenbihl an Subramani 1992). C. elegans *Drosophila* and in humans (McKay *et al.* 1996). Rec8 a related protein in fission yeast, is required for sister chromatid cohesion during meiosis (Molnar *et al.* 1995). A common cohesion apparatus might therefore be used during mitosis and meiosis in all eukaryotic cells."
"Sister Chromatid Cohesion Proteins - By identifying mutations that allow yeast cells lacking APC function to undergo some sembiance of anaphase, we have discovered four proteins necessary for sister chromatid cohesion. Two of these, Smc1p and Smc3p, are members of the SMC family of putative ATPases with colled-coil domains (Hirano *et al.* 1995). The third Scc1p, is an unstable protein that binds to chromosomes during late G1 or S phase (following its synthesis during late G1) and remains tightly-associated with sister chromatids until metaphase. Proteins similar to Scc1 exists in a wide variety of eukaryotes including humans. Proteins of this family contain conserved

domains at their N and C termini. Sequences related to the conserved C-terminal domain exists also in the Cdb4 protein from fission yeast, which is thought to bind bent DNA (YAMADA *et al*. 1994). The fourth protein, Scc2p, has a homolog in S.pombe but remains otherwise uncharacterized.
In wild-type cells, sister chromatids remain assoiated for an appreciable period after formation of mitotic spindles. In scc1, scc2, smc1 and smc3 mutants, sister chromatids separate prematurely, soon after the formation of bipolar spindles. Smc1p, Smc3p, and Scc1p are associated with chromosomes and are essential for the cohesive force that opposes microtubule-induced chromosome splitting. They might therefore be suitably called "cohesins." The premature separation of sister chromatids in scc and smc mutants is consisten with the currently accepted view that sister chromatids are under tension during metaphase and that this is an intrinsic aspect of chromosome alignment."
Chromo domain, chromo box (chromo = chr + o + mo = chromatin organization modifier): PARO & HOGNESS (1991) - These authors published a paper entitled "The polycomb protein shares a homologous domain with a heterochromatin-associated protein of *Drosophila*" had coined the terms chromo domain and chromo box on the basis of the following biochemical data and consideration, cf. PARO & HOGNESS 1991, p. 264:
"A comparison of the Pc protein sequence with different protein daba bases did not reveal a homology to functionally characterized protein domains. The only significant homology, excluding those due to the histidine repeats, was to the HPI protein (formerly CIA9) encoded by the suppressor of variegation gene Su(var) 205 (19, 29). This homology is restricted to a stretch of 37 aa in the N-terminal portion of both proteins (Figs. 1-3). Since the two similar domains occur in two proteins that are involved in the organization of the chromatin we have named this the "chromo domain" (chormatin organization modifier). The 111 bp encoding the chromo domain is called the "chromo box." Fig. 3 shows that the two chromo domains are to 65% identical over their 37 aa, with conservative replacements accounting for another 19%. No other significant similarities between the two proteins were found in the remaining sequences."
The meaning given by PARO & HOGNESS to their chromo domain and chromo box, cannot be accepted. Indeed, the prefix chromo belongs to the classic chromosome-chromatin terminology and consequently the expression chromo domain (box) is a short for chormosome domain (box), without any relation to an organization modifier.
However the prefix chromo, sensu PARO & HOGNESS (1991) has been acritically accepted and utilized by the biochemical literature, see e.g. LINDROTH *et al*. (2001: also Chromomethylase), JACOBS *et al.* (2001; 2004), FLANAGAN *et al*. (2005: "double chromodomain", and "CHD, for chromo-ATPase/helicase-DNA binding proteins").

Condensin: HIRANO T., KOBAYASHI, HIRANO M., may 1997: *"Condensins, Chromosome Condensation, Protein Complexes Containing XCAP-C, XCAP-E and a Xenopus Homolog of the Drosophila Barren Protein"* - The term condensin has been proposed by HIRANO T.KOBAYASHI and HIRANO M. as briefly quoted below (op. cit. pp. 511-512).
"We report here purification and characterization of chromosome condensation protein complexes (termed condensins) containing XCAP-C and XCAP-E, two Xenopus members of the SMC family. Sucrose density gradient centrifugarion reveals two major forms of condensins. The 8S form is a heterodimer of XCAP-C and XCAP-E, whereas the 13S form contains three additional subunits. One of them is identified as a homolog of the *Drosophila* Barren protein whose mutation shows a defect in chromosome segregation. Chromosomal targeting of condensins is mitosis-specific and is independent of topoisomerase IIα. 13S condensin is required for condensation, as demonstrated by immunodepletion and rescue experiments. Our results suggest that the condensin complexes represent the most abundant structural components of mitotic chromosomes and play a central role in driving chromosome condensation."
"To investigate further the role of XCAP-C and XCAP-E in mitotic chromosome condensation, we have purified protein complexes containing the two polypeptides from Xenopus egg extracts. We find that the majority of XCAP-C and XCAPE exists in two distinct forms in the extract: the 8S form (termed 8S condensin) consists of XCAP-C and XCAP-E, whereas the 13S form (13S condensin) contains three additional subunits. One of them, XCAP-H, is found to be a Xenopus homolog of the *Drosophila* barren gene product (BHAT *et al*. 1996).
Immunodepletion and rescue experiments show that 13S condensin is absolutely required for

chromosome assembly in vitro. Our results also suggest that chromosomal targeting of condensins is mitosis-specific an is independent of topoisomerase IIα."

Cyclomere (1072)*, Cyclin* (1983) *and Cyclosome* (1995) - These terms deserve a joint discussion since they are as well linguistically as cytologically very related.
Cyclin: Evans et al. (1983) - The term cyclin has been coined by Evans et al. (1983) as follows:

Op. cit. pp. 389-390:
"Cleavage in embryose of the sea urchin Arbacia punctulata consists of eight very rapid divisions that require continaul protein synthesis to sustain them. This synthesis is programmed by stored maternal mRNAs, which code for three or four particularly abundant proteins whose synthesis is barely if at all detectable in the unfertilized egg. One of these proteins is destroyed every time the cells divide. Eggs of the sea urchin Lytechinus pictus and oocytes of the surf clam Spisula solidissima also contain proteins that only start to be made after fertilizationi and are destroyed at certain points in the cell division cycle. We propose to call these proteins the cyclins.
There are clear differences between the patterns of proteins made before and after activation. The most striking change is the appearance of the prominent new bands A, B, and C after fertilization or activation with A23187, much as happens in Spisula (Rosenthal et al., 1980). However, closer inspection reveals other interesting features, of which the most unexpected is the behavior of protein A, which we shall call "cyclin" henceforth. It is the most strongly labeled protein at early times after fertilization, but by 85 min after fertilization (lane g, fertilized) it has almost disappeared. It gets stronger again in lanes h and i, only to decline again in lane k. These oscillations in the level of cyclin are extremely reproducible, as can be seen in Figures 2,3, and 6, which show similar behavior in different batches of fertilized Arbacia eggs."
Given that currently the ending "-in" stands for protein, the term cyclin is a short for cyclic-protein. Consequently it is a compound term rightly proposed and has been accepted by the modern literature, cf. e.g. Murray (2004), Potapova *et al.* (2006).

Cyclomere: Engelhardt & Pusa (1972) - As early as 1972 Engelhardt & Pusa coined the term cyclomere on the basis of the following experimental data and related interpretative considerations: Cf. op. cit., pp. 163, 164:
"The replicating sites of eukaryotic chromosomes appear, mostly, though not always[3], bound to the nuclear envelope and from bacterial analogies a nuclear envelope-associated polreplicon[4] has been postulated. Attachment of chromosomes to the nuclear envelope can be seen by light microscopy, especially for heterochromatin[5] and telomeres, and by electron microscopy. Nuclear pore complexes are seen as "multiple attachment sites" in whole mount preparations. What is the nature and substructure of the attachments?
Such elements might congregate, after "synaptic detachment" into the lateral elements of the synaptonemal complex building up for synapsis. The very same attachment elements could be responsible for synaptic recognition.
We propose, nevertheless, that the nuclear pore complex is essentially a permanent chromosomal element appearing in its familiar position where chromosomes make contact with the emerging nuclear envelope.
By direct inspection of normal and centrifuged material, there is a short "synaptic detachment" at about zygotene in various organisms but the chromatin-nuclear envelope connexions are restored rather early in pachytene[6,7]. The bipartite nuclear pore complex could implement these abrupt changes.
The nucleoplasmic half of the bipartite nuclear pore complex often stains more intensely with ruthenium red than the cytoplasmic half (Fig. 1d). We suggest that this nuclear half and the central plug make up a detachable chromosome element. Because it may have a central role in the organization and function of the chromosome, we propose to call it cyclomere. The exterior portions remaining in the outer nuclear membran, hypothetically, receptors, could peel off in nuclear envelope derived annulate lamellae to be involved in the construction of the envelope at telophase."
A part form the consideration that there are many cytological compound terms having the prefix cyclo-, linguistically cyclomere means only circular piece, from the Greek kyklos, circle, thus without any cytological relation.

Cyclosome: SUDAKIN et al. (1995) - The term cyclosome has been coined and interpreted by Sudakin and collaborators (1995, p. 185) as shortly reported below:
"The ubiquitin-mediated degradation of mitotic cyclins is required for cells to exit from mitosis. Previous work with cell-free systems has revealed four components required for cyclin-ubiquitin ligation and proteolysis" a nonspecific ubiquitin-activating enzyme E_1, a soluble fraction containing a ubiquitin carrier protein activity called E_2-C, a crude particulate fraction containing a ubiquitin ligase (E_3) activity that is activated during M-phase, and a constitutively active 26S proteasome that degrades ubiquitinated proteins. Here, we identify a novel ~ 1500-kDa complex termed the cyclosome, which contains a cyclin-selective ubiquitin ligase activity, E_3-C. E_3-C is present but inactive during interphase; it can be activated in vitro by the addition of cdc2, enabling the transfer of ubiquitin from E_2-C to cyclin. The kinetics of E_3-C activation suggest the existence of one or more intermediates between cdc2 and E_3-C. Cyclosome-associated E_3-C acts on both cyclin A and B, and requires the presence of wild-type N-terminal destruction box motifs in each cyclin. Ubiquitinated cyclins are then rapidly recognized and degraded by the proteasome. These results identify the cyclosome-associated E_3-C as the component of the cyclin destruction machinery whose activity is ultimately regulated by cdc2 and, as such, the element directly responsible for setting mitotic cyclin levels during early embryonic cell cycles."
These authors apparently were unaware of the very similar term cyclomere, proposed earlier by ENGELHARDT & PUSA (1972).
Since cyclosome etymologically means circular body and, just as cyclomere, is without any specific cytological implication, it should be refused at least in the biochemical field here analyzed.

Izumo: INOUE et al. 2005 - N. INOUE, M. IKAWA, A. ISOTANI and M. OKABE published a paper entitled "The immunoglobulin superfamily" protein Izumo is required for sperm to fuse with eggs. They coined the term Izumo on the base of the following biochemical data and related interpretations: Cf. op. cit. p. 234.
"Recently, CD9 on the egg membrane was found to be essential for fusion [2-4], but sperm-related fusion factors remain unknown. Here, by using a fusion-inhibiting monoclonal antibody[5] and gene cloning, we identify a mouse sperm fusion-related antigen and show that the antigen is a novel immunoglobulin superfamily protein. We have termed the gene *Izumo* and produced a gene-disrupted mouse line. Izumo $^{-/-}$ mice were healthy but males were sterile. They produced normal-looking sperm that bound to and penetrated the zona pellucida but were incapable of fusing with eggs. Human sperm also contain Izumo and addition of the antibody against human Izumo left the sperm unable to fuse with zona-free hamster eggs.
We termed the antigen 'Izumo' after a Japanese shrine dedicated to marriage."
The gene encodes a novel immunoglobulin superfamily (IgSF), type I membrane protein with an extracellular immunoglobulin domain that contains one putative glycosylation site (Fig. 1a, b). Mouse Izumo was shown to be a testis (sperm)-specific 56.4-kDa antigen by western blotting with a polyclonal antibody raised against recombinant mouse Izumo (Fig. 1c). Izumo was also detectable as a 37.2-kDa protein by western blotting of human sperm with anti-human Izumo antibody (Fig. 1d) Izumo was not detectable on the surface of fresh sperm.

Nestin: Lendahl, Zimmerman, McKay 1990 - The term nestin has been coined by LENDAHL, ZIMMERMAN and MCKAY (1990) and justified as follows:
"We describe a gene whose expression distinguishes the stem cells from the more differentiated cells in the neural tube. This gene was named nestin because it is specifically expressed in neuroepithelial stem cells. The predicted amino acid sequence of the nestin gene product shows that nestin defines a distinct sixth class of intermediate filament protein."
Aside from any biochemical evaluation, the author suggests neurostin in the place of nestin for the sake of terminological coordination with already established analogous terms such as neuropil and neuropilin.

Nesprin: ZHANG et al. 2001 - The term nesprin (acronym) has been coined by ZHANG *et al.* 2001 as follows:
"In search of vascular smooth muscle cell differentiation markers, we identified two genes encoding members of a new family of type II integral membrane proteins. Both are ubiquitously expressed, and tissue-specific alternative mRNA initiation and splicing generate at least two major isoforms of each

protein, with the smaller isoforms being truncated at the N-terminus. We have named these proteins nesprin-1 and –2 for nuclear envelope spectrin repeat as they are characterized by the presence of multiple, clustered spectrin repeats, bipartite nuclear localization sequences and a conserved C-terminal single transmembrane domain. Transient transfection of EGFP-fusion expressoin constructs demonstrated their localization to the nuclear membrane with a novel C-terminal, TM-domain-containing sequence essential for perinuclear localization. Using antibodies to nesprin-1, we documented its colocalization with LAP1, emerin and lamins at the nuclear envelope, and immunogold labeling confirmed its presence at the nuclear envelope and in the nucleus where it colocalixed with heterochromatin. Nesprin-1 is developmentally regulated in both smooth and skeletal muscle and is relocalixed from the nuclear envelope to the nucleus and cytoplasm during C2C12 myoblast differentiation. These data and structural analogies with other proteins suggest that nesprins may function as 'dystrophins of the nucleus' to maintain nuclear organization and structural integrity."
Given that the nesprins function as nuclear distrophins the author would propose the alternative term karyodistrophin.

Netrins: Serafini et al. 1994, Kennedy et al. 1994 - Netrin is a term coined by Serafini *et al.* (1994), followed by Kennedy *et al.* (1994), to define a family of axon outgrowth-promoting proteins homologous to the *Caenorhabditis elegans* UNC-6.
The biochemical data have been summarized as follows by Serafini *et al.* (1994, p. 409):
"In vertebrates, commissural axons pioneer a circumferential pathway to the floor plate at the ventral midline of the embryonic spinal cord. Floor plate cells secrete a diffusible factor that promotes the outgrowth of commisural axons in vitro. We have purified from embryonic chick brain two proteins, netrin-1 and netrin-2, that each possess commissural axon outgrowth-promoting activity, and we have also identified a distinct activity that potentiates their effects. Cloning of cDNAs encoding the two netrins shows that they are homologous to UNC-6, a laminin-related protein required for the circumferential migration of cells and axons in C.elegans. This homology suggests that growth cones in the vertebrate spinal cord and the nematode are responsive to similar molecular cues."
The choice of the term netrin has been justified as quoted below:
"Outgrowth-promoting activity cofractionated with each of the two major proteins of 75 kDa and 78 kDa …
Because they guide axons (see the following paper, Kennedy *et al.* 1994) the proteins of 78 and 75 kDa have been termed netrin-1 and netrin-2, respectively: the root "netr" derives from the Sanskrit "one who guides".
The author fully disagrees as regards the linguistic choice of netr, a root based on the Sanskrit language since the scientific literature, as an orthodox procedure, refers to the Latin and Greek classic languages.
As regards the need of proposing an alternative term, as f.i. chemotropins (= chemotropiproteins), this alternative can be advanced only within a general terminological revision of these cytokinetic questions.

Plectin: Wiche, Hermann, Leichtfried, Pytela 1982 - Wiche *et al.* (1982) wrote a paper entitled "Plectin: a High-molecular-weight Cytoskeletal Polypeptide Component That Copurifies with Intermediate Filaments of the Vimentin-Type". The term plectin, linguistically, was proposed and justified as follows:
"In reference to its cellular localization and to its postulated function as a cross-linker of cytoskeletal filaments, we propose to term this high-M, component, plectin (from the Greek word πλεκτη, meaning net or mesh)."
Further biochemical investigations greatly encreased plectin's role as mechanical linker and stabilizer of structural elements. As regards the choice of this term, it is quite evident that plectin requires a further qualification, just for instance, neuroplectin.

Pontin: Bauer, Huber, Kemler 1998 - Andreas Bauer, Otman Huber and Rolf Kember published a paper entitled "Pontin 52, an interaction partner of β-catenin, binds to the TATA box binding protein". They coined the term Pontin on the basis of the following biochemical data and consideration, cf. op. cit. p. 14789:
"Of particular interest was the high homology to the recently described rat protein TIP49 (rTIP49),

which was identified as a binding partner of the TBP, a component of the basic transcription machinery (24). This finding suggested that the 52-kDa protein also could bind to TBP and thus bridge β-catenin to TBP. The 52-kDa protein therefore was named Pontin52 (pons, bridge in Latin)."
The term pontin is linguistically fitting, however these authors overlooked the occurrence of an earlier almost identical term, namely ponticulin, see, e.g., The Oxford Dictionary of Biochemistry and Molecular Biology, Oxford Press, 1997.

Reptin: BAUER et al. 2000 - A few years later the discovery of pontin, BAUER, HUBER, KEMLER and other members of the scientific staff, cf. BAUER *et al.* 2000, published an additional account on this biochemical matter and claimed the discovery of "an interacting partner of pontin", termed reptin of the basis of the following data and considerations:
"Here we report that TIP49b, which we isolated independently as an interacting partner of Pontin52 and named Reptin52 (repressing Pontin52), is able, like Pontin 52, to bind β-catenin and TBP directly. Moreover, we demonstrated by reporter gene assays that Reptin52 represses gene activation mediated by TCF- β-catenin while Pontin52 can stimulate gene activation. To address their function in Wg/Wnt signalling *in vivo*, we isolated and mutagenized the orthologous genes in *Drosophila: dpontin (dpon)* and *dreptin (drep)*. Consistent with the reporter gene assays, removal of one copy of either *dpon* or *drep* modifies, in an opposite manner, the phenotypes generated by *arm* loss or gain of function. Our results provide evidence for a new regulatory mechanism of Wg/Wnt signalling where Pontin52 and Reptin52 act antagonistically on target gene activation."
The author disagrees as regards both the linguistic procedure and the meaning ascribed to reptin. Linguistically, there is no relation between the term reptin and the claimed concept of repressor assigned to this term. In Genetics, the concept of repression is traditionally termed "repressor" and consequently the author believes that repressopontin (repress + o) is a better linguistical alternative to the present reptin.

Selectin: BEVILACQUA et al. 1991 - Es early as 1991, a large group of biochemists working on the cell surfaec proteins, see BEVILACQUA *et al.* (1991, Cell 67, p. 233: "Selectins: A Family of Adhesion Receptors) proposed this term on the base of the following data and considerations:
"Recent data have shown that a group of cell surface proteins, originally studied independently as lymphocyte homing receptors or as activation-induced surface proteins of platelets and/or endothelial cells (STOOLMAN 1989) are structurally related. Each is an integral membrane protein with an N-terminal, C-type lectin domain followed by an EGF-like module, multiple copies of the consensus repeat units characteristic of complement0binding proteins, a transmembrane segment, and a short cytoplasmic domain. The three known proteins having this structure are encoded by closely linked genes on the long arm of human and mouse chromosome 1 (WATSON *et al.* 1990). The gene sructures are related, and the genes clearly arose by gene duplication.
These proteins are all involved in cell-cell adhesion events and constitute a new family of cell adhesion receptors. A wide variety of names are used to designate these proteins, owing to their independent discovery by different laboratories working in several fields. This diversify of nomenclature interferes with the dissemination of information about these proteins. After consultation among the researchers working on these proteins be named selectins to reflect the involvement of carbohydrate recognition in their functions. Individual members of the family will be designated by a prefix capital letter, as is done for the cadherins (e. g., E-, N-, P-). Letters can be chosen based on the source of the original discovery but are not intended to imply cell type specificity.
The three known selectins are:
E-selectin
L-selectin
P-selectin (CD62)
We suggest that all future publications concerning these proteins should use these names (and CD numbers when they exist) to facilitate communication of data both within the field and more generally."

Syntaxin: BENNET, CALAKOS, SCHELLER 1992 - These authors published a paper entitled "Syntaxin: A Synaptic Protein Implicated in Docking of Synaptic Vesicles at Presynaptic Active Zones" (1992), and summarized their biochemical data as follows:
"Synaptic vesicles store neurotransmitters that are relased during calcium-regulated exocytosis.

The specificity of neurotransmitter release requires the localixation of both synaptic vesicles and calcium channels to the presynaptic active zone. Two 35-kilodalton proteins (p35 or syntaxins) were identified that interact with the synaptic vesicle protein p65 (synaptotagmin). The p35 proteins are expressed only in the nervous system, are 84 percent identical, include carboxyl-terminal membrane anchors, and are concentrated on the plasma membrane at synaptic sites. An antibody to p35 immunoprecipitated solubilized N-type calcium channels. The p35 proteins may function in docking synaptic vesicles near calcium channels at presynaptic active zones."
The choice of the term syntaxin deserves full quotation and namely, cf. op. cit. p. 258.
"The molecular properties of p35 that we have described suggest that it may be involved in synaptic vesicle docking of fusion. Because of this, we propose the name syntaxin, from the Greek συνταζνσ meaning "putting together in order." Our working model is that syntaxin, by virtue of its interactions with p65 and N-type calcium channel, brings into close proximity the two membranes involved in the fusion reaction and the source of a factor that regulates membrane fusion. This arrangement would ensure that exocytosis occurs both at restricted sites and with an extremely rapid time course. The interaction between p65 and syntaxin could serve as an intermembrane scaffold on which the molecular machinery that catalyzes the fusion reaction is assembled."
The author criticizes this term by a consideration as well simple as obvious, that is syntaxin is not a biochemical term. It is, indeed, a linguistic suffix that would require a prefix able to qualify biochemically the resulting full compound term.

The eph gene, eph protein (Hirai et al. 1987) *and the Ephrins (Eph Nomenclature Committee, cf. CELL, 1997)* - Hisamuru Hirai and colleagues published a paper entitled "A Novel Putative Tyrosine Kinase Receptor Encoded by the eph gene" and coined the expression eph gene and eph protein, cf. Hirai *et al.* (1987, p. 1717-1718):
"Growth factors and their receptors are involved in the regulation of cell proliferation and also play a key role in oncogenesis. In this study, a novel putative kinase receptor gene, termed *eph*, has been identified and characterized by molecular cloning. Its primary structure is similar to that of tyrosine kinase receptors thus fra cloned and includes a cysteine-rich region in the extracellular domain. However, other features of the sequence distinguish the eph gene product from known receptors with tyrosine kinase activity. Thus the *eph* protein may define a new class of these molecules. The *eph* gene is overexpressed in several human carcinomas, suggesting that this gene may be involved in the neoplastic process of some tumors.
….In an erythropoietin-producing human hepatocellular carcinoma cell line (ETL-1), the novel gene, which we have termed *eph*, is overexpressed 10- to 20-fold but not amplified (Fig. 1, B and C)."
This *eph* acronym referring to the expression erythropoietin-producing hepatocarcinoma. Further biochemical investigations, documented the function role of the "EPH-family receptor Nuk and its transmembrane ligands".
Such a nomenclatural disorder justified the establishment of an international "Eph Nomenclature Committee 1987 (Cf. CELL 1997, vol. 90, p. 404. "The Committee consists of Flanagan J-G., Gale N.W., Hunter T., Pasquale E.B. and Tessier-Lavigne M. (chair). The considerations and the proposals advanced by this International Committee deserves the following quotation:
"Because of the rapid pace of discovery of receptors and ligands in various species, many different names have been used to designate them, making it difficult for the general scientific community to follow developments in this exciting field. To address this problem, representatives of over 20 laboratories involved in research on the Eph family initiated extensive discussions at the "Molecular Biology of Axon Guidance" workshop held at the EMBL, Heidelberg, in September, 1996. As a result, a proposal was put forth to unify and to systematize the nomenclature for these ligands and receptors, and an Eph Nomenclature Committee was elected to refine the proposal in consultation with the community al large. The resulting nomenclature has now been endorsed by over 70 scientists, many of whom contributed extensively to defining the nomenclature and to preparing this letter, as well as by the Human and Mouse Gene Nomenclature Committees.
Ligands
It is proposed that the ligands be known as ephrins (pronounced eff-rins), which can be derived as an abbreviation for Eph family receptor interacting proteins or from the ancient Greek word (ephoros), meaning overseer or controller. The ligands are naturally divided into two structural

types, being membrane-anchored either by a glycosylphosphatidylinositol (GPl) linkage or through a transmembrane domain."

As regards the coining of the term ephrin the author disagrees from the evaluations of the Committee and advances what he considers the only orthodox terminological procedure to be applied in this case.

Given that the acronym eph refers to the expression erythropoietin-producing hepatocarcinoma to the receptors encoded by such gene should be assigned the acronym ephr. Indeed, HIRAI and collaborators in their paper quote the wide utilization ofthe letter R in coining acronyms referable to receptors, e.g.:

CSF-1-R : COUSSENS *et al.* 1985 (Colony-Stimulating Factor 1);
EGF-R-1 : ULLRICH *et al.* 1984 (Epidermal Groth Factor);
EGF-R-2 : COUSSENS *et al.* 1986 (" " ");
IGF-I-R : ULLRICH *et al.* 1986 (Insulin-like Groth Factor);
IR : ULLRICH *et al.* 1985 (Insulin Receptor);
PDGF-R : YARDEN *et al.* 1986 (Platelet-Derived Growth Factor).

Once established the acronym ephr the following classic procedure would be suggested that is the further addition of the suffix in, see e.g. chromatin, nuclein, cyclin, thus giving rise to ephrin!

Tubulin: MOHRI 1968 - BORIS & TAYLOR (1067), investigating the binding of colchicine to celllular protein (tissue culture of Hela cells) write: "the binding site had a sedimentation constant of 6S and it is suggested that the protein is a subunit of microtubules".

The following year MOHRI (1968) isolated the protein of microtubules of flagella and cilia of the sea-urchins (*Pseudocentrotus*, Anthocidaris) and termed such a protein as tubulin on the basis of the following considerations:

"The composition is entirely different from that of flagellin which constitutes bactreria flagella … (MOHRI 1968, p. 1054).

"The appearance of the microtubules is also different from that of actin filaments or thin filaments of muscle. From these facts, we believe that the microtubule constituent is a different protein for which we propose the nema "tubulin" (YANAGISAWA, HASEGAWA, MOHRI; Exper. Cell. Res. in press).

As regards modern literature on this matter see e.g. DRYKOVA *et al.* (2003), HORIO & OAKLEY (2003; 2005), DIXIT & CYR (2004), MURATA *et al.* (2005), GRISHCHUK *et al.* (2005) and LÜDERS, PATEL, STEARNS (2006).

F³. *The mono-polychromosome terminology* - The author confines himself to quote only the main data and the papers of historical interest.

a) Older historical data.
b) Monocromosomic and polychromosomic: GREGOIRE and WYGAERTS (1903), CHODAT (1925).
c) Monochromosome: WINGE (1917).
d) Haplochromosome: MORGAN (1924), CHODAT (1925).
e) Diplochromosome: MORGAN (1924), diplochromosome and monochromosome of WHITE (1935 a; b); polychromosome and diplobivalent of BARBER (1940).
f) Tetradi somatiche: DELLA VALLE (1907).
g) Tetrachromosome: BERGER and WITKUS (1946).
h) Quadruplochromosome: BIESELE, POYNER and PAINTER (1942).

a) Older historical data.

The terminology regarding the multi-partite chromosome structure begins with HÄCKER's papers published in the years 1890, 1891, 1892, 1894. This author distinguished Einzelelement, Doppelelement (1890), Doppelchromosom (1891; 1892), Plurivalent Mitosen, Bivalent, Plurivalent Chromosomen (1894).

A few years later MCCLUNG proposed chromatid (1900) and later (1905) an historical classification of the chromosomes which deserves mention (cf. MCCLUNG, 1905, p. 339):

"NEW TERMS EMPLOYED. Definitions and Classifications of Chromosomes.

Chromosomes are chromatin elements acting as unit structures during mitosis. Chromosomes are of two general classes.

1. Simple – containing two chromatids in metaphase.
2. Multiple – containing more than two chromatids in metaphase and formed by the union of simple chromosomes:
 • Tetrads, containing four chromatids.
 • Hexads, containing six chromatids (not yet observed).
 • Octads, containing eitht chromatids (not yet observed).
 • Decads, containing ten chromatids.

A chromatid is a half of a simple chromosome.
The univalent-bivalent terminology became enriched by many terms coined in the period 1931-1957, for instance:
 • hemiunivalent: Edman (1931); see also semiunivalente Battaglia (1945b);
 • amphibivalent: Häkansson (1931 a; b; c).
 • pseudobivalent: Levan (1937);
 • diplobivalent: Barber (1940);
 • quasibivalent: Östergren and Vigfusson (1953);
 • autobivalent: Häkansson and Levan (1957).

These terms together with some other analogous modern terms certainsly deserve redefinition on the base of the present biochemical data. This task is beyond the purpose of the present paper.

b) *Monocromosomic and polychromosomic.*

The adjectives monochromosomic and polychromosomic have been coined by Gregoire and Wygaerts (1903) ascribing to them the meaning occurrence of one or more chromosomes, namely: Grégoire & Wygaerts (1903 p. 49) write:
"De plus, nous sommes bien ici en présence d'une recontitution de noyau par caryomérites. N'ayant pas observé le début de la télophase, nous ne saurions dire si parfois il se forme autant de vésicules que de chromosomes, ni si les caryomérites, mono- ou polychromosomiques, sont souvent, au début, tour à fait indépendants. Masi ce qui est certain, c'est que *le noyau résulte de la confluence de vésicules, ou monochromosomiques ou polychromosomiques, soit que cette confluence se produise dès le début, soit qu'elle s'effectue seulement plus tard*. ».
The same terminology can also be found in Chodat (1925, p. 15). Chodat wrote:

« V. Grégoire et A. Wygaerts, ont publié, sous le titre de: "Reconstitution des noyaux et la formation des chromosomes dans les cinèses somatiques (*Trillium cernuum*) et télophase, nous ne saurions dire si parfois il se forme autant de vésicules que de chromosomes, ni si les caryomérites, mono- (ou polychromosomiques) son souvent au début indépendantes." in *La Cellule,* 21 (1903) 47.
As regards the meaning of Karyomeriten and Idiomeren see also Goldschmidt (1904a; b; c) and Häcker (1902a; b).
Lastly the Jackson's Glossary of Botanical Terms (1928) quotes: "monochromosomic: an idiomere having only the chromosome (Chodat); polychromosomic: an idiomere having many chromosomes (Chodat)."

c) *Monochromosome.*

This term has been coined by Winge (1917): heterochromosomes (monochromosomes), and reproposed by White (1935a; b, overlooking the priority of Winge), together with diplochromosome (see further).

d) *Haplochromosome.*

This term was proposed by Morgan (1924, p. 271, footnote), together with diplochromosome. It is notewerthy to quote that almost contemporaneously the term haplochromosome is recorded by Chodat (1925) as follows: Chodat (1925, p. 18):
"De cet état stepsinema, on passe insensiblement, par raccourcissement, au stade brachynema et, en même temps, les tours de spires diminuent. Certains auteurs veulent admettre que, durant la synapsis et encore après, il y ait fusion des paires (myxochromosomes) et qu'à ce mement l'individualité des haplochromosomes disparaisse (Bonnevie, 1911), tandis que les autres (Grégoire, en particulier), plus nombreux, admettent une simple juxtaosition suivie d'une disjunction totale au stade métaphase.

Dans le premier cas (BONNEVIE, etc.), le myxochromosome subirait un clivage longitudinal à la façon d'un chromosome somatique, tandis que, selon GRÉGOIRE, il s'agirait simplement d'un décollement des deux chromosomes accolés dans la paire bivalente, donc une pseudo-mitose."

e) *Diplochromosome.*

As mentioned in the preceeding pages, MORGAN (1924) quoted contemporaneously diplochromosome and haplochromosome.
However the complet mono-diplochromosome became a current expression in cytology by virtue of some classic papers published in the period from 1935 to 1949.
First WHITE (1935 a; b) describing the effects of X-rays on mitosis in the spermatogonial divisions of *Locusta migratoria* chosen the terms monochromosome, diplochromosome and mitotic bivalent. Meanings and definitions ascribed by WHITE to these terms descrive documentation for their noticeable historical interest., see Text-Figs 1, 2. Cf. White (1935 a, p. 300):
"Diese eigentümlichen Strukturen, die im Gegensatz zu den gewöhnlichen Monochromosomen "Diplochromosomen" genannt werden mögen, stellen offensichtlich ein Analogon zu den "Attached-X"-Chromosomen bei *Drosophila melanogaster* dar. Die Diplochromosomen entstehen durch eine zweifache Teilung der Chromatiden, ohne daß inzwischen eine Anaphasetrennung stattfindet. Da Diplochromosomen nur in röntgenbestrahltem Material, nicht dagegen in den sehr ausgedehnten Kontrollen gefunden wurden, darf man diese Abnormität als eine Folge der Bestrahlung betrachten. Daß es sich bei der Erscheinung um eine Allgemeinreaktion des Kernes handelt, geht aus der Tatsache hervor, daß stets sämtliche Chromosomen eines Kernes Diplochromosomen darstellen, niemals nur einzelne von ihnen."
Cf. WHITE (1935 b, p. 28):
"I shall refer to these structures as *diplochromosomes*, an ordinary chromosme of the type represented in fig. 8 being a *monochromosome*. Monochromosomes consist of four chromatids and a spindle attachment; in chromosomes which have hitherto been considered to have terminal spindle attachments two of these are very short and constitute the "polar granules." Diplochromosomes consists of eight chromatids (in the present case four long ones and four polar granules)."
Cf. WHITE (1935 b, pp. 22-23):
"Most frequent of all the abnormalities in 32-hour material are chromosomes with two points of attachment to the spindle, in which it is clear that fusion has taken place between two chromosomes. The structures tabelled M.b. and D.a. in figs 9 and 11 are examples of this type of aberration. Some of them are difficult to analyse in terms of chromatids, but it is probable that all are *reciprocal chromatid fusions*. The clearest example is M.b. in fig. 9, represented diagrammatically in fig. 18. Here it is clear that a sort of somatic crossing over has taken place between two of the four chormatids at the level in question. This has resulted in a structure which may be described as a "mitotic bivalent." It differs from a true meiotic bivalent, fig. 19, in that one of the four chromatids has two spindle attachments, while one of the others has none. At the next division the latter will appear as a fragment."
White quoting the complet mono-and diplochromosome did not mention or at least overlocked the earlier priorities over these two terms.
A few years later the chromosome terminology became enriched by the neoterm coined by BARBER (1940), namely diplobivalent BARBER (1940, pp. 174, 184) investigated the effect of abnormal temperatures (30° - 40° C) on the meiotic divisions of the pollen-grains of *Fritillaria meleagris*. Owing to this treatment the diplotene nucleus lapses directly into a pollen grain resting nucleus. The pollen-grain chromatid division takes plade to give, at the metaphase of the pollen-grain mitosis, diplochromosome bivalents (diplobivalents) consisting of eight chromatids. "Furter, in discussing the occurrence of diplochromosomes BARBER chose the term polychromosome for chromosome with eight, sixteen etc. chromatids, already known; for instance in *Culex* (BERGER 1938 a; b), commented as follows, cf. BARBER 1940, p. 140):
"The diplochromosomos in *Culex* and *Antirrhinum* are more complex. More than four chromatids can be associated at one centromore. Chromosomes, with eight, sixteen, etc., chromatids may be formed (see BERGER's figures 9 and 11y). They are polychromosomes. The behaviour at anaphase of polychromosomes has not been described completely, but they occur together with cells containing the 8-ploid or 16-ploid number of monochromosomes. We muste therefore assume that they break up into their separate chromatids at anaphase. This is probably the origin of the cells figured by

BORGOR (1938, figures 17,18, 19 plate 1).
The conditions responsible for the formation of diplochromosomes are very diverse. They may be produced by the direct action of X-rays or by Light temperatures. They are apparently a normal part of the developmental cycle in certain tissues as in *Culex* at metamorphosis, or in the older parts of roots. Their occurrence may also be genetically determined by a single recessive gene (*Antirrhinum*)."

f) *Tetradi somatiche.*

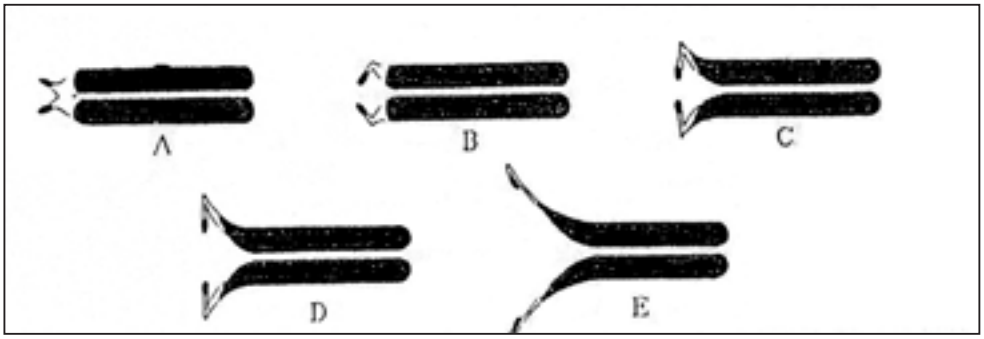


Fig. 1a — From Fig.s A: prometaphase; B: metaphase; and C-E: stages of anaphase-separation in a chromosome with "terminal" (really sub-terminal) spindle attachment. From WHITE (1935 b; Fig. 8).

Fig. 1b — From Fig.s A=Schema eines Monochromosoms, B=eines Diplochromosoms. Spindelanheftungen sind punktiert. From WHITE (1935 a; Fig. 2).

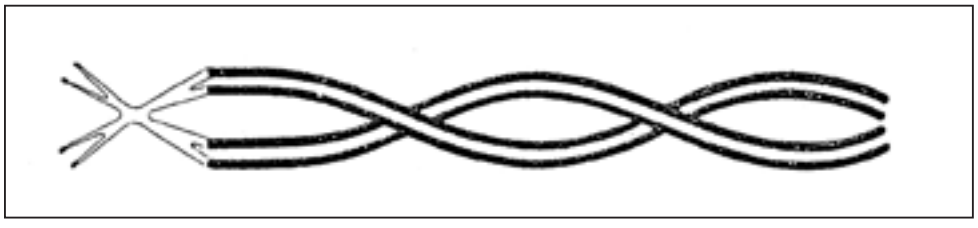


Fig. 1c — Diagram of a diplochromosome in early prophase when the two limbs are still spirally wound round one another. From WHITE (1935 b; Fig. 26).

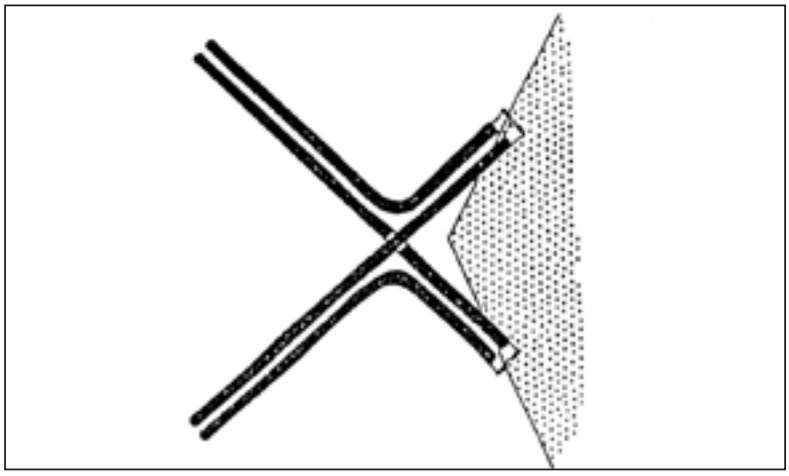


Fig. 2a —- From Fig. 19 - Diagram of a meiotic bivalent with a single chiasma-to compare with fig.18. From WHITE (1935 b; Fig 19).

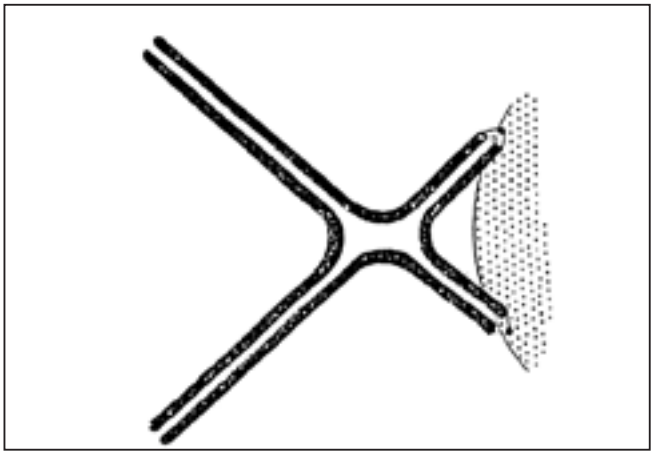


Fig. 2b — Diagram of a "miotic bivalent" (reciprocal chormatid fusion). From WHITE (1935 b; Fig 18).

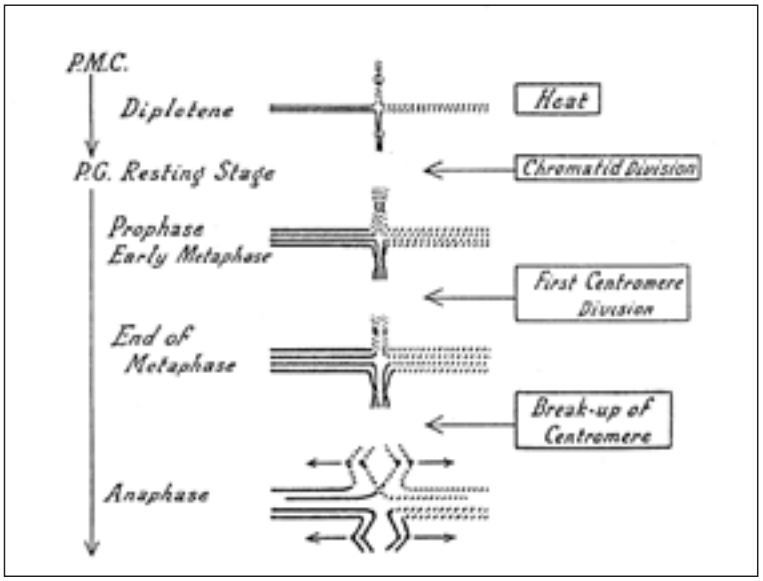


Fig. 2c — Diagram showing the origin and behaviour of diplobivalents. From BARBER (1940; Fig. 4).

In the present context, the author must also duly mention that the occurrence of somatic chromosomes showing a four-stranded structure had been fairly described by P. DELLA VALLE (1907: tetradi in cellule somatiche) and observed again the following year by M. POPOFF (1908: Tetradenchromosomen in der Leberzellen).

g) *Tetrachromosome.*

The term tetrachromosome has been coined by BERGER and WIKTUS (1946, *Allium cepa*, dividing tetraploid cells) and described as follows: "At prometaphase such cells showed the diploid number (16) of tetrachromosomes, i.e., two chromosomes united at a single SA-region and relationally coiled. The two chromatids of each chromosome were also relationally coiled."
The synonimy tetrachromosome = diplochromosome can also be found in KATO (1957, p. 8, endosperm of *Allium cepa*).

h) *Quadruplochromosome.*

The concept of quadruplochromosome, spelled ad quadruple chromosome, is recorded by the paper BIESELE, POYNER and PAINTER (1942, nuclear phenomena in mouse cancer) as follows: "EMMY STEIN (1935b) saw double and quadruple chromosomes in the cancerous growths (determined by a homozygous recessive mutant gene produced through radium irradiation) in snap-dragons, and she interpreted them as chromoso es undergoing somatic reduction divisions."

G. *Soma terms in Cytology*

a) Historical old terms.
b) Terms quoted by the present biological literature.
c) Soma compound terms pertinent to the classic chromosome terminology: MONTGOMERY (1904; 1905).
d) The mono, di, tri,… endekasome and the simplex, duplex (etc.) system of BLAKESLEE (1921).

a) *Historical old terms (1880-1899).*

These historical old terms deserve quotation because the term soma (body wide sense) has been largely utilized by the cytologists of the nineteenth century, namely:

1867 Parasoma: LA VALETTE ST. GEORGE;
1880 Mikrosom (en) HANSTEIN;
1882 Cyto-, Nucleo-, Chromato-, Mikrosomata (somen): STRASBURGER;
1883 Karyosoma, Plasmosoma: OGATA;
" Plasmotosomen: WIESNER;
1888 Centrosoma: BOVERI;
" Hyalosomen: LUKJANOW;
" Chromosom(en), Chromosoma: WALDEYER;
1889 Chromatosom(en): DAVIDOFF;
" Mitosoma: PLATNER (1889b);
1890 Plasom(en):WIESNER (1890a; b);
1891 Diplosom: HÄCKER (1891 and 1892a);
1892 Leukosom: ZIMMERMANN;
1893 Idiosomes: WHITMAN;
" Pseudosome: HÄCKER;
1894 Amylosome: ZIMMERMANN (1894c);
" Dermatosoma: ZIMMERMANN (1894c);
1895 Nucleolo-Centrosoma: KEUTEN;
1896 Nucleomicrosoma: FOL;
1898 Monosom (-e, -a): HENRY; ZIMMERMANN.

The full references can be found in classic literature as e.g. SHARP (1934), WILSON (1925) and DARLINGTON (1937; 1939).

b) *Terms quoted by the present biological literature.*

There are many soma-compound terms quoted in the present cytological literature. However their criticism is not within the purpose of the present paper. In any case, for the sake of accuracy their prefix are recorded below:
achro- (acro-, akro-), allo-, amphi-, ampho-, archo-, atracto-, auto-, bi-, (di-, tri-, tetra-, penta-, ….poly-), bio-, brachy-, calcio-, calypto-, caryo- (karyo-), centro-, centronucleo-, chlarago-, chondrio-, chromatin-, chromatino-, chromidio-, chromo-, chromomicro-, cineto- (kineto-), crypto-, cyto-, cytogranulo-, cytoliso- (cytolyso-), cytomicro-, dermato-, desmo-, deuto-, deuthyalo-, di-, dictyo-, dinucleo-, diplo-, ditto-, duocto-, ecdy-, eclecto-, ecto- (ekto-), elekto-, endo-, eo-, epi-, epinucleo-, ergasto-, exo-, fibro-, gamo-, geno-, glyoxi-, Golgi-, gono-, grano-, hetero-, haplo-, hyalo-, (deuthyalo-, prothyalo-), idio-, idioecto-, idioendo-, idiogranulo-, idiophtharto-, idiosphaero-, informo-, kayo-, kariocentro-, karyomicro-, karyomito-, kineto- (cineto-), kinetoplasma-, kino-, lepido-, leuco- (leuko-), lexo-, lino-, lipido-, lipo-, lyo-, lyso-, macro-, (makro-), mastigo-, mega-, meio-, meso-, metachromatino-, metanucleo-, micro (mikro-), mito-, mitoribo-, mixo-, mono-, monochromo-, mononucleo-, monotelodi-, (tri-, etc.)-, monoteloiso-, myo-, neuro-, nucleo-, nucleocentro-, nucleomicro- (nucleomikro-), nucleolo-, nucleocaryo-, nucleocentro-, oleo-, oo (oö-), oxydo-, pangeno-, para-, parabaso-, paranucleo-, percno-, peridio-, perisoleno-, peroxy-, phago-, (phagolyso-, lysophago-), phragmo-, pla-, plasma-, plasmalemma-, plasmamikro-, plasmo-, plasto-, plastomo-, platy-, poly-, polyribo-, primo-, pro-, proteo-, proto-, prothyalo-, protomakro-, protomikro-, pseudo-, pseudocaryo-, pseudomono-, pyreno-, quanta-, quanto-, repli-, ribo-, sarco- (sarko-), schizo-, sidero- (sydero-), soleno-, spermacentro-, spermato-, sphero (sphaero-), spliceo-, sporo-, stauro-, stigmo-, submicro-, synapto-, syntelo-, tego-, tri-, tetra-, zygo-.

c) *Soma compound terms pertinent to the classic chromosome terminology.*

MONTGOMERY (1904, pp. 145,146) proposed the classic term heterochromosome as follows:
"3. The Heterochromosomes.
I offered this name to include those peculiarly modified chromosomes to which have been given the names "accessory chromosomes" by MCCLUNG, "small chromosomes" by PAULMIER and "chromatin nuceoli" by myself. They have been described for the Hemiptera by HENKING (l.c.), PAULMIER, and myself; for the Orthoptera by WILCOX, McCLung, SUTTON, DE SINÉTY; and for the spider by Miss WALLACE.
Now there are two kinds of these. In the Orthoptera there is an unpaired one in the spermatogonia, larger than the other chromosomes; in the Hemiptera they are paired in the spermatogonia, and usually smaller than the other chromosomes. Otherwise in their behavior they are very similar in these two groups of insects. To include both these kinds the name "heterochromosomes," as expressing a difference from the other chromosomes, can be advantageously applied; and this would include (1) the "accessory chromosomes" (unpaired in the spermatogonia), and (2) "the chromatin nucleoli" or "small chromosomes" (paired in the spermatogonia). MCCLUNG regards them as sex determinants; I have considered them to be chromosomes that are in the process of disappearance, in the evolution of a higher to a lower chromosomal number."
Two years later this author (MONTGOMERY 1906) published an article of large historical interest on "The terminology of aberrant chromosomes" which deserves adequate documentation, namely:
"Chromosome, a name introduced by WALDEYER, to be retained on account of its long usage as a convenient collective term, and also to be applied in those cases where all the chromosomes of a cell show essentially the same behavior. But when more than one kind occurs in a cell, they are to be distinguished as follows:
1 Autosoma (*or autosome*), the usual or non-aberrant chromosomes, called by me previously *ordinary chromosomes*.
2 Allosoma (*or allosome*), the modified chromosomes that behave differently from the preceding. This term is much more convenient than the appellative *heterochromosome* previously proposed and used by me, for the latter has an excessive lenght. Two kinds of allosomes are known in spermatogenesis and may be nemed respectively:
Monosoma (or monosome), allosomes that are unpaired in the spermatogonia. These have been variously termed *accessory chromosomes* (MCCLUNG), *chromosomes spéciaux* (DE SINÉTY), *chromosomes*

x and *unpaired ordinary chromosomes* (MONTGOMERY), and *heterotropic chromosomes* (WILSON).
Diplosoma (or diplosome), allosomes that are paired in the spermatogonia. These correspond to what have been previously denominated *chromatin nucleoli* (MONTGOMERY), *Chromosome nucleoli* (in parte), *small chromosomes* (PALUMIER), and *idiochromosomes* (WILSON)."
Clearly MONTGOMERY assumed the word soma (some) as a short for chromosome, so that the complet monosoma-diplosoma became abbreviation for monochromosome and diplochromosome.
These considerations account for the sentence of WINGE (1917, p. 207): heterochromosomes ("monochromosomes").

d) *The mono, di, tri… endekasome and the simplex, duplex (etc.) system.*

BLAKESLEE, in 1921, investigating the numerical chromosome mutation found in *Datura stramonium*, once more assuming the word some short for chromosome, proposed a classic terminological system of high historical interest.
This system is worthy of large documentation, namely BLAKESLEE 1921, p. 259, footnote 1:
"The followings terms are suggested to designate sets with numbers of chromosomes from 1 to 12: monosome, disome, trisome, tetrasome, pentasome, hexasome, heptasome, oktasome, enneasome, dekasome, hendekasome, dodekasome.
The number of sets affected by duplication may be indicated by the terms: simple, double, triple, quadruple, quintuple, sextuple, septuple, octuple, nonuple, decuple, undecuple, duodecuple.
The Poinsettia and Globe are simple trisomic mutants. If the Globe and Poinsettia could be combined to form a mutant with 3 chromosomes each in two of the 12 sets, such a mutant would be called a double trisomic mutant. If differential viability of gametes does not interfere, the triploid plant already mentioned should produce, theoretically, offspring of all the trisomic types from simple to duodecuple. Haploid, diploid, triploid, tetraploid, etc., are terms already employed to designate plants with the same number of chromosomes in all the sets."
BLAKESLEE's (1921) paper is noticeable because also records the terms simplex, duplex, triplex, etc., namely:
"The set of 3chromosomes in the diagram, Table II, may be called the *Poinsettia* set, or the purple set. A *Poinsettia* plant may, to speak in terms of the dominant factor, be consider nulliplex with no dominant genes, or simplex, duplex or triplex with, respectively, 1, 2, or 3 dominant factors. There are therefore two types of heterozygotes, and under greenhouse conditions these apparently can be distinguished from each other as well as from the homozygous dominants by different intensities of pigmentation. Simplex heterozygotes when selfed throw offspring with 5 dominants to 4 recessives among the normals, and 7 dominants to 2 recessives among the *Poinsettias*; while duplex heterozygotes should give a ratio of 8:1 among the normals and all dominants among the *Poinsettias*."
For the sake of clarity it is necessary to recall that terms simplex, duplex, multiplex have been introduced in Cytogenetics by BLAKESLEE, BELLING and FARHAM (1920): "Chromosomal duplication and Mendelian phenomena in *Datura* mutants" and commented as follows, (op. cit. p. 389):
"The mutant *Poinsettia* which appears to be caused by a duplication of one of the chromosomes carrying determiners for purple or white flower color will serve as an example. *Poinsettia* plants have 2 chromosomes in all the sets except in the one carrying the gene for flower pigmentation, which has three. Considering only the latter, we may have *Poinsettia* mutants, as regards their purple pigment, either triplex PPP, duplex PPp, simplex Ppp or nulliplex ppp. "

H. *Endomitosis: history and terminology.*

In this shortened analysis of the main features of endomitosis, the author confines himself to discuss this matter basically from the etymological and the historical points of view, summarized as follows:
a) Historical priority (HEIDENHAIN 1919) endomitose, endoamitose and compound derivates.
b) The endomitosis of GEITLER (1939).
c) Cytological literature from 1939 to 1945.

a) *Historical priority (Heidenhain 1919: Endomitose, Endomamitose) and compound derivates.*

Regarding this classic cytological term, the present literature quotes only Endomitosis (GEITLER 1939) and accepts the wide reinterpretation given to endomitosis by WHITE (1942). On the con-

trary, as early as 1919, HEIDENHAIN coined "Endomitose" together with "Endoamitose", and his statement deserves documentation. " Grössenwachstum des Myoblasten. Wir unterscheiden die Mitose und Amitose von der Endomitose und Endoamitose. In den beiden letzteren Fällen findet zwar die Teilung des Kerns un die entsprechende proportionale Vermehrung des Plasmas statt, es fehlt aber die äussere Zelleibsteillung. Auf diese Weise entstehen dann durch einen besonderen Akt der enwickelungsgeschichtlichen Sun. these mehrkernige Gebilde, deren Formwert der Zahl der Kerne entsprechend ein Mehrfaches einer einkernigen Zelle ist (Pliomeren oder höhere Hologen der Zelle)."
There are some papers, published before GEITLER's (1939) account, which record HEIDENHAIN's "Endomitose" and "Endoamitose", for instance: JACOBJ[1] (1929, p. 122).
CLARA (1930). This paper is interesting in that CLARA distinguishes, within the Endo-amitose, an Endoschisis from a Phaenoschisis (cf. CLARA, p. 206).
It is to be noticed that the interpretative change on this matter occurred in more recent years. In the year 1953 LEVAN and HAUSCHKA coined Endomitotic Reduplication or Endoreduplication, while BAUER (1953) claimed the occurrence of the Kryptoendomitose and LIPP (1953) proposed a rather ambiguous Pseudoendomitose.
Today, however, endomitosis has been replaced by a non equivalent endoreduplication term which shares the meaning of repeated endonuclear chromosome duplication. Such a modified meaning, as ascribed to endoreduplication, increased the interpretative ambiguity between this term and some classical terms such as polysomaty and polyteny (see chapters L and P).

b) *The endomitosis of GEITLER (1939).*

GEITLER (cf. 1937; 1938a; b; c) comment "Die Analyse des Kernbaus und der Kernteilung" in both plant and animal tissues. Further in the year 1939 published an account on the polyploidy in *Gerris lateralis*, induced "durch eine Art von Mitose im Innern des Kerns (Endomitose)".
The following sentence is worthy of documentation: GEITLER (1939, p. 7):
"Es muß demnach folgender Kernform wechsel angenommen werden (vgl. dazu auch Abb.3): Umbildung der Chromozentren des Ruhe (Interphase) Kerns zu einem Spirem. Verkürzung und Verdickung der Chromosomen, wäwelcher die zunächst nicht erkennbare Spaltung erfolgt, gleichzeitige, aber etwas unregelmäßßTrennung der Chromatiden unter Aneinanderhaften der Enden, Später völlige Trennung und Übergang zur Ruheckernstruktur, wobei aber die Tochterchromatiden noch lange Zeit beisammen liegen bleiben. Dieser Teilungsvorgang sei als *Endomitose* bezeichnet; analog kann von einer *Endoprophase*, *Endometaphase* usw. gesprochen werden."
GEITLER, writing Endomitose, apparently overlooked the paper of HEIDENHAIN (1919) which first recorded this term. GEITLER also proposed the terms "endoprophase… endotelophase" to qualify the following endonuclear features. The endoprophase is similar to the prophase stage of the normal mitosis (that is the occurrence of bipartite chromosomes).
The following stage of maximum degree of chromosome contraction is called endometaphase.
After attaining their maximum condensation, the two chromatids of each chromosome separate slightly (e.g. endoanaphase stage) and finally undergo reversion to the resting stage (endotelophase). This process occurs entirely within the intact nuclear envelope. In the following years this terminoogy became enriched by endochromozentren (GEITLER 1953) and endochromosomen (TSCHERMAK-WOESS 1971).

c) *Cytological literature from 1939 to 1945.*

To accomplish the purposes of the present paper the author must record some of the main papers on this matter, published from 1939 to 1946.
PFUHL (1939) reinterpreted both endomitose (= endocelluläre mitose) and endoamitose (see also endoschisis in CLARA 1930), as follows, PFUHL (1939, p. 117):
"Darunter versteht CLARA die einfache Volumenverdoppelung des Kerns, die er sonst auch

[1] Die Endomitoses ist auch, wie M. HEIDENHAIN bei den Megakaryozyten zeigen konnte durch eine entsprechende Vermehrung der Zentriolencharakterisiert.

als “Endoschisis” bezeichnet. “Innere Amitose” oder “Endoschisis” sind also nicht identisch mit “Endoamitose”, d.h. der Kernzerschnürung innerhalb eines ungeteilten Zellleibes. Diese Bezeichnungen sind zum Teil sehr unglücklich gewählt; wir werden sie, wie wir sehen werden, glücklicherweise zum großen Teil entbehren Können.”

PFUHL (1939, p. 130): “6. Die Mitose in der Leberzellen führt nicht nur zur Entstehung neuer Zellen, sondern als Endomitose nuch zur ersten Ausbildung der Zweikernigkeit. In diesem Falle ist jeder der beiden Doppelkerne dem Ausgangskern größengleich, die Mitose hat also zu einer Verdoppelung der Zellgröße gefürt.”

PAINTER and REINDORP (1939): Endomitosis in the nurse cells of the ovary of Drosophila melanogaster) - A few months after GEITLER’s account, just in the same journal Chromosoma, PAINTER & REINDORP (1939), published the second paper claiming the occurrence of endomitosis and endomitotic cycle in animals and namely in the nurse cells of the ovary of *Drosophila*.

This paper is a noticeable paper in history of endomitosis and is worthy of large quotation.

“The idea that concommitant with nuclear growth there is a rhythmical reduplication of the nuclear contents is not new to cytology. The evidence, prior to the salivary gland chromosome era, and first adduced by JACOBJ from nuclear volume considerations, was entirely indirect. Nor is the sporadic occurrence of plyploid nuclei in diploid tissues very uncommon in animals. But the formation of plyploid cells as a regular and normal growth process, in insect larval tissues, is a concept which has come into the foreground only recently. And the nuclear phenomena exhibited by the nurse cells of the *Drosophila* ovary is a very striking example of the same process extended over into the germinal tissue of the adult insect.

Our interest in this polyploidy, of course, centers about the reduplication process, and in the foregoing account we have presented the evidence which shows that the method is similar to that which obtains in normal mitosis except for the absence of the spindle mechanism and the sequelae of this. Because there is non spindle, there is no metaphase plate oreintation of the chromosome bundles nor any anaphase movement and, in the absence of any mechanism for a wide separation, homologous chromatids remain together. As a result during early and late prophase stages we have either discrete polytene chromosomes (fig. 6) or, later, loose felt-like masses of chromatids. We conclude from the evidence that during the growth of the nurse cells there must been about 8 division cycles and that nuclei averaging 40 μ in diameter are about 512-ploid.

While in general the behavior of the chromosomes in nurse cells is similar to the endomitotic cycle first decribed by GEITLER for tissues of *Gerris lateralis*, there are differences in details which should be pointed out. The most conspicuous difference is the tendency for the chromatids to associate together in discrete bundles during the prophase stages in nurse cells. GEITLER points out that in *Gerris* homologous chromosomes tend to lie in the same part of the nucleus but there is no indication of any attraction between homologues such as is found in the ovary of the fruit fly. The cause for the attraction between chromatids in the latter form is not entirely clear. We have noted that in earlier cycles the chromatids are most closely joined in the region of the centromere and it is possible that a delay in contromere cleavage is responsible for the close union seen in figure 6. In later cycles the chromatids are more scattered and their tendency to collect about centers may be an expression of the same force which causes the somatic pairing of chromosomes in Diptera.

The second most notable difference between *Drosophila* and *Gerris* is that in the latter form the chromosomes appear to be much more discrete than in the fruit fly and so in the latter we have a more complete parallelism between mitosis and endomitosis.

From a broader point of view there are two phases of cytology upon which our work has a bearing. The first is that our findings are in entire accord with the multiple strand concept of salivary gland chromosome structure. The bundles of chromatids in nurse cells differ from salivary chromosomes principally in the very close association of the elements in the latter and their great extension. In an article now in press the senior author has discussed the possible causes of this difference (PAINTER 1939).

A second aspect is that the principle of the endomitotic cycle undoubtedly has a very wide application and will explain many cytological phenomena now obscure. Thus, from slides which Dr. BERGER sent the senior author, it is obvious that in the intestinal tract of the mosquito the increase in chromosome number ist brought about by a series of changes essentially like that described for *Gerris* and the nurse cells of *Drosophila*. In all probability the variations in the

staining of salivary chromosomes in a single gland are due to the fact that in different nuclei different phases of the endomitotic cycle are present. And undoubtedly many of the cases of polyploidy reported in the past and interpreted as being due to incomplete cytokinesis are really teh sequelae of inner division cycles of the chromosomes, without nuclear cleavage. The giant nuclei in malignant growths may have a similar origin."

D'ANCONA (1939) *Grandezze nucleari e poliploidismo nelle cellule somatiche*.

This is the third account, published in 1939 claiming the occurrence of andomitosis in animal tissues. D'ANCONA investigating the cytology of the liver cells of mous, pig and lamb, found miotic stages strictly similar to the endoprophases … endotelophases described by GEITLER (1939) in *Gerris lateralis*.

It is to be noticed that D'ANCONA quotes the terminological priority of HEIDENHAIN over endomitosis as follows: "HEIDENHAIN chiamava invece endomitosi la moltiplicazione miotica del nucleo non seguita da divisione del corpo cellulare".

Two years later, D'ANCONA published an additional and related paper, cf: D'ANCONA (1942) - "Verifica del poliploidismo delle cellule epatiche dei mammiferi nelle cariocinesi provocate sperimentalmente" and pointed out the following conclusions (op. cit. p. 282):

"3) Nelle mitosi stesse si notano numeri di cromosomi estesamente variabili, che molto spesso superano di parecchio il numero che si ritiene caratteristico per questa specie nella fase diploide; si osservano infatti anche piastre con più di 100 cromosomi.

4) Le osservazioni fatte inducono a ritenere che le mitosi più frequenti siano tetraploidi; accanto ad esse sarebbero meno frequenti quelle diploidi, più rare quelle ottoploidi.

5) Si ammette quindi che le diverse grandezze dei nuclei a riposo delle cellule epatiche siano dipendenti dal fatto che fra essi sono rappresentati nuclei diploidi, tetraploidi e ottoploidi, che da stimoli sperimentali possono essere tutti indotti in mitosi.

6) Lo stato poliploide di questi nuclei viene ascritto a un processo di poliploidizzazione endonucleare per endomitosi."

HUSKINS (1942) *Structural differentiation of the nucleus.*

HUSKINS qualified as endomitosis the double chromosome reproduction which a few years earler was described by GENTCHEFF and GUSTAFSSON (1939): "The double chromosome reproduction in *Spinacia"* and by LEVAN (1939) in *Allium"*, cf. HUSKINS (1942, p. 117):

"The clearest case of endomitosis in plants occurs in spinach, 2n=12, where somatic polyploidy has long been known, but its origin due to endomitosis was shown only recently by GENTCHEFF and GUSTAFSSON (1939)…".

LEVAN (1939) obtained similar results in auxin-treated cortical cells of spinach. In *Allium*, auxin produced endomitosis differing only in that the kinetochores were delayed in their division relative to the arms, and "diplochromosomes" were therefore present at metaphase. In these experiments with auxin, cellular enlargement precedes the increase in nuclear volume, and endomitosis appears to be initiated thereby. In most of the other cases cited, chromosome or chromonema multiplication precedes and apparently initiates the increase in nuclear volume."

BIESELE, POYNER and PAINTER (1942) *Nuclear phenomena in cancer*.

Again in 1942 PAINTER (cf. BIESELE, POYNER, PAINTER 1942) emphasized the concept of endomitotic cycle and distinguished two types of endomitosis, that is an endomitosis with division of centromeres, as in *Gerris*, and an endomitosis without division of centromeres giving rise to diplochromosomes. Conseguently he also described the Drosophila salivary glands polytene chromosomes as structures formed by repeated endomitoses in which the reduplicated chromosomes fail to separate.

Further, he adopted expressions such as reduplication of centromeres and reduplication by endomitosis.

WHITE (1942) *Nucleus, chromosomes and genes. in* BOURNE G., *Cytology and Cell Biology,* Chapter V, 1942, Oxford.

The term endopolyploidy has been invented by WHITE (1942, p. 147) and interpreted as follows:

"*d.* Endopolyploidy and Salivary Gland Chromosomes. It has been known for a long while that many of the somatic nuclei of insects are normally polyploid, but the extent and nature of this phenomenon has only been realized in recent years. Most of the tetraploid, octoploid, 16-ploids, & c., nuclei which occur in the hypodermis, fat body, oenocytes, & c., have been derived from diploid nuclei by a process of repeated division of the chromosomes without any true mitosis. The cells

which undergo this "endopolyploidy" seem, in fact, to have lost the power of division, but they go on increasing in size and from time to time their chromosome number is doubled."
The author quotes this entire paragraph since the terminological paternity over endopolyploidy has been widely overlooked by the following scientific literature.
The author's comments, as regards both interpretation and use of endopolyploidy, are also further discussed in the chapter N.
PAINTER (1943) *Cell growth and nucleic acids in the pollen of Rhoeo discolor*.
This account is the first report of the occurrence in plant material of a cytological behaviour specifically called "endomitotic" and thus deserves citation (cf. Painter, 1943, pp. 64, 65, 68):
"Since growth of the pollen mother cells involves the reduplication of the chromosomes, the question arises: Is the growth of the tapetal cells accompanied by a similar doubling of the chromosomes? COOPER has reported that in *Rhoeo* the nucleus may divide mitotically one ore more times, and if the resulting nuclei do not fuse multinucleate cells result. In the writer's material no multinucleate tapetal cells have been observed, nor has there been any case in which the nuclear wall has been broken down. On the other hand, various normal prophase stages are common, showing that the chromosomes are condensing by coiling, and dumbbell-shaped nuclei are frequent (figs. 10-21). Such figures suggest that, in addition to the normal mitoses and fusion observed by COOPER, tapetal nuclei also increase in volume by an intranuclear, or endomitotic, division cycle."
The very interesting documentation of Painter's paper is recorded in the Plate III (figs. 10-22).
FAVARGER (1944) *Sur quelques phénomenes de pseudo-appariement des chromosomes dans les tissues somatiques.* (1946) - *Recherches caryologiques sur la sous-famille des Silénoïdées* - Since the occurrence of endomitosis in plants (cf. tapetal cells) became largely known by merit of a paper by RUTH WITKUS published in 1945 (see further), the author must also duly mention and adequately document two analogous accounts published by CLAUDE FAVARGER in 1944 and 1946, which have been largely disregarded by the cytological literature.
FAVARGER (1944), in his first account *Sur quelques phénomènes de pseudo-appariement des chromosomes dans les tissus somatiques.* distinguishes: "…prophases à chormosomes courts ed dédoubles (prophases dites du premier type)". These stages were unfrequently seen "dans l'assise nourricière des microspores", cf. Plate III lower half, figs. 1, 2: in several species belonging to the genera *Silene* and *Viscaria*.
In both *Silene italica* and *S. dubia*, again in the tapetum and together with prophases of the first type, FAVARGER describes the occurrence of:
"a) des prophases à chromosomes longs, flexueux, au contour un peu flou, nettement dédoublés et dont les deux moitiés sont plus ou moins enroulées l'une autour de l'autre à la maniere d'un strepsinema (fig. 3). Text-Fig. 3.
b) des métaphases extrêmement remarquables. Celles-ci sont tétraploïdes, à 48 chromosomes disposés par paire avec la plus grande régularité (fig. 4). Les chromosomes sont à peu près de la même taille que ceux des métaphases normales à 24 chromosomes qu'on voit ici ou là dans des cellulex voisines (fig. 5). Signalons la réelle heauté de ces images qui apparaissent en assez grand nombre au moment de la première division du noyau dans les cellules du tapis. cf. Plate III, figs. 4,5."
As regards the interpretation of the stages cited above, FAVARGER, (by analogy with the case of polysomaty in *Spinacia*, op. cit. p. 581: "Les deux derniers phénomenes que nous venons décrire présent une grand analogie avec ceux étudiés dans *Spinacia oleracea* per DE LITARDIÉRE") hypothesizes the occurrence of arrested metaphases.
The second paper published by FAVARGER (1946) is of higher interest since here FAVARGER quotes the term "endomitose", borrowed from the account of WITKUS (1945), unfortunately not seen owing to the war circumstances and indirectly noticed. Favarger once more distinguishes the mitotic anomalies observed in his "Recherches caryologiques sur la sous-famille des Silénoïdées" into:
"Endomitoses…, Elles se présentent soit dans les cellules du tapis, soit dans le périblème des racines (cf. FAVARGER, 1946, p. 438)"; "Prophases anormales à chromosomes court set fortement clivés."
FAVARGER (1946, p. 441-442) writes:
« Dans presque toutes les espèces étudiées, lo tapis renferme pendant la prophase hétérotypique des noyaux d'un type très curieux. Ils sont en prophase (apparemment une prophase tardive) et ont des chromosomes courts et droits, fortement contractés et épaissis, et si nettement clivés que

la plupart du temps les deux chromatides sont placées parallèlement à quelque distance l'une de l'autre (planche 18, figures 14 et 18). La différence avec le clivage prophasique ordinaire est telle en général qu'on ne peut hésiter sur le caractère anormal de ces images, mais l'aspect contracté des chromosomes parait les caractériser également. Parfoïs, c'est un unique noyau qui offre la prophase anormale, mais la plupart du temps, le phénomène atteint les deux noyaux d'une cellule binuclééo, tandis que les cellules voisines ont déjà des noyaux hyperdiploïdes et plus ou moins confondus. En général, ces prophases offrent, dans chaque noyau, le nombre diploïde de chromosomes, mais nous avons aussi relevé des nombres plus grands, ce qui prouve que le phénomène pout atteindre également les noyaux tétraploïdes.

Les prophases anormales sont rares, ce qui en rend l'étude difficile, mais dans chaque espèce nous en avons observé quelques-unes et elles sont assez nombreuses dans certaines anthères (*Viscaria alpina*, par exemple) ……

Quelle est l'évolution des noyaux offrant la prophase à chromosomes contractós et quelle relation y a-t-il entre ce phénomène et les endomitoses? Il est très difficile de répondre à ces deux questions. Dans certains cas (anthères de *Gypsophila repens*) nous avons cru entrevoir la réponse à la première en constatant des pseudo-méthaphases et pseudo-anaphases ayant l'allure d'une stathmocinêse, avec cette différence que les chromosomes étaient très contractós. Toutefois, il ne peut ètre question de stathmocinèses proprement dites, puisque dans celles-ci la prophase n'est jamais que normale; voir à ce sujet l'étude remarquablement précise de NANGENOT sur la racine d'*Allium Cepa;* c'est pourquoi nous nous conterons de dire qu'il s'agit d'un processus apparenté à la stathmocinèse. Quant à la deuxième question, elle est encore plus difficile à résoudre. Nous pouvons cependant écarter l'idée d'une filiation directe entre les deux ordres de phénomènes puisqu'ils peuvent se présenter indépendamment l'un de l'autre, les endomitoses étant d'ailleurs moins répandues dans la sous-famille que les prophases anormales. Toutefois, leur présence dans les mêmes régions (cellules du tapis ou méristèmes radiculaires) suggère qu'ils peuvent être causés par des conditions ambiantes analogues. Il est curieux de constater que dans le tapis un même résultat, à savoir la formation de deux noyaux tétraploïdes, peut être amené de troïs manières différentes:

1. par des mitoses simultanées normales;
2. par une endomitose suivle d'oxomitose;
3. par une mitose apparentée aux stathmocinèses, atteignant les deux noyaux en même temps. ».

The last sentence is also noteworhy because, incidentally and whithout any reference, it mentions the term "exomitose".

Given that it is not the purpose of the present account to include more detailed discussion fo Favarger's paper, the author confines himself in reproducing in Fig 3 - lower part - some of most significative stages of FAVARGER's paper, and namely figs. 14, 18 (*Viscaria*: prophases anormales dans le tapis); figs. 1, 16, 17 (prophase d'endomitoses dans le périblème), fig. 2 (metaphase a chromosomes appariés), *Vaccaria* (figs. 1, 2), *Silene* (fig. 16) and *Dianthus* (fig. 17).

Last but not least the author must quote the question of the priority over exomitose. At the present the author is still looking for the priority over the term exomitose, see also next pages.

WITKUS (1945) *Endomitotic tapetal cell divisions in Spinacia*

The occurrence in plants of endomitosis, became widely known by merit of an account of RUTH WITKUS (1945) on the tapetum of *Spinacia*. E.R. WITKUS (1945, p. 326) wrote: "A careful study of these cells showed that a type of division occurs in the tapetum of *Spinacia*, which is new to tapetal cells literature. The ctyological details of this process are worth mentioning, cf. WITKUS (1945), p. 330:

"The tapetal cells of *Spinacia* undergo two divisions during meiosis. Both of these divisions take place while the sporocytes are in the zygotene synizesis stage. The first division may be one of three types. Normal mitosis may take place but no cell plate is formed and a binucleate cell results. Secondly, the nucleus may undergo an abnormal mitosis due to the presence of sticky chromosomal bridges. As a result a uninucleate cell is formed with a dumb-bell-shaped nucleus. Thirdly, the cell may undergo a type of division new to tapetal cell cytology which is called endomitosis. The endomitotic cycle consists of endoprophase, endometaphase, endoanaphase and endotelophase. The chromosomes undergo contraction to the metaphase condition, the spindle attachment regions divide and the daughter chromosomes separate slightly and revert to the resting stage condition. Throughout the

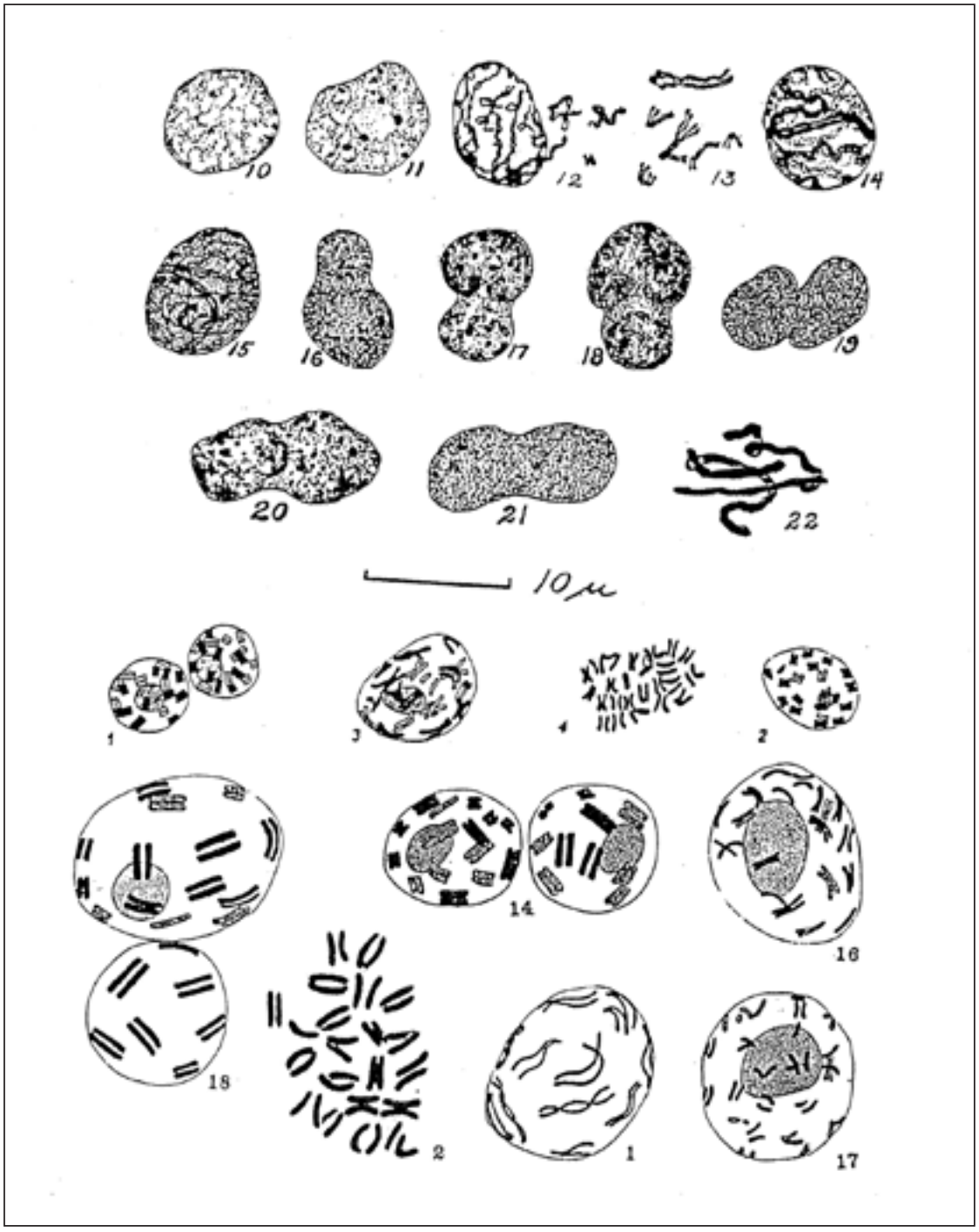


Fig. 3 — Upper half: Fig.s 10-22 from PAINTER (1943). PAINTER'S explanations: "Various endomitotic division stages in tapetal nuclei. Figs. 10, 11, resting stages. Figs. 12, 13, split and coiling prophase chromosomes. Figs. 14, 15, maximum degree of condensation of chromosomes observed. Figs. 16-21, constriction of nuclear wall following condensation of chromosomes. Fig. 22, normal somatic metaphase showing size of dividing chromosomes." Lower half: Fig.s 1, 3, 4, 2 from FAVARGER (1944). FAVARGER'S explanations: « 1. Prophase du 1" type dans l'assise nourricière de *Viscaria alpina.* 2. Idem dans la coiffe de la racine de *Silene nemoralis*. 3. Prophase du 2" type dans l'assise nourricière de *Silene dubia*. 4. Métaphase à chromosomes appariès (ibidem). Figs. 14, 16, 17, 18 and 1, 2 from **FAVARGER** (1946, Pl. 18 and 19). FAVARGER'S explanations: « Figs. 14, 18: prophase anormale dans le tapis, (*Viscaria alpina*); Fig. 2: métaphase à chromosomes appariés 1re assise du périblème, (*Vaccaria pyramidata*); Fig. 16: prophase d'endomitose dans le périblème, (*Silene saxifraga*); Fig. 1: prophase éndomitotique dans le 1re assise du périblème, (*Vaccaria pyramidata*); Fig. 17: prophase d'endomitose dans le périblème, (*Dianthus carthusianorum*).

whole process the nucleolus is present, the nuclear membrane remains intact, there is no spindle and consequently no true anaphase movement of the chromosomes. Thus all the chromosomes remain in the same nucleus, increasing the degree of polyploidy.
The resulting nuclei may remain in the resting condition or may undergo a second division. The second division is in all cases endomitotic. The cell resulting from this division is either a uninucleate octoploid cell, in which case the nucleus is dumb-bell-shaped, or a binucleate cell with two tetraploid nuclei.
It seems possible that endomitosis may not be peculiar to the tapetal cells of *Spinacia* but may have a wider application and may explain many of the cytological phenomena occurring in the tapetal cells of other plants, which up to now have been obscure."
Revaluation of the papers of WINGE (1914) *The pollination and fertilization processes in Humulus lupulus L. and H. japonicus Sieb. et Zucc.* and (1917) *The Chromosomes. Their number and general importance* - Since referable to the topics here discussed the author wish quote two relevant accounts by WINGE, which have been exclusively recorded by D'AMATO (1952, p. 339) in his very comprehensive review "Polyploidy in the differentiation and function of tissues and cells in Plants", as follows:
"*Humulus japonicus* - To our knowledge, it is in the tapetum of this species that the first description of endomitosis – according to the scheme of *Gerris*, as discovered by GEITLER (1939) – has been reported WINGE (1917). The sequence of stages from "endoprophase" to "endoanaphase", as described by GEITLER in *Gerris*, was observed, but the assumption was made that to the "andoanaphase" stage the organization of a normal bipolar spindle followed. Thus, WINGE, althout pointing out that a "special method of miotic nuclear division, presumably due to anticipated chromosome splitting" (l.c. pag. 262) was present in *Humulus*, did not realize the true significance of endomitosis, the interpretation of which is the merit of Prof. GEITLER.
Atriplex littoralis - As pointed out by WINGE (1917), the occurrence of diakinesis-like stages in the tapetum of this species is evidence of the same type of division as observed in *Humulus*."
The author thinks it useful to complete D'AMATO's considerations by the documentating some interesting stages from WINGE (1914, figs 26a and b: tapetum of *Humulus*) and from WINGE (1917, figs 43 a and d and fig. 4: tapetum of *Humulus*; fig. 46: tapetum of *Atriplex*), together with WINGE's original comments, namely: "From WINGE (1914), p. 17 and Fig. 26 a, b, cf. *Humulus Japonicus* Sieb et Zucc.:
"In fig 26 is shown a peculiar diakinesis-like prophase in *H. Japonicus* in two sections, which has only been noticed this once; 16 (17) divided chromosomes can be observed. The picture calls to mind a tetrad division in which only the chromosomes, but not the nuclei themselves are dividing (comp. fig. 46). I suppose that it is a case of abnormal, indirect vegetative reduction like those of NĚMEC (1910)."
From WINGE (1917, pp. 256-262 and Figs. 43a and 43d., 44: *H. japonicus*; Fig. 46: *Atriplex littoral*; see Plate IV):
"In my work already quoted on the *Humulus* (1914) I stated that I had once, in a tapetal cell of an anther, observed a diakinesis-like prophase, where 16 to 17 chromosomes lay distributed throughout the nucleus in an absolutely diakinesis-like manner. I illustrated this in my Pl. I, Fig. 26, and was compelled to regard the phenomenon for the time being as abnormal. Since then, however, I have encountered it so frequently in the same species, *Humulus Japonicus*, that I am surprised that I should not have noticed it more often in my earlier studies. In reality, it would at least seem that the diploid nuclei in the tapetum and those of higher valency seem at any rate continually to go through the diakinesis stage in preparation for further divisions, and only the brief duration of the phenomenon prevents it from occurring more frequently in fixed material.
I shall in the following endeavour to describe this method of nuclear division, which, owing to its peculiar course, cannot be compared with anything elsewhere in sporophytic tissue, but which is undoubtedly of a nature connected with the hyperchromatic qualities of the tapetal cells…
Fig. 43 a-d shows the process at its height, inasmuch as we have here a stage altogether diakinesis-like, save for the augmented number of chromosomes. The chromosomes lie in pairs in the periphery of the nuclear cavity…
The chromosomes lying together are always of the same shape, which bears witness to their common origin. I have now and again found that a pair of such chromosomes were distinctly split (Fig. 43 c)

parallel with the plane of division. In Fig. 44, the gemini are for the most part seen separated, only a few appearing still to lie together. …
The only explanation of the phenomenon – which is one of considerable theoretical interest – seems to me to be that we have here a special method of mitotic nuclear division, normally including – as regards the cytological view – a typical diakinesis stage, presumably due to anticipated chromosome splittings. ……
It would be interesting to follow up this question further, also in the case of other plant species. I have myself observed exactly corresponding diakinesis-like stages in *Chenopodium album* and in *Atriplex littorale* again, the nuclear divisions of the tapetum appear to proceed on similar lines, though I have not here observed quite so marked diakinesis stages (Fig. 46). …….
In the hyperchromatic cells in the tapetum of phanerogams, nuclear division takes place according to a peculiar system, in which a typical diakinesis stage appears – albeit with doubled or manifold chromosome number; this does not, however, indicate any reduction division".
Conclusively, the author wishes to draw the attention of the readers to the following conclusion of Winge, owing to historical interest: "The only explanation of the phenomenon – which is one of considerable theoretical interest – seems to me to be that we have here a special method of mitotic nuclear division, normally including – as regards the cytological view – a typical diakinesis stage, presumably due to anticipated chromosome splittings …".

Criticism of endomitosis (Geitler) *and alternative terminology: endocaryopseudomitosis, endocaryopseudoprophase (etc.), endocaryorestitution cycle, see also "nucleo di endorestituzione"* Battaglia (1945b).

The author does not agree to the terminology proposed by Geitler (1939) since this cytological cycle (endomitosis) lacks real meta and anaphase stages which are characterized by the dissolution of nucleoli and the breakdown of the nuclear envelope and by the occurrence of spindle fibers and the relative polar movement of the chromatids. The telophase stage too, being characterized by the reorganization of nucleoli and reconstruction of the nuclear envelope, cannot be described as actually occurring during the endomitotic process. Thus should be more adequate to speak of endocaryopseudomitosis together with endocaryopseudoprophase (etc.). Actually the endomitotic process (sensu Geitler) is an endocaryochromosome division.
Now, since in the classic cytology a mitotic chromosome division ending into the distribution of all sister chromatids into a single nucleus is defined restitution nucleus Rosenberg (1927), as early as 1945 the author Battaglia (1945 b.) suggested the expression "nucleo di endorestituzione" (endorestitution nucleus) to indicate any chromosome division taking place within an intact nuclear membrane (Cf. Battaglia 1945b, p. 53: "Per quest'ultimo caso, come pure in tutti quei casi in cui nel nucleo profasico, dopo la differenziazione cormosomica (e quindi l'inizio della profase), si realizzasse la dissociazione di ciascun cromosoma nelle sue due metà trapassando poi nella fase quiescente, poiché l'intero processo si realizza entro la medesima vescicola nucleare, la formazione del nucleo di restituzione potrebbe essere ulteriormente precisata come formazione di *nucleo di endorestituzione"*). Incidentally, in the year 1945 the author owing to war condition, was unaware of Geitler's (1939) paper.
Finally, in order to avoid ambiguity, the endocaryorestitution cycle as discovered and described by Geitler (1939) could be further qualified as endocaryorestitution cycle *Gerris* type.

Endomitose and exomitose. Resende (1956), Levan and Müntzing (1963), Resende (1964).

Resende (1956) published a short communication entitled "Endomitose e Endomitose." In it Resende considers the second division of meiosis such as a "Processo contrario a este de Endomitose", qualifying it by the term "Exomitose".
Since this matter has been widely ignored by the cytological literature it deserves an adequate documentation and discussion. Resende (1956 p. 95) wrote:
"Processo contrário a este de Endomitose será aquele em que una cariocinese comseparação anafásica oxista, sem que haja durante ela qualquer crescimente cromonemático. Ref. tem-se esforçado, desde 1944, por demonstrar que este processo existe na II divisão é nitidamente uma cariocinese sem multiplicação cromonemática e pertanto a única responsável pela passagem de 2n-n.
Nos objectos de centromero localizado a II divisão é, quanto a isto, perfeitamente identica à dos de

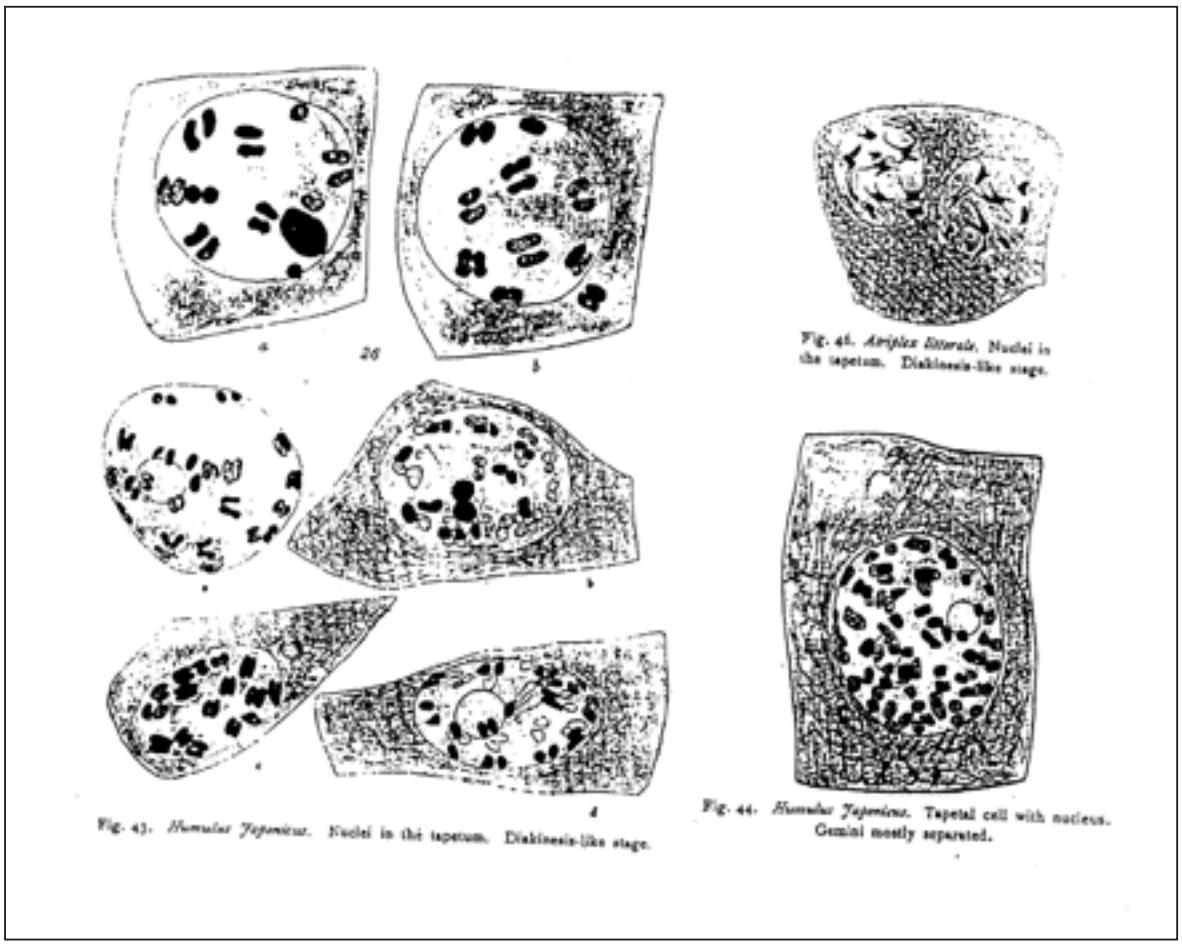


Fig. 4 — Text of Fig. 4. Fig. 26 a-b, from WINGE (1914: "*Humulus Japonicus* Sieb. et Zucc."), see the text. Fig. 43 a-d, 44, 46, from WINGE (1917), see the text. Fig. 46 *Atriplex littorale*. Nuclei in the tapetum. Diakinesis-like stage. Fig. 43 *Humulus Japonicus*. Nuclei in the tapetum. Diakinesis-like stage. Fig. 44 *Humulus Japonicus*. Tapetal cell with nucleus. Gemini mostly separated.

Kinetochore difuso, só diferindo deles pelo facto de haver, na maior parte dos casos, uma calescencia na regido centromérica, de maneira a terse pensado durante várias décadas, que a multiplicação do Kinetocóro se fazia na II, enquanto todo o restante cromosoma se dividia na I.
Ref. está hoje convencido que, em todos os objectos conhecidos, a II divisão meiótica é uma cariocinese "em falso" isto é apenas aparente, pois o acontecimento essensial da mitose, o crescimento cromonemático, não se passa nesta mitose em nenhuma regido cromosómica. Deve lògicamente designar-se esto processo per Exomitose.
As chamadas reduções somáticas (IIUSKINS, RESENDE 1951) serão de incluir nesta designação.
Assim, as variações somáticas no número de cromosomas, se devem fundamentalmente a processos endo- e exomitóticos. E, se houver independencia de cromosoma para cromosoma de mesma guarnição, poderemos comprendere tambéa existência de números somáticos anouploides por assincronismo de cormosoma para cromosoma na mecânica destes processos."
A few years later LEVAN and MÜNTZING (1963) published a widely quoted paper entitled Terminology of Chromosome Numbers. At the page 11 of this paper can be found the following foot note: "(1) Editor's note: RESENDE (1956), analzing minutely the 2nd division of meiosis, regarded this as the reverse of endomitosis and designated this karyokinetic process ectomitosis. It represents a division of the nucleus without division of the chromonemata cf. RESENDE, 1947, fig. 1 7I, 7II."
It is here, worth noting that RESENDE's Exomitose is spelled ectomitosis. This apparently linguistic question has been closed the following year by RESENDE himself.

At the page 276 of RESENDE's paper (1964): General principles of sexual and asexual reproduction and life cycles is published the following foot-note: "The second mitosis of meiosis is the reductional division and hence named "ektomitosis" (RESENDE 1956c; LEVAN and MÜNTZING 1963)."
Unexpectedly all authors cited above overlooked the papers of FAVARGER.
Conclusively, the author criticizes the coining and the interpretation of exomitosis on the basis of the following consideration: since the Greek prefixes exo- and ecto- mean outside, out for (cf. e.g. ectoplasma), thus linguistically exomitosis would signify mitosis out of the nucleus by antithesis with endo-mitosis or mitosis within the nucleus.

I. *Polyploidy*

a) Strasburger's priorities (1905-1910).
b) Earlier historical data, DELPINO (1875-1903).
c) Synhaploid and syndiploid, STRASBURGER (1907).
d) Octoploid, STRASBURGER (1910) and octaploid.
e) The terminology of NEMEC (1910).
f) The terminology of LANGLET (1927 a; b).
g) Further historical data.
In the present context, the terminology concerning the polyploidy deserves a critical comment. However such a criticism will be confined to wrongly quoted priorities and to linguistic inaccuracy.

a) *Strasburger's priorities* (1905-1910) – The terms haploid, diploid, triploid, tetraploid, octoploid, Diploidie, Tetraploidie and Polyploidie, have been coined by Strasburger in a series of papers published from 1905 to 1910. Since Strasburger's priorities are still today widely ignored or wrongly ascribed to other authors (e.g. NEMEC 1910; WINKLER 1916), the first question to be faced is the quotation of Strasburger's terms summarized as follows:

haploid: STRASBURGER 1905, p. 62;
diploid: STRASBURGER 1905, p. 62;
syndiploid: Strasburger 1907, p. 489 (syndiploiden Kerplatten);
synhaploid: STRASBURGER 1907, p. 509 (synhaploiden Zellen);
tetraploid: STRASBURGER 1909, p. 511;
triploid: STRASBURGER 1910, p. 414;
octoploid: STRASBURGER 1910, p. 405;
oktoploid: STRASBURGER 1910, p. 407, 427;
Diploidie: STRASBURGER 1910, p. 415;
Tetraploidie: STRASBURGER 1910, p. 410;
Polyploidie: STRASBURGER 1910, p. 406.
STRASBURGER's terminology deserves and suggests many considerations analitically subdivided as follows:

b) *Earlier historical data* DELPINO (1875; 1903) – STRASBURGER was certainly aware of earlier analogous terms just as those coined by DELPINO (1875) - aplonte, diplonte, triplonte and Aplogenesi – Diplogenesi DELPINO (1903). DELPINO (1875, p. 152): "Adunque secondo la nostra maniera di vedere le specie vegetali possono essere semplici o multiple; quindi le dividiamo in due categorie, in *aplonte* e *pleionte*. La gran maggioranza è quella della aplonte.

Le specie pleionte si dividono in doppie o triple; quindi abbiamo specie *diplonte* e specie *triplonte*. Le specie triplonte, quelle almeno sin qui conosciute appartenenti ai generi *Lythrum*, *Oxalis*, *Pontederia* e a pochi altri, sono tutte zoidiofile, e producono tre sorta d'individui, macrostili, mesostili, microstili.
Le specie diplonte possono essere o zoidiofile (specie di *Linum*, *Primula*, *Hottonia*, *Faramea* e di molti altri generi) o anemofile (specie unica fin qui nota *Iuglans regia*)".

c) *Synhaploid and syndiploid* by STRASBURGER (1907) – This paper records:

p. 489: Fig. 1 syndiploiden Kernplatten,
p. 500: syndiploid,

p. 509: Die synhaploiden Zellen.
These terms refer to the fusion of two haploid or diploid nuclei. STRASBURGER, coining these terms, increased an already large syn-terminology. cf. for instance:
syncytium: HAECKEL 1872, p. 160,161;
synapsis: MOORE 1895, p. 296;
synkaryon: MAIRE 1900 a, p. 94;
syndesis: HAECKER 1904, p. 200;
synmixis: HAECKER 1904, p. 191, 199, 200.

d) *Octoploid* STRASBURGER (1910) *and octaploid* – The prefixes haplo-, diplo- (etc.) selected by Strasburger for coining the compound terms haploid, diploid (etc.) derive from the corresponding Greek terms aploos, diploos etc.
Since the prefix referable to the number eight is octa-, the term octaploid is the linguistically pure form (Greek - Greek) within the series haploid, …, polyploid.
On the contrary octoploid should be recognized to be the hybrid form (Latin - Greek) of the same term.
Clearly, STRASBURGER writing octoploid (and oktoploid) did not pay attention to a related linguistic historical documentation published by WILHEM BISCHOFF as early as 1833 (p. 52) and quoted below:
"b - Bestimmte Wusbrüde für die Zahlenverhaltnisse:

gewöhnliche Zahlwörter:

	In der Zusammenseßung	
	lateinisch:	griechisch:
eins (unus - un)	uni	mono -
zwei (dus - deux)	bi	di -
drei (tres - trois)	tri	tri -
vier (quatuor – quatre)	quatri	tetra -
fúnf (quinque - cinq)	quinque	penta -
sechs (sex - six)	sex	hexa -
sieben (septem - sept)	septem	hepta -
acht (octa - huit)	octo	octa -
neun (novem - neuf)	novem	ennea -
zehn (decem - dix)	decem	deca -
elf (undecim - onze)	undecim	endeca -
zwólf (duodecim - douze)	duodecim	dodeca -
zwanzig (viginti - vingt)	viginti	icosa - u. s. w.

However the prefix octa-, in the place of the usual octo-, did not escaped to the attention of the cytologists thus, for instance, BLAKESLEE (1921) coined octasome and the text-book of DARLINGTON (1937) records the following entry: "Polyploid, an organism with more than two sets of homologous chromosomes. The terms used are triploid, tetraploid, pentaploid, hexaploid, heptaploid, octoploid (for octaploid), nonaploid (for enneaploid), decaploid, undecaploid (for hendecaploid), dodecaploid and so on. Higher multiples are best referred to as 14x, 22x and so on (v. Haploid, Diploid and Tetraploid). WINKLER, 1916."

e) *The terminology of* NEMEC (1910*)* – Besides its historical interest, NEMEC's terminology deserves quotation since the terms triploid and tetraploid have been repeatedly ascribed to this author, cf. e.g. DARLINGTON (1937) and RIEGER, MICHAELIS and GREEN (1991).

NËMEC (1910) published his "Das Probem der Befruchtungsvorgänge" a few months after Strasburger's account. NËMEC accepted the terminological system of STRASBURGER and coined some other selfexplanatory terms as summarized below:

didiploid,		synhaploid,	haploid,
tetradiploid,	tetratriploid,	syndiploid,	diploid,
oktodiploid,	oktotriploid,	syntriploid,	triploid,
			tetraploid.

The terms coined by NEMEC have been underlined.

f) *The terminology of* LANGLET (1927a; b) – LANGLET in two papers published in 1927 proposed the terms monoploid (=p), diploid (=2p), etc. and a terminological system circumstatially analyzed in the next chapter I.

g) *Further historical data* – The author believes it to be very useful to quote the following series of terms related to the matter here analized, because they are today overlooked or wrongly ascribed as regards their true priority.

For the sake of conciseness most of them are here quoted without comment.

WINKLER (1916): hyperploid,
hyperdiploid,
hypoploid, orthoploid, orthohaploid,
hypodiploid, anorthoploid, anorthodiploid,
heteroploid.

WINKLER (1920): hemidiploid. Later other authors increased this series with hemihaploid and hemipolyploid.

SAX (1921): allopolyploid,

TÄCKHOLM (1922): euploid, eneuploid,

KIHARA (1924): allopolyploid,

JEFFREY (1925): artioploid,
perissoploid,
disploid.

KIHARA and ONO (1926): allopolyploidy,
autopolyploidy.

NAWASHIN (1927): amphiploid.

JARETZKY (1928): verkappte polyploidie,

NEMEC (1931): Mixoploidy and the cellular Theory; mixoploid:
"Many plants contain under normal conditions both diploid and polyploid cells. It is easy to get experimentally plants containing a varying number of polyploid cells. The author designates such plants as mixoploid."

CHIARUGI (1932): criptopoliploidia
This is a translation of the Verkappte Polyploidie of JARETZKY (1928), and is quoted as follows:
"… soltanto quando fosse dimostrata un'importanza generale del fenomeno della *criptopoliploidia* ("*Verkappte Polyploidie*", JARETZKY 1928), per il quale specie in realtà poliploidi, per fusione dei cromosomi omologhi in larghe unità cromatiche, possono ritornare in condizioni apparenti di diploidismo. Allora anche da forme altamente poliploidi, potrebbero sorgere tipi disploidi."

SHARP (1934): homoploid ("Non-heteroploid groups may be called homoploid").

MALHEIROS-GARDÉ (1950): agmatopolyploidy.

BATTAGLIA (1956): pseudopolyploidy, agmatopseudopolyploidy.

BATTAGLIA (1996): phenopolyploidy.

J. *Polysomaty:* LANGLET (1927a; b).

The adjectives somatisch… polysomatisch corresponding to STRASBURGER's diploid… polyploid terms, were suggested by LANGLET (1927a, b) to indicate a nuclear condition of a tissue in which diploid and polyploid cells are found. He also introduced the terminology p (=monoploid), 2p (= dip-

loid), 3p (=triploid) etc. to indicate a polyploid series and namely: Cf. LANGLET (1927 a, p. 3):
"DE LITHARDIERE (1923) fand in Wurzelspitzen von Spinacia Kerne, die teils durch die normale somatische Chromosomenzahl 12, teils durch die doppelte Zahl gekennzeichnet waren. Die letzteren Kerne wurde von ihm didiploid genannt. Didiploid, tetradiploid, syndiploid usw. sind aber samtlich im Einklang mit diploid = somatish gebildet, und deshalb als zweideutig nich gut zu verwenden. Im Anschluss an die Bezeichnung somatishc = 2n, schlage ich vor, die Zellen einer Chromosomenchimäre, welche Multipla der somatischen Zahl enthalten, polysomatisch zu nennen. Die einzelnen Glieder der Reihe sollen dann: haploid = n, somatisch = 2n, disomatisch (didiploid) = 4n, trisomatisch = 6 n, tetrasomatisch (tetradiploid) = 8n, usw. heissen.
Zum Unterschiede von den Bezeicnungen n, 2n, 3n, usw., welche die Glieder der polysomatischen Reihe kennzeichnen, und welche im allgemeinen zu verwenden sind, wenn man das Vielfache irgend einer haploiden Zahl meint, können viellecht die Glieder der polyploiden Reihe z.B. als p (= monoploid), 2p (= diploid), 3p (= triploid), 4p, 5p, usw., bezeichnet werden, wenn man das Vielfache einer monoploiden Chromosomenzahl auszudrücken beabsichtigt."
Cf. LANGLET (1927b, p. 397).
"Es er scheint mir daher angebracht, hier alles zusammenzufassen, was auf diesem Gebiete bisher geschriebe ist; gleichzeitig beabsicthige ich auch selbst über einige Fälle von Polysomatic zu berichten. Ich bin auch in del Lage, nach Kontrolluntersuchungen einige frühere Angaben bestätigen zu können.
Um die Unkarheit zu vermeiden, welche die Bezeichnung "diploid" für die nicht reduzierte Chromosomenzahl im Gegensatz zur haploiden Zahl zur Folge hat, wird hier aus Gründen, welche früher (LANGLET 1927) mitgeteilt worden sind, die nicht reduzierte Zahl die somatische genannt. Die Kerne, welche eine, zwei, vier oder mehrere somatische Chromosomengarnituren enthalte, werden demgemäss mono-, bzw. di-, tetra- und polysomatisch genannt. Diese Bezeichnungen entsprechen demnach diploid, didiploid oder tetraploid, tetradiploid oder octoploid und syndiploid."
Since there is no true linguistic difference between somic and somatic, LANGLET's monosomatic… polysomatic series do not really differ from the well-known series monosomic …polysomic as earlier established by BLAKESLEE in 1921.

K. *Aneusomaty:* ALLEN in DUNCAN (1945).
DUNCAN (1945) introduced in Cytology the new term andusomaty describing the "Production of variable aneuploid number of chromosomes within the root tips of *Paphiopedium Wardii*." He wrote: cf. DUNCAN (1945, p. 509):
"Various ancuploid complements of chromosomes are present in isolated cells of the root tips of *Paphiopedilum Wardii*. Of the twenty types fo chromosomes making up the idiogram, three types may be present in an equatorial plate in numbers ranging from three to six. This replication at trisomic to hexasomic level occurs through a process which closely resembles that responsible for polysomaty except that not all chromosomes are replicated. The name aneusomaty is suggested for this phenomenon."
Cf. DUNCAN (1945, p. 506): "Since the mechanism by which the change in number is brought about can be followed with considereble ease in *P. Wardii*, a brief investigation was made. The process involves only certain members of the chromosome set and leads to cells polysomic, in Blakeslee's terminology, for those members of the complement. The causal mechanism bears close resemblance to that of polysomaty. These facts lead to the adoption of the word "*aneu-somaty*"[1] as a name for the phenomenon.
[1] The author wishes to express his appreciation for Prof. C.E. Allen's advice in selecting an appropriate name."
Both polysomaty and aneusomaty are recorded by modern biological dictionary, see e.g.: LAWRENCE E., editor, 1995: Henderson's Dictionary of Biological Terms:
Aneusomic: a. appl. organisms whose cells have varying numbers of chromosomes.
Polysomic: a. appl. cells or organisms carrying more than the normal number of any particular chromosome.
Polysomy: n. condition in which more than two copies of any particular chromosome are present in diploid cells.
Obviously the author today does not support any further choice of both polysomaty and aneusomaty.

L. *Endopolyploidy:* WHITE (1942; 1945).

The term endopolyploidy has been introduced in Cytology by J.D. WHITE (1942). It has become largely known because it has been discussed again in the very successful book "Animal Citology and Evolution" WHITE (1945, 1st edition). WHITE (1942) did not condition on the number of chromosomes, the concept of endoploypoidy and consequently his endoploydy, refers to a polyploid status due to a process of a repeated division of the chromosomes, without any true mitosis, (cf. WHITE 1942, p. 147), that is an endomitosis sensu PAINTER (1939).

The author does not agree with the choice of the term endopolyploidy for the following considerations:

First, linguistically, endopolyploidy is not an abbreviation of endomitotic polyploidy.

Second, the term polyploidy, from a correct cytological point of view, cannot be qualified by the prefixes endo and exo. By analogy, the prefix endo cannot justifiably be associated to the term meiosis, cf. endomèiose MATTHEY (1945). The prefix endo is clearly superfluous since the polyploid status is always an endocaryo (or endonuclear) condition. Thus, in other words, the term endo-nuclear polyploidy NORDENSKIÖLD (1951) is nothing else than a tautological word for polyploidy. It is, also, necessary to state that to define endopolyploidy as a somatic polyploidy arisen through endo-cycles (NAGL 1978, p. 216), that is as an endocycle-polyploidy, does not change the terminological debate.

Indeed, even the term cycle, in this case, cannot be qualified by the prefixes endo or exo. Clearly an exo-cycle is not proposable. The author recalls once more, that the prefix endo cannot properly be used as an abbreviation for endomitotic. Thus such a terms as endochromocenter and endochromosome, do not convey the meaning of nuclear structure originated by endomitosis (cf. TSCHERMAK WOESS 1971).

M. *Ploidy, taxoploidy and somatoploidy*.

Owing to the unanimous acceptance of the haploid … polyploid terminology coined by STRASBURGER (1905-1910), the suffix –ploid became the linguistic basis chosen by the classic cytologist to form analogous terms referable to the number of chromosomes. However, in modern years, the cytological literature has been enriched by many related new compound terms already quoted, thus causing confusion or discordancy on this matter.

Consider first the suffix –ploid. This suffix should be chosen to qualify or to define the relation to as many times, the chromosome set (not necessaryly consisting of homologous chromosomes) is present in the nucleus.

In other words –ploid should convey the meaning of a simple numerical evaluation.

A first ambiguity or uncertainty arises when the nucleus, numerically recognized as diploid, bears the diploid number of diplo-… polychromosomes (cf. the current endopolyploidy).

A second uncertainty arises when the nucleus to be taken into consideration, belongs to a species (genus etc.) taxonomically recognized to be polyploid.

For the purpose of avoiding this ambiguity and, at the same time, to propose a related correct terminology, the author here suggests the following terminology.

1. Taxoploidy = taxonomic polyploidy - This term should refer to the different degrees of polyploidy pertinent to taxonomic unities. Further, following a well-known traditional pattern, (see the choice of the symbol n=haploid, etc.) the following abbreviations would be assigned to the Taxo-ploidy:

t= taxoploidy),

n^t = taxohaploid, 2 n^t = taxodiploid …8 n^t = tazooctaploid, etc.

2. Somatoploidy (shorter somaploidy) = somatic polyploidy - This term should refer to the degree of polyploidy pertinent to a single nucleus (cell, etc.) indipendently from the individual degree of polyploidy.

The following series of abbreviations should be assigned to the somatoploidy:

s = somatoploydy (somaploidy);

n^s = somahaploid; 2 n^s = somadiploid.., 8 n^s = soamoctaploid, etc.

Thus, for instance, by parthenogenesis an haploid egg should give rise to somahaploid cells (n^s cells).

N. *Polytene:* KOLLER (1935).

Polyneme, syn-polyneme, caryopolynemy, polygenonemy - The term polytene, in Cytology, quali-

fies the giant chromosomes of salivary glands of *Drosophila* (etc.) and has been coined by KOLLER (1935).

A critical analysis of the very great amount of literature on this matter is beyond the purpose of the present paper. The author, however, is compelled to quote at least some main data and relative interpretations which will justify the alternative terms here proposed.

In 1933, T.S. PAINTER discovered the genetical correspondence between the bands of the giant chromosomes in the salivary glands of *Drosophila* and the loci in the related genetical map. The following year, N. KOLTZOFF (1934) discussed the question "what nuclear structures are multipllied in the development of these chromosomes?" and advanced the hypothesis of "the multiplication of the genonemes". Finally, a few months later, P.C. KOLLER (1935) investigating the chromosome "Pairing and Coiling in Salivary Gland Nuclei of *Drosophila*", coined the term "Polytene" and defined the giant chromosomes "multiple chromosomes", as follows: Cf. KOLLER (1935 p. 372):

"It seems that we can regard these chromosomes as corresponding with paired pachytene chromosomes at meiosis in which the intercalary parts between chromomeres have been stretched and separated into smaller units and in which, instead of two threads lying side by side, we have 16 ore even more. Hence they are "polytene" rather than pachytene; I do not, however, propose to use this term; I shall refer to them as "multiple threads." Further, it seems that the nuclei must be regarded as resting or prophase nuclei, and we may therefore look for a structural similarity between the arrangement of the chromosomes found in these nuclei and that found in the ordinary resting or prophase nucleus."

Cf. KOLLER (1935 p. 378): "It is most probable that the great increase in volume of cytoplasm and nucleus is correlated with the multiplication of the chromosomes by division of the individual threads two, three, or four times, as in the process found in the octoploid cells of the tracheal tissues. In the salivary glands the sister threads remain in close association and compound or multiple chromosomes arise."

The author believes that the meaning of KOLLER's sentence "I do not, however, propose to use this term" has been widely underestimated and consenquently also ignored…

Polytene is a term that linguistically (by analogy with diplotene, pachytene etc.) would refer to a terminological series unanimously ascribed by the cytologists to chromosome meiotic morphology. Consequently KOLLER does not recommended the choice of the meiotic-like polytene term to define the mitotic chromosomes of the salivary glands.

However, and in contrast with KOLLER's recommendation, DARLINGTON (1937 p. 580) - "Recent Advances in Cytology" accepted the definition "polytene chromosomes": "Polytene, of chromosomes in the salivary gland nuclei of *Diptera* KOLLER, 1935."

DARLINGTON (1937 p. 378): "In other words each of the pairing chromosomes has divided four or five times, and the products of its division have remained in side-by-side association (BRIDGES 1935; METZ 1935; KOLLER 1935). It is possible that they are associated closely in pairs resulting from primary attraction and that these paris are more loosely held together by a secondary attraction corresponding to the secondary attraction characteristic of somatic chromosomes in the *Diptera* (ELLENHORN, PROKOFIEVA and MULLER 1935). The original plane of association of the paired multiple chromosomes is, however, soon lost, and the whole bundle of threads becomes a uniform cylinder, a *polytene* chromosome, as we might call it."

The quotation of Darlington's considerations allows the author to condense his criticism and proposals as follows: since the suffix neme is classically specific of the mitotic chromosomes, in this case the choice of the term polyneme in the place of the present polytene, is the most appropriate terminological alternative.

Further, since the chromosomes of the salivary glands nuclei are characterizated by somatic synapsis (which occurs before their repeated reproduction), these chromosomes should be further qualified as syn-polyneme chromosomes.

Lastly, as regards a general terminology referable to the polynemic cytological status, the author propose: *Caryopolynemy and Polygenonemy.*

Occurrence of a multistranded status due to repeated multiplication of a specific neme unit, respectively the caryoneme and the genoneme.

The author (BATTAGLIA (1993) wrote: "Third, the hypothetical association or co-operation of more than two genonemes, should lead to additional terms such as *tetragenonemes … polygenonemy*."

O. *Documentation. Caryodineme (monochromosome), caryotetraneme (diplochromosome), caryooctaneme (quadruplochromosome) division (kineses) in the root-tips of Scilla peruviana L. (Liliaceae).*

The author wishes to conclude the present paper with a microphotographic documentation concerning the morphology of the caryodineme… caryooctaneme division (kineses). Such a documentation integrates and also supports the caryological nomenclatural system proposed in the present paper.

The selection of a plant material and namely the root-tips of the liliaceous species *Scilla peruviana L.* is motivated by the personal evaluation and choice of a set of caryological data together with their history and terminology.

The diplo … polychromosome divisions represent basic morphological details within that more complex cytological state, which occurs during the tissue development and differentiation in both animals and plants.

As regards the nomenclature, the somatic cytological differentiation has variably defined by the biological literature, namely as somatic polyploidy, polysomaty, endopolyploidy, polyteny, and it has been already analyzes and discussed in this paper. Regarding the caryological details is worthy to recall that the histological growth is associated with two different chromosome behaviours that is a numerical change and a structural change, both co-existing in the same tissue.

The numerical chromosome change results into nuclei having multiple chromosome sets and currently termed tetraploid … polyploid nuclei.

The structural chromosome change results into multistranded chromosome sets (diplo-quadruplo … polychromosomes) due to repeated chromatid duplication, thus leaving unchanged the pre-existing chromosome-ploidy. This last structural change nomenclaturally corresponds to the caryotetraneme … caryopolyneme series of the author. Necessarily also the choice of the plant material specifically the root-tips of the liliaceous *Scilla peruviana* L., together with the relative cytological technique, deserves motivation. As regards this question it is essential to mention that Francesco D'Amato and collaborators (at the Botanical Institute of the University of Pisa) in the years 1948 – 1952, by experiments of mitotic stimulation induced by the 2-4 dichlorophenoxyacetic acid documented the caryology, (diplo-polychromosome divisions), in many genera of Liliaceae and Graminaceae (cf. D'Amato 1948; 1950; 1951; 1952a, b; Avanzi 1951).

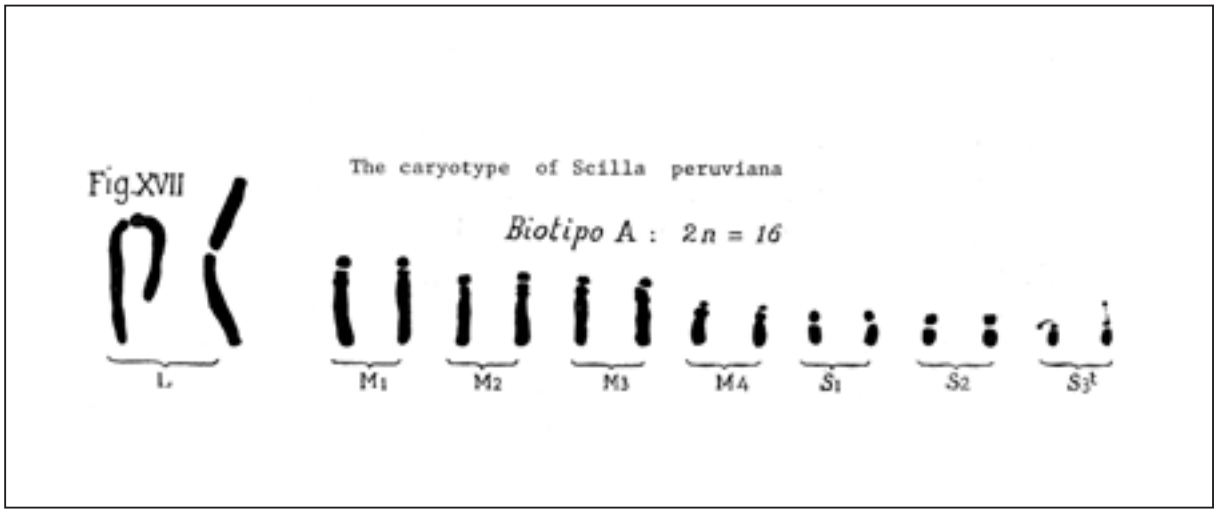
The cytological technique adopted by D'Amato and collaborators included the staining of the chromosomes by the so-called Feulgen method.

In those years the author, as a member of the scientific staff of the Botanical Institute of the University of Pisa, was fully aware of all details of the Feulgen staining method, a technique which the author himself later improved with the introduction of a "cold hydrolysis" Battaglia (1951).

With such Feulgen method, the author documented the normal caryotype of *Scilla peruviana*, together with several chromosome mutations discovered in plants coming from different geographical habitats (Battaglia 1949a; b; 1950; Battaglia, Cesca and Maggini 1969). By the improved Feulgen method, together with the mitotic stimulation, the author also investigated the somatic polyploidy of the root-tips of *Scilla peruviana* L.

In this case, after 6 days of the experimental treatment, a large amount of mono-diplo and quadruplo-chromosome divisions were observed. The full paper is still unpublished because the author left the University of Pisa and became fully engaged in human cytogenetics (cf. Battaglia 1971).

A series of caryological microphotographs from the paper mentioned above, is utilized here to assemble the plates 1-12. These plates show the normal diploid caryotype of *Scilla peruviana* L. (2n=16) and the finest details of the diplo- and quadruplochromosome divisions or the caryotetraneme caryooctaneme kineses of the author's present new terminology.



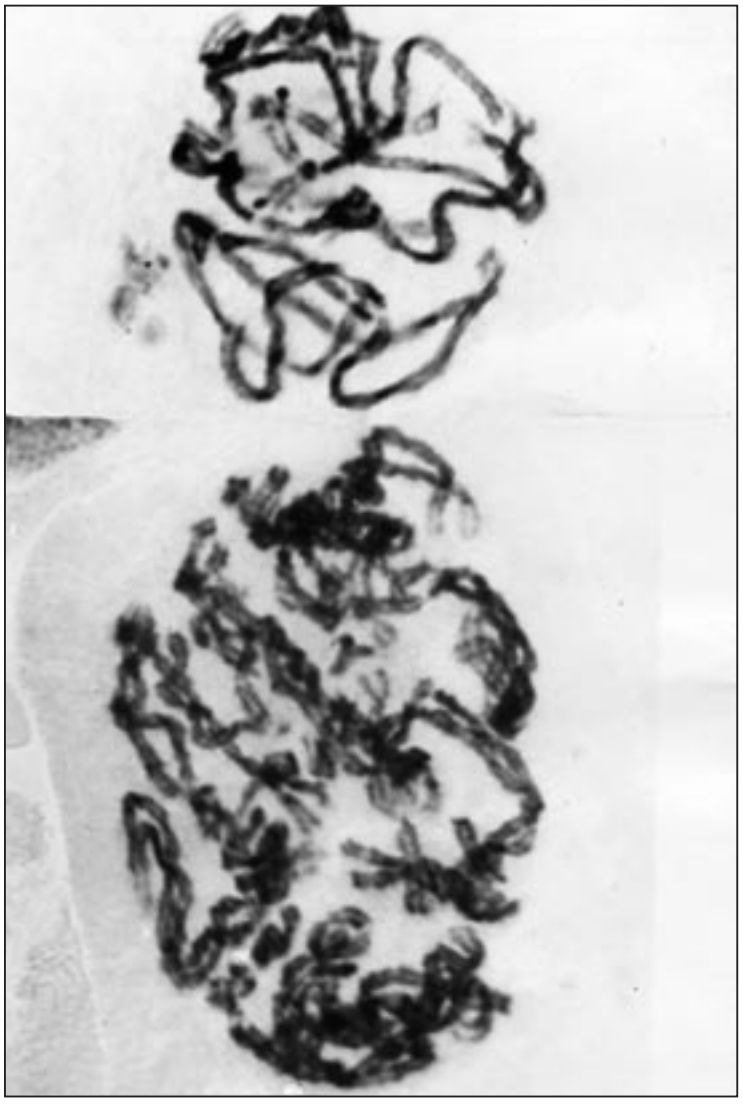


Plate 1 — Prophase: dinemes (left) and tetranemes (right).

Plate 2 — Prophase: octanemes.

Plate 3 —Prometaphase: dinemes (left) and groups of two dinemes (right).

Plate 4 — Prometaphase: groups of four dinemes.

Plate 5 — Metaphase: only dinemes.

Plate 6 — Metaphase: only dinemes.

Plate 7 — Early anaphase: only mononemes.

Plate 8 — Early anaphase: only mononemes.

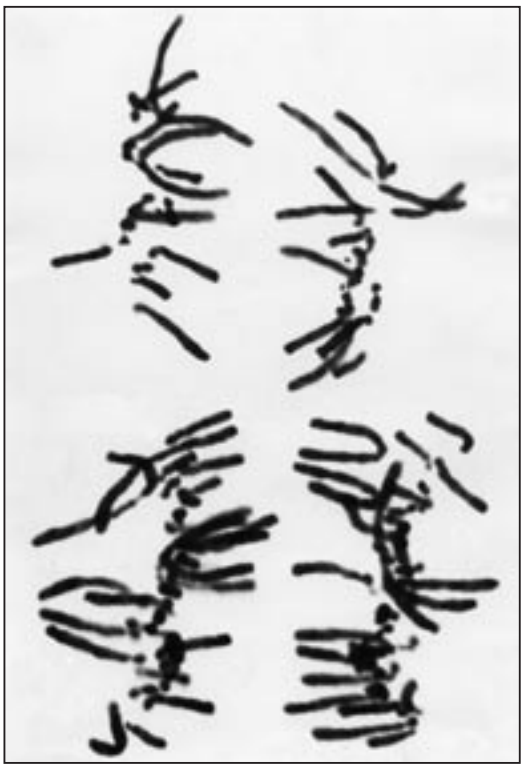


Plate 9 — Middle anaphase. Left: two diploid mononeme sets. Right: two tetraploid mononeme sets.

Plate 10 — Middle anaphase. Two octaploid mononeme sets.

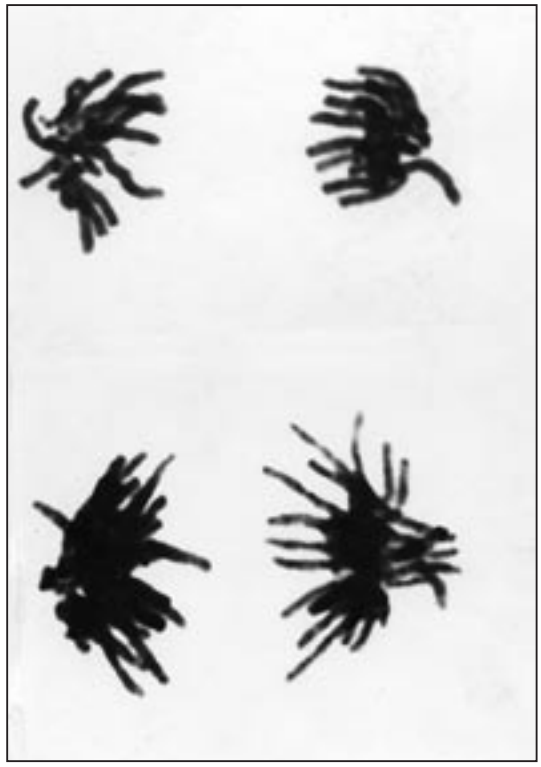


Plate 11 — Late anaphase. Çeft: two diploid mononeme sets. Late anaphase. Right: two tetraploid mononeme sets.

Plate 12 — Late anaphase: two octaploid mononeme sets.

CONCLUSIONS

The author believes that the present collection of terms, analytically commented from both the historical and the linguistic points of view, may well represent the basis for achieving a sound terminological system for the modern cytogenetics.

Acknowledgements — The author started the collection of the data presented in this article in the years 1954 and 1955 when, as Fulbright Fellow he worked at the Department of Biology, Fordham University, New York, under the direction of the eminent Prof. Charles Berger S.J.

In the years 1955-1956 he also became engaged in human cytogenetics by Dr. R. Wallerstein, head of the Marcia Slater Lab., Jewish Memorial Hospital, New York.

Dr. Wallerstein was involved in early leukemia research and became an authority on the disease. He was also a leading figure in the movement to establish blood banks in the early 1930's.

Dr. Wallerstein and a collegue, Dr. Walter Levy, performed the first exchange transfusion in 1945. The procedure replaces the infant's blood and makes possible the survival of babies born to parents whose blood is Rh incompatible.

It is only recently that the author has had the opportunity of completing the collection and the elaboration of the data and compiling the present paper.

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Fig. A — Fordham University Department of Biology, New York, 1955. Witkus E. R., Battaglia E., Berger C. A..

Fig. B — Dr. Harry Wallerstein, Marcia Slater Lab., Jewish Memorial Hospital, New York

Tables 1-10 - The present state of affairs in the cytological literature is simply chaotic and often contradictory. There are many terms interpreted not in agreement with their etymological meaning, cf. e.g. the couplet mitosis-amitosis. A different meaning has been frequently ascribed to each of two synonymous compound terms only because one term is non-hybrid (that is to say Latin-Latin or Greek-Greek) whilst the other terms is hybrid (that is to say Latin-Greek of Greek-Latin), cf. the couplets karyotype-nucleotype and karyosome-nucleosome. In addition, in many modern cytological papers and also text-books, the terminological priority is wrongly ascribed or ignored. The present Tables 1-10 summarize a selection of terms which the author considers of historical and cytogenetic interest obviously in relation to the purposes of the present paper.

Table 1 — The classic cytological terminology established from 1874 to 1899.

Year	Chromato-, chromo-	Caryo-, karyo-	Mito-
1874		Karyolysis *Auerbach*	
1878		Karyoplasma, Karyoparaplasma *Flemming*	
1878		Karyokinesis *Schleicher*	
1880	Chromatin, achromatin *Flemming*		
1881	Chromatogen *Pfitzner*		
1882	Chromato-Chylema *Strasbuger*	Karyota, Akaryota *Flemming*	Mitom, Paramitom *Flemming*
”	Chromatoplasma *Strasburger*	Karyenchym *Flemming*	Mitose, amitotischer Teil. *Flemming*
”	Chromatosomata *Strasburger*	Karyomitom *Flemming*	Mitoschisis *Flemming*
”		Karyomitosis *Flemming*	
”		Karyaster *Flemming*	
1883	Parachromatin *Pfitzner*	Karyosoma *Ogata*	
”	Prochromatin *Pfitzner*		
1884		Karyomitose *Flemming*	
”		Karyon *Strasburger*	
1885		Caryodiérèse *Carnoy*	
1886	Pseudochromatin *Pfitzner*		
1887		Karyomerit *Böhm*	
”		Pseudokaryokinese *Van Beneden*	
1888	Chromosome (-en), Chromosoma *Waldeyer*		
1889	Chromatosomen *Davidoff*		Mitosoma *Platner*
”		Karyogamie *Maupas*	
1890			Amitose *Lowit*
1891	Chromatomere *Hartog*	Karyosymphysis *Hartog*	Cytomitom *Schiefferdecker and Kossel*
”	Chromomere *Fol*	Karyomitoplasma *Schiefferdecker and Kossel*	Mitoplasma *Schiefferdecker and Kossel*
”	Chromatoid *Benda*	Karyomit (-en) *Schiefferdecker and Kossel*	Cytomit (-en) *Schiefferdecker and Kossel*
”	Achromin *Haeckel*		
”		Karyobasis *Haeckel*	
”		Karyolymphe *Haeckel*	
”		Karyotheke, Cytotheke *Haeckel*	
1894	Basichromatin *Heidenhain*	Karyoide *Palla*	
”	Oxychromatin *Heidenhain*		
1895		Karyologie *Trow*	
1896		Karyochyl *Fol*	
”		Karyomere *Fol*	
1897		Endo-karyogamie *Hartog*	
1899	Chromidia *Hertwig*		
”	Chromiole *Eisen*		
”	Chromoplasma *Eisen*		

Table 2 — Tene and nema terms.

Tene		Nema	
		dolichonema	Rosen (1896)
		strepsinema	Dixon (1901)
diplotene	Winivarter (1900)	diplonema	Gregoire (1907)
leptotene	Winivarter (1900)	letonema	Gregoire (1907)
pachytene	Winivarter (1900)	pachynema	Gregoire (1907)
synaptene	Winivarter (1900)		
amphitene	Janssens (1905)		
strepsitene	Gregoire (1907)	strepsinema	Gregoire (1907), see Dixon (1901)
		prostrepsinema	Janssens (1905)
zygotene	Gregoire (1907)	zygonema	Gregoire (1907)
zygotenie	Janssens (1909)	péricaryonème, périnème	Renault & Dubreil (1906)
		chromonema	Vejdowsky (1912)
		prochromonema	Hollande (1943, 1944)
		plectaneme	Bolles Lee (1911a)
		plectonemic coil	Sparrow, Huskins, Wilson (1941)
brachytene	Chodat (1925)	brachynema	Bolles Lee (1911 b)
synaptotene	Wilson (1925); Moses (1969)	synaptinemal complex	Moses (1958 b p. 637, 1968); Nebel & Hacket (1961); Roth (1966)
synaptotenic complex	Moses (1969)	complex synaptotenematique	Folliot & Maillet (1966, p. 395)
polytene	Koller (1935)	synaptonemal complex	Wettstein & Sotelo (1967); Smith & King (1968); Moses (1969)
diatene	McClung (1941)		
peritene	McClung (1941)	synapticonemal complex	Moses (1969, p. 49)
		synaptonemata	Moses (1969)
		haptonema	Parke, Manton, Clarke (1955, p. 581)
		haplonema	cf. Ettl (1980)
		hyalonema	Fujii (1931)
		centronema	cf. Sharp (1934, p. 223)
		genoneme	Koltzoff (1934)
		haplo, diplogenonema, tetragenonemes… polygenonemy	Battaglia (1993)
		namamere	Nebel (1939)
		kinetonema	Matsuura (1941 a, b).
		nucleolonema	Estable and Sotelo (1950)
		mononeme	Crick (1971)
		uninema (bi-, multineme)	Laird (1971)
		uninema (polynemy)	Gay et al. (1970)
		karyoneme	Battaglia (1993)
		idionema	Battaglia (1993)
		caryomononeme	This article
		caryodineme	This article
		caryotetraneme	This article
		caryooctaneme	This article
		caryopolyneme (-nemy)	This article
		synpolyneme (-nemy)	This article

Table 3 — Gen-o, gen-e, gen-i terms.

Genoblast	Minot 1877
Genocyte	E.G. Bertrand in Hartog 1897 p. 700
Genoide	L'Héritier & Teissier 1937
Genom	Winkler 1920 p. 165; progenom: Lamprecht 1949, 1954
Genomatie	Winkler 1920 p. 166 (Homo-, Polygenomatie)
Genomatisch	Winkler 1920 p. 165-166 (Hetero-, Homo-, Iso-, Anisogenomatisch, Mono-, Di-,Tri-, Polygenomatisch), Levan 1937, p. 364: autogenomatic species;
Genomere	Eyster 1928: suggested by P.W. Whiting, Belling 1931, p. 157
Genoneme	Koltzoff 1934 p. 313. See also hemi-, mono-, di-, tetra-, haplo-, polygenon-eme: Battaglia 1993.
Genophore	Ris 1961, p. 112
Genoplasma	Winkler 1924, p. 253
Genoplast(ic)	Clark 1912, p. 140.
Polygenoplast(ic)	" " "
Genoplast, paragenoplast	Blejer 1930, p. 108, 109
Genoplastin, paragenoplastin	Blejer " p. 109
Genosome	Cf. Knight 1948
Genospecies	Raunkiaer 1918; Turesson 1922
Genoholo, genolecto, genosyntype	Schuchert & Buckman cf. Jackson 1928
Genotype	Schuchert 1897, p. 639; Johansen 1909, 1911
Genotypus, phaenotypus	Johannsen 1909, p. 130
Pangenosom	Strasburger 1905, p. 13
Epigenotype	Waddington 1939.
Pangenesis	Darwin 1859, 1868; Jäger 1879
Pangene	De Vries 1889
Gene	Johannsen 1909
Antigènes (substances)	Deutsch 1899
Antigen, Antisomatogen	Deutsch & Feistmantel 1903, see also Lindenmann 1984
Catagenesis, Kinetogenesis	Cope 1884
Diplogenesis	Cope 1889
Diplogenesi, Aplogenesi	Delpino 1903
Palingenese	Haeckel 1875
Perigenesis	Haeckel 1876, see Wilson 1925, p. 1167
Orthogenese	Haacke 1893
Autogenese	Plate 1903
Ektogenese	" " "
Genetics	Bateson 1907
Epigenetic	Waddington 1939
Epigenetics	Waddington 1942
Cytogenetics	Babcock 1931, Clausen 1931, Schulz-Schaeffer 1976, 1980
Phänogenetik	Haecker 1918
Phenogen	Camp & Gilly 1943, p. 334, 373
Phenon	Camp & Gilly 1943, p. 335
Phenomic species	Camp & Gilly 1943, p. 336
Homogeneon species	Camp & Gilly 1943, p. 334
Parageneon species	Camp & Gilly 1943, p. 337
Paragenesis	Hartog 1891, p. 73; McClung 1941, p. 578
Genidion	Jucci 1943, p. 395
Genite	McClung 1941 p. 578

Table 4 — Chromatin terms.

Achromatin	Flemming 1880 a
Basichromatin	Heidenhain 1894
Centrochromatin	Lindegren 1949
Chromatin	Fleming 1880 a
Chromatinfäden	Pfitzner 1881
Chromatinkuglen	Pfitzner 1881
Chromatinmikrosome	Lenhossek 1898
Cytochromatin	Prenant 1898 cf. Wilson 1925 p. 724; Maziarski 1910
Epichromatin	Stubblefield & Wray 1971
Euchromatin	Heitz 1928
Fisiocromatina	Gerola 1950
Gene chromatin	Belling 1931
Hemichromatin	Fol 1896 p. 268
Heterochromatin	Heitz 1928
Idiochromatin	Lubosch 1902: idio (tropho) chromatische Substanz; Goldschmidt 1904: idio (tropho) chromatin
Karyochromatin	Bluntschli 1904; Schaxel 1910; Wildman 1913
Kinochromatine	Camp 1924
Métachromatine	Guillermond 1902; 1904, cf. Wager & Peniston 1910; Dangeard 1916a,b; Dangeard 1919: métachrome
Metachromatischen Körperchen	Babes 1887, cf. Babes 1895
Olistherochromatin	Resende 1945
Orthochromatin	Brink 1960: órtho-parachromatin system
Oxychromatin	Heidenhain 1894
Parachromatin	Pfitzner 1883
perichromatin fibril	Monneron & Bernhard 1969
perichromatin granule	Yamamoto *et al*. 1969
Plasmachromatin	Bluntschli 1904, Schaxel 1910
Plasmochromatin	Schrader & Leuchtenbergen 1950
Plastochromatin	Wildman 1913
Prochromatin	Pfitzner 1883
Pseudochromatin	Pfitzner 1886b
Trophochromatin	Lubosch 1902; Goldschmidt 1904c

Table 5 — Chromatin-o terms.

chromatinmicrosom	Lenhossék 1898
chromatinsome	Haapala & Niestedt 1976 p. 52-53
chromatinosome	Dangeard 1922 p. 1658, 1931
chromatinomere	Haapala & Nienstedt 1976, p. 52-53
euchromatinosome	Fernandes 1948
hétérochromatinosome	Fernandes 1948
métachromatinosome	Hollande & Hollande 1931

Table 6 — Chromat-o, -ic, -id, -oid terms.

chromatocyte	Asvadourova 1913
chromatogen	Pfitzner 1881, p. 295- 297
chromatolysis	Flemming 1887
cromatoma	Giglio-Tos & Granata 1908 p. 39
chromatomere	Hartog 1891, p. 54, 55
chromatophore	Schaarschmid 1880; Schmitz 1882, cited by Wilson 1896
Chromatoplasma	Strasburger 1882 b p. 479
Chromatosomata	Strasburger 1882 b, p. 479; Macallum 1891
Chromatosomen	Davidoff 1889 p. 132, 153, 158; Weisman 1891 (cf. 1892 p. 691); Simpson 1978 p. 5524
chromatosperite	cf. Knight 1948
Chromato-Chylema	Strasburger 1882b p. 479
endo-, parachromatic granules	Eisen 1899b
chromatisch (a-, holo-, mero-)	Schaxel 1911, p. 588
autochromatid	Battaglia 1991 p. 101
chromatid	McClung 1900 p. 78
hemichromatid	Rhoades 1961 p. 69
isochromatid	Rhoades 1961 p. 69
semicromatidio	Battaglia 1950, p. 49
Chromatoid	Benda 1891; Hermann 1891

Table 7 — Chrom-id, -iole, -it, -oid terms.

chromidia	Hertwig 1899
chromidien, chromidial	Hertwig 1902
chromidiome	Bernard *et al*. 1952
chromidiocentrum	Wager 1913
chromidiogamy	Minchin 1912
chromidium (=gonidium)	cf. Jackson 1928
chromidium = chromium	Dangeard 1931 p. 355, 359
endochromidies=endochromies	Dangeard 1931 p. 359
gameto- & somatochromidia	Schaudin 1905 p. 26
idio-, trophochromidia	Mesnil 1905
interchromidia	Monné 1948
kinetochromidien	Schaxel 1911
chromiole	Eisen 1889 p. 131, 1899 b
achromite	McClung, cf. Schrader 1935, p. 424
eu- & heterochromities	Klingstedt 1941
chromoid	Benda 1891, cf. chromosomoid Reuter 1909

Table 8 — Chromosom –a, -e, -in, -oid terms.

Chromosom, Chromosoma (=Chromatinkugel)	Waldeyer 1888 pp. 27, 54, see also Einzelelement, Doppelelement: Henking 1891; 1892.
Doppelchromosom	Haecher 1891 p. 3; doppelchromosoma: Bonnevie 1905 p. 501
allo-, auto-, mono-, diplosome	short for allochromosome, etc. cf. Montgomery 1906,
Einzelchromosom	Schleip 1911 p. 94
Sonderchromosom	Krüger 1911 p. 179
Sammelchromosom	Schleip 1912 p. 6
autochromosomen	Nawashin 1927 p. 416; Kuster 1935 p. 37
cytochromosome	Maziarski 1910 p. 536
diplochromosome	cf. Morgan in Cowdry 1924 p. 721, foot note 1, together with haplochromosome; White 1935 a, b
endochromosome	Tschermak-Woess 1971
euchromosome:	McClung 1914 p. 697
gonochromosome	Wilson 1906 p. 28
haplochromosome	cf. Morgan in Corwdry 1924 p. 721, foot note1, together with diplochromosome; Chodat 1925 p. 18
hemichromosome	Darlington 1965 p. 719
heterochromosome	Montgomery 1904 p. 145-146
idiochromosom	Henking 1892; Wilson 1905 p. 375
isochromosome	Darlington 1939 a p. 355, 357
macro (micro) chromosome	Wilson 195, p. 375; Fillon *et al*. 1998; Masabanda *et al*. 2004
mega (micro) chromosome	Bonnet 1911, p. 234
metachromosome	cf. Jackson 1928
minichromosome	Griffith 1975; Clarke & Carbon 1985; Tease & Fisher 1998; Kaname *et al*. 2005
mixochromosome	Winiwarter & Sainmont 1909; Fernandes 1948; see also myxosome: Chodat 1925 p. 4: “ou bivalent”
chromosomin	Stedman & Stedman 1943
chromosomoid	Reuter 1909, (cf. chromoid Benda 1891)
monochromosome	cf. Winge 1917 p. 207 “heterochromosomes (‘monochromosomes’); White 1935a p. 390, 1935 b p. 78; cf. Barber 1940: “mono… polychromosomes”
mono, polychromosomic	Gregoire & Wygaerts, 1903 vesicule monochromosomique (polychromosomique); Chodat 1925 p. 15 “les caryoimérites, mono (ou polychromosomiques)
olisterochromosome	Resende, de Lemos-Pereira, Cabral 1944 pp. 39-40
polychromosomic	cf. monochromosome
polychromosomic	cf. monochromosome
pollychromosome	Barber 1940 p. 180
prochromosome	Overton 1905 p. 207
protochromosome	Maire 1902, Guillérmond 1904
pseudochromosom	Heidenhain 1900 p. 518, 522
pseudo-isochromosome	Caldecott & Smith 1952
quadruplochromosome	Biesele, Poyner, Painter, 1942; Levan & Hautschka 1953
tetrachromosom (e)	Berger & Witkus 1946; Kato 1957

Table 9 — Chromo-terms.

Chromoblaste	cf. Guilliermond 1901; 1903 see Guilliermond, Mantenot, Plantefol 1933
Chromocentro	Baccarini 1908 p. 195
endochromozentre	Geitler 1953
euchromocentre	Gregoire 1932
chromochondrien	Prenant 1913
chromochondries	Asvadourova 1913 p. 293
chromogene & cytogene	cf. Lindegren 1949; Serra 1955
chromokinesin	Wang & Adler 1995
chromoleucite	van Thiegem 1884, p. 487
chromomère	Fol 1891 a, p 397
heterochromomere	Montgomery 1904; Blejer 1930 p. 121
interchromomere	Monné 1948
homochromomere	Blejer 1926
telochromomere	Brown 1949
chromomite	Giglio-Tos & Granata 1908 p. 39
chromomikromosom	Haecker 197 p. 22
chromo-Mikrosomen	Fick 1905 p. 200
chromonema	Vejdowsky 1912 p. 12
prochromonema	Hollande 1936, cf. Hollande 1944 p. 165
chromoplasma	Eisen 1899a p. 132
chromoplasm	Eisen 1899b p. 104
chromoplastid	Schimper 1882 c
chromoplast	Meyer 1882; Strasburger 1884b; Eisen 18889a p. 130; Janssens 1905 p. 393 (chromoplaste)
chromosin	Mirsky & Pollister 1946
chromospire (s)	Dangeard 1902
chromotaxis	Haecker 1902b p. 379
cromotipo	Battaglia 1956 p. 256

Table 10 — Nucleo-Karyo Synonyms (some instances of historical interest).

Nukleoid	Karsten 1893 p. 560	karyoide	Palla 1894 p. 153
Nucleo-Mikrosom(en)	Strasburger 1882	karyomikrosomen	Schiefferdecker 1891 p. 9
Nucleoplasma	van Beneden 1875	karyoplasma	Flemming 1878 p. 360
Nucleosome	Hollande & Hollande 1931; Oudet *et al.* 1975; Battaglia 1994	karyosoma	Ogata 1883 p. 414
Nucleomere	Kiryanov *et al.* 1976	karyomere	Fol 1896 p. 242, 259
Nucleotype	Bennet 1971; 1973	karyotypus	Delaunay 1923; Lewitsky 1924

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ALLEN — Cf. DUNCAN R.E. 1945.

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