The Golgi Apparatus

Study of these elements waited upon the development of special techniques for their demonstration. They are impossible to see except in living spermatocytes. Silver impregnation techniques demonstrate that the axon is an outgrowth of the cyton, and this same (....) led Golgi to discover the internal apparatus now known as the Golgi apparatus. They were first seen in the nerve cells of the owl. This network never met the surface of the cell; on the outside there are nerve endings of a different character 1898

Negri discovered the apparatus in many types of cells, including non-nervous tissue. Cajal (1914) modified the technique, surveyed the Golgi in many tissues.

Kopsch (1902) accidentally found the osmication technique. Applied to many different tissues by v. Bergen (1041), particularly vertebrates. All histologists now use it widely.

Huecibler investigated invertebrates 1912-1914.

Golgi techniques are rather capricious, variable. But the structures they do reveal, when they do, are rather consistent in structure, even throughout the animal kingdom.

Golgi described the apparatus as a series of strands broadening into plates and discs. Not reticular

Review: Musich, C.C. Protoplasma Monographien 8 (1939). Formed and Dechaud der Golgi Apparat. Complete bibliography, but biased text.

Weisman + Severinghaus — Anat Rec 1938 uncritical

Jacobs Eng Biol II:357 (1927)

Always ~~modified~~ stuck, according to Pollister.
An intermediate density of osmication is optimal for analysis; it permits 3-dimensional reconstruction.
lines, dots mean threads
areas, lines mean laminae

Nassonoff ... 1928: Hirudo. In invertebrates, they are usually organized into dictyosomes: cup-like structures

Pollister & JMS (1938) In Amphibia, they are fundamental cribbled collars. Frequently the thickness can be approximated; this proves to be ≈ 25μ.

No Golgi rapid screen method

11/6/42 Transitions occur in invertebrate dictyosomes. In pulmonates they may run together. In each cell dividing the Golgi fragments, apparently diminishing in amount. In somatic early anaphase, the Golgi may almost disappear, reappearing at telophase.

Johnson In late spermatogenesis, the Golgi is sloughed off, first breaking up. Each fragment is cup like. Hirschler misinterpreted this as a multiplication.

The cup may be considered as a fundamental sort of crystalline orientation of the Golgi material.

Ultracentrifuge shows its specific gravity between oil and mitochondria.

Skepticism has frequently been expressed as to the real existence of Golgi material in vertebrates. The invertebrate dictyosomes are easily seen. The acrobastic homology of Golgi is thus stressed.

Why do acids destroy the structures called the dictyosomes and Golgi?

Hirschler Golgi as closed vesicles; osmophobic interior.

Hirsch Small granules. a Golgi septum. Synthesis of granular products. ... May be mistaken as fat droplets.

1928 Parat Neutral red accumulates in vacuoles, superficially resembling plant "saccome". Secretion in the saccules. No organized Golgi apparatus. He concedes now however three types of formed components of cells: centrioles, chondriosomes and lipodromes = Golgi.

Gatenby, Bowen The one proved function of Golgi is the formation of the acrobast which secretes the accrosome in spermatogenesis. The accosome however is still quite mysterious. The acrobast may be a single large cup, or a group of smaller ones.

1923 Nassonowa in pancreas, secretory granules grow from vacuoles and pushed on osmophil surface.

Cowdry Gen Cytology

The Golgi is usually quite polarized, and has been used to detect changes of polarity in enamel organ, thyroid etc.

Trypan blue is absorbed in the Golgi region, or rather ends up there after absorption. Indicates vacuolar or secretory, excretory functions.

Maksarov Biol Bull 62
Protoplasma 19

32

Plant homologues to Golgi

Bowen, Zeitschr. Zellf. 6:689 1928 Osmiophil platelets, believed by Kisphaw to be stages of plastids

Weier A.J.B. 29 Plastids may have lamellar structure, are osmophile; participate in lemonplane production in bryophytes. But mitochondria, proplastids are also homologizable.

Dec Adv Anatomy Bloch.

11/11/42

CELL DIVISION

Amitosis no longer upheld by cytologists. No future in it! Even amoeba, supposedly dividing by binary fission actually has a modified promitosis. Protozoologists, working on relatively badly fixed material are the general supporters of amitosis, now conceded in only a very few cases.

Modified mitosis?

"Indirect division; karyokinesis Mitosis.

Define phases—

Interphase, resting phase. Loose, flocculent, almost homogeneous nuclei (chromatin) without ordinary features.

Prophase - loose stuff into a thready form gradually forms chromosomes. Usually in this phase splitting appears obviously and suddenly.

Metaphase - chromosomes congress, coonsit. Simultaneously the spindle appears, the nuclear wall disappears.

Anaphase - separation of chromosomes to opposite poles.

Telophase - chromosomes become diffuse nuclear wall is reformed.

Interphase—

Little agreement on time relations.

Spindle, in ideal zoological form, amphiastral.

In many cases, appears anastral.

But the presence or absence of centrioles is not

so important as the existence of an aster on a fundamental cytical configuration (chondrio somes in plants).

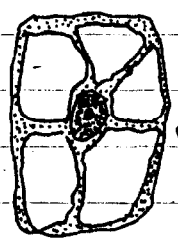
Cell Walls (after Wilson)

Plasma membrane – peripheral cytoplasm, membrane
"True" membrane – maybe lacking; secretory prod

Plant Cell Division

The phragmoplast is an organ derived from the interzonal spindle. By a running together of the fibers, a cell plate is formed which becomes continuous with the plasma membrane.

Even vacuolated cells can divide, especially on wound stimulus. A strand of cytoplasm exists in the line of the cell plate.



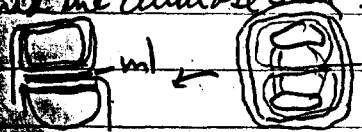
← phragmoplast. Orientation during prophase.

Duration of Mitosis. Tremendous differences in opinion and species variation. In following Tabulation, Telophase and interphase are combined:

	Minutes	Pr	Meta	Ana	Telo-Inter
Lewis & Lewis Anat Rec 13 (1917)	Mesenchyme, 39°	35	5	3	50
Zimmerman Z. Bot 15 (1923)	Spirogyra	10	7	4	9
Laughlin Cam 76	allium	55	1	1	35
Dalmorority J Morph 69 (1941)	Diss. 99	4	.3	1.0	4.3 !

In general, one can say that there is considerable variation, but that meta, and anaphase are generally the most rapid.

Precise relationships of the middle lamella, plasma membranes and the cellulose wall ??



Schmidt & Bloch PNAS 26 (1940)

See Sharp.

Clarke & Lumsdale, interpretation

v. Sha
M.
Fr
St

Sollas

Schrade
E & Haw

Analog
Cell is a
Seed

Erlanger
McClendon
Roberts

v. Sharp
Nellicott
Fresnes
Stafelt ... 1921

Periodicity of Cell Division
do not confuse with spawning periods; has nothing to do with egg laying in birds.
Complex of cavities. Various disagreement

Arbitrarily distinguish cell division and nuclear division

In most animals cell-division is largely cortical.
There is considerable independence of cell and nuclear division: Syncytial cleavages in fishes. Contrary to general opinion, centrolecithal eggs of insects have a total cytoplasmic cleavage; each nucleus has its own cytoplasm around it.

Cell division may occur in the absence of nuclei. In
Jollos & Peterfi Biol Centbl 43 (1923) the axolotl, removed ♀ pronucleus, ♂ pronucleus degenerates in hybrid crosses. Cleavage occurs nevertheless.
Schrader doubtful: fragmentation?
E B Harvey Biol Bull 71 (1936) Parthenogenetic stimulation of merogonic eggs (from which the ♀ pronucleus has been removed by ultra centrifugation. ?

11/13/42 CYTOPLASMIC DIVISION
Analogies work in simple systems
Cell is a very heterogeneous complex
See Wilson for diagrams....
Erlanger, Biol Centbl 17 (1897)
McClendon Arch Entw 37 (1913)
Robertson Arch Entw 35 (1913)

Mechanisms [Analogy analysis mainly]
1. Surface Tension [Butschli, Quincke] If a small surface on an oil drop is in contact with soap solution, currents are established inside, which tend to divide the drop. Erlanger presumed analogous currents in the Rhabditis egg. McClendon confirmed the oil drop experiment.

Spek Arch Entwm 44 (1918) Robertson employed soaked linen thread; but the furrow appeared at the wrong place; he may have touched the drop and he used a floating drop of oil. Did not mitot; negative concession.

Spek repeated earlier experiments; used solid NaOH. Critical of earlier technique. He noted analogous currents in various eggs.

Emphas.. Polar lobe formation, blebs at anaphase.

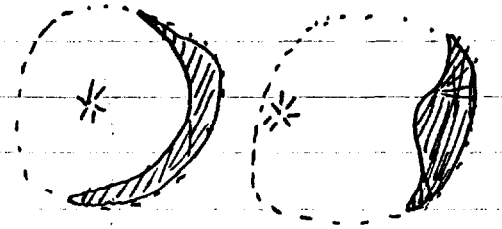
Just Arch Ph. 61 (1922) Echinarachnius (Meroblastic) eggs burst at poles.

?? Reconstruction of cell wall at furrow

Dan, Yanagita, Sugiyama Pr. 28 '37 Marked egg surface with kaolin particles, and followed their movement.

2. Hyaloplasm. The cleavage furrow is preceded by the hyaloplasm, "cleavage head". But correlates with monasters:

Painter, J. Exp. Zool 24 (1918)



Herbst Arch Entwm 9 (1900) But, also.. There is no hyaloplasm in Ca-free seawater but such eggs do cleave.

3. Asters. a. No cleavage in monastral eggs. If there are more than two, furrows appear between all of them. No spindle is formed necessarily for cleavage. The size of cleaved cells is proportional to the size of the asters. But complete cleavage is rare. The aster therefore is of some importance.

Fry J Ex Zool 43 (1925)

The aster is usually faintly visible in vivo.

Chambers J Exp Zool 23 (1917)

The aster may be produced by a system of centripetal lines of flow. By its growth, the homogeneous central material increases. [Echinoderm eggs.] Attempt to demonstrate this movement by injection of carmine particles, but this may have been seen between rays.

Detergent effects?

Forces of cytoplasmic movement.

Cremation of normal eggs?

Pollester '41: canals are not seen, but the diffusion stream current long molecules. Current flows between them.

Heilbrunn J Exp Zool 30 ('20)

Astral rays are gel strings. In centrifuge experiments the entire figure was displaced, bodily. Even contraction of cell surface. (Rejuvenation of elastic protein hypotheses.) W Heilbrunn
What then moves the centrioles? There is some small movement of them sometimes, but in other cases not.?

Viscosity changes (Heilbrunn, Chambers; Fry + Parker)

Greatest increase just before the anaphase cleavage. As you increase the polar surface, division ensues.

Gray .... (BJ Exp Biol; Biol Rev 1:)

11/18/42 NUCLEAR DIVISION

1. The separation of chromosome halves.

Clearly splitting occurs very early in mitosis, possibly in preceding anaphase. Has no relation to the achromatic figure. The earliest steps of anaphase is autonomous of spindle and aster.

a. If a chromosome gets lost from its group. Possibly acentric chromosomes split autonomously also.

Geitler — b. Endomitosis (polysomaty): A division of chromosomes in the nucleus; halves never separate very far. In

(Induced by heteroauxin; Gruenberg)

Gerris, some cells continue to endomitosis as indicated

Astragalus Vilkomerson — by the multiplication of pycnotic X.

Culex, Spinacia Berger. — c. Monasters in Echinoderm eggs, after Mechanical disturbance.

(Drosophila)

d. "Deleterious conditions" cause disappearance of

Wilson, Lillie — spindle and aster. the chromosomes continue to divide. (to 128 ploidy).

Levan, Federberg.... — e. C-Mitosis

Does colchicine dissolve out spindles once formed? Yes?? — This autonomous migration is very limited.

Centers do not disappear under ether treatment; the

See Harvey 128 (anoxia) — centers divide, producing polycentric eggs: to 64 centers. After recovery, new asters form from centers.

11/20/42. THEORIES OF MITOSIS

Electrostatic theory. Largely based on various attraction and repulsion, on the similarity of the mitotic figure to electrical lines of force. Asters would have to be ~~the~~ of different signs.

Fundamental Objections:

1. Diagonal figures, quadri, tripolar figures
2. If asters are of different sign, they should attract each other.
4. The peripheral rays cross!

Various formulations

Gallardo — where?

1 aster of like sign and chromosomes of the other sign. But spindles occur without chromosomes. In many cases spindles form completely before breakdown of nuclear membrane.

Haecker

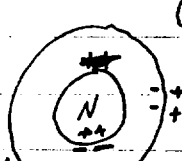
1 pole is more neutral than the other (s) in di and multipolars. Only very small remnants of astral type figures.

Lillie, RS Am J Phys 15 1905
J Morph 22 1911
Lady, McClendon, etc.

More thorough electrical theory of mitosis. Electrical analogues. Cells with high Electrolyte content cataphoreze anodically

Chauncey + Klein Brief Bull 72 '37

Supports charge on sol. chromosomes. (+)

Lillie see pgm. In interphase: 

"What initiates mitosis is a local increase in permeability of the poles, neutralizing the dipole. Then the negative cytoplasm develops lines of force to the poles. The centrioles and chromosomes all have negative charges. At anaphase the charges reverse." The scheme has been adopted uncritically by various cytogeneticists.

(Later on magnetic) Floating coil models.

But:

Prasse 1941 ♂

1. Magnetic fields have no known influence
2. Hydrostatic pressure, although presumably not directly an electrical agent, does affect anaphase movement.

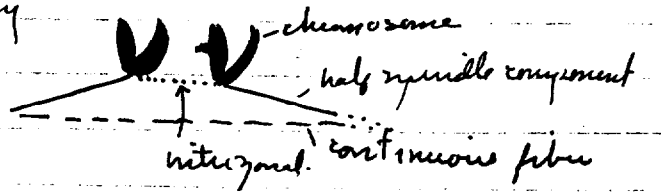
Morphology of the Amphiaster.

1. (Asters). Easily seen in vivo. The spindle is only a clear zone, outlined by mitochondria, with no visible fibrillar structure, usually. But, see —— on Pediculopsis. In this case, there are neither centrioles, nor asters. The spindle is more viscous than the cytoplasm.

Cooper PNAS 27:480 1941 ♂

Chambers & Sands J.M.P. 5 ♂ 123

Terminology



The continuous fiber is generally very fine and at the limit of visibility. Half-spindle fibers may attach to cont. fibers (e.g. a chromosome fiber).

The interzonal generally seems structureless if there is a distinct half spindle.

Thixotropy

Bovери: spindle derived from archoplasm; this is probably a Golgi remnant.
Betsaibli: transformation of cytoplasmic alveoli
Lillie, RS Polarization: orientation of long molecules.

Faris 1910

In some cases (Arion, Amphibia) spindle is made of cytoplasmic materials, and may be formed before nuclear membrane breakdown. The centers are involved

in spindle formation. The chromosomes migrate (congression) to the spindle fibers and attach to them (with coorientation).

More commonly, the centers are amphipolar before spindle formation, and the fibers grow toward each other, meet and fuse!! The nuclear membrane becomes corrugated by the active impressing of the fiber! They rupture, or dye the nuclear wall, and penetrate, etc.

as in the figures of Griffin J Morph 15 ✓ 1899.

In Hemiptera heteroptera there is an outpushing of the nucleus at various points toward the centers at an early stage. The cytologist cannot distinguish astral nipplelike from that of spindles. ✓ Science 81: 598 (1935) Cleveland upholds this view, on Protozoa material

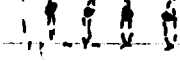
Which?

There exist spindles without continuous fibers
There exist anastral spindles
If asters formed spindles, the asters would have to connect only with chromosmes.

If there is an extra nuclear spindle, it connects only continuous fibers until the nuclear wall breaks down.

Special cases:

Belling J Gen 18 (1927) ✓ Univalents in heteroploids; form separate spindles
In Drosera (hybrids) in flattened cells, independent spindle components



Hughes-Schrader J Morph 39 (1924) ✓ (Flavesia, Nematococcus —) In late prophase
2. Zelle 13 (1931) the half spindle components are independent. Later

Compound fiber with localized kinetochore?

These ~~are~~ evidence that chromosomes are on a plane. These half spindles are intranuclear, clearly.

Belar

Then, in Slavids the chromosomes organize the half spindle components.

The interpolar is part of the continuous fiber, and not a neomorph. The chromosomes slide along the continuous fiber.

Ellenhorn 2.2ff 20

The interpolar is the trail or track left in the nuclear matter by the moving ~~interpolar~~ chromosome.

Schrader

(Particularly in Syromastes, other bugs): a hypothetical sheath about chromosome. This is drawn out into a collapsed tube. In some cases, low density of medium, etc., there may persist a circular cross-section

Interpolars Fraulgm positive

Infoto: Cleveland maintains a cytoplasmic spindle
Wada a nuclear origin

In living figures, asters are visible; spindles not. ? fibers can be seen in asters? in Protozoa ?.

11/27/40 The Reality of Spindle Fibers.

Artifact opposition...

Do there some morphological [not just microscopic] basis for spindle structure?"

Contra:

1. Invisible in vivo

Chambers, Gen Cyt

2. By micro dissection, pulling in half-spindle should cause chromosomes to move; fibers cannot be

pulled out of the spindle. He neglected, however, to fix the material in final configuration.

Lewis, MR Bull Johns Hopkins Hospital 34 1923 — 3 In fibroblast mitosis, acid conditions cause a reversible denaturation of the spindle.

Gregoire — 4. In a "very good" fixation, fibres do not appear. [Stain reactions may be a factor.]

Pro:

Cooper, (Schrader) — 1. In some coccid, aphid oEgytes they can be seen in spindle at metaphase, but these may be semi-morbid.

Bibl Anat Centrum 118 (1929) 437 — 2. a. In hypertonic media, spindles contract laterally, may bend. Shortening lines of force would not lead to a bending.

b. Spindles may be split, always longitudinal.

(The possibility of reversible coagulation must be considered).

? — ?? — c. Brownian movement within spindles is limited to the longitudinal direction.

But very few cells recover if treated at metaphase.

Schrader Biol Bull (1934) — Centrifugation banding; species variation.

Schultze Chromosoma 1939 — Perhaps the final word on the matter is the birefringence: in Echinoderm eggs.

Schmidt Cell Net 15 1940 — These deal with the ½ spindle component.

The interzonals persist after telophase, particularly in some Orthoptera, even for several divisions. Lines of force would not persist past the new nuclear wall. They stain somewhat differently. The interzonals are early

Emphasizes difference | distorted.
gebn, Fortschr. d. Zool 8 (1935) | Husichle has a fantastic theory of the persistence of spindle fibrillae.

12/2/42. Further required laboratory: plasmosomes in mitosis
3 Feulgen slides.
Further on spindles.