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 them that the axon is an outgrowth of the cyton, and the 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 (04), particularly vertebrates. All histologists now use it widely.

Review: Hirsch, G.C. Protoplasma Monographien 18 (1939). Form und Wechsel der Golgi Apparat. Complete bibliography, but biased text.

Kirkman + Severinghaus – Anat Rec 1938 uncritical

Jacobs Erg Biol II: 357 (1927)

Hirschler 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

Always ~~modified~~ ~~shock~~ 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

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

Pollister & JMS (1938) In Amphibia, they are fundamental circled 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 division 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 accoblastic homology of Golgi is thus far stressed.

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

Hirschler Golgi as closed vesicles; osmophobic interior.

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

1928 Parat Neutral red accumulates in vacuoles, superficially resembling plant "saccome". Osmiophilia 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 acroblast which secretes the acrosome in spermatogenesis. The acrosome however is still quite mysterious. The acroblast may be a single large cup, or a group of smaller ones.

1923 Nassonowa in pancreas, secretory granules grow for most part at osmiophilic surface.

Cowdry Gen Cytology

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

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

Mathews Biol Bull 62

Protoplasma 19

32

Plant homologues to Golgi

Bowen, Zeitschr. Zellf.	6:689	1928
Weier A.J.B.	29	
v. Dec Adv Anatomy Biol.		

Osmiophil platelets, believed by Kiyohara to be stages of plastids

Plastids may have lamellar structure, are osmiophile; participate in limoniphene production in bryophytes. But mitochondria, proplastids are also homologizible.

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, coonient. 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 finer relations.

Spindle, in ideal zoological form, amphiastral

✳ In many cases, appears anastral.

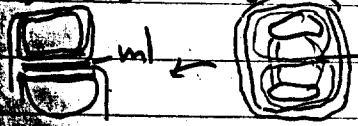
But the presence or absence of centrioles is not

so important as the existence of an astra or a fundamental festial configuration (chromosomes in plants).

Cell Walls (after Wilson)

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

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

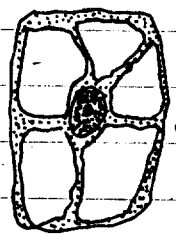


Sinnott & Bloch PNAS 26 (1940)

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 persists in the line of the cell plate.



← phragmosome. Orientation during prephase.

See Sharp.

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)	Mesocyclops, 31°	35	5	3	50
Zimmerman Z. Bot 15 (1923)	Spirogyra	10	7	4	9
Laughlin Cam 265	Allium	55	1	1	35
Belar Univ J Morph 69 (1941)	Drosophila	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.

Clark & Lumsdale, interphase

v. Shaw
Kellicott
Freesner
Stafelt ... 1921

Periodicity of Cell Division.
do not confuse with spawning periods; has nothing to do with egg laying in birds.
Complex of causes. 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 ultracentrifugation. ?

11/13/42 CYTOPLASMIC DIVISION

Analogies work in simple systems — Mechanisms [Analogy analysis mainly]
Cell is a very heterogeneous complex — 1. Surface Tension [Butschli, Quincke] If a small surface
See Wilson for diagrams — on an oil drop is in contact with soap solution, currents
Erlanger, Biol Centbl 17 (1897) — are established inside, which tend to divide the drop.
McClendon Arch Entwm 37 (1913) — Erlanger presumed analogous currents in the Rhabditis
Robertson Arch Entwm 35 (1913) — 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 insist; negative conclusion.

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.

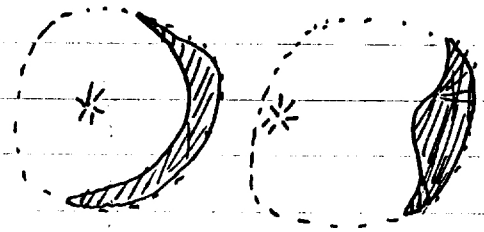
Just Am J Ph. 61 (1922) Echinarachnius (by hypotony) eggs burst at poles.

?? 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 monoastral 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 effect?

Forces of cytoplasmic movement.

Creation of normal eggs?

Pollister '41: canals are not real, but the diffusion stream current [org 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. Coagulation of cell surface. (Rejuvenation of elastic protoplasmic 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:)

11/12/42 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 Gerris, some cells continue to endomitoses as indicated by the multiplication of pycnotic X.

Induced by heteroauxin; Greenleaf

Astragalus Vilkomerson

Culex, Spinacia Berger.

(Drosophila)

c. Monasters in Echinoderm eggs, after Mechanical disturbance.

Wilson, Lillie

d. "Deleterious conditions" cause disappearance of spindle and aster. the chromosomes continue to divide. (to 128 ploidy).

Levan, Feldberg....

e. C-Mitosis

Does colchicine dissolve out spindles once formed? Yes??

This autonomous migration is very limited.

See Harvey 128 (anoxia)

Centers do not disappear under ether treatment; the 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 — Asters of like sign and chromosomes of the other sign. | But spindles occur without chromosomes.

where? — In many cases spindles form completely before break-down of nuclear membrane.

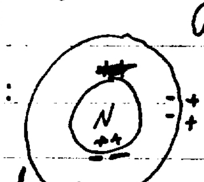
Hartog — 1 pole is more neutral than the other(s) in di and multipolars. | Only very small amounts of astral type figures.

Lillie, RS Am J Phys 15 1905 — More thorough electrical theory of mitosis. Electrical analogues.

J Morph 22 1911 — Cells with high chromatin content

Hardy, McClendon, etc. — cataphorese anodically

Churney & Klein Biol Bull 72 '37 — Supports charge on salivary chromosomes. (+)

Lillie see paper. In interphase:  "What initiates mitosis is a local increase in permeability at the poles, neutralizing the dipole. Then the negative cytoplasm develops line of force to the poles. The centers and chromosomes all have negative charges. At anaphase the charges reverse." The scheme has been adopted uncritically by various cytogeneticists.

Static or magnetic

Floating cork 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.

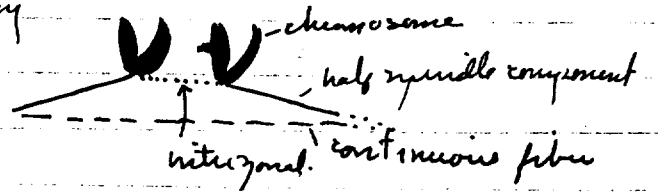
Morphology of the Amphiaster.

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 JMP 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.

Betsaïbli: transformation of cytoplasmic alveoli

Lillie, RS Polarization: orientation of long molecules.

Fauré 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 fibers! 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 aberrant spindles

If asters formed spindles, the asters would have to connect only with chromosmes

If there is an extra nuclear spindle, it consists only of 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, Nautococcus—) In late prophase

2. Zellf 13 (1931) the half spindle components are independent. Later

Compound fiber with delayed kinetochore? — These orient so that chromosomes are on a plane. These half spindle are intranuclear, clearly.

Thus, in Flavcida the chromosomes organize the half spindle components.

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

Ellenhorn 2.2ff 20 — The interzonal is the trail or track left in the nuclear matrix by the moving ~~interzonal~~ 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.

Interzonals Feulgen positive

In toto: Cleveland maintains a cytoplasmic spindle
Wada a nuclear origin

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

11/27/48 The Reality of Spindle Fibers.
Artifact opposition...
"Is there some morphological [not sub microscopic] basis for spindle structure?"
Contra:
1. Invisible in vivo
2. In microdissection, pulling in half-spindle should cause chromosomes to move; fibers cannot be — Chambers, Gen Cyt

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

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 oocytes they can be seen in spindle at metaphase, but these may be semi-morbid.

Biol Centrbl 118 437 (1929) Z — 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 bending; species variations.

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 easily

Emphasis Influence	destroyed.
Zeitschr. f. Zool 8 (1935)	Huseby has a fantastic theory of the persistence of spindle fibrillae.
12/2/42.	Further required laboratory: plasmomeres in mitosis 3 Feulgen slides. Further on spindles.