referred to at page 215, finds that after treatment with magnesium chloride unfertilized sea-urchin eggs (*Arbacia*) may give rise to perfect *Pluteus* larvæ — a result which if well founded seems to place the new formation of true centrosomes beyond question.

Taken together, these researches give strong ground for the conclusion that true (*i.e.* physiological) centrosomes may arise *de novo* from either the cytoplasmic or the nuclear substance and may play the usual *rôle* (whatever that may be) in mitosis. If this conclusion be sustained by future research, we shall no longer be able to accept Van Beneden's and Boveri's conception of the centrosome as a persistent organ in the same sense as the nucleus; but on the other hand we shall have gained important ground for further inquiry into the nature and source of that power of division which is so characteristic of living things and upon which the law of genetic continuity rests.

Morphology of the Centrosome. — In its simplest form (Fig. 152, *A*) the centrosome appears under the highest powers as nothing more than a single granule of extraordinary minuteness which stains intensely with iron-hæmatoxylin, and can scarcely be distinguished from the cyto-microsomes except for the fact that it lies at the focus of the astral rays. In this form it always appears at the centre of the very young sperm-asters during fertilization (Figs. 97, 99), in the early phases of ordinary mitosis (Figs. 27, 32), and in some cases also in the resting cell, for example, in leucocytes and connective tissue corpuscles (Figs. 8, 49), where, however, it is often triple or quadruple. In the course of division the centrosome often increases in size and assumes a more complex form, becoming also surrounded by various structures involved in the aster-formation. The relation of these structures to the centrosome itself has not yet been fully cleared up and there is still much divergence of opinion regarding the cycle of changes through which the centrosome passes. It is, therefore, not yet possible to give a very consistent account of the centrosome, still less to frame a satisfactory morphological definition of it.

It is convenient to take up as a starting-point Boveri's ('88) account of the centrosomes in the egg of *Ascaris*, supplemented by Brauer's ('93) description of those in the spermatocytes of the same animal. During the early prophases of the first cleavage Boveri found the centrosome as a minute granule which steadily enlarges as the spindle forms, until shortly before the metaphase it becomes a rather large, well-defined sphere in the centre of which a minute *central granule* or *centriole* appears (Fig. 152, *B*, *C*). From this time onward the centrosome decreases in size until in the daughter-cells it is again reduced to a small granule which divides into two and goes through a similar cycle during the second cleavage and so on. The centrosome is at all stages surrounded by a clear zone ("Heller Hof") in which the astral rays are thinner and stain less deeply than farther out. Brauer's account is substantially the same, though no definite "Heller Hof" was found, and the astral rays were traced directly in to the boundary of the centrosome. He added, however, two important observations, viz. (1) that the central granule is visible at every period; and (2) *division of the centrosome is preceded by division of the central granule* (Fig. 148) — an observation recently extended by Boveri to the division of the egg-centrosome.[1] Van Beneden and Neyt ('87), on the other hand, gave a quite different account of the

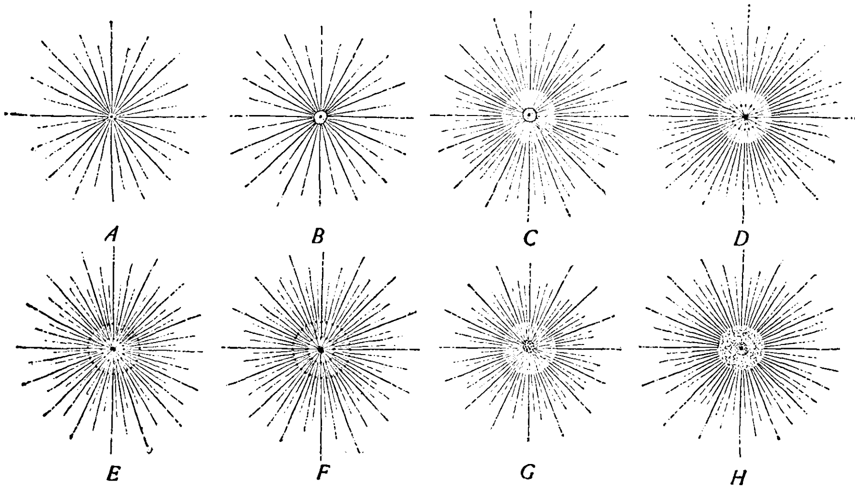

Fig. 152. — Diagrams illustrating various accounts of centrosome and aster.

A. Centrosome, a simple granule at the centre of the aster; *ex*. sperm-aster in various animals. *B*. "Centrosome," a sphere enclosing a central granule or centriole; *ex*. Brauer's account of spermatocytes of *Ascaris*. *C* Like the last, but "centrosome" surrounded by a "Heller Hof"; *ex*. Boveri's account of the centrosome of the *Ascaris* egg. *D*. Central granule surrounded by a radial sphere ("centrosome") bounded by a microsome-circle, and lying in a "Heller Hof"; *ex*. polar spindles of *Thysanozoön*, Van der Stricht. *E*. Central granule ("centrosome") surrounded by medullary and cortical radial zones, each bounded by a microsome-circle; *ex*. polar spindle of *Unio*, Lillie. *F*. Van Beneden's representation of aster of the *Ascaris* egg; like the last, but the "corpuscule central" consisting of a group of granules. *G*. "Centrosome," a group of granules surrounded by a "Heller Hof"; *ex*. the echinoderm-egg. *H*. "Centrosome" (central granule) surrounded by a vague larger body lying in a reticulated centrosphere; *ex*. *Thalassema*. [GRIFFIN.]

structures at the centre of the aster. The "corpuscule central" (usually assumed by later writers to be the centrosome), described as a "mass of granules," is surrounded by two well-defined astral zones, formed as modifications of the inner part of the aster, and constituting the "attraction-sphere." These are an inner "medullary zone," and an outer "cortical zone," each bounded by a very distinct layer of microsomes (Fig. 152, *F*).

[1] Reported by Fürst, '98, p. 111.

The discrepancy between these results on the part of the two pioneer investigators of the centrosome has led to great confusion in the terminology of the subject, which has not yet been fully cleared away. Many of the observers who followed Boveri (Flemming, Hermann, Van der Stricht, Heidenhain, etc.) found the centrosome, in various cells, as a much smaller body than he had described, often as a single or double minute granule, staining intensely with iron-hæmatoxylin. Heidenhain ('93, '94) and Drüner ('94, '95) found further that the asters in leucocytes and other forms often show several concentric circles of microsomes, and that the sphere bounded by the innermost circle often stains more deeply than the outer portions and may appear nearly or quite homogeneous (Fig. 156). To this sphere, with its contained central granule or granules Heidenhain applies the term *microcentrum* ('94, p. 463), while Kostanecki and Siedlecki suggest the term *microsphere* ('96, p. 217). Still later Kostanecki and Siedlecki ('97) found that even in *Ascaris*, as in other forms, sufficient extraction of the colour (iron-hæmatoxylin) reduces the centrosome to a minute granule to which the astral rays converge, and which is presumably identical with Boveri's "central granule." Heidenhain ('93, '94) found that in leucocytes the central granule is often double, triple, or even quadruple, while in giant-cells of certain kinds there are numerous deeply staining granules (Fig. 14). He therefore proposed to restrict the term *centrosome* to the individual granules, whatever be their number, applying the term *microcentrum* to the entire group ('94, p. 463).

With these facts in mind we can gain a clear view of the manner in which both the confusion of terminology and the contradiction of results has arisen. Brauer ('93) found in *Ascaris* (see above) that *division of the central granule precedes division of the "centrosome,"* and therefore suggested that only the former is equivalent to Van Beneden's "corpuscule central," while the body called "centrosome" by Boveri is really the medullary astral zone, the "Heller Hof" being the cortical zone. This is substantially the same conclusion reached by Heidenhain, Rawitz, Lenhossék, Kostanecki and Siedlecki, Erlanger, Van der Stricht, Lillie, and several others. The confusion of the subject is owing, on the one hand, to the fact that those who have accepted this conclusion continue to use the word *centrosome* in two quite different senses, on the other hand to the fact that the conclusion is itself repudiated by Boveri ('95), MacFarland ('97), and Fürst ('98).

As regards the terminology we find that most recent writers agree with Heidenhain, Kostanecki and Siedlecki, in restricting the word *centrosome* to the minute, deeply staining granules, whether one or more, at the centre of the aster. On the other hand, Brauer, Francotte, Van der Stricht, Meves, and others apply the term to the central granule or granules plus the surrounding sphere ("centrosome" of Boveri), which they regard as equivalent to the medullary zone of Van Beneden, the "corpuscule central" of the last-named author being identified with the central granule or "centriole" of Boveri, though the latter structure is considerably smaller than the former as described by Van Beneden.

The matter of fact turns largely on the question whether the astral rays traverse the larger sphere to the central granule. That such is the case in *Ascaris* is positively asserted by Kostanecki and Siedlecki, ('97) and as positively denied by Fürst ('98) with whose observations

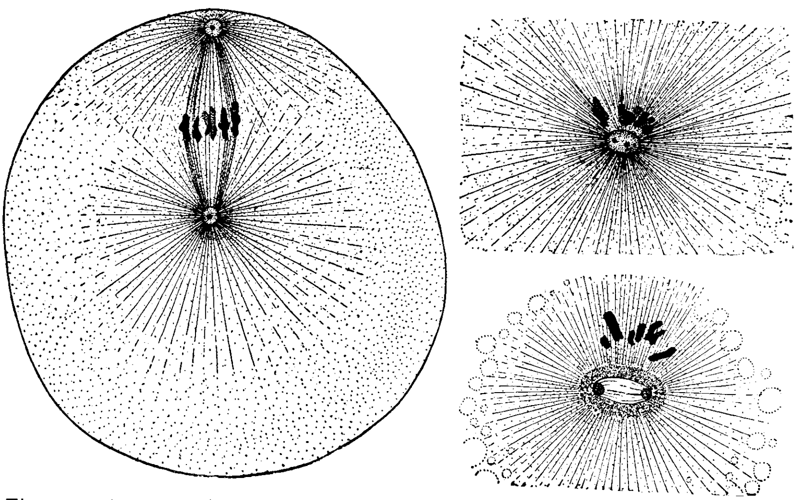

Fig. 153. — Structure of the centrosome in the polar asters of a gasteropod, *Diaulula*. [MACFARLAND.]

A. Mitotic figure, formation of first polar body. *B.* Inner aster at final anaphase; central granule double within the "centrosome." *C.* Elongation of old "centrosome" to form second polar spindle.

those of MacFarland ('97) on gasteropod-eggs agree. On the other hand, in the turbellarians the observations of Francotte ('97, '98) and Van der Stricht ('98, 1) seem to leave no doubt that the larger sphere ("centrosome"), here very sharply defined and staining deeply in iron-hæmatoxylin, is traversed by well-defined astral rays converging to the central corpuscle, and both these observers agree further that *both the corpuscle and the sphere divide to persist as the "centrosomes" of the daughter-cells* — a result in conformity with Van Beneden's conclusion in the case of *Ascaris*.

Lillie's valuable observations on the polar asters of *Unio* ('98) afford, I believe, conclusive evidence as to the nature of the sphere. In the earlier stages the aster has exactly the structure described by Van Beneden in *Ascaris*, except that the innermost body (*i.e.* the "corpuscule central") is a single minute granule. This is surrounded by typical medullary and cortical zones, through both of which the

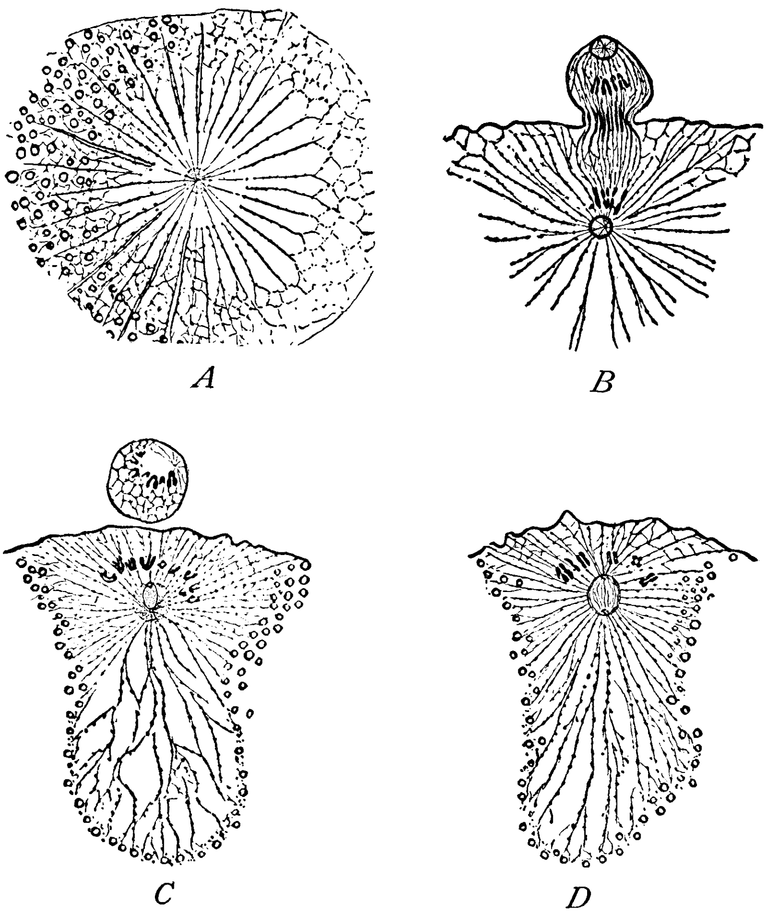

Fig. 154. — Centrosome and aster in the polar mitoses of *Unio*. [LILLIE.]

A. Aster of the first polar figure; central granule (centrosome) surrounded by medullary (entosphere) and cortical (ectosphere) zones. *B*. Late anaphase of second polar mitosis; radial entosphere bounded by continuous membrane. *C*. *D*. Prophases of second mitosis; formation of central spindle within and from the substance of the old entosphere.

rays pass (Fig. 152, *E*, Fig. 154). The inner sphere, consisting of a dense and deeply staining substance, has at first a typical radiate structure and is bounded by a microsome-circle. In later stages (late anaphase) the central granule divides into two and afterward into four or more granules, of which, however, only one or two actually persist. The inner sphere is now bounded by a definite membrane, and its radiate structure becomes obscure, the astral rays extending only to the boundary of the sphere, though a few rays persist within it (Fig. 154, *B*). It is clear from this that the inner sphere and central granule pass through phases that bridge the gap between Van Beneden's and Boveri's descriptions. Lillie's observations fully sustain the conclusion that the *central granule* (*"centriole" of Boveri*) *corresponds to the "corpuscule central" of Van Beneden, and the inner sphere* (*medullary zone*) *to Boveri's "centrosome."* A comparison of the polar aster of *Unio* with that of *Thysanozoön*, as described by Van der Stricht ('98), leaves hardly room for doubt that the cortical zone represents Boveri's "Heller Hof"; for in both forms the rays of the cortical zone are much thinner and lighter than the more peripheral portions, thus giving a clear zone, which in *Unio* is bounded by only a fairly definite microsome-circle and in *Thysanozoön* by none.

Lastly, we must recognize the justice of the view urged by Kostanecki, Griffin, Mead, Lillie, Coe, and others, that the term *centrosome* should be applied to the central granule and not to the sphere surrounding it (medullary zone), despite the fact that historically the word was first applied by Boveri to the latter structure. For in both *Diaulula* (MacFarland) and *Unio* (Lillie) the second polar spindle arises from the substance of the inner sphere, while the central granule, becoming double, gives rise to the centrosomes at its poles. By following Boveri's terminology, therefore, MacFarland is driven to the strange conclusion that the second polar spindle is nothing other than an enormously enlarged "centrosome" — a result little short of a *reductio ad absurdum* when we consider that in *Ascaris* the polar spindle arises by a direct transformation of the germinal vesicle (p. 277). The obvious interpretation is that the central granule is the only structure that should be called a centrosome, the surrounding sphere being a part of the aster, or rather of the attraction-sphere. Thus regarded, the origin of the spindle in *Diaulula* presents nothing anomalous and a similar interpretation may be placed on the polar spindles of *Ascaris* as described by Fürst ('98).[1]

[1] In echinoderms the concurrent results of Reinke ('95), Boveri ('95), myself ('96–'97), show that the "centrosome" is a well-defined sphere containing a large group (ten to twenty) of irregularly scattered, deeply staining granules. I have shown in this case that in the early prophases there is but one such granule, which then becomes double and finally multiple, forming a pluricorpuscular centrum (Fig. 52) not unlike that described by Heidenhain in giant-cells. Kostanecki, who asserts that the centrosome of echinoderms is a single granule ('96, 1, '96, 2, p. 248), has not sufficiently studied the later phases of mitosis. *Cf.* also Erlanger ('98). The centrosomes described in nerve cells by Lenhossék ('95) are apparently of somewhat similar type. Until the facts are more fully known the exact nature of these "centrosomes" remains an open question. Lillie's observations on *Unio* show that here, too (first polar spindle), the centrosome divides to form a considerable number of

The genesis of the concentric spheres surrounding the centrosome will be considered in the following section. We may here only emphasize the remarkable fact that the centres of the dividing system are bodies which are in many cases so small as to lie almost at the limits of microscopical vision, and which in the absence of the surrounding structures could not be distinguished from other protoplasmic granules. Full weight should be given to this fact in every estimate of the centrosome theory, and it is no less interesting in its bearing upon the corpuscular theory of protoplasm.

Watasé ('93, '94) made the very interesting suggestion that *the centrosome is itself nothing other than a microsome* of the same morphological nature as those of the astral rays and the general meshwork, differing from them only in size and in its peculiar powers.[1] Despite the vagueness of the word "microsome," which has no well-defined meaning, Watasé's suggestion is full of interest, indicating as it does that the centrosome is morphologically comparable to other elementary bodies existing in the cytoplasmic structure, and which, minute though they are, may have specific chemical and physiological properties.

An interesting hypothesis regarding the historical origin of centrosome is that of Bütschli ('91) and R. Hertwig ('92), who suggest that it may be a derivative of a body comparable with the micro-nucleus of Infusoria, which has lost its chromatin but retained the power of division; and the last-named author has suggested further that the so-called "archoplasmic loops" discovered by Platner in pulmonates may be remnants of the chromatic elements. A similar view has been advocated by Heidenhain ('93, '94) and Lauterborn ('96). Heidenhain regards central spindle and centrosomes as forming essentially a unit ("microcentrum") homologous with the micro-nucleus of the Infusoria, the centrodesmus (p. 79) representing a part of the original achromatic elements. The metazoan nucleus is compared to the protozoan macro-nucleus. The improbability of a direct derivation of the Metazoa from Infusoria, urged by Boveri ('95) and Hertwig ('96), has led Lauterborn ('96) to the view that the metazoan centrosome and nucleus are respectively derivatives of two equivalent nuclei, such as Schaudinn ('95) describes in *Amœba binucleata*, the "Nebenkörper" of *Paramœba* (*cf.* p. 94), being regarded as an intermediate step, and the micro-nucleus of Infusoria a side-branch. R. Hertwig ('96), on the other hand, regards the metazoön centrosome as a derivative of an intra-nuclear body such as the "nucleolo-centrosome" of *Euglena* (p. 91), which has itself arisen through a condensation of the general achromatic substance. With this view Calkins ('98), on the whole, agrees; but he regards it as probable that the "nucleolo-centrosome"

granules of which one or two remain as the persistent centrosome, while others are converted into microsomes or other cytoplasmic structures. It is probable that something similar occurs in the echinoderms.

[1] The microsome is conceived, if I understand Watasé rightly, not as a permanent morphological body, but as a temporary varicosity of the thread, which may lose its identity in the thread and reappear when the thread contracts. The centrosome is in like manner not a permanent organ like the nucleus, but a temporary body formed at the focus of the astral rays. Once formed, however, it may long persist even after disappearance of the aster, and serve as a centre of formation for a new aster.

of *Euglena* and *Amœba* and the sphere of *Noctiluca* and *Paramœba* are to be compared with the attraction-sphere, while the centrosome may have had a different origin.

It appears to me that none of these views rests upon a very substantial basis, and they must be taken rather as suggestions for further work than as well-grounded conclusions.

F. The Archoplasmic Structures

1. *Hypothesis of Fibrillar Persistence*

The asters and attraction-spheres have a special interest for the study of cell-organs; for they are structures that may divide and persist from cell to cell or may lose their identity and re-form in successive cell-generations, and we may here trace with the greatest clearness the origin of a cell-organ by differentiation out of the structural basis. Two sharply opposing views of these structures have been held, represented among the earlier observers on the one hand by Boveri, on the other by Bütschli, Klein, Van Beneden, and Carnoy. The latter observers held that the astral rays and spindle-fibres, and hence the attraction-sphere, arise through a morphological rearrangement of the preëxisting protoplasmic meshwork, under the influence of the centrosome. This view, which may be traced back to the early work of Fol ('73) and Auerbach ('74), was first clearly formulated by Bütschli ('76), who regarded the aster as the optical expression of a peculiar physico-chemical alteration of the protoplasm primarily caused by diffusion-currents converging to the central area of the aster.[1] An essentially similar view is maintained in Bütschli's recent great work on protoplasm,[2] the astral "rays" being regarded as nothing more than the meshes of an alveolar structure arranged radially about the centrosomes (Fig. 10, *B*). The fibrous appearance of the astral rays is an optical illusion, for they are not fibres, but flat lamellæ forming the walls of elongated closed chambers. This view has recently been urged, especially by Erlanger ('97, 4, etc.), who sees in all forms of asters and spindles nothing more than a modified alveolar structure.

The same general conception of the aster is adopted by most of those who accept the fibrillar or reticular theory of protoplasm, the astral rays and spindle-fibres being regarded as actual fibres forming part of the general network. One of the first to frame such a conception was Klein ('78), who regarded the aster as due to "a radial arrangement of what corresponds to the cell-substance," the latter

[1] For a very careful review of the early views on this subject, see Mark, *Limax*, 1881.

[2] '92, 2, pp. 158–169.

being described as having a fibrillar character.[1] The same view is advocated by Van Beneden in 1883. With Klein, Heitzman, and Frommann he accepted the view that the intra-nuclear and extra-nuclear networks were organically connected, and maintained that the spindle-fibres arose from both.[2] "The star-like rays of the asters are nothing but local differentiations of the protoplasmic network.[3] . . . In my opinion the appearance of the attraction-spheres, the polar corpuscle (centrosome), and the rays extending from it, including the achromatic fibrils of the spindle, are the result of the appearance in the egg-protoplasm of two centres of attraction comparable to two magnetic poles. This appearance leads to a regular arrangement of the reticulated protoplasmic fibrils and of the achromatic nuclear substance with relation to the centres, in the same way that a magnet produces the stellate arrangement of iron filings."[4]

This view is further developed in Van Beneden's second paper, published jointly with Neyt ('87). "The spindle is nothing but a differentiated portion of the asters."[5] The aster is a "radial structure of the cell-protoplasm, whence results the image designated by the name of aster."[6] The operations of cell-division are carried out through the "contractility of the fibrillæ of the cell-protoplasm and their arrangement in a kind of radial muscular system composed of antagonizing groups."[7]

An essentially similar view of the achromatic figure has been advocated by many later workers. Numerous observers, such as Rabl, Flemming, Carnoy, Watasé, Wilson, Reinke, etc., have observed that the astral fibres branch out peripherally into the general meshwork and become perfectly continuous with its meshes, and tracing the development of the aster, step by step, have concluded that the rays arise by a direct progressive modification of the pre-existing structure. The most extreme development of this view is contained in the works of Heidenhain ('93, '94), Bühler ('95), Kostanecki and Siedlecki ('97), which are, however, only a development of the ideas suggested by Rabl in a brief paper published several years before. Rabl ('89, 2) suggested that neither spindle-fibres nor astral rays really lose their identity in the resting cell, being only modified in form to constitute the mitome or filar substance (meshwork), but still being centred in the centrosome. Fission of the centrosome is followed by that of the latent spindle-fibres (forming the linin-network); hence each chromosome is connected by pairs of daughter-

[1] It is interesting to note that in the same place Klein anticipated the theory of fibrillar contractility, both the nuclear and the cytoplasmic reticulum being regarded as contractile (*l.c.*, p. 417).

[2] '83, p. 592. [3] '83, p. 576. [4] '83, p. 550. [5] '87, p. 263. [6] *l.c.*, p. 275. [7] *l.c.*, p. 280.

fibres with the respective centrosomes. Heidenhain, adopting the first of these assumptions, builds upon it an elaborate theory of cell-polarity and cell-division already considered in part at pages 103–105. Sometimes the astral rays ("organic radii") retain their radial arrangement throughout the life of the cell (leucocytes, Fig. 49); more commonly they are disguised and lost to view in the cytoplasmic meshwork. All, however, are equal in length and in tension — assumptions based on the one hand on the occurrence of concentric circles of microsomes in the aster, on the other hand on the analogy of the artificial model described at page 104. Bühler ('95) and Kostanecki and Siedlecki ('97) likewise unreservedly accept the view that besides the centrosome the entire system of "organic radii," including astral rays, mantle-fibres, and central spindle-fibres, persists in the resting cell in modified form, and is centred in the centrosome. Kostanecki finally ('97) takes the last step, logically necessitated by the foregoing conclusion, and apparently supported also by the crossing of the astral rays opposite the equator of the spindle and the relations of their peripheral ends, concluding that the monocentric astral system is converted into the dicentric system (amphiaster) by *longitudinal fission of the rays*.[1] Thus the entire mitome of the mother-cell divides into equal halves for daughter-cells; and since the radii consist of microsomes, each of these must likewise divide into two.[2]

Could this tempting hypothesis be established, Roux's interpretation of nuclear division (p. 224) could be extended also to the cytoplasm; and the aster- and amphiaster-formation, with the spireme-formation, might be conceived as a device for the meristic division of the entire cell-substance — a result which would place upon a substantial basis the general corpuscular theory of protoplasm. Unfortunately, however, the hypothesis rests upon a very insecure foundation: first, because it is based solely upon the fibrillar theory of protoplasm; second, because of the very incomplete direct evidence of such a splitting of the rays; third, because there is very strong evidence that in many cases the old astral rays wholly disappear, to be replaced by new ones.[3] We may best consider this adverse evidence in connection with a general account of the opposing archoplasm-hypothesis.

2. *The Archoplasm Hypothesis*

Entirely opposed to the foregoing conception are the views of Boveri and his followers, the starting point of which is given by

[1] '97, p. 680.

[2] This view had been definitely stated also by O. Schultze in 1890.

[3] There is, however, no doubt that the aster as a whole does, in some cases, divide into two — for instance, in the echinoderm-egg, Fig. 95.

Boveri's celebrated archoplasm-hypothesis. Boveri has from the first maintained that the amphiastral fibres are quite distinct from the general cell-meshwork. In his earlier papers he maintained ('88, 2) that the attraction-sphere of the resting cell is composed of a distinct substance, "*archoplasm*," consisting of granules or microsomes aggregated about the centrosome as the result of an attractive force exerted by the latter. From the material of the attraction-sphere arises the entire achromatic figure, including both the spindle-fibres and the astral rays, and these have nothing to do with the general reticulum of the cell. They grow out from the attraction-sphere into the reticulum as the roots of a plant grow into the soil, and at the close of mitosis are again withdrawn into the central mass, breaking up into granules meanwhile, so that each daughter-cell receives one-half of the entire archoplasmic material of the parent-cell. Boveri was further inclined to believe that the individual granules or archoplasmic microsomes were "independent structures, not the nodal points of a general network," and that the archoplasmic rays arose by the arrangement of these granules in rows without loss of their identity.[1] In a later paper on the sea-urchin this view underwent a considerable modification through the admission that the archoplasm may not preexist as formed material, but that the rays and fibres may be a new formation, crystallizing, as it were, out of the protoplasm about the centrosome as a centre, but having no organic relation with the general reticulum; though Boveri still held open the possibility that the archoplasm might preëxist in the form of a specific homogeneous substance distributed through the cell, though not ordinarily demonstrable by reagents.[2] In this form the archoplasm-theory approaches very nearly that of Strasburger, described below.

There are three orders of facts that tell in favour of Boveri's modified theory: first, the existence of persistent archoplasm-masses or attraction-spheres from which the amphiasters arise; second, the origin of amphiasters in alveolar protoplasm; and, third, the increasing number of accounts asserting the replacement of the old asters by others of quite new formation. In at least one case, namely, that of *Noctiluca*, the entire achromatic figure is formed from a permanent attraction-sphere lying outside the nucleus and perfectly distinct from the general cell-meshwork.[3] Other cases of this kind are very rare, and in most cases the attraction-sphere sooner or later disintegrates,[4] but in the formation of the spermatozoa we have many examples of archoplasmic masses (Nebenkern, attraction-sphere, idiozome), which apparently consist of a specific substance having a special relation to the achromatic figure.

[1] '88, 2, p. 80.
[2] '95, 2, p. 40.
[3] Ishikawa, '94, '98; Calkins, '98, 2.
[4] *Cf.* p. 323.

The amphiastral formation in alveolar protoplasm gives very clear evidence against the theory of fibrillar persistence. Here the fibrillar rays can be seen growing out through the walls of the alveoli[1] quite distinct from, though embedded in, them. At the close of mitosis every trace of the fibrillar formation may disappear, *e.g.* in echinoderm-eggs after formation of the polar bodies, the protoplasm retaining only a typical alveolar structure.

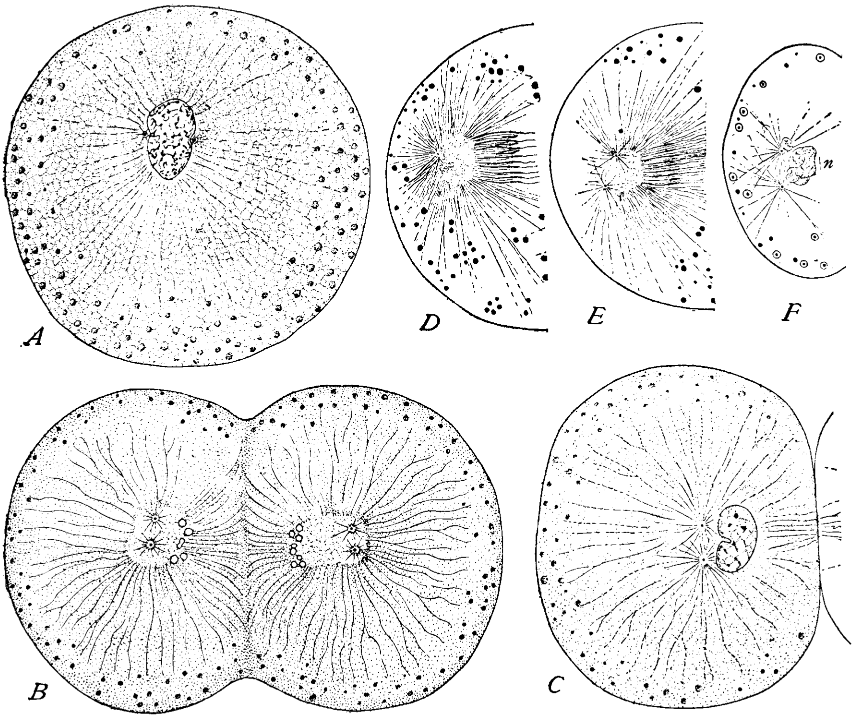

Fig. 155. — Stages in the first cleavage of the egg in *Cerebratulus* (*A–C*, COE) and *Thalassema* (*D–F*, GRIFFIN).

A. First appearance of the cleavage-centrosome at the poles of the fused germ-nuclei; cleavage-asters forming within the degenerating sperm-asters. *B*. Final anaphase of first cleavage, showing persistent centrosomes and new asters forming. *C*. Immediately after division. *D–F*. Three stages of the late anaphase in *Thalassema*, showing formation of new asters within the old. (*Cf.* Fig. 99.)

The strongest evidence against fibrillar persistence is, however, given by recent studies on mitosis, showing on the one hand that the new astral centres do not coincide with the old ones, on the other that the old rays degenerate *in situ*, to be replaced by new ones. Aside from many earlier observers, who believed the entire aster to disappear at the close of mitosis, the first to assert the wholly new

[1] *Cf.* Reinke ('95), Wilson ('99).

formation of the rays was Drüner, who maintained in the case of the mitosis of salamander testis-cells, that "not a single fibre of the astral system of the mother-cell is carried over unchanged into the organism of the daughter-cell" ('95, p. 309). The same conclusion was soon afterward supported by Braus ('95) in the case of the cleavage-mitoses of *Triton*. The most convincing evidence of this fact has been given by studies on the maturation and fertilization of the egg by Griffin ('96, '99), MacFarland ('97), Lillie ('99), and Coe ('99), all of whom find that the new astral centres, arising by division of the centrosome, move away from the old position, *to which, however, the old rays still converge while the new asters are independently forming* (Fig. 155). This is shown with especial clearness in the egg of *Cerebratulus* (Coe), where the peripheral portions of the old asters persist until the new amphiaster is completely formed. This observation seems conclusively to overturn Kostanecki's hypothesis of the persistence and division of the rays, and together with the work of MacFarland gives a very strong support to Boveri's later view.

It still remains an open question whether the rays actually arise from the substance of the centrosome, from a specific surrounding archoplasm, or by differentiation out of the general substance of the meshwork. The first of these possibilities has been urged in a very interesting way by Watasé ('94), who believes that the centrosome "spins out the cytoplasmic filaments" [1] of the spindle and aster, and that ordinary microsomes may in like manner spin out the fibrillæ of ordinary cytoplasmic networks.[2] This view is sustained by the mode of origin of the axial filament in the spermatozoa and that of the cilia in plant spermatozoids. It is, on the other hand, opposed by the almost infinitesimal bulk of the centrosome as compared with that of the aster that may form about it, and by the formation of the spindles in higher plants in the apparent absence of centrosomes. On the whole, the facts do not seem at present to warrant the acceptance of Watasé's ingenious hypothesis, and the most probable view is that of Drüner and Boveri, that the rays are differentiated out of the walls of the meshwork. In cases where the protoplasm is reticular or fibrillar the differentiation of the rays may be indistinguishable from a mere rearrangement of the thread-work; in alveolar protoplasm they may be seen as new formations, while in either case the material of the old aster may be more or less directly utilized in the building of the new. The feature common to all is the periodic activity either of the centre itself or of the surrounding protoplasm, and the coincidence or non-coincidence of the new aster with the old is apparently a secondary matter.

[1] *l.c.*, p. 283.

[2] See the same paper for a suggestive comparison of the astral fibrillæ to muscle-fibres.

In its original form the archoplasm hypothesis, as stated by Boveri, was developed with reference only to the material of the spindle-fibres and astral rays. Later writers have greatly extended the conception on the basis of Boveri's earlier view that archoplasm is a specific form of protoplasm, possessing specially active properties. Strasburger ('92–'98), whose views have already been considered in part, believes the protoplasm to consist of, or to show a tendency to differentiate itself into, two distinct substances, namely, a specially active fibrillar *kinoplasm* and a less active alveolar *trophoplasm*. The former gives rise to the mitotic fibrillæ, constitutes the peripheral cell layer, or *Hautschicht*, from which the membrane arises, forms the substance of the centrosomes, and gives origin to the contractile substance of cilia and flagella. The kinoplasm is thus mainly concerned with the motor phenomena of the cell, the trophoplasm with those of nutrition; and this physiological difference is morphologically expressed in the fact that the former has in general a fibrillar structure, the latter an alveolar. Beyond this the two forms of protoplasm show a difference of staining-reaction, the kinoplasmic fibrillæ staining deeply with gentian-violet and iron-hæmatoxylin, while the trophoplasm is but slightly stained.

Prenant ('98, '99) still further extends the hypothesis, adopting the view that the "ergastoplasmic" (Garnier) fibrillæ of gland-cells[1] are equivalent to the kinoplasmic or archoplasmic fibrillæ of the mitotic figure, and to the fibrillæ of nerve- and muscle-fibres as well. He is thus led to the conception of a dominating or "superior" cytoplasm (including "archoplasm," "kinoplasm," "ergastoplasm"), which arises by differentiation out of the general cytoplasm, plays the leading *rôle* in the elaboration of active cell-elements ("cytosomes"), such as mitotic, neural, and glandular fibrillæ, and finally, its *rôle* accomplished, may disappear. Under the same category with the foregoing structures are placed the centrosome, attraction-sphere, mid-body, idiozome, Nebenkern, and yolk-nucleus.

Such a generous expansion of the archoplasm-hypothesis brings it perilously near to a *reductio ad absurdum;* for the step is not a great one to the identification of the "superior protoplasm" with the active cell-substance in general, which would render the whole hypothesis superfluous. Physiologically, we can draw no definite line of demarcation between the more and the less active protoplasmic elements, and it may further be doubted whether such a boundary exists even between the latter and the metaplasmic substances.[2] It is further quite unjustifiable to infer physiological likeness from similarity in staining-reaction[3] or in fibrillar structure. For these reasons the hypothesis of "superior protoplasm" seems one of doubtful utility.

[1] *Cf.* the pancreas, p. 44. [2] *Cf.* p. 29. [3] *Cf.* p. 335.

In its more restricted form, however, the archoplasm or kinoplasm hypothesis is of high interest as indicating a common element in the origin and function of the mitotic fibrillæ, the centrosome and mid-body, and the contractile substances of cilia, flagella, and muscle-fibres. The main interest of the hypothesis seems to me to lie in the definite genetic relations that have been traced between the archoplasmic structures of successive cell-generations (as is most clearly shown in the phenomena of maturation and fertilization). It has been pointed out at various places in the preceding chapters[1] how many apparently contradictory phenomena in cell-division, fertilization, and related processes can be brought into relation with one another under the assumption of a specific substance, carried by the centrosome or less definitely localized, which gives the stimulus to division, which is concerned in the formation of the mitotic figure and of contractile elements, and which may be transmitted from cell to cell without loss of its specific character. There seems, however, to be clear evidence that such substance (or substances), if it exists, is not to be regarded as being necessarily a permanent constituent of the cell, but only as a phase, more or less persistent, in the general metabolic transformation of the cell-substance.[2]

3. *The Attraction-sphere*

As originally used by Van Beneden[3] the term *attraction-sphere* was applied (in *Ascaris*) to the central mass of the aster surrounding the "corpuscule central" and consisting of medullary and cortical zones, as already described (p. 310). The cortical zone is bounded by a distinct circle of microsomes from which the astral rays proceed; and at the close of cell-division the rays were stated to fade away, leaving only the attraction-sphere, which, like the centrosome, was regarded as a permanent cell-organ. Later researches have conclusively shown that the attraction-sphere cannot be regarded as a permanent organ, since in many cases it disintegrates and disappears. This occurs, for example, in the early prophases of mitosis in the testis-cells of the salamander,[4] where the sphere breaks up and scatters through the cell as the new amphiaster forms (Fig. 27). A very interesting case of this kind occurs in the cleavage of the ovum in *Crepidula*, as described by Conklin ('99). The spheres here persist for a considerable period after division (Fig. 192), but have no direct relation to those of the ensuing division, finally disappearing *in situ*. The new spheres are formed about the centrosomes, which Conklin believes to migrate out of the old spheres (somewhat as occurs in the spermatid, p. 167) to their new position. The interesting point here is that the old sphere

[1] *Cf.* pp. 111, 215. [2] *Cf.* p. 171. [3] '83, p. 548.
[4] Drüner, '95, Rawitz, '96, Meves, '96.

takes up such a position as to pass entirely into *one* of the grand-daughter-cells, while the new sphere-substance is equally distributed between them and in its turn passes into one of the cells of the ensuing division.[1]

In *Crepidula*, as in *Ascaris*, the attraction-sphere represents only the central part (centrosphere) of the aster. In some cases, however, *e.g.* in leucocytes, the entire aster may persist, and the term *attraction-sphere* has by some authors been applied to the whole structure. Later workers have proposed different terminologies, which are at present in a state of complete confusion. Fol ('91) proposed to call the centrosome the *astrocentre*, and the spherical mass surrounding it (attraction-sphere of Van Beneden) the *astrosphere*. Strasburger accepted the latter term but proposed the new word *centrosphere* for the astrosphere and the centrosome taken together.[2] A new complication was introduced by Boveri ('95), who applied the word "astrosphere" to the *entire aster* exclusive of the centrosome, in which sense the phrase "astral sphere" had been employed by Mark in 1881. The word "astrosphere" has therefore a double meaning and would better be abandoned in favour of Strasburger's convenient term *centrosphere*, which may be understood as equivalent to the "astrosphere" of Fol.

Besides these terms we have Heidenhain's *microcentrum* (p. 311), equivalent to the centrosome or group of centrosomes at the centre of the aster, with its surrounding sphere;[3] Kostanecki's and Siedlecki's *microsphere*, applied to the central region of the aster surrounding the centrosome whether bounded by a distinct microsome-circle or not;[4] Erlanger's *centroplasm*, equivalent to microsphere;[5] Ziegler's *ectosphere* and *entosphere*, applied to the cortical and medullary zones respectively; and Meves's *idiozome*, applied to the "attraction-sphere" of the spermatids.[6] This profusion of technical terms has arisen through the desire to avoid ambiguity in the use of the term "attraction-sphere," which, like the word "Nebenkern" (p. 163), has been applied to bodies of quite different origin and fate. If we adhere to Van Beneden's original use of the term it must be confined to the body surrounding the centrosome, forming a part of, or directly derived from, an aster, and giving rise wholly or in part to the succeeding aster. Meves ('96), Rawitz ('96), Erlanger ('97, 2), and others have, however, clearly shown that the "attraction-sphere" surrounding the centrosome (in testis-cells) may not only contain other material derived from the cytoplasm, *e.g.* the "centrodeutoplasm" of Erlanger, but may take no direct part in the succeeding aster-formation, disintegrating and scattering through the cell as the new aster forms (Fig. 27). In

1 *Cf.* p. 424.
2 '92, p. 5.
3 '94, p. 463.
4 '96, p. 217.
5 '96, 3, p. 8.
6 '97, 4, p. 315.

other cases a sphere closely simulating an attraction-sphere may arise in the cytoplasm without apparent relation to the centrosomes or to the preceding aster, *e.g.* the yolk-nucleus or the sphere from which the acrosome arises in mammalian spermatogenesis.[1] To call such structures "attraction-spheres" or "archoplasm-masses" is to beg an important question; and in all such doubtful cases the simple word *sphere* should be used.[2] In case of the aster itself we may, for descriptive purposes, employ Strasburger's convenient and non-committal term *centrosphere*, to designate in a somewhat vague and general way the central mass of the aster surrounding the centrosome, leaving its exact relation to Van Beneden's attraction-sphere to be determined in each individual case. Where the centrosphere shows two concentric zones (medullary and cortical), they may be well designated with Ziegler as *entosphere* ("centrosome" of Boveri) and *ectosphere*.

As regards the structure of the centrosphere, two well-marked types have been described. In one of these, described by Van Beneden in *Ascaris*, by Heidenhain in leucocytes, by Drüner and Braus in dividing cells of Amphibia, and by Francotte, Van der Stricht, Lillie, Kostanecki, and others, in various segmenting eggs, the centrosphere has a radiate structure, being traversed by rays which stretch between the centrosome and the peripheral microsome-circle (Fig. 152, *D*, *E*, *F*), when the latter exists. In the other form, described by Vejdovský in the eggs of *Rhynchelmis*, by Solger and Zimmermann in pigment-cells, by myself in *Nereis*, by Rückert in *Cyclops*, by Mead in *Chætopterus*, Griffin in *Thalassema*, Coe in *Cerebratulus*, Gardiner in *Polychœrus*, and many others, the centrosphere has a non-radial reticular or vesicular structure, in which the centrosomes lie (Figs. 152, *H*, 155). Kostanecki and others have endeavoured to show that such structures are artifacts, insisting that in perfectly fixed material the astral rays always traverse the centrosphere to the centrosome. This interpretation is, however, contradicted by the fact that the new asters developing in the centrospheres during the anaphases and telophases of such forms as *Thalassema* or *Cerebratulus* (Figs. 99, 155) show perfect fixation of the rays. The reticular centrosphere almost certainly arises as a normal differentiation of the interior of the aster, which, as Griffin ('96) has suggested, probably marks the beginning of the degeneration of the whole astral apparatus, to make way for the newly developing system.

The radial centrosphere is in *Ascaris* divided into cortical and medullary zones, as already described (p. 310), the aster being bounded by a distinct circle of microsomes. The true interpretation of these zones was given through Heidenhain's beautiful studies on the asters in leucocytes, and the still more thorough later work of Drüner on the sper-

[1] *Cf.* p. 170. [2] *Cf.* Lenhossék, '98.

matocyte-divisions of the salamander. In leucocytes (Fig. 49) the large persistent aster has at its centre a well-marked radial sphere bounded by a circle of microsomes, as described by Van Beneden, but without division into cortical and medullary zones. The astral rays, however, show indications of other circles of microsomes lying outside the centrosphere. Drüner found that a whole series of such concentric circles might exist (in the cell shown in Fig. 156 no less than nine), but that the innermost two are often especially distinct, so as to mark off a centrosphere composed of a medullary and a cortical zone precisely as described by Van Beneden. These observations show conclusively that the centrosphere of the radial type is merely the innermost portion of the aster, which acquires a boundary through the especial development of a ring of microsomes, or otherwise, and which often further acquires an intense staining-capacity so as to appear like a centrosome (p. 313). In *Thysanozoön* (Van der Stricht) only a single ring of microsomes exists, and this lies at the boundary between the medullary and cortical zones (Fig. 152, *D*), the latter differing from the outer region only in the greater delicacy of the rays and their lack of staining-capacity, thus producing a "Heller Hof." In other cases, no "microsome-circles" exist; but even here a clear zone often surrounds the centrosome (*e.g.* in *Physa*, *t.* Kostanecki and Wierzejski), like that seen in the cortical zone of *Thysanozoön*.

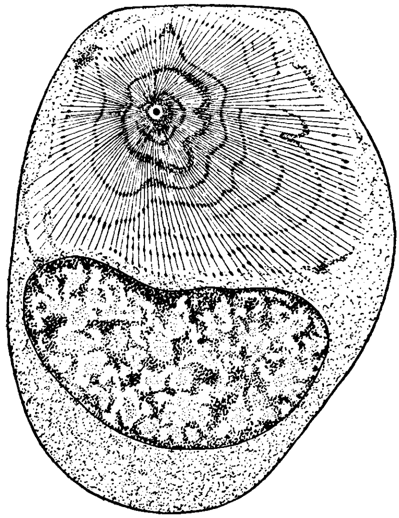

Fig. 156. — Spermatogonium of salamander. [DRÜNER.]

The nucleus lies below. Above is the enormous aster, the centrosome at its centre, its rays showing indications of nine concentric circles of microsomes. The area within the second circle probably represents the "attraction-sphere" of Van Beneden.

There are some observations indicating that the entosphere (medullary zone) may be directly derived from the centrosome (central granule). This is the conclusion reached by Lillie in the case of *Unio* referred to above, where, during the prophases of the second polar spindle, the central granule enlarges and breaks up into a group of granules from which the new entosphere is formed. Van der Stricht ('98) reaches a similar conclusion in case of the first polar spindle of *Thysanozoön*. We may perhaps give the same interpretation to the large pluricorpuscular centrum of echinoderms (p. 314). This observation may be used in support of the probability that the astral rays may be actually derived from the centrosome (p. 321); but Lillie finds in some cases that in the same mitosis the entosphere is formed by a different process, arising by a differentiation of the cytoplasm around the central granule. The former case, therefore, may be interpreted to mean simply that the centrosome may give rise to other cytoplasmic elements (as has already been shown in the formation of the spermatozoön, p. 172), the material of which may then contribute either directly or indirectly to the building of the aster; and the facts do not come into collision with the view that the astral rays are in general formed from the cytoplasmic substance.

G. Summary and Conclusion

A minute analysis of the various parts of the cell leads to the conclusion that all cell-organs, whether temporary or "permanent," are local differentiations of a common structural basis. Temporary organs, such as cilia or pseudopodia, are formed out of this basis, persist for a time, and finally merge their identity in the common basis again. Permanent organs, such as the nucleus or plastids, are constant areas in the same basis, which never are formed *de novo*, but arise by the division of preëxisting areas of the same kind. These two extremes are, however, connected by various intermediate gradations, examples of which are the contractile vacuoles of Protozoa, which belong to the category of temporary organs, yet in many cases are handed on from one cell to another by fission, and the attraction-spheres and asters, which may either persist from cell to cell or disappear and re-form about the centrosome. There is now considerable evidence that the centrosome itself may in some cases have the character of a permanent organ, in others may disappear and re-form like the asters.

The facts point toward the conclusion, which has been especially urged by De Vries and Wiesner, that the power of division, not only of the cell-organs, but also of the cell as a whole, may have its root in a like power on the part of more elementary masses or units of which the structural basis is itself built, *the degree of permanence in the cell-organs depending on the degree of cohesion manifested by these elementary bodies.* If such bodies exist, they must, however, in their primary form, lie beyond the present limits of the microscope, the visible structures arising by their enlargement or aggregation. The cell, therefore, cannot be regarded as a colony of "granules" or other gross morphological elements. The phenomena of cell-division show, however, that the dividing substance tends to differentiate itself into several orders of visible morphological aggregates, as is most clearly shown in the nuclear substance. Here the highest term is the plurivalent chromosome, the lowest the smallest visible dividing basichromatin-grains, while the intermediate terms are formed by the successive aggregation of these to form the chromatin-granules of which the dividing chromosomes consist. Whether any or all of these bodies are "individuals" is a question of words. The facts point, however, to the conclusion that at the bottom of the series there must be masses that cannot be further split up without loss of their characteristic properties, and which form the elementary morphological units of the nucleus.

In case of the cytoplasm the evidence is far less satisfactory. Could Rabl's theory of fibrillar persistence, as developed by Heidenhain and Kostanecki, be established, we should indeed have almost a demonstration of panmeristic division in the cytoplasm. At present, however, the facts do not admit the acceptance of that theory, and the division of the visible cytoplasmic granules must remain a quite open question. Yet we should remember that the dividing plastids of plant-cells are often very minute, and that in the centrosome we have a body, no larger in many cases than a "microsome," which is positively known to be in some cases a persistent morphological element, having the power of growth, division, and persistence in the daughter-cells. Probably these powers of the centrosome would never have been discovered were it not that its staining-capacity renders it conspicuous and its position at the focus of the astral rays isolates it for observation. When we consider the analogy between the centrosome and the basichromatin-grains, when we recall the evidence that the latter graduate into the oxychromatin-granules, and these in turn into the cytomicrosomes, we must admit that Brücke's cautious suggestion that the whole cell might be a congeries of self-propagating units of a lower order is sufficiently supported by fact to constitute a legitimate working hypothesis.

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