ULTRASTRUCTURAL ANALYSIS OF THE INITIATION AND DEVELOPMENT OF CYTASTERS IN SEA-URCHIN EGGS

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SUMMARY

Two approaches were used to study the origin and overall development of cytasters in relation to the emergence and maturation of new centrioles in sea-urchin eggs. A continuous hypertonic treatment was used to gather information on cytoplasmic areas of potential cytaster formation and the subsequent development of these cytastral areas. A two-step parthenogenetic stimulation procedure was used to analyse various cytastral changes during and after mitosis. Potential cytastral areas are associated with extensive Golgi complexes and astral formation occurs only about newly induced centrioles. The construction of a single aster involves a large redistribution of local cytoplasmic structures, concentrating some components, excluding others and orienting more and more microtubules in an increasingly focussed arrangement. These events are correlated with an extensive accumulation of astral endoplasmic reticulum, an increase in the size of the astral area, and a gradual acquisition of a more typical radial configuration. The astral shape becomes more pronounced during mitosis, after which the cytasters regress, but retain the mature centrioles. The data reveal that cytaster formation is initiated after the activation and appearance of centriolar precursor bodies, and that both centrioles and associated cytasters are complementary structures, which develop in unison. The results suggest that developing centrioles, from the moment of their emergence, control and direct the events of cytastral formation.

INTRODUCTION

The phenomena of artificial parthenogenesis and cytaster formation have been of interest to embryologists for nearly a hundred years (Wilson, 1911; Morgan, 1927; Tyler, 1941; Dirksen, 1961; Kallenbach, 1982a). First described by Morgan (1896, 1899, 1900) and Wilson (1901), cytasters were found to be readily induced in a variety of organisms by numerous parthenogenetic procedures (Harvey, 1910; Loeb, 1913; Harvey, 1956; Kallenbach, 1983a). Cytasters can form in both unfertilized and fertilized eggs, as well as in nucleated and enucleated egg fragments (Morgan, 1899; Fry, 1932; Harvey, 1936, 1938). Scattered throughout the cytoplasm, the asters are frequently present in great numbers, a feature determined essentially by both the type and the timing of the parthenogenetic treatment. Initially detectable as what have been termed clear areas at the light-microscopic level, cytasters become very conspicuous features of eggs at the time of mitosis. The asters are independent structures, some forming near the nucleus while others form away from the perinuclear zone; at mitosis, the cytasters at the nucleus behave as active mitotic poles, while the others remain unassociated with the cleavage figure (Wilson,
1925). Since cytasters typically interfere with normal mitosis, causing irregular cleaving and multiple furrowing, they are considered to be functionally equivalent to regular mitotic asters (Mazia, 1978).

Though early cytologists gave excellent descriptions of cytasters, specific details about the structure and formation of these asters could not be discerned until the advent of electron microscopy (EM). The EM studies could detect no significant differences in ultrastructural make-up between cytasters and typical cleavage asters seen in normally fertilized eggs (Dirksen, 1961, 1964; Van Assel & Brachet, 1966; Miki-Noumura, 1977). These fine-structural studies of mature cytasters have revealed a normal organization of astral components, such as microtubules and vesicles. Furthermore, centrioles have also consistently been seen in cytasters (Dirksen, 1961; Kato & Sugiyama, 1971; Miki-Noumura, 1977; Kallenbach, 1982a, 1983a; Kuriyama & Borisy, 1983), indicating that centrioles are a regular feature of parthenogenetically induced asters. Such asters have not yet been ultrastructurally described from their inception during the parthenogenetic procedure, and this paper will deal with their origin, maturation and cycling in response to the cycling cells of the parthenogenetic embryos. Various aspects relating to the origin and differentiation of induced centrioles, without which the cytasters would not form, have already been reported in detail (Kallenbach, 1982b, 1983a; Kallenbach & Mazia, 1982), and the fine-structural data will be presented here as an overview, describing the development and growth of cytasters in toto in relation to associated centrioles.

**Materials and Methods**

**Continuous hypertonic treatment**

Eggs of the species, *Strongylocentrotus purpuratus*, were shed in accordance with normal sea-urchin procedures and placed directly in hypertonic seawater at 17°C. The details of this particular procedure have already been reported (Kallenbach & Mazia, 1982). Eggs were periodically removed from the hypertonic solution and immediately put into a fixative and processed for electron microscopy.

**Two-step parthenogenetic procedure**

*Lytechinus pictus.* Standard procedures were used to spawn and handle these sea-urchin eggs. Eggs were dejellied by passing eggs through bolting silk. Eggs were chemically activated by immersion in ammoniacal seawater at pH 9.1 to 9.3 for 20 min, during which they entered the cell cycle (Mazia, 1974; Mazia & Ruby, 1974; Paweletz & Mazia, 1979). Following a rinse with regular seawater, the eggs were parthenogenetically stimulated by exposure to deuterated (2H₂O) seawater at pH 8.1 for 40 min. 2H₂O–seawater was prepared by substituting 55% of the H₂O with 2H₂O when making up artificial seawater (Mazia, 1977, 1978). Eggs were then washed and cultured in seawater at 21°C.

*Strongylocentrotus purpuratus.* Following shedding, eggs were dejellied and treated with 2–5 mM-dithiothreitol in seawater raised to pH 9.1 with Na₂CO₃ to remove the vitelline layer (Epel, Weaver & Mazia, 1970) in preparation for ease of cytaster isolation from the eggs. Eggs were activated in a 1 mM-urea solution containing 0.1 mM-CaCl₂ for 6 min. This procedure is as effective as NH₄OH–seawater in chemically activating eggs of this species. After activation, eggs were rinsed and kept in artificial seawater containing only 0.1 mM-Ca₂⁺ for 12 min. Eggs were then parthenogenetically activated with hypertonic seawater prepared by adding 32 ml of 2.5 M-NaCl to
100 ml of artificial seawater containing only 0.1 mM Ca\(^{2+}\); pH was adjusted to 8.9 with NaHCO\(_3\). After 45 min, eggs were rinsed and cultured in low-Ca\(^{2+}\) seawater at pH 8.2 and at 17°C. Cytasters were isolated from these eggs at 3 h with an aster isolation medium (Mazia, Paweletz, Sluder & Finze, 1981) and prepared for electron microscopy (Kallenbach, 1983a).

**Electron microscopy**

Eggs of *S. purpuratus* during the continuous hypertonic treatment and eggs of *L. pictus* following the pathogenetic procedure were periodically sampled and immediately fixed in the standard fixative that has been used for these eggs: 1% OsO\(_4\) in 0.1 M sodium acetate buffer at pH 6.1 (Harris, 1962) for 1–1.5 h. This fixation procedure has proved excellent for the overall preservation of cell structure in these eggs and is distinctly superior to fixation in seawater or seawater at high pH; the low pH of the osmium fixative is crucial to the preservation of microtubules (Harris, 1978a). Eggs were then dehydrated with acetone and embedded in Spurr’s embedding medium; sections were stained with 4% aqueous acetate for 10 min followed by lead citrate for 10 min, and observed with a Philips 200 electron microscope.

**RESULTS**

**Cytaster formation in continuously exposed eggs**

Mature sea-urchin eggs typically exhibit a relatively uniform distribution of organelles and cytoplasmic inclusions between the cortex and the nucleus, and reveal no cytoplasmic areas that can really be identified as presumptive cytasters. After 30 min of exposure to the hypertonic stress, a variety of intracellular modifications have taken place (Kallenbach, Paweletz & Finze, 1983), some of which indicate regions of probable cytaster formation. The formation of endoplasmic reticulum (ER) whorls is one such modification. These temporary formations of the ER are frequently associated with early astral areas and are often a direct source of membranes for enlarging cytastral areas. Another modification of the cytoplasm that is perhaps even more indicative of areas of potential cytaster appearance are aggregations of Golgi bodies. These are sometimes located near endoplasmic reticulum whorls (Kallenbach, 1981) and are often situated adjacent to areas of cytoplasm that are less densely populated with large organelles (Fig. 1). These areas frequently contain annulate lamellae and heavy bodies, both of which have been shown to be loci for newly appearing centriolar precursor bodies (Kallenbach, 1982b).

After 60 min in the hypertonic seawater eggs have entered the cell cycle, proof of which was given in a previous paper (Kallenbach & Mazia, 1982). The cytoplasm of eggs begins to exhibit a general spottiness, which at the ultrastructural level is seen to be due to the presence of many small nascent cytasters. These developing cytastral areas are scattered throughout the cytoplasm and are characteristically different from the rest of the cytoplasm in terms of composition, number and distribution of organelles and cytoplasmic inclusions (Fig. 2). The one unique feature that unmistakably identifies these areas as nascent cytasters is the presence of centriolar precursor bodies (Fig. 3). As reported before, these osmiophilic bodies are initially associated with either annulate lamellae or heavy bodies during cytastral formation (Kallenbach, 1982b).
As the cytastral areas continue to enlarge following egg activation, they gradually take on more distinctive aster-like characteristics. Fig. 4 depicts an example of an early cytaster in a 24-h egg, revealing an area composed primarily of endoplasmic reticulum elements and microtubules, and excluding many of the larger organelles. These areas typically contain developing centrioles, which now often appear as relatively compact dense bodies (Fig. 5). The larger osmiophilic masses, which

Fig. 1. A presumptive cytastral area in the cytoplasm of a sea-urchin egg exposed for 30 min to a hypertonic solution. The area is presumptive not only because of the presence of a large aggregation of Golgi bodies (G), but also by the presence of heavy bodies (arrows), with which 'de novo' centrioles in the form of osmiophilic precursor bodies are known to appear. ×18 000.

Fig. 2. An early cytastral area in a 1-h hypertonic-exposed egg. These areas form around the time of egg activation and always contain centriolar precursor bodies (cp). The area is beginning to look distinctive from the rest of the cytoplasm by the redistribution of its organelles and cytoplasmic inclusions. The centriolar precursor bodies are typically associated with either annulate lamellae or heavy bodies (h), as well as with Golgi bodies (G). ×22 500.

Fig. 3. A relatively more-developed early cytastral area in a 1-h hypertonic-exposed egg than the one in Fig. 2. The area exhibits microtubules (arrowheads) and a large concentration of ER. Larger cytoplasmic particles, such as yolk bodies (y), are in the process of being displaced toward to the peripheral zones of the astral area. Centriolar precursor bodies (cp) are always detectable and are beginning to become somewhat more removed from associated annulate lamellae or heavy bodies (arrows). ×17 000.
The development of cytasters

Figs 2 and 3
The development of cytasters

The development of cytasters, can also still be observed, but these generally tend to be associated with smaller, less-developed aster-like areas. Cytastral areas take on variable shapes, something that appears to be related to the number of nascent centrioles present. Those areas with single centriolar precursor bodies are often spherical, whereas those with more than one nascent centriole tend to be elongated or oddly shaped.

In cases where single centrioles are developing they gradually become more centrally positioned within asters, as these develop (Fig. 6). These astral structures at 3±h are often of substantial size and are readily detectable with the light microscope as distinct clear areas and display considerable birefringence when viewed under a polarization microscope (Kallenbach, 1982a). Organelles such as yolk and lipid bodies, Golgi, mitochondria and heavy bodies are now mostly excluded from the astral zone, which is essentially composed of only ER membranes and microtubules. A large population is in fact present, and many of the microtubules can be observed to traverse long distances from the central to the peripheral region of an aster. These asters do not develop at exactly the same rate, but the more developed cytasters at 3±h now frequently reveal mature centrioles. The presence of mature centrioles is correlated with asters that have acquired a more typical astral configuration. This configuration is caused primarily by an increased radial arrangement of microtubules, as well as a certain degree of radially taken on by some annulate and ER lamellae (Fig. 7).

The degree of radial orientation of astral elements increases, so that by 6h all eggs display very conspicuous cytasters. These asters become slightly more pronounced but basically show few additional changes even after 8h of hypertonic treatment (Fig. 8). The microtubules have become radially directed, originating at the centrosphere and ending at the astral terminus. Radially oriented annulate and ER lamellae are generally confined to the peripheral regions of asters. The cytasters all reveal centrosphere-like areas, which are essentially microtubule-free and in which both centrioles and diplosomes are located (Kallenbach, 1982a). After 6h the eggs

Fig. 4. An extensive developing cytastral area located next to the cortex in a 2±h hypertonically exposed egg. This area can be considered a clear area, in that it is mostly composed of ER with the majority of large cytoplasmic particles excluded from the central astral zone. Whereas this particular thin-section does not reveal any nascent centrioles, it does exhibit a sizeable population of microtubules throughout the astral area (arrowheads). ×14000.

Fig. 5. A large clear area in a 2±h treated egg displaying evidence of at least two developing centrioles (arrows). This time-point reveals neither very well-developed cytasters nor mature centrioles. The larger developing cytastral areas typically exhibit nascent centrioles more developed than those in less-differentiated clear areas. A large population of microtubules is in evidence (arrowheads), many of which extend for long distances. The small, dark-staining granules are unique to developing cytastral areas within constantly hypertonically stressed eggs; they are not related to pericentriolar material and appear to be a condensation product from disrupted pore complexes from both annulate lamellae and heavy bodies (authors' unpublished data). ×14750.
The development of cytasters

Fig. 8. A well-developed cytaster in an 8-h hypertonic-treated egg. The area is now completely clear of any large particles and displays a high degree of radiality. There is evidence of much radially directed membrane material, most of which is located in the outer astral zone, and an astral array of both single and bundles of microtubules originating from the centrosphere-like area (cs), which contains the centrioles. ×14750.

are held in early prophase, from which they cannot continue in mitosis since the hypertonic stress prevents the breakdown of the nuclear envelope.

Cytaster formation in two-step parthenogenetically treated eggs

Aspects of both cytastral and centriolar development in eggs treated with two-step parthenogenetic procedures have already been discussed (Kallenbach, 1983a). With

Fig. 6. Image of a cytastral area displaying some degree of radiality about a developing centriole (c) closely associated with pericentriolar material. The central astral zone in this 3½-h stressed egg is free of any large cytoplasmic particles and reveals that many microtubules originate with the pericentriolar material. ×22500.

Fig. 7. A cytaster in a 3½-h exposed egg displaying a larger degree of radial configuration than the aster in Fig. 6. Though some organelles seem to linger within the astral area, the majority of large organelles have become repositioned toward the aster periphery. The more developed cytasters at this time now exhibit mature centrioles (c), which are centrally located and serve as distinct focal points for the astral radiations. Annulate lamellae at this time also become radially positioned, seemingly in response to the greater degree of radiality acquired by the microtubular array upon centriolar maturation. ×12300.
the exception that the cytasters and centrioles develop more rapidly in these eggs, due to their return to normal seawater, no significant differences could be ascertained in the maturation of asters in these eggs, as compared to those in constantly stressed eggs. The eggs are generally loaded with cytasters at the time of nuclear envelope breakdown (Mazia, 1977), which occurs between 2 and 3 h after the start of treatment. Those asters that are part of the multipolar mitotic apparatus are nearly identical to cytasters elsewhere in the cytoplasm except that they are actively involved in mitosis (Fig. 9). All asters reveal centrioles within their centres, from which the radiating microtubules emanate. Radiating ER lamellae are also observed, but annulate lamellae are not detectable, supporting other reports that they are absent during mitosis. An analysis of thin sections through compacted cytasters isolated from eggs at 3 h (Kallenbach, 1983a) revealed that many asters possessed more than one centriole (Fig. 10).

Immediately following mitosis, cytasters begin to lose their distinct radial configurations, gradually reverting back to small astral areas similar to those seen at earlier times. The loss of radially oriented microtubules accompanies a substantial
The development of cytasters

Fig. 10. View of a central region of an isolated cytaster showing the presence of two centrioles. This aster, isolated from an S. purpuratus egg 3 h after the start of the two-step parthenogenetic treatment, was not yet in mitosis, since centrioles typically move closer together within the centrosphere at the time of mitosis. Astral microtubules are directly associated with the centrioles, something that is not unusual in isolated asters, but is not usually seen in developed asters in vivo. \( \times 11500 \).

decrease in the number of astral microtubules. This is followed by normally excluded organelles and cytoplasmic inclusions gradually re-entering the peripheral astral areas. Mitochondria, because of their relatively small size, are some of the first organelles to enter the dissipating cytasters (Fig. 11). With the dispersion of astral ER and the encroachment of the larger organelles, the cytastral areas diminish considerably in size, losing most of their characteristic astral features. However, the centrioles that originated during the parthenogenetic treatment remain, staying confined to the central region of the small, interphase astral areas (Fig. 12). These areas begin to enlarge again as the eggs prepare for the next mitosis, but this time the pattern of astral growth is more similar to that seen in normal asters.

DISCUSSION

The main object of this work was to examine the origin and development of cytasters in relation to the emergence and maturation of induced centrioles. These related events are readily studied in eggs continually exposed to a hypertonic stress, since this particular parthenogenetic procedure produces a gradual development of all cytastral activities (Kallenbach, 1982a; Kallenbach & Mazia, 1982). Distinctive intracellular changes induced by this procedure (Kallenbach et al. 1983) also allow the identification of presumptive astral areas in the cytoplasm, whereas two-step
Figs 11 and 12
The development of cytasters

treated eggs reveal no evidence of any potential cytasters before the actual parthenogenetic step. Areas destined to become cytasters quickly begin to rearrange and reorganize their cytoplasmic components. The earliest cytasters detectable are small irregularly shaped areas distinctly different from adjacent regions of cytoplasm. These areas are unique in that they contain centriolar precursor bodies, which are typically associated with either annulate lamellae or heavy bodies (Kallenbach, 1982b) at this stage. A small population of microtubules originating with the nascent centrioles is also evident in these early astral areas (Kallenbach, 1982b; Kallenbach & Mazia, 1982). Since nascent centrioles can be clearly detected in potential cytastral areas even before any other astral features are apparent, the data indicate that centrioles in their precursor forms are the first cytastral structures to appear during the parthenogenetic treatment. This supports the hypothesis that parthenogenetic procedures induce the appearance of cytasters only through the activation and formation of latent egg centrioles (Kallenbach, 1983a).

The subsequent differentiation and enlargement of the small astral areas into fully mature cytasters occurs in a closely coordinated and integrated fashion. As greater amounts of ER accumulate, some of which are derived from adjacent ER whorls in the case of constantly stressed eggs (Kallenbach, 1984), longer microtubules and larger numbers can be seen within the clear areas. This is directly correlated with both the continued expulsion of large organelles and the steady increase in size of the astral areas. As development continues, greater numbers of microtubules become more radially oriented. All these events correspond well with those observed during the formation of other asters (Luykx, 1970; Nicklas, 1971; Little et al. 1977; Paweletz, 1978; Paweletz & Finze, 1981). An important feature of cytastral growth is the continuous link that exists between cytaster development and centriole formation. This was also observed during cytaster formation in two-step parthenogenetically treated eggs (Kallenbach, 1983a). In both instances, the small, aster-like areas are associated only with early centriolar precursor bodies, whereas the more developed astral areas typically are associated with procentriole-like and procentriolar forms. Cytasters do not begin to acquire a pronounced radial configuration until the parthenogenetic centrioles have reached mature forms, details of which have already been described by this author. The findings thus reveal a closely coordinated set of intracellular events during the formation of cytasters.

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Fig. 11. An example of a cytaster observed immediately after mitosis in an L. pictus egg parthenogenetically stimulated with $^2$H$_2$O. The aster reveals a smaller population of microtubules than seen in asters during mitosis, though it still contains a substantial amount of astral ER. Normally excluded organelles are re-entering the astral area, and mitochondria appear to be some of the first organelles to come back into the aster. The centrioles (c), though still confined to the astral centre, appear to be more free to move after the dissolution of the centrosphere following mitosis. ×9500.

Fig. 12. View of a cytastral area seen after mitosis in a two-step parthenogenetically treated L. pictus egg. The area exhibits few microtubules, a small population of astral ER, and a considerable loss of astral shape and size. Further loss of astral ER results in the formation of small astral areas containing few microtubules and the de novo centrioles (c). Which become a permanent part of the cytoplasm. ×11 500.
which are confined to separate and distinct areas of cytoplasm and occur exclusively about developing centrioles.

As eggs enter mitosis, all cytasters rapidly attain full maturity. They become very conspicuous radial structures with microtubules originating from now relatively well-defined centrospheres. The ultrastructure of these mature asters corresponds to that of cytasters reported elsewhere (Dirksen, 1961, 1964; Kato & Sugiyama, 1971; Miki-Noumura, 1977; Kuriyama & Borisy, 1983). Cytasters are independent structures and only those located at the nucleus become actively involved in multipolar mitotic figures, as light-microscopic images have regularly depicted (Wilson, 1925). Following mitosis, asters lose their radial forms and rapidly diminish in size, irrespective of cytokinetic events. Whereas the cytasters regress back to small, interphase-like asters, the centrioles retain their mature form and appear to become permanent additions to the cytoplasm. Some centrioles in the continually treated eggs are able to replicate during the 8 h of hypertonic stress (Kallenbach, 1982a), but centrioles in two-step treated eggs do not form diplosomes until after the first division (unpublished observations). Duplication and movement of asters following mitosis, as noted by various investigators (Wilson, 1925; Dalcq, 1931; Fankhauser, 1934; Harvey, 1936, 1940; Lorch, 1952; Lorch, Danielli & Harstadius, 1953), were not studied here. Renewed astral enlargement is not seen until eggs re-enter the next mitosis and occurs, as expected, only about the centrioles.

Thus, cytastral events, as observed over a period of two mitotic cycles, reveal links to the cell cycle to varying degrees. The second cycle displays events more similar to those observed in normal mitotic eggs (Schmekel, 1975): small asters are maintained during interphase and large astral structures are generated only at the time of mitosis. In contrast, events of the first cycle reveal the development of large mitotic asters during interphase, attaining full maturity only after eggs have entered mitosis. These differences in astral behaviour appear to be related to the presence of mature centrioles. With centrioles present, cytasters behave more like normal asters, fluctuating in accordance with regular cell cycle events. Artificial induction of centrioles and cytasters during the first cycle seems temporarily to over-ride normal cell-cycle controls that inhibit mitotic aster formation during interphase. However, those controls over the asters are soon re-established at the time of mitosis.

In addition to a general control by the egg as a whole over cytastral formation, the simultaneous occurrence of many separate cytastral events implies additional controls at more local cytoplasmic levels. As with all asters, independent cytastral events must include an alteration in the local ionic environment suitable for microtubule polymerization (Stephens & Edds, 1976; Raff, 1979), a systematic accumulation of astral ER for the regulation of Ca\(^{2+}\) concentration (Harris, 1975, 1978b; Hepler, 1977, 1980; Moll & Paweletz, 1980; Pawaletz & Finze, 1981; Kallenbach, 1984), and continuous importing and distribution within the astral area of a variety of chemicals and molecules required for constant astral growth. Whereas these events normally occur within two astral areas only, in parthenogenetic eggs these complex and well-coordinated sets of events occur within numerous distinct
The development of cytasters

astral areas, each of which develops totally independently. The growth of asters about already-present mature centrioles, as seen in fertilized eggs (Kurosumi, 1958; Gross, Philpott & Nass, 1958; Harris, 1961, 1962) and in parthenogenetic eggs after the first cell cycle, provides evidence suggesting that centrioles exert a considerable influence over astral events. In parthenogenetically activated eggs, where numerous cytastral structures assemble, radiate and expand only about sites where new centrioles are being constructed, there are strong indications suggesting that the developing centrioles are the local controlling entities, coordinating and directing the activities of surrounding astral events.

Local cytoplasmic control by induced centrioles is more clearly apparent in cases where cytasters form in either enucleated eggs or egg fragments (Yatsu, 1905; Harvey, 1936, 1938; Kato & Sugiyama, 1971), ruling out any control or participation by the nucleus. Observations on astral formation induced by artificially injected centrioles (see Raff, 1979) also provide a clear illustration, even more than the usual case of the construction of mitotic asters about already-present mature centrioles, of centriole control and direction over astral growth. The injected centrioles definitely appear to play some active role in the restructuring of their surrounding cytoplasm, seeming to coordinate all aspects of astral formation, including the organization of the pericentriolar material that possesses microtubule-organizing centre (MTOC) activity (Borisy & Gould, 1977; Endo, 1979; Peterson & Berns, 1980; De Brabander, 1982). Such control over the pericentriolar material and centrosphere has been suggested before (Weisenberg & Rosenfeld, 1975; Gould & Borisy, 1977; Heidemann, Sander & Kirschner, 1977; Galareo-Gillam et al. 1983) and is most likely to be located with the RNA that is within the centrioles (Peterson & Berns, 1980; Wheatley, 1982). This RNA has been shown to be involved in both centriolar replication and aster formation (McGill, Highfield, Monahan & Brinkley, 1976; Snyder & McIntosh, 1976; Zackroff, Rosenfeld & Weisenberg, 1976; Heidemann et al. 1977; Pepper, 1979). The existence of centriolar RNA corresponds to the recent discovery of ribosome-like granules in centrioles (Kallenbach, 1983b; Kallenbach, unpublished). These granules have been interpreted to be centriolar ribosomes, possibly involved in the production of special proteins. These could be regulatory in nature and the means by which the centriole would control local cytoplasmic events. Centriolar RNA and ribosomes also seem to be present within the unstructured centriolar precursor bodies, directing cytastral events even at this early stage while the centriolar ultrastructure is being assembled around them.

REFERENCES


R. J. Källenbach


FANKHAUSER, G. (1934). Cytological studies on egg fragments of the salamander Triton. IV. The cleavage of egg fragments without the egg nucleus. J. exp. Zool. 73, 349.


The development of cytasters


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