ARTICLE

# A Complete Second Gut Induced by Transplanted Micromeres in the Sea Urchin Embryo

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**Founder cells for most early lineages of the sea urchin embryo are probably specified through inductive intercellular interactions. It is shown here that a complete respecification of cell fate occurs when 16-cell stage micromeres from the vegetal pole of a donor embryo are implanted into the animal pole of an intact recipient embryo. Animal pole cells adjacent to the transplanted micromeres are respecified from presumptive ectoderm into vegetal plate founder cells. These induced vegetal plate cells express the entire battery of genes characteristic of the endogenous vegetal plate cells. The ectopic vegetal plate invaginates during gastrulation to form a second archenteron which differentiates properly into a tripartite gut, as shown by the spatial pattern of expression of an endoderm-specific marker gene. Thus, transplanted micromeres can signal neighboring cells to induce them to change their fate.**

The sea urchin embryo is representative of a diverse group of invertebrate embryos with an invariant early cell lineage. In these embryos, the fates of the lineage elements that give rise to various parts of the embryo are specified during the cleavage stage. One embryonic axis is established by the time of fertilization, and the second axis is determined (by various species-specific mechanisms) within the first few cleavage cycles. In embryos of this general type, zygotic transcription is active from the time of fertilization onward. The expression of cell-lineage marker genes is instituted almost immediately after segregation of lineage founder cells from one another (*1–4*). In the sea urchin embryo, the primordial axis is the animal-vegetal axis. At the fourth cleavage, four cells (micromeres) arise at the vegetal pole, and these cells appear to be autonomously specified by the polar egg cytoplasm that they inherit. The fourth-cleavage micromeres give rise to the small micromeres and the skeletogenic mesenchyme cells. The sole function of the latter is to produce the larval skeleton (spicules). If micromeres are removed from the embryo and cultured, or if they are transplanted to other positions in the embryo, their progeny nonetheless carry out skeletogenesis. They express skeletogenic genes and proceed through a lineage-specific morphogenetic program to form syncytial cables, within which they secrete the calcite skeletal elements (*1, 5–7*). The following experiment demonstrates that the micromeres are also capable of a powerful inductive interaction.

By the sixth cleavage, the sea urchin embryo has been partitioned into five polyclonal territories, each of which will express a unique set of genes and produce specific structures of the advanced embryo (pluteus) (*4*). From the vegetal pole upward these territories are: (i) the small micromeres, (ii) the skeletogenic territory, (iii) the vegetal plate territory, (iv) the aboral ectoderm, and (v) the oral ectoderm territories (Fig. 1A). The specification of an ectopic vegetal plate from blastomeres normally contributing only to ectodermal territories is described below. The vegetal plate is so called because at the late-blastula stage, the vegetal side of the embryo consists of a single layer of about 60 cells arranged as a disc of thickened epithelium. These vegetal plate cells invaginate during gastrulation and form a single cell thick tube, the archenteron. Four morphological elements subsequently differentiate from the archenteron. From proximal to distal, these are the hindgut or intestine, the midgut or stomach, the foregut or esophagus, and the secondary mesenchyme and its various derivatives (Fig. 1, D and E). Once specified, the vegetal plate functions in an essentially autonomous fashion. It has been shown that isolated vegetal plates invaginate (*8*), and that the gut differentiates as in a normal embryo even in exogastrulae, in which the archenteron protrudes outwards rather

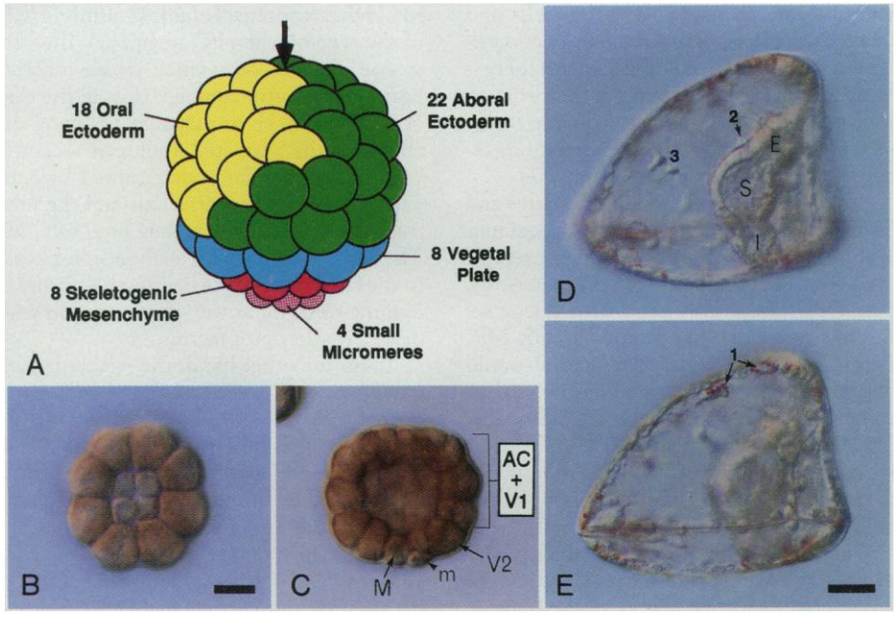


**Fig. 1.** Territory diagram and vegetal plate development. (**A**) Schematic representation of a 60-cell embryo with the five territories labeled and color-coded. The original animal pole is marked by an arrow. (**B**) Vegetal pole view of 28-cell stage *S. purpuratus* embryo clearly illustrating the cleavage asynchrony that results in four fourth-cleavage micromeres surrounded by eight fifth-cleavage macromeres. (**C**) Optical cross section (side view) of an approximately 60-cell *S. purpuratus* embryo, with the large micromeres (M), the small micromeres (m), the vegetal 2 tier (V2), and the vegetal 1 tier plus the animal cap (AC + V1) indicated. (**D** to **E**) Two different optical sections of the same 72-hour early pluteus stage *S. purpuratus* embryo, oriented with the oral surface to the right. Four morphological components have differentiated from the vegetal plate: intestine (I), stomach (S), esophagus (E), and secondary mesenchyme [derivatives of which include pigment cells (*1*), muscle cells adhering to the gut (*2*), and mesenchymal cells (*3*)]. Scale bars, 20 μm.

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than invaginating. In exogastrulae the archenteron cannot make lateral contacts with other cells, extracellular matrix components, or blastocoelic fluid (*9, 10*).

## Historical Perspective

Experimentalists have found that the sea urchin embryo has extensive regulative ability. Driesch (*11*) and Hörstadius (*12*) demonstrated that early-cleavage blastomeres are redirected to new fates if intercellular relations are altered, or when cells are ectopically juxtaposed. Evidence from both classical (*11, 12*) and modern (*4*) experiments has established that many of the territorial founder cells are conditionally specified; that is, their fate is determined by informational cues derived from neighboring cells. Thus, a contemporary interpretation is that the regulative ability of the early sea urchin embryo is a manifestation of the conditional specification of founder cells. Considered as a whole, the evidence indicates that sea urchin embryo blastomeres through sixth cleavage have an extensive capacity for intercellular interaction. The implication is that founder cell specification in normal embryos depends on cell interactions between adjacent blastomeres (*1, 4, 13*).

Hörstadius reported experiments in 1935 (*14*) that clearly demonstrate a respecification of cell fate as a result of cell interactions, although he did not interpret the results he obtained in these terms. The most remarkable and clear results of Hörstadius that are relevant to our experiments were obtained by placing four micromeres against the vegetal sides of isolated animal-halves (the animal cap) of fifth- or sixth-cleavage embryos. Complete embryos developed from these chimeric recombinants, including the archenteron, even though (i) the animal-half blastomeres are normally destined only to give rise to parts of the oral and aboral ectoderm (Fig. 1); (ii) the micromeres in the chimera contributed only skeletal mesenchyme; and (iii) the construct lacked any of the cells that normally serve to found the vegetal plate, which normally produces the archenteron. Hörstadius consistently interpreted the outcome of this and similar recombination experiments, that is, the generation of whole embryos from partial embryos, in terms of a gradient field theory that was then popular (*12*). In that model, the micromeres were thought to provide a polar "vegetalizing center," which together with the resident "animalizing center" at the opposite pole, would function to recreate all the states of specification in between the two polar centers, including the vegetal plate. An entirely different interpretation (*4*) is that the micromeres may respecify any cells they are placed adjacent to into vegetal plate founder cells, by means of short-range intercellular interactions.

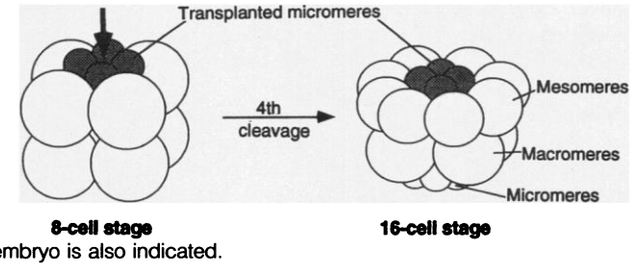


**Fig. 2.** Chimeric embryos resulting from micromere transplantations. Labeled micromeres (shaded) from a stained donor embryo are placed at the animal pole (arrow) of a recipient 8-cell (left) or 16-cell (right) embryo. For reference, each of the three cell types present in the 16-cell stage embryo is also indicated.

A few of Hörstadius' other experiments (*14*) provide preliminary evidence from which it could be hypothesized that micromeres might indeed possess a direct inductive capacity. He reported several experiments in which micromeres had been transplanted to the animal hemisphere or equatorial region of intact recipient embryos at the 32-cell stage. These embryos produced uninterpretable monsters in some cases, but in three examples, Hörstadius reported the appearance of small vesicles at the site of the transplantation. These vesicles were interpreted to be rudimentary induced archenterons, though his figures showed no specific features, and he explicitly states that the presumed archenteron-like vesicles failed to differentiate. In the course of the experiments described below, we discovered why the archenteron-like vesicles in Hörstadius' experiments did not differentiate; in order to obtain a completely differentiated secondary archenteron, it was necessary to carry out the transplant prior to the mid–16-cell stage.

Hörstadius based his conclusions on observations of morphological characters because molecular markers of gut differentiation were not available. Recently, several relevant experiments have been carried out with the use of specific endoderm markers (*15–18*). If animal pole cells of 16-cell embryos (the mesomeres) are separated by dissociation, then reaggregated and cultured, they form embryoids that frequently give a positive histochemical reaction for gut alkaline phosphatase, and react with antibodies to Endo-1 (a gut antigen) (*15, 16*). In contrast, when isolated as complete caps the mesomeres produce only ectodermal vesicles (*16*). When mesomere pairs are isolated and cultured they generally develop into ectodermal vesicles as well (*15*), but in some cases they express endoderm markers (*16*). Markers for gut differentiation are also expressed in embryoids that develop from micromeres combined with reaggregated mesomeres (*17*) or added to isolated mesomere pairs (*18*) in various ratios.

## Micromere Transplantation

Our experiments were carried out according to a different protocol. In contrast to Hörstadius, we used 8- and 16-cell stage host embryos and we assessed the progressive differentiation of the endogenous and secondary archenterons by monitoring the spatial expression of a vegetal plate–specific gene. In contrast to recent studies (*15–18*) we avoided any dissociation of the mesomeres and transplanted a complete set of four fourth-cleavage micromeres to a region near the animal pole of a complete, normal recipient embryo. We show that with this protocol, a second vegetal plate and subsequently a second archenteron were produced. With differentiation as a criterion, the respecification of the ectodermal cells to an endodermal fate was complete; all the component parts of a second archenteron formed on a normal developmental schedule.

*Strongylocentrotus purpuratus* embryos were used for all of the experiments reported here. The micromeres were transplanted to the animal pole region of 8- or 16-cell stage recipient embryos (Fig. 2). The most significant results were obtained with 8-cell stage hosts, and the following account refers specifically to these cases. Two cytological detection methods were required to obtain interpretable results. (i) The donor micromeres were labeled with a fluorescent lineage tracer so that they (and their progeny) could be identified throughout development. (ii) The transformation of the cell fate of the ectodermal precursors to vegetal plate founder cells, as well as the subsequent differentiation of the archenteron that they formed, were monitored by a whole-mount in situ hybridization method. This method provided a visual assay for transcripts from the *Endo-16* gene, a gene that encodes a gut-specific cell surface protein (*19*). This gene is first expressed in 20-hour blastulae throughout the vegetal plate, and expression continues in the entire invaginating archenteron through midgastrulation. However, *Endo-16* expression is extinguished in the tip of the archenteron as the secondary mesenchyme cells delaminate. Subsequently, *Endo-16* transcripts disappear from the foregut and hindgut regions so that, by the mature pluteus larva

stage, expression of the *Endo-16* gene is confined exclusively to the midgut. Exogastrulae exhibit the same progressive pattern of differential *Endo-16* expression as do normal embryos (*20*). This suggests that the initial phases of the genetic regulatory process controlling gut development are programmed into the vegetal plate cells because in exogastrulae the differentiating cells of the archenteron cannot receive lateral instructions from other cells in the embryo. The distribution of *Endo-16* transcripts provides a precise indicator of the specific stage of differentiation of the induced vegetal plate.

For micromere transplantation, donor embryos were labeled by immersion in rhodamine B isothiocyanate (RITC) (*21*), and then dissected by hand with a fine glass needle at the 16-cell stage to obtain an intact set of four micromeres. These were pressed against the animal pole side of an unlabeled 8-cell stage host embryo whose cell contacts had been loosened by incubation in $Ca^{2+}$-free artificial seawater. Perfusion of these constructs with normal seawater promoted adhesion between cells, and within minutes, the chimeric embryos could be transferred to normal seawater for long-term culture.

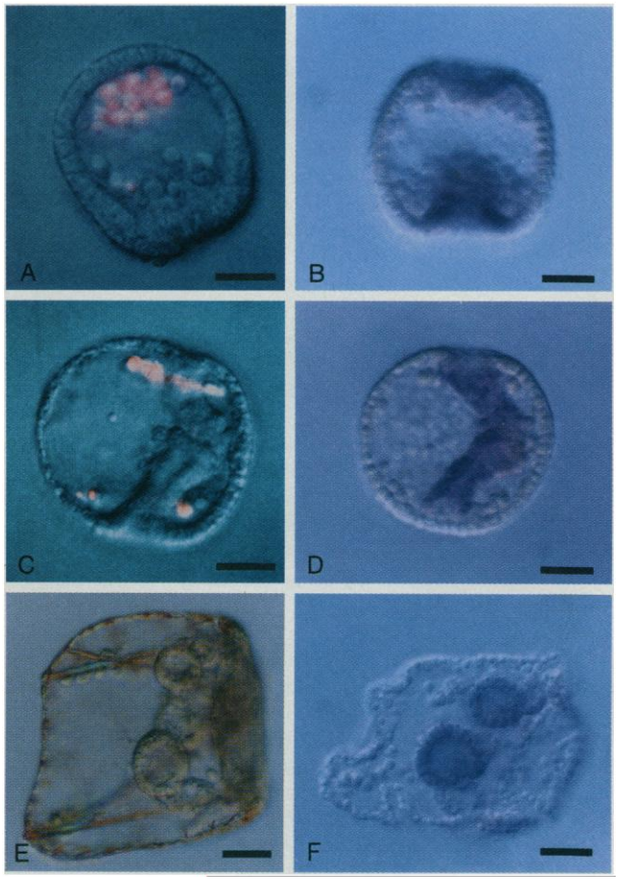


**Fig. 3.** Development of experimental embryos with induced vegetal plates. (A, C, and E) show development after addition of labeled micromeres; (B, D, and F) whole-mount in situ hybridizations of experimental embryos with the use of antisense *Endo-16* probe. (**A**) Processed video image of a 24-hour mesenchyme blastula stage of *S. purpuratus* with two populations of primary mesenchyme. Primary mesenchyme cells derived from the transplanted micromeres are labeled red in (A) and (C). (**B**) Photograph of an approximately 32-hour gastrula of *S. purpuratus* with two invaginating archenterons stained purple in cells expressing *Endo-16*. (**C**) Processed video image of a 40-hour gastrula of *S. purpuratus* with two archenterons. The primary mesenchyme cells are arranged in rings around the base of each invagination. Most labeled mesenchyme cells remain around the induced archenteron (top), but a few have incorporated into the endogenous population around the true archenteron (bottom). (**D**) Photograph of the same embryo as shown in (C) after whole-mount in situ hybridization. Both archenterons are expressing *Endo-16* along their entire length at this stage. (**E** and **F**) Two photographs of the same *S. purpuratus* 72-hour pluteus stage equivalent. (E) shows the living specimen observed with differential interference contrast optics and (F) shows this embryo again after whole-mount in situ hybridization with a probe for *Endo-16*. The archenterons have become regionalized, and in both, the expression of *Endo-16* is restricted to the stomach region. Scale bars = 20 μm. Induction is not a rare occurrence in these experiments. In one experiment, some degree of induction was observed in five out of ten transplant embryos, and two of these generated complete secondary archenterons. Our whole-mount in situ procedure, which is modified after Harkey *et al.* (*27*), is described in detail elsewhere (*20*). We utilized antisense RNA probes in which digoxygenin-11-UTP was incorporated. The probe corresponded to a 650-base region of the *Endo-16* coding sequence contained within a subclone derived from a full-length *Endo-16* genomic clone (*20*). To visualize the probe, digoxygenin polyclonal antibodies conjugated to alkaline phosphatase were incubated with the embryos after the hybridization step, then a standard histochemical assay for alkaline phosphatase was performed to visualize the location of the bound antibodies. Endogenous alkaline phosphatases were apparently inactivated during the in situ protocol, because control experiments which omitted antibodies showed no alkaline phosphatase staining.

In normally developing embryos raised under our laboratory conditions (15° to 16°C in filtered seawater plus antibiotics), ingression of the micromere descendants into the blastocoel begins at about 20 hours after fertilization. In the experimental embryos, two populations of primary mesenchyme cells could be observed ingressing from opposite sides of the embryo at this time. As expected, an RITC-labeled population ingressed from near the animal pole (Fig. 3A). In normal embryos after ingression, the skeletogenic mesenchyme cells become migratory and explore the blastocoel, but as gastrulation begins they cluster in the vicinity of the vegetal plate in response to an as yet uncharacterized target signal. In the experimental embryos, the transplanted labeled mesenchyme cells coalesced at the original animal pole of the embryo at the same time as the endogenous mesenchyme cells were forming clusters at the opposite end of the blastocoel. The creation of two centers for skeletogenic mesenchyme aggregation provided an initial indication that the prospective ectodermal cells of the animal pole had undergone respecification into a vegetal plate region. In contrast, whenever skeletogenic mesenchyme cells are introduced into the blastocoel of an otherwise normal late-blastula embryo by injection near the animal pole (*22*), they migrate to the vegetal pole, where they mingle with the endogenous skeletogenic mesenchyme.

When experimental embryos at the late-blastula stage were reacted with an antisense-RNA probe to detect *Endo-16* mRNA (Fig. 3), two areas of *Endo-16* expression were detected. One area of expression was in the true vegetal plate (identical to controls) and the other was in the cells near the animal pole that were immediately adjacent to the initial location of the transplanted micromeres (Fig. 3B). In control embryos, these prospective ectodermal cells never expressed *Endo-16*. As development of the experimental embryos progressed, this region exhibited definitive characteristics of a second vegetal plate. At gastrulation, two archenterons invaginated and each was flanked by a bilaterally arranged ring of skeletogenic mesenchyme cells (Fig. 3C). The two archenterons invariably met, and turned toward the same site on the inner ectodermal wall in preparation for mouth formation. By the equivalent of the pluteus stage, the major internal morphological structures of the embryo were present in duplicate. Thus, these embryos contained two complete arrays of skeletal rods (spicules) and two regionalized guts (Fig. 3E). The second set of spicules arose from the transplanted micromeres and the second gut arose from the differentiation of the ectopically induced archen-

teron. We cannot yet state with certainty that secondary mesenchyme was generated by the induced archenterons.

In situ hybridizations with the *Endo-16* probe at various stages of gastrulation and morphogenesis confirmed that molecular differentiation progressed in the same pattern in the induced archenterons as in the endogenous archenterons. *Endo-16* transcripts were found throughout the secondary archenteron initially, and just as in the endogenous archenteron they were progressively localized to the midgut region. The equivalence of these patterns in the induced and the endogenous archenterons is illustrated at a late gastrula stage (Fig. 3D) and at the pluteus stage (Fig. 3F).

## Early Intercellular Interactions and Induction of a Differentiated Second Gut

These experiments show that fourth-cleavage micromeres (or their immediate progeny) can present signals to prospective ectodermal blastomeres and thus respecify the ectodermal blastomeres to a vegetal fate. Instead of giving rise to oral and aboral ectoderm, the progeny of the respecified cells produced endoderm and probably definitive mesoderm (that is, secondary mesenchyme). The progeny of the transplanted micromeres did not themselves contribute at all to the induced vegetal plate structures; as expected, they generated only skeletogenic mesenchyme and small micromeres. Thus, the role of the transplanted micromeres is entirely one of providing a short-range signal that induced the respecification of the prospective ectodermal cells. Only the cells in the immediate vicinity of the transplanted micromeres were affected, as shown by the results obtained with the *Endo-16* probe in blastula and gastrula stage embryos (Fig. 3B). The experiment also shows that the animal pole blastomeres are competent to receive and respond to the micromere signals. An implication is that the molecular apparatus required for signal reception and downstream response is globally distributed at least through the 8-cell stage.

The transplantation technique described preserved the natural associations among the animal pole cells (the mesomeres) and their immediate progeny, and thus minimized potentially artifactual stimuli. It has been shown that progeny of the mesomeres will express a broad range of developmental potentials after prolonged culture of isolated blastomere pairs, or dissociation and reaggregation (*15, 16*). In such altered conditions, the progeny of these blastomeres display gut markers. On the other hand, if these mesomeres are left in association with their natural neighbors, they express only ectodermal characteristics (*7, 12, 16*). Our data indicate that, without any disturbance of the organization of the host embryo, ectopically apposed micromeres (used in the same number as normally present at the vegetal pole) could induce vegetal plate specification even in prospective ectodermal cells at the animal pole. This result supports our model for conditional blastomere specification in the sea urchin embryo (*4*), which proposes that gene regulatory factors required for all territorial fates are present globally in all the early blastomeres, but that the activation of key factors for most founder cell types depends on transduction of signals from adjacent blastomeres. In the context of the model, vegetal plate specification would occur as a consequence of a signaling interaction between the four micromeres and the four macromeres (or their eight fifth-cleavage progeny), or between the fifth-cleavage progeny of the micromeres and the definitive sixth-cleavage vegetal plate founder cells themselves (the $veg_2$ ring), which coexist in time (*23, 24*). Although our results are consistent with this model, a definitive conclusion concerning vegetal plate specification in normal development must await experiments that directly address the significance and requirement for the interactions in which these cells and their immediate ancestors actually participate.

The progeny of the responding blastomeres proceeded to execute the whole complex developmental program of archenteron formation and morphogenesis. The genetic organization of this program is such that it can be triggered by an initial early signaling event, and thereafter operates autonomously. Downstream of the initial event, batteries of vegetal plate–specific genes must be activated. They, in turn, regulate the activation and repression of different batteries of genes expressed during diversification of the archenteron. At each stage, new zygotic transcription factors must be required. We would predict that the immediate early target of the micromere signal in the responding cells is likely to be a set of maternal transcription factors. Analysis of the regulators that control expression of the early vegetal plate marker gene *Endo-16* may lead us directly to some of these target transcription factors.

## Later Morphogenesis

Additional observations pertain to cell interactions controlling morphogenetic processes later in development. The spatial relations among the various parts of the embryo are profoundly altered by the development of two archenterons originating from opposite sides of the blastocoel. In considering the structure of these aberrant pluteus larvae, two observations merit further discussion. (i) A double set of skeletal structures emerges. In the normal embryo, the originating points for the skeleton are two bilateral clusters of skeletogenic mesenchyme cells that form at ectodermally determined target sites (*1, 22*). Our experimental embryos with two sets of skeletal structures demonstrate that the positioning of these target sites is not dependent solely on cues from the oral ectoderm, but rather is dependent on cues emanating from the boundary between oral ectoderm and the supra-anal aboral ectoderm (*25*). An extra set of target sites may arise as a result of the creation of a second supra-anal ectoderm region from cells adjacent to the blastopore of the induced gut, which in turn creates a second boundary between oral and supra-anal ectoderm territories. (ii) The induced archenteron fuses to the endogenous archenteron in the foregut region, and one mouth is ultimately formed. The induced archenterons have never been observed to remain independent, or form a separate mouth. Experiments of Hardin and McClay (*26*) led them to propose that the archenteron locates a target site, the future stomodaeum, on the inner wall of the oral ectoderm by means of exploratory filapodia extended from the secondary mesenchyme cells at the tip of the archenteron. The behavior of the induced archenterons in this study is consistent with their proposal, although more study is required to demonstrate that secondary mesenchyme cells are present in the induced guts. The double archenteron embryos thus provide a new experimental vehicle for exploring long-standing questions of morphogenesis, as well as for analyzing the initial processes of founder cell specification.

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23. In the normal 16-cell embryo, the four micromeres abut the four macromeres, their sister cells after the fourth cleavage (Fig. 2). However, because the next division of the micromeres is delayed relative to that of the macromeres, the fourth-cleavage micromeres also underlie the eight, fifth-cleavage macromere progeny (Fig. 1B). The macromere progeny divide horizontally at the sixth cleavage, separating the eight vegetal-plate founder cells, known as the $veg_2$ ring (*12*) (Fig. 1, A and C), from an overlying $veg_1$ ring that gives rise only to portions of the oral and aboral ectoderm (*24*). When the micromeres do finally divide, it is by an unequal cleavage that produces a skeletogenic founder blastomere and a small micromere From these four skeletogenic founder cells, several cleavages generate the 32 skeletogenic mesenchyme cells present at the late blastula stage. The small micromeres divide only once more to produce eight cells that ultimately contribute to postembryonic imaginal development [R. A. Cameron, S. E. Fraser, R. J. Britten, E. H. Davidson, *Development* **113**, 1085 (1991), J. R. Pehrson and L. H. Cohen, *Dev Biol.* **113**, 522 (1986).] It is unlikely that the small micromeres play a role in this process, because they lack the inductive capabilities of the (skeletogenic) micromeres in blastomere recombination experiments (*17*).
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28. We are pleased to thank R J. Britten and R A. Cameron for their critical and helpful reviews. Supported by NIH grant HD-05753; and an NIH training grant HD-07257 (A.R.).

RESEARCH ARTICLE

# Live Iron-60 in the Early Solar System

A. Shukolyukov and G. W. Lugmair

**Isotopic analyses of nickel in samples from the differentiated meteorite Chervony Kut revealed the presence of relative excesses of $^{60}$Ni ranging from 2.4 up to 50 parts per $10^4$. These isotopic excesses are from the decay of the now extinct short-lived nuclide $^{60}$Fe and provide clear evidence for the existence of $^{60}$Fe over large scales in the early solar system. Not only was $^{60}$Fe present at the time of melting and differentiation (that is, Fe-Ni fractionation) of the parent body of Chervony Kut but also later at the time when basaltic magma solidified at or near the surface of the planetesimal. The inferred abundance of $^{60}$Fe suggests that its decay alone could have provided sufficient heat to melt small (diameters of several hundred kilometers) planetary bodies shortly after their accretion.**

An important parameter for describing the earliest stages of the evolution of the solar system is the time interval between the last event of nucleosynthesis contributing to solar system matter and formation of the first solid bodies. Nucleosynthetic production and subsequent rapid introduction into the nascent solar system of relatively short-lived radionuclides with half-lives of millions to hundreds of millions of years could provide information on the extent of this time interval provided that the short-lived species, although now extinct, were still alive at the time of the formation of solids. Thus, ancient solid bodies such as meteorites would reveal evidence for the original presence and subsequent decay of these short-lived radionuclides in the form of isotopic anomalies on the daughter isotopes.

These thoughts were formulated almost half a century ago by Brown (*1*) and Süss (*2*) and later were further developed by Urey (*3*) and Kohman (*4*). Evidence for the first such short-lived radionuclide, $^{129}$I [half-life $T_{1/2}$ of 16 m.y. (million years)], was discovered in 1960 by Reynolds (*5*). Since then the presence in the early solar system of several short-lived species has been well established: $^{244}$Pu ($T_{1/2}$ = 82 m.y.) (*6*), $^{26}$Al (0.7 m.y.) (*7*), $^{107}$Pd (7 m.y.) (*8*), $^{146}$Sm (103 m.y.) (*9*), and $^{53}$Mn (3.7 m.y.) (*10*). Together with long-lived radionuclides, such as $^{87}$Rb, $^{40}$K, $^{147}$Sm, $^{235}$U, and $^{238}$U, the abundance of these short-lived radionuclides has already provided extensive information and constraints on the nature of nucleosynthesis and the chronology of the early evolution of the solar system. In this article, we present evidence for the presence in the early solar system of another short-lived radionuclide, $^{60}$Fe, and discuss its usefulness as a chronometer and its importance as a heat source for early planetary melting.

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**History.** The composition and texture of differentiated meteorites such as achondrites, irons, and pallasites reflect igneous differentiation processes within asteroidal-sized parent bodies. This igneous differentiation can only be the result of extensive melting of these planetesimals. However, these bodies, which had radii of 500 km or less, are much too small to have melted extensively as a result of accretional energy or radioactive decay of long-lived nuclei (*11*). Thus, the nature of the heat source has remained uncertain, although heating by both external [electromagnetic induction (*12*)] and internal [radioactive decay of short-lived nuclei (*3*, *4*, *13*)] mechanisms has been suggested. Urey (*3*) proposed that the decay of $^{26}$Al (3.18 MeV) could have been an efficient heat source for the processing of meteorites; Kohman and Saito (*4*), in consideration of the high iron content of many meteorites, suggested that a yet unknown nuclide, $^{60}$Fe, might be an important heat source if it had a suitable half-life and sufficient primordial abundance. Roy and Kohman (*13*) subsequently discovered the nuclide $^{60}$Fe, which has a total decay energy of 3.04 MeV, and estimated its half-life as ~0.3 m.y. with an uncertainty of a factor of 3. However, at that time both $^{26}$Al and $^{60}$Fe were discounted as useful chronometers and adequate heat sources because of their short half-lives. Nevertheless, extensive efforts were made to find the vestiges from extinct $^{26}$Al in meteorites. The first clear evidence for the presence in the early solar system of $^{26}$Al was found by Lee *et al.* (*7*) in refractory Ca-Al–rich inclusions (CAI) from the Allende meteorite in the form of relative excesses of its daughter, $^{26}$Mg. Thereafter, $^{26}$Al again attracted attention as a possible heat source [see, for example, (*14*)]. Further studies on other meteorite inclusions, however, showed that not all samples of comparable antiquity contain excess $^{26}$Mg; this evidence suggested that $^{26}$Al was heterogeneously distributed in the early solar