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Development of the Infusoriform Embryo of *Dicyema japonicum* (Mesozoa: Dicyemidae)

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Abstract. The cleavage pattern and cell lineage of the infusoriform embryo of the dicyemid mesozoan *Dicyema japonicum* were studied in fixed material with the aid of a light microscope. The early cleavages are holoblastic and spiral. At the 16-cell stage, the animal pole consists of four mesomeres, the equatorial region consists of four macromeres with four alternating sub-macromeres, and the vegetal pole is composed of four micromeres. At around the 20- to 24-cell stage, cleavage becomes asynchronous and its pattern changes from spiral to bilateral. The four micromeres, namely, the presumptive germinal cells, do not divide further and are finally incorporated into the cytoplasm of four urn cells, which are generated after divisions of the sub-macromeres. The blastomeres situated in the animal hemisphere give rise to ciliated cells that cover the posterior part of the embryo. Two blastomeres ($2a^2$ and $2d^2$) undergo extremely unequal divisions and the much smaller sister blastomeres degenerate and ultimately disappear during embryogenesis. The fully formed embryo consists of 37 cells. These cells are produced after only four to eight rounds of cell division. The cell lineage appears to be invariant among embryos, apart from the derivation of the lateral cells.

Introduction

The bodies of dicyemid mesozoans consist of only 20 to 40 cells and are organized in a very simple fashion (Nouvel, 1948; McConnaughey, 1951). Although Hyman (1940, 1956) considered dicyemids to be truly primitive multicellular animals, until some twenty years ago many zoologists regarded the simple body organization of dicyemids as the result of degeneration due to parasitism in the cephalopod kidney (Nouvel, 1948; McConnaughey, 1951; Stunkard, 1954; Ginetsinskaya, 1988). However, recent studies on the base compositions and sequences of their nucleic acids have suggested that dicyemids are somewhat closer to ciliate protozoans than to flatworms (Lapan and Morowitz, 1974; Hori and Osawa, 1987).

In any attempt to evaluate the phylogenetic position of an organism, a knowledge of the normal development of the organism can be crucial. In the case of dicyemids, such information may also attract the attention of developmental biologists because, in the animal kingdom, the development of dicyemids may represent one of the simplest patterns of cell differentiation that occurs during embryogenesis. Nevertheless, the development of the infusoriform embryo of dicyemids has been minimally studied (McConnaughey, 1951; Sponholtz, 1964; Lapan and Morowitz, 1975) and the details of the cell lineage during embryogenesis remain to be determined.

In this report, we describe the pattern of cleavage and the cell lineage during the development of the infusoriform embryo of *Dicyema japonicum*. In the complex life cycle of dicyemids, the vermiform embryo and the infusorigen each develop asexually from an axoblast (agamete) and the stem nematogen is believed to develop asexually from a germinal cell of the infusoriform embryo (McConnaughey, 1951; Lapan and Morowitz, 1975; Hochberg, 1982, 1983). The infusoriform embryo is the only form that develops from a fertilized egg and the development that we discuss herein is that of infusoriform embryos. In individuals of *Dicyema japonicum*, they are ultimately composed of 37 cells.

Materials and Methods

Seventeen host octopuses, *Octopus vulgaris*, were purchased or collected personally in the western part of Japan. Although, in this region, four species of dicyemids are found in the kidneys of *Octopus vulgaris* (Furuya *et al.*,

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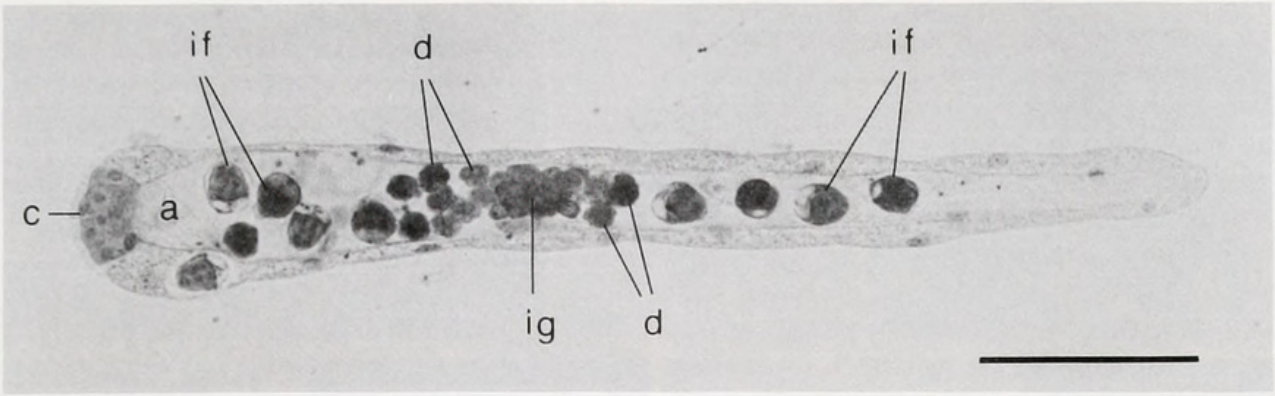

Figure 1. Light micrograph of a rhombogen of *Dicyema japonicum*. a, axial cell; c, calotte; d, developing infusoriform; if, infusoriform embryo; ig, infusorigen (hermaphroditic gonad). Scale bar = 100 μm.

1992), only those of *Dicyema japonicum* Furuya et Tsuneki, 1992 were examined throughout this study. After the octopus had been sacrificed, its kidneys were taken out and smeared directly on glass slides. Smeared dicyemids were immediately fixed with Carnoy's fixative or alcoholic Bouin's solution (absolute ethanol saturated with picric acid: formalin: acetic acid, 15:5:1). Specimens fixed with Carnoy's fixative were stained with Feulgen's stain or by the PAS method and were poststained with Ehrlich's hematoxylin and light green. Some specimens were treated with saliva before the PAS staining. Specimens fixed with alcoholic Bouin's solution were stained with Ehrlich's hematoxylin and light green only. The embryos in the axial cell of rhombogens were observed with the aid of a light microscope under an oil-immersion objective at a magnification of 2000 diameters. Blastomeres were identified by criteria such as position within the embryo, size of nucleus and cell, and stainability of nucleus and cell. By paying careful attention, we identified each swollen nucleus that was about to divide and each metaphase figure in terms of the blastomere that was going to divide and the resulting two daughter blastomeres. Each developing embryo with or without dividing blastomeres was sketched at three different optical depths and a three-dimensional diagram was reconstructed from these sketches. The fully formed embryo consisted of only 37 cells and special techniques such as injection of a tracer and videoscopy were not required for determination of the cell lineage. The early cleavages of *Dicyema japonicum* were spiral and, therefore, the terminology of blastomeres that is generally used for embryos with spiral cleavages was adopted in designating the blastomeres. The cells of the infusoriform were named according to the earlier authors (Nouvel, 1948; McConnaughey, 1951; Short and Damian, 1966; Ridley, 1969; Matsubara and Dudley, 1976).

Results

In individuals of *Dicyema japonicum*, there is usually only one infusorigen, which is functionally a hermaphroditic gonad, and it is located in the center of the axial cell of a rhombogen (Fig. 1). A sperm enters the oocyte, which is located around the axial cell of the infusorigen. Then the oocyte undergoes meiosis and produces the polar bodies, and the two-pronucleus stage follows (Fig. 2a–d). Fertilized eggs are about 12.3 μm in diameter. As development proceeds from the 2-cell to the 4-cell stage and beyond (Fig. 2e–h), the embryo leaves the infusorigen and moves toward the anterior or posterior end of the axial cell of the rhombogen. In large specimens, there are more than 20 embryos, including fully formed infusoriforms, in a single rhombogen. In some cases, therefore, nearly the entire series of developmental stages can be observed in a single fixed rhombogen.

Cleavage is holoblastic and early cleavages proceed spirally. The first cleavage is meridional and equal, and produces two blastomeres, AB and CD (Figs. 2e, 3a). The second cleavage is latitudinal and equal, and produces four blastomeres, A, B, C, and D (Figs. 2f, 3b). Blastomeres A and C are in contact with each other at the animal pole, and blastomeres B and D are in contact at the vegetal pole. The third cleavage is again equal and four blastomeres, 1a, 1b, 1c, and 1d, are formed at the animal hemisphere (Figs. 2g, 3c). When viewed from the animal pole, these blastomeres are organized spirally clockwise to their sister blastomeres (1A, 1B, 1C, 1D), which form the vegetal hemisphere. The 8-cell embryo, thus, consists of two tiers of four cells (quartet). The descendants of blastomeres A and 1B are destined to form the left side of the infusoriform and the descendants of blastomeres C and 1D form the right side of the embryo.

The fourth cleavage is unequal and results in the 16-cell embryo (Figs. 2i, 3d). Four blastomeres, 1a, 1b, 1c, and 1d, divide and produce the mesomeres $1a^1$, $1b^1$, $1c^1$, and $1d^1$ at the animal pole, and the macromeres $1a^2$, $1b^2$, $1c^2$, and $1d^2$ in the equatorial region. These divisions are not typically spiral. Blastomeres $1a^1$, $1b^1$, $1c^1$, and $1d^1$ undergo no further division. Blastomeres $1a^1$ and $1c^1$ become the dorsal caudal cells (DC) of the left and right

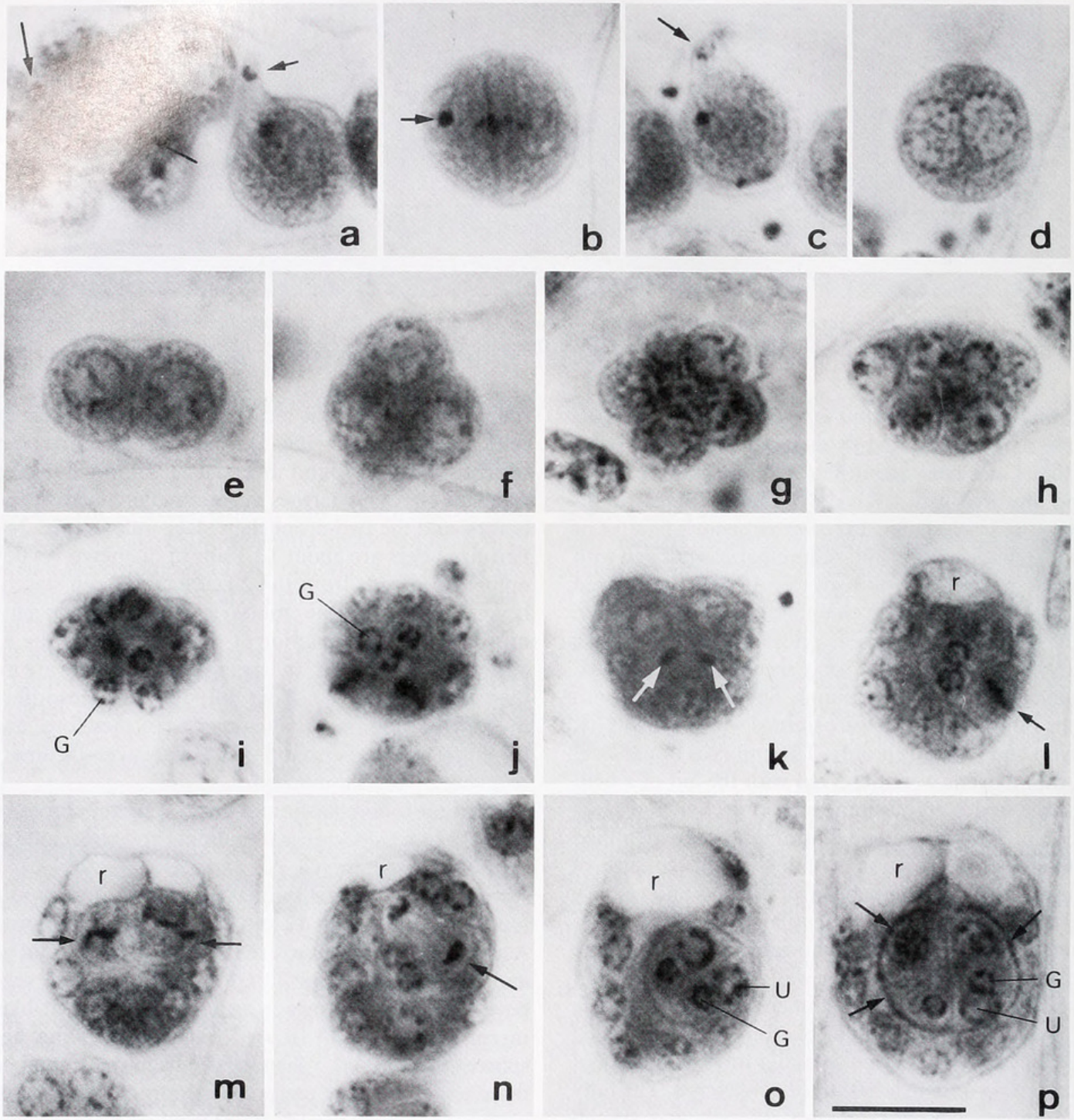

Figure 2. Light micrographs of eggs, developing infusoriform embryos, and fully formed infusoriform embryos of *Dicyema japonicum*. Photomicrographs were taken at magnifications of 2000 diameters under an oil-immersion objective. Scale bar = 10 μm. **a.** An infusorigen (left) and an oocyte undergoing meiosis (right). The short arrow indicates the first polar body and the long arrows indicate spermatozoa. **b.** An oocyte undergoing the second meiotic division. The arrow indicates a spermatozoon. **c.** An oocyte finishing meiosis (center). The arrow indicates the second polar body. **d.** A fertilized egg at the 2-pronucleus stage. **e.** Two-cell embryo. **f.** Four-cell embryo. One blastomere is out of focus. **g.** Eight-cell embryo. An axial cell nucleus is seen in the lower left corner. **h.** Twelve-cell embryo (optical section). **i.** Sixteen-cell embryo (optical section). **j.** Twenty-four-cell embryo (optical section). **k.** Twenty-nine-cell embryo (ventral view). The arrows indicate degenerating cells produced after extremely unequal divisions. **l.** Twenty-nine-cell embryo (sagittal optical section). The arrow indicates a metaphase figure of $2d^2$. Two small nuclei in the center are those of germinal cells. r = refringent body. **m.** Thirty-three-cell embryo (horizontal optical section). Arrows indicate metaphase figures of $2b^{211}$ and $2c^{211}$. r = refringent body. **n.** Thirty-six-cell embryo (sagittal optical section). The arrow indicates a telophase figure of $2c^{212}$. r = refringent body. **o.** Fully formed embryo (sagittal optical section). r = refringent body. **p.** Fully formed embryo (horizontal optical section). Arrows indicate granules in capsule cells. r = refringent body.

side of the embryo, respectively. Blastomeres $1b^1$ and $1d^1$ become the median dorsal cell (MD) and the ventral caudal cell (VC), respectively. Macromere $1d^2$ also does not divide further and ultimately becomes the couvercle cell (C). These three cells (MD, VC, C) are located in the midline of the embryo and, thus, are not paired. Among the other macromeres, $1a^2$ and $1c^2$ usually undergo no further divisions and become the lateral caudal cell (LC) of the left and right side, respectively. Macromere $1b^2$ subsequently divides once more (Fig. 3j). The resultant sister blastomeres gradually accumulate a refringent body in the cytoplasm and finally become the apical cells (A).

The fourth division in the vegetal hemisphere generates four sub-macromeres, 2a, 2b, 2c, and 2d, in the subequatorial region, and four micromeres, 2A, 2B, 2C, and 2D, at the vegetal pole. Micromeres 2A, 2B, 2C, and 2D do not divide further and they ultimately become the germinal cells (G). After the fourth division, the cleavages are not synchronized among the blastomeres (Figs. 2j–n, 3e–1, 4).

The 20-cell stage is achieved by the unequal division of blastomeres 2a, 2b, 2c, and 2d (Fig. 3e). When the embryo is viewed from the vegetal pole, the daughter blastomeres $2a^1$, $2b^1$, $2c^1$, and $2d^1$ occupy the left side of $2a^2$, $2b^2$, $2c^2$, and $2d^2$, respectively. At around this stage, the four micromeres 2A, 2B, 2C, and 2D (the presumptive germinal cells) are incorporated into the inside of the embryo as the other blastomeres grow and rearrange themselves. Blastomeres $2a^1$ and $2d^1$ undergo no further divisions and eventually they become the posteroventral lateral cells (PVL) of the left and right side, respectively.

The cleavage pattern beyond the 20-cell stage is not spiral but bilateral. Beyond this stage, the order of divisions of blastomeres is not necessarily identical among developing embryos and the subsequent developmental stages, such as the 24-cell stage and so on, become increasingly less well defined. For example, in the embryo shown in Figure 3f (23-cell stage), blastomere $2c^{22}$ has already divided into its daughter cells while, in the embryo shown in Figure 3h (24-cell stage), the same blastomere is still intact.

Blastomeres $2b^1$ and $2c^1$ usually divide once more and generate the paired dorsal cells (PD) and lateral cells (L) on the left and right side, respectively. In some individuals, however, these blastomeres ($2b^1$ and $2c^1$) do not divide further and simply become the paired dorsal cells. In these embryos, macromeres $1a^2$ and $1c^2$ divide once more and produce the lateral cells and the lateral caudal cells. In every case, the embryos become slightly oval in shape.

Blastomeres $2a^2$, $2b^2$, $2c^2$, and $2d^2$ exhibit complex patterns of cleavages. Blastomere $2a^2$ usually undergoes extremely unequal division (Fig. 2k); the much smaller sister blastomere (not named here) becomes pycnotic and is destined sooner or later to degenerate. The much larger sister blastomere soon divides again and produces $2a^{21}$ and $2a^{22}$. Blastomere $2a^{21}$ becomes the capsule cell (CA), while blastomere $2a^{22}$ divides once more and produces the anterior lateral cell (AL; $2a^{221}$) and the second ventral cell (V2; $2a^{222}$). The capsule cell has a large nucleus and later accumulates PAS-positive granules in the cytoplasm. These granules are PAS-positive even after the saliva-test is applied. The second ventral cell later extends a long cytoplasmic process medially. The cleavage pattern and cell lineage of blastomere $2d^2$ are the same as those of blastomere $2a^2$, although $2d^2$ produces the cells that occupy the right side of the embryo.

Blastomere $2b^2$ first divides into $2b^{21}$ and $2b^{22}$, and blastomere $2b^{22}$ soon divides again. The resultant blastomere $2b^{221}$ becomes flattened (Fig. 4d); it covers the anterior region of the embryo and eventually it is transformed into the enveloping cell (E). The sister blastomere $2b^{222}$ becomes the first ventral cell (V1). The blastomeres generated from $2b^{21}$ are gradually incorporated into the inside of the embryo as the blastomeres derived from the animal hemisphere grow and rearrange themselves. Blastomere $2b^{211}$ then divides (Fig. 2m) to produce blastomeres $2b^{2111}$ and $2b^{2112}$. Blastomere $2b^{2111}$ becomes transparent apart from its nucleus and it is ultimately designated the dorsal internal cell (DI). Blastomere $2b^{2112}$ eventually projects cilia into a small cavity, the urn cavity, and becomes the ventral internal cell (VI). The urn cavity is a cleft formed between the ventral internal cells and the urn that is composed of four urn cells. Blastomere $2b^{212}$ finally divides and produces two urn cells (U) of the left side. The cleavage pattern and cell lineage of blastomere $2c^2$ are the same as those of blastomere $2b^2$: the descendants of $2c^2$ ultimately contribute to the right side of the embryo's body. The urn itself apparently rotates as a mass and, thus, it cannot be determined for each urn cell whether it was originally the right one or left one.

After all cells of the embryo have been laid down, one germinal cell is incorporated into the cytoplasm of each of the four urn cells (Fig. 5d). In individuals of *Dicyema japonicum*, the nucleus of each urn cell does not divide and each urn cell contains only one nucleus throughout. As the infusoriform matures, the nuclei of most of the cells tend to become pycnotic. Nuclear pycnosis takes place first in the second ventral cell. However, the nuclei of the germinal cells and the urn cells do not become pycnotic, even in the mature infusoriform.

The cell lineage of the infusoriform embryo of *Dicyema japonicum* is summarized in Figure 6. Blastomeres A and D follow exactly the same pattern of cleavages. Blastomeres B and C follow a very similar pattern of cleavages. A difference is found only in blastomeres $1b^2$ and $1c^2$; the former divides once to produce the apical cells but the latter does not. Even in the A and D series, however, corresponding blastomeres do not necessarily produce the

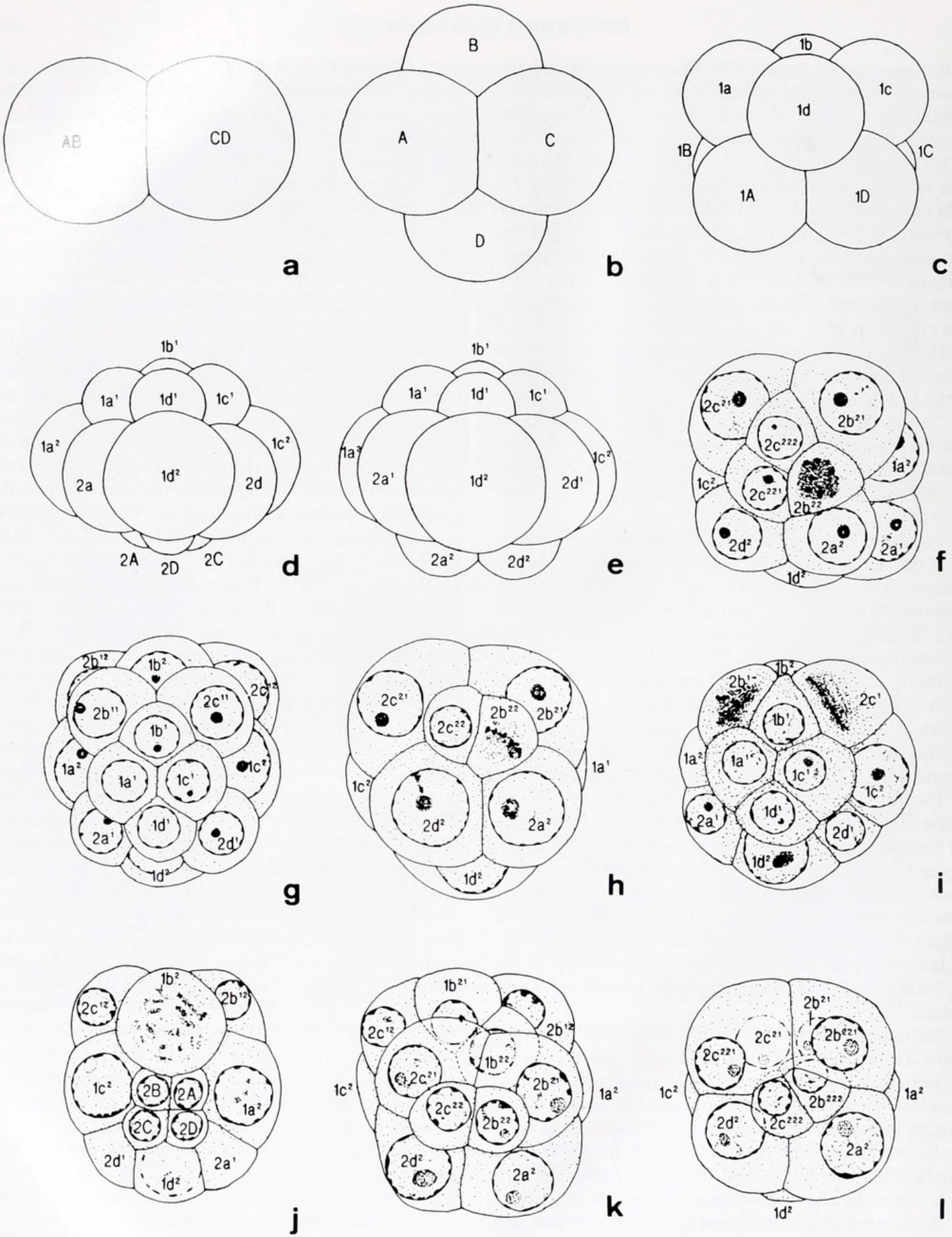

Figure 3. Sketches of early embryos of *Dicyema japonicum*. Blastomeres are named according to the notation system for spiral cleavages. Scale bar = 10 μm. **a.** Two-cell stage (from the animal pole). **b.** Four-cell stage (from the animal pole). **c.** Eight-cell stage (lateral view). **d.** Sixteen-cell stage (lateral view).

same types of cell. For example, blastomere $1a^1$ becomes the dorsal caudal cell of the left side, while blastomere $1d^1$ produces the ventral caudal cell in the midline. Ultimately, four to eight rounds of cell division take place, excluding extremely unequal divisions, until each cell is established (Table I). Germinal cells are one type of cell that is determined early in embryogenesis. The cell lineage is invariant, apart from the derivation of the lateral cell. As mentioned above, it is usually derived from $2b^1$ and $2c^1$ (see Fig. 6), but in some embryos it is derived from $1a^2$ and $1c^2$. Extremely unequal divisions, accompanied by degeneration of the much smaller daughter blastomeres, usually occur in blastomeres $2a^2$ and $2d^2$. However, it remains to be determined whether the unequal divisions occur consistently in these blastomeres in every embryo, and whether such divisions never occur in the $2b^2$ and $2d^2$ series.

The fully formed embryo consists of 37 cells (Fig. 5). Two enveloping cells (E) are flat and enclose the anterior half of the embryo; these cells are not depicted in Figure 5. Two apical cells (A) are completely enclosed by these cells and each contains one large refringent body in the cytoplasm. The nucleus is in the dorsocaudal part of each apical cell. The refringent body is known to contain magnesium inositol hexaphosphate, at least in individuals of *Dicyema typus* (Lapan, 1975). The external cells that are distinctly ciliated are as follows: two paired dorsal cells (PD), a median dorsal cell (MD), two dorsal caudal cells (DC), two lateral caudal cells (LC), a ventral caudal cell (VC), two lateral cells (L), and two posteroventral lateral cells (PVL). The cells forming the ventral surface of the embryo do not have cilia. They include two first ventral cells (V1), two second ventral cells (V2), two anterior lateral cells (AL), and a couvercle cell (C) which covers up the urn. Five cell types constitute the interior of the embryo. Two ventral internal cells (VI) have cilia that project into the urn cavity. Two dorsal internal cells (DI) and two capsule cells (CA) are not ciliated. The dorsal internal cells were once called glycogen cells (McConnaughey, 1951), but they appear to be PAS-negative. By contrast, the capsule cells have PAS-positive granules in their cytoplasm. Each of the four urn cells encloses a germinal cell in its cytoplasm. The body length, excluding cilia, of the fully formed embryo is about 24 μm and the body width is about 19 μm.

Discussion

The processes of fertilization and extrusion of the polar body in dicyemid mesozoans were studied in detail by Short and Damian (1967). However, the development of the infusoriform embryo, which is the only organism that is produced directly after fertilization, has only been studied to a limited extent (McConnaughey, 1951; Sponholtz, 1964; Lapan and Morowitz, 1975). The pattern of development in *Dicyema japonicum,* which is described herein in detail, is very different from that briefly described for *Dicyemennea adscita* and some other species by McConnaughey (1951) and from the cursory depiction in the case of unspecified species by Lapan and Morowitz (1975), although these earlier reports indicated that the early cleavages followed a spiral pattern, as we observed in this study. A spiral pattern of early cleavages appears to be universal among dicyemids.

Spiral cleavage in dicyemids is reminiscent of that in flatworms (Platyhelminthes) and this similarity may be used as an argument for a phylogenetic relationship between dicyemids and flatworms. In acoels, however, cleavages proceed by duets and small blastomeres are not produced at the vegetal pole (Apelt, 1969; Henley, 1974). In polyclads, early cleavages proceed by quartets as in dicyemids, but four small macromeres produced at the vegetal pole of the polyclad embryo are later absorbed during embryogenesis (Hyman, 1951; Kato and Minegishi, 1983). Details of developmental patterns, thus, are different between dicyemids and flatworms. In sponges (Porifera), the early cleavages are usually radial and, in coelenterates (Cnidaria), it is radial, bilateral, or partly spiral (Uchida and Yamada, 1983). The cleavage patterns of these primitive invertebrates are so diverse that a similarity in cleavage pattern *per se* may not necessarily reflect a phylogenetic relationship between the organisms concerned. Development of placozoans, *Trichoplax adhaerens,* has been only partly described (Grell, 1972), and development of fertilized eggs of the Orthonectida has never been described. Detailed comparative studies on the development of these "mesozoan" animals are necessary if we are to gain any insight into details of the evolution of these animals.

In the infusoriform embryos of dicyemids, there is no germ layer and groups of cells are roughly distinguished only as outer cells and inner cells. The outer cells, which

e. Twenty-cell stage (lateral view). Blastomeres 2A–D have been incorporated inside the embryo and, thus, they are not seen from outside. **f.** Twenty-three-cell stage (ventral view). Note a prophase figure in $2b^{22}$. **g.** Twenty-four-cell stage (dorsal view). **h.** Twenty-four-cell stage (ventral view). Note a metaphase figure in $2b^{22}$. **i.** Twenty-four-cell stage (dorsal view). Note prophase to metaphase figures in $2b^1$ and $2c^1$. **j.** Twenty-five-cell stage (horizontal optical section). Note an early prophase figure in $1b^2$. **k.** Twenty-five-cell stage (ventral view). **l.** Twenty-six-cell stage (ventral view).

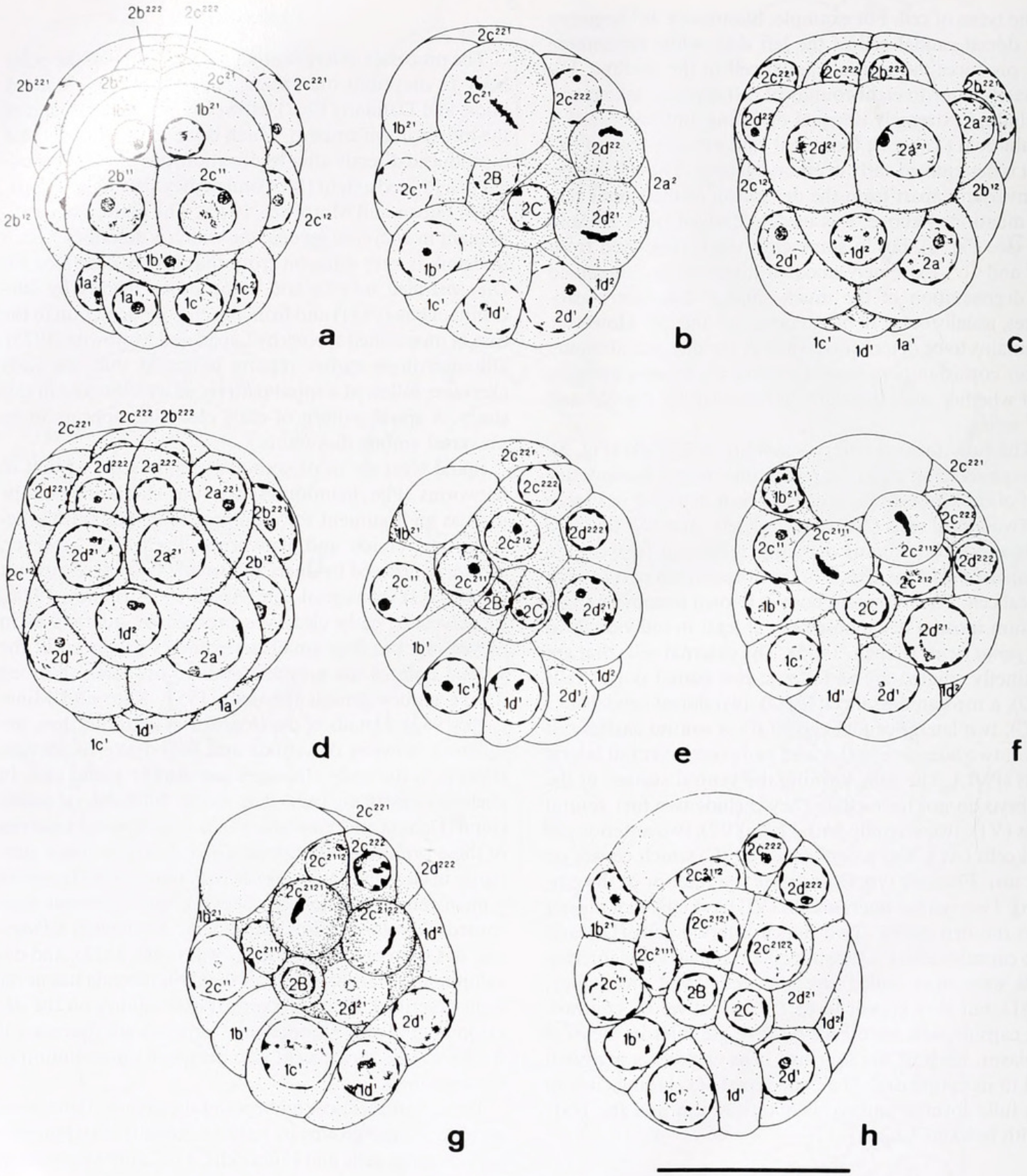

Figure 4. Sketches of late embryos of *Dicyema japonicum*. Scale bar = 10 μm. **a.** Twenty-nine-cell stage (dorsal view). **b.** Twenty-nine-cell stage (sagittal optical section). Note a metaphase figure in $2c^{21}$ and a telophase figure in $2d^{2}$. **c.** Twenty-nine-cell stage (ventral view). **d.** Thirty-three-cell stage (ventral view). Large capsule cells ($2a^{21}$ and $2d^{21}$) are still situated on the ventral surface. **e.** Thirty-three-cell stage (sagittal optical section). **f.** Thirty-three-cell stage (sagittal optical section). Note a telophase figure in $2c^{211}$ that is dividing to produce dorsal and ventral internal cells ($2c^{2111}$ and $2c^{2112}$). **g.** Thirty-six-cell stage (sagittal optical section). Note a telophase figure in $2c^{212}$ that is dividing to produce two urn cells ($2d^{2121}$ and $2d^{2122}$). **h.** Early 37-cell stage (sagittal optical section). Cell divisions have been completed, but germinal cells (2B and 2C) have not yet been incorporated into the cytoplasm of urn cells ($2c^{2121}$ and $2c^{2122}$).

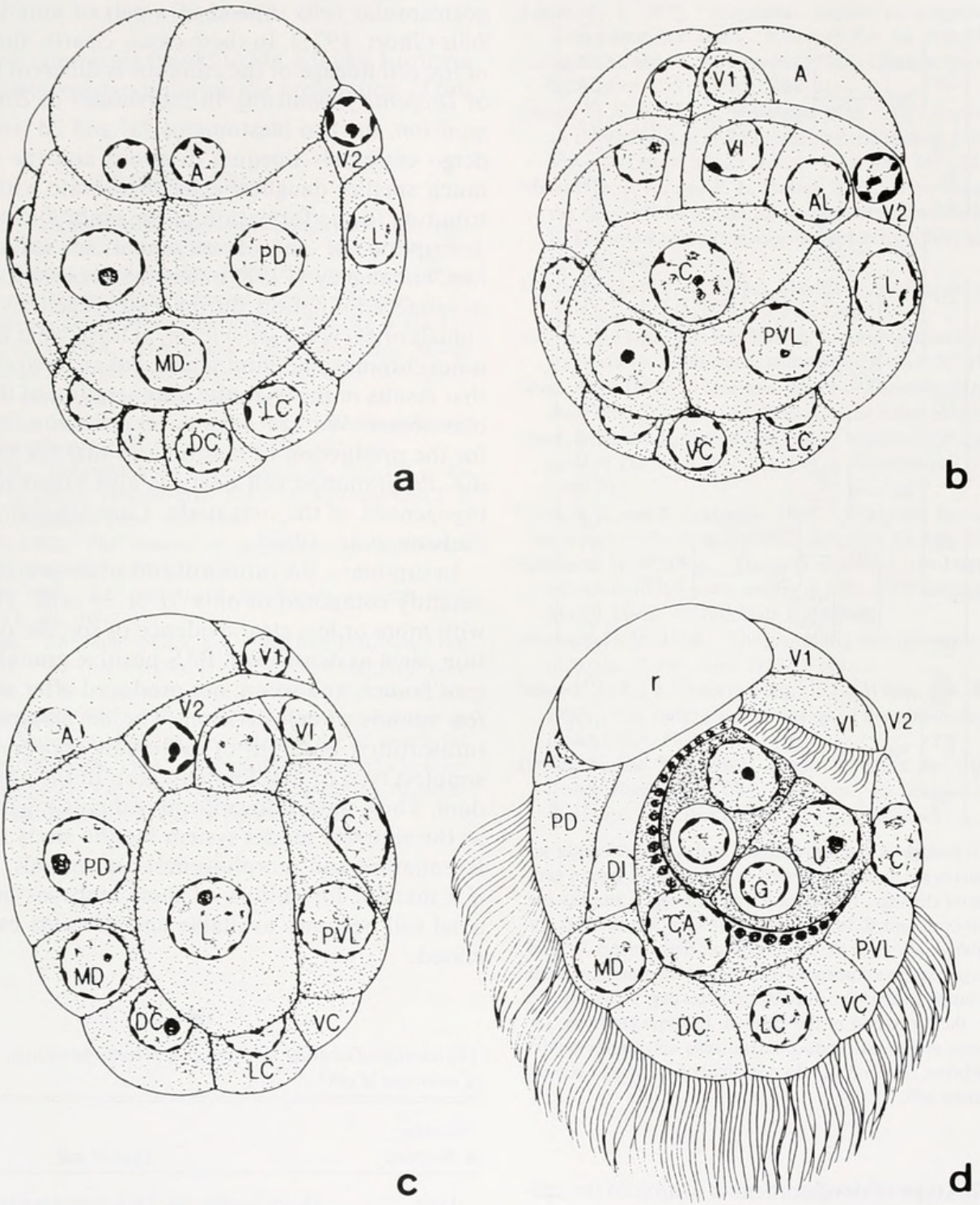

Figure 5. Sketches of a fully formed infusoriform embryo. Scale bar = 10 μm. **a.** Dorsal view. **b.** Ventral view. **c.** Lateral view. **d.** Sagittal optical section. Enveloping cells are not depicted. Cilia are omitted in **a, b,** and **c.** r = refringent body.

occupy the dorsal and caudal surfaces of the embryo, are ciliated and are derived from the blastomeres of the animal hemisphere of the embryo, and the inner cells are derived from the blastomeres of the vegetal hemisphere. The innermost germinal cells are derived from the cells that form the vegetal pole. These processes of cellular rearrangement are observed in many other groups of animals and appear to represent the basic pattern of the early development of animals. It is also apparent that the outer ciliated cells differentiate much earlier than the inner cells, with the exception of the germinal cells (Fig. 6 and Table I). In infusoriform embryos, the cells of the vegetal hemisphere are apparently incorporated passively into the interior of the embryo as the cells of the animal hemisphere

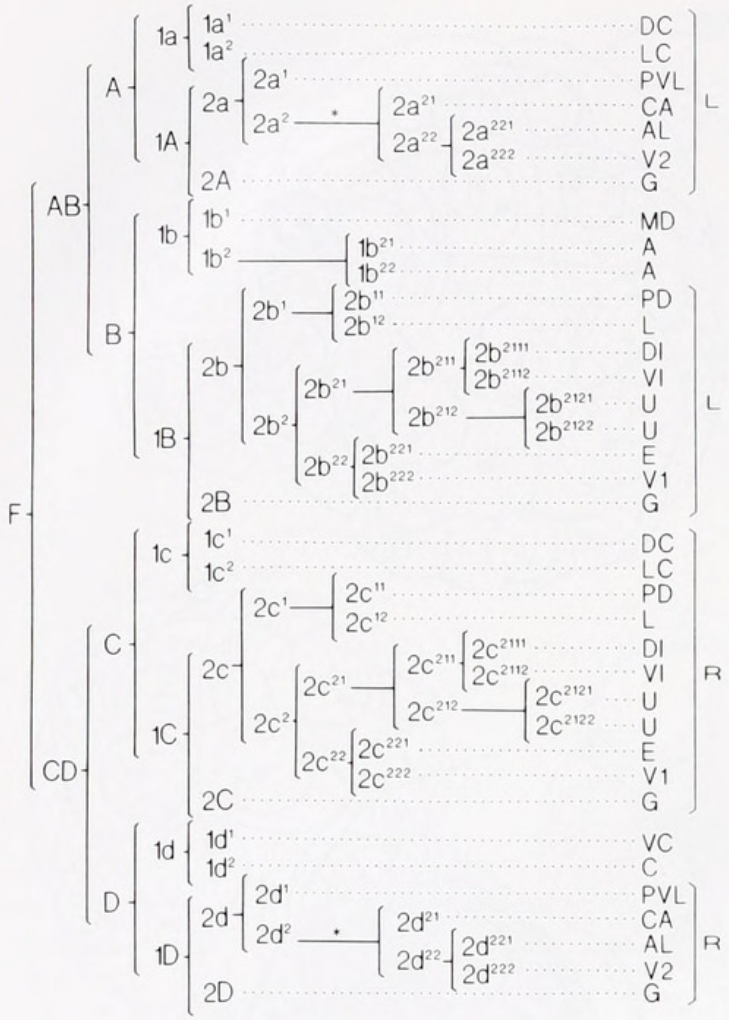

Figure 6. Cell lineage of the infusoriform embryo of *Dicyema japonicum.* Blastomeres are named according to the notation system generally used for spiral cleavage. F implies a fertilized egg. L implies the left side of the embryo and R implies the right side. See the text for explanations of abbreviations in the right column. Blastomeres $2a^2$ and $2d^2$ usually undergo extremely unequal divisions at the poinis marked by asterisks. The much smaller daughter blastomeres degenerate and do not contribute to the formation of the embryo. In some embryos, $1a^2$ and $1c^2$ divide once more and produce lateral cells and lateral caudal cells. In these embryos, $2b^1$ and $2c^1$ do not divide further and simply become paired dorsal cells.

proliferate. This type of development is similar to the epiboly seen in the stereoblastulae of some invertebrates including flatworms (Hyman, 1951; Henley, 1974). In dicyemids, a cavity called the urn cavity appears between the ventral internal cells and the urn, but this slit-like space is certainly formed secondarily and cannot be taken to represent a blastocoel.

In many species of dicyemid including *Dicyema japonicum,* the infusoriform finally consists of 37 cells, but in some species belonging to the genus *Dicyema* or *Dicyemennea* the infusoriforms consist of 39 cells (Short, 1971). In these latter species, there is a pair of third ventral cells in addition to the standard 37 cells. In peculiar cases such as in *Dicyema knoxi,* the infusoriform is composed of 37 cells, but there is a pair of postcapsular cells instead of a pair of anterior lateral cells (Short, 1971). In these cases, clearly, the last part of the cell lineage of the embryos is different from that of *Dicyema japonicum.* In individuals of *Dicyema japonicum,* the two blastomeres $2a^2$ and $2d^2$ usually undergo extremely unequal divisions and the resultant, much smaller daughter cells degenerate without contributing to the formation of the embryo. In his short description of the development of infusoriforms, McConnaughey (1951) noted the occurrence of chromosome elimination during embryogenesis. In individuals of *Dicyema japonicum,* at least, what takes place is not chromosome elimination, but an unequal division that results in the pycnotic degeneration of the smaller blastomere. We can offer no explanation, at present, for the production of blastomeres that are destined to die. Programmed cell death is also noted in the embryogenesis of the nematode, *Caenorhabditis elegans* (Sulston *et al.,* 1983).

In summary, the infusoriforms of dicyemids are consistently composed of only 37 or 39 cells. These cells, with more or less clear evidence of specific differentiation, such as dense cilia, PAS-positive granules, refringent bodies, and so on, are produced after only a very few rounds of cell division. The development of the infusoriform embryos of dicyemids appears to be the simplest type of development seen in the animal kingdom. Thus, these infusoriform embryos might be useful as the simplest model system for the study of cell differentiation and morphogenesis in animals, especially if a method for culture of these embryos outside the axial cell becomes available and mutants can be generated.

Table I

*The number of cleavage divisions that precede formation of each type of cell**

Number of divisions	Type of cell
Four	Dorsal caudal cells (DC), lateral caudal cells (LC), median dorsal cell (MD), ventral caudal cell (VC), couvercle cell (C), and germinal cells (G)
Five	Posteroventral lateral cells (PVL), apical cells (A), paired dorsal cells (PD), and lateral cells (L)
Six	Capsule cells (CA)
Seven	Anterior lateral cells (AL), first ventral cells (V1), second ventral cells (V2), and enveloping cells (E)
Eight	Dorsal internal cells (DI), ventral internal cells (VI), and urn cells (U)

* Extremely unequal divisions are not counted. In some embryos, paired dorsal cells are formed after four rounds of division and lateral caudal cells after five rounds of division (see text).

Acknowledgments

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