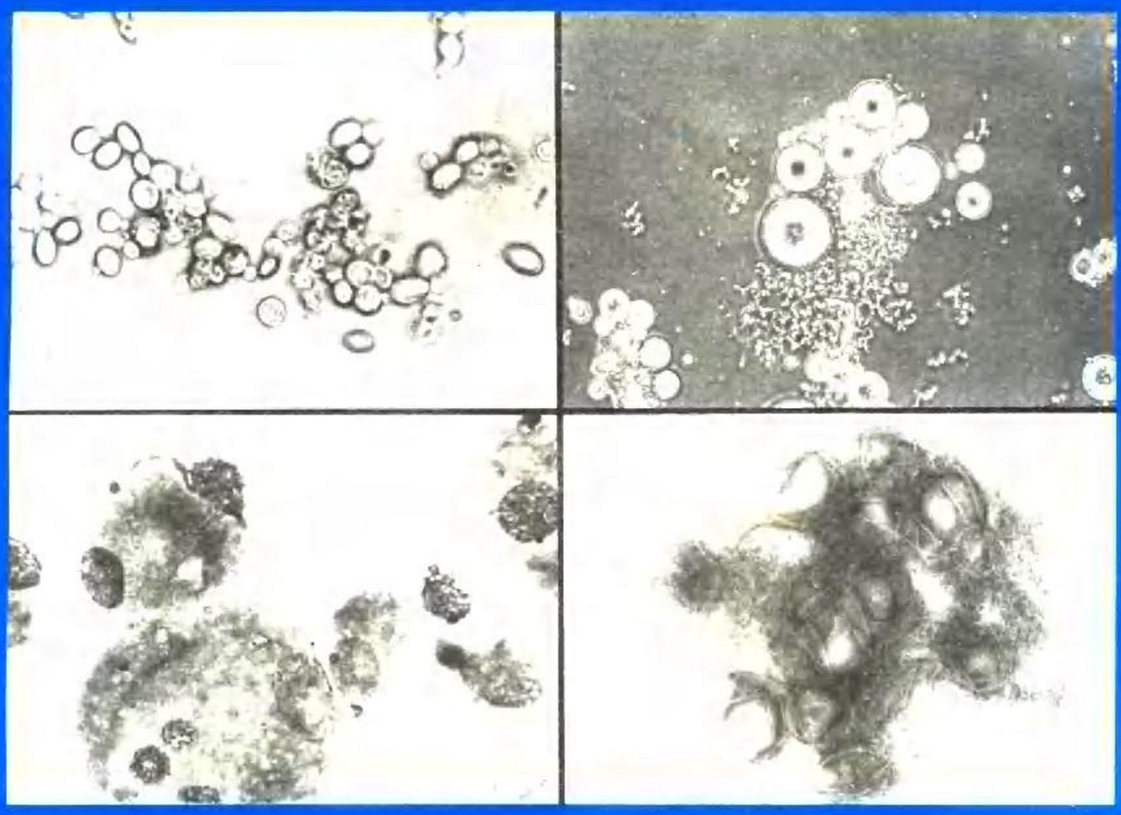
细胞重建 第一集

CELL REFORMATION Series 1

贝时璋 主编
Edited by Bei Shizhang



科学出版社
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1988

内 容 简 介

本文集由中国科学院生物物理研究所细胞重建组的24篇尚未发表过的论文汇集而成.论文集较全面地阐述了鸡胚体细胞、丰年虫中间性生殖细胞、成体小鼠骨髓细胞和沙眼衣原体细胞的重建,以及根瘤菌的繁殖与大豆根瘤细胞的关系.这些研究说明细胞可在生物体内或离体情况下自行组装,是细胞繁殖增生的一个重要途径.论文集提供了大量光学显微镜和电子显微镜照片,以资佐证.

本文集可供生物科学研究工作者和教学工作者参考.

封面: 细胞重建照片	Cover: Photos of Cell Reformation
左上: 丰年虫中间性卵黄颗粒的细胞重建	The upper left: Cell reformation of yolk granules of *Chirocephalus intersex*
右上: 鸡胚卵黄球的细胞重建	The upper right: Cell reformation of yolk spheres of chicken embryo
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细 胞 重 建

第一集

贝时璋 主编

责任编辑 白松乾 卢素芳 朱咸滨 崔永平

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关于细胞重建的研究

1932 年春天，我在杭州郊区松木场稻田里采集到的南京丰年虫（*Chirocephalus nankinensis*）中，发现中间性（Intersex）个体．丰年虫属甲壳类动物的叶足类．中间性是指个体在发育过程中的一定阶段同时呈现雌雄性征．根据呈现的性征偏于雌性或雄性的程度不同，中间性有五种类型，并对其生殖腺的性转变进行了研究．在转变过程中，我还观察到生殖细胞转变的全部过程，包括细胞的解体（细胞解形 cell deformation）和细胞的重新形成（细胞重建 cell reformation）．1934 年，在浙江大学生物系的一次讨论会上，我报告了这些现象和我的看法．但论文的发表却已经是 1942 年和 1943 年[1]的事情了．迟迟未予发表是因为抗日战争时期浙江大学屡次迁校，动荡不安．另外，没有一个合适的可以投稿的期刊也是一个原因．到 1942 年，《科学记录》（《Science Record》）创刊，这项工作才得以正式发表．这些，是客观存在的事实．而主观上我多少也曾有所犹豫．我在这两篇论文里，分析了全部五种中间性类型丰年虫性转变过程中生殖细胞的解形和重建的情况，叙述了从卵黄粒转变为完整的细胞的现象，探讨了它的机制．我称它是重建而不是新生，因为重建是复兴，表现在卵黄粒具备组成细胞的一切原料．细胞解形产生了卵黄粒，卵黄粒反过来提供了重建细胞的材料．这说明，当组成细胞的物质基础存在以及环境合适的时候，可以不通过细胞分裂的方式形成细胞．而生物学界认为一切细胞来自细胞，认为细胞分裂是细胞繁殖增生的唯一途径．如果说可以通过细胞分裂以外的细胞重建的方式繁殖增生细胞，势将被看作是对生物学的亵渎，是可笑的愚昧和狂妄．这样的疑虑当然不足取．好在我终究将论文发表了，而且并未受到责难．但是可能有人认为细胞重建即使存在，也不是那么容易见到和经常见到的现象，而传统的观点已成为金科玉律．它的压力毕竟是巨大而又深远的．因此，我的工作显得似乎只是一个孤证，不足以说明规律性的问题．既无响应，难免寂寞，当时又忙忙碌碌，腾不出手来，我只得把这项工作放了下来．

这一放，放过了二十多个年头．一直到 1970 年，才又重新开展细胞重建的研究．和 30 年代相比，我们已经处在一个新的时代，我们的工作也换了新的面貌．原先基本上是一个人干，现在有一个集体——中国科学院生物物理研究所细胞重建研究组．原先的研究材料只有南京丰年虫一种，现在除丰年虫外，我们还研究鸡胚、小鼠骨髓以及沙眼衣原体、大豆根瘤菌等．原来的研究方法只是光学显微镜观察，现在我们应用了包括电子显微镜、显微缩时电影、相差定位观察、放射自显影、荧光偏振、双荧光标记能量转移、荧光漂白恢复、拉曼光谱等以及生化方面的其他各种新技术、新方法．在原先工作的基础上，我们获得了新的发现、新的知识．例如，我们发现了鸡胚卵黄颗粒内有 DNA、组蛋白和染色质．卵黄颗粒的染色质和细胞核的染色质有同样的结构和行为．DNA 分子的形状也与核 DNA 很相似．染色质一直被认为是

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1) Pai, S., *Science Record*, **1**(1942), 187; **2**(1943), 573.

细胞核特有的. 卵黄颗粒内有染色质,这是生物学史上的第一次发现,不能不引起生物学工作者的注目.

总的说来,根据我们的实验研究,已经有了一些比较系统的认识,可以概括地作如下的叙述:

1. 细胞重建是一个自组织(self-organization)、自装配(self-assembly)的过程. 只要具备组成细胞的物质基础和合适的环境,在生物体内,或在离体培养的不存在细胞的制备中,都有可能发生细胞重建或核重建.

2. 细胞重建在自然界内广泛存在. 不仅真核细胞能重建,原核细胞也能重建. 不仅生殖细胞能重建,胚胎的或成长个体的体细胞也能重建.

3. 在鸡胚卵黄颗粒内有DNA、组蛋白和染色质,在合适的环境下能重建细胞. 染色质不是细胞核独有的物质. 卵黄颗粒也不是没有生命的细胞内含物.

4. 细胞和细胞核可以从细胞质重建,说明细胞质、细胞核之间本来就没有森严的壁垒.

5. 细胞重建很可能是地球上细胞起源在今日生命世界的反映,是简单的生命形态发展为细胞的漫长过程的一个缩影. 细胞重建的研究,有助于生命进化的阐释.

6. 细胞分裂是"闭锁性"的繁殖,细胞在分裂过程中和它的环境是以细胞膜隔离的. 细胞重建是"开放性"的繁殖,在重建过程中细胞组分始终和周围环境打成一片. 把细胞分裂和细胞重建结合起来研究,把模拟和诱导自组装结合起来研究,对改变细胞的结构和性质,对改造细胞的性状,选优汰劣,控制定向生产,也就是说对促进和发展细胞工艺和细胞工程,将提供新的手段和途径.

关于这些,部分地在本论文集的各篇论文里分别作了报道. 另外还有五篇论文[1]已于1982年发表在《中国科学》B辑. 再有二十几篇论文在整理中,将编入论文集第二集.

我们做了一些工作,有的已经发表,有的写出了论文,有的正在整理,有的工作还在进行,当然还有大量工作要做. 继续要做的工作,有的属于广泛取证的性质,有的属于深入本质的探讨,有的则是新课题的开解. 例如,我们说细胞重建在自然界是广泛存在着的. 这里指的广泛,包含两个方面的内容. 其一,是广泛存在于各类物种. 目前我们的实验还只限于丰年虫、鸡、小鼠、沙眼衣原体、大豆根瘤菌. 它们包括了无脊椎动物、脊椎动物和微生物,但毕竟只有五种生物,需要在广阔的范围内进一步探索. 另一方面,细胞重建广泛存在于生物体的各个部分和各种生命过程. 我们研究了生殖细胞和体细胞的细胞重建. 各种组织的干细胞,以及创伤愈合、再生、变态等过程中的细胞繁殖增生是否也有细胞重建现象,值得注意.

具体地说,细胞自组装包括了细胞的自我合成,这是一种生物合成过程,可以在人工条件下模拟. 细胞的自组装和自我合成,对于细胞来说,最重要的是细胞核. 对于细胞核来说,最重要的是染色质和核膜. 关于染色质,我们做了些工作,对卵黄颗粒的DNA和组蛋白自组装为染色质,染色质相变成为染色体及其可逆性,作了分析和模拟. 但是这些工作与人工条件下系统地模拟染色质的自组装及其在细胞周期中的变化和离体情况下染色质的自我合成相去尚远. 关于核膜,我们认为它在分裂过程中消失(细胞分裂中期)和重新形成(末期)与微环境的变化有关. 我们准备用人工建立的微环境模拟核膜的消失和重建.

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1) 曹懋孙等,中国科学B辑,1982,9:798;陈楚楚等,同上,1982,10:888;李玉安等,同上,1982,11:1007;1982,12:1089;1982,12:0192.

另一方面,是细胞重建(自组装)的诱导问题. 诱导因素可能是多种多样的,可以是体内的,即自身诱导,也可以用各种环境因素人工进行诱导. 目前已在进行的是以某些物理因素对细胞自组装诱导作用的研究. 关于环境对细胞重建的影响,在诸多物理因素当中,我们尤其重视电场、磁场和重力场. 以重力场为例,失重或微重力对细胞的生长、繁殖、分化的影响是很显著的. 重力影响细胞贴壁,影响细胞间相互作用和细胞间粘连,以及细胞与任何背景的粘贴,而粘贴和粘连与核重建和细胞重建有关.这些问题在理论上和实践上都有重要的意义.

有一大堆问题摆在我们面前. 例如细胞重建与细胞分裂的关系如何? 在怎么样的条件下细胞以重建或分裂的方式繁殖? 已经观察到丰年虫和鸡胚的重建细胞是能分裂的. 原则上,重建的细胞是否都能分裂? 在进化的阶梯上哪种方式比较原始? 哪种方式比较进化? 肿瘤细胞的来源和繁殖与细胞重建有什么关系? 这些问题都需要回答.

所以,我们有大量的工作要做. 工作量大,涉及面广,对于已经完成的工作更需要及时总结. 本论文集的第一集已经延误四年了. 今后我们将在抓紧工作的同时努力做好论文的撰写工作,及时发表我们的研究成果.

我们的工作得到中国科学院基金的资助;本论文集的完成得到应幼梅和郑竺英同志在文字上加工,并提了许多宝贵意见,以及生物物理研究所的领导和同志们,尤其是电子显微镜室同志们的支持和帮助,谨此一并表示衷心的感谢!

贝时璋

一九八八年四月,北京

ON THE RESEARCH OF CELL REFORMATION

Early in the spring of 1932, I found an intersex strain of *Chirocephalus nankinensis*, which belongs to Phyllopoda of Crustacea, among the specimens collected in a paddy field of Songmuchang on the outskirts of Hangzhou. Intersex, which denotes the individual having characteristics of both sexes at the same time during a certain period of developing stage, in *Chirocephalus* has not been recorded before. The intersex of *Chirocephalus* could be divided into five types according to the extents of sexual inclination to male or female. The whole process of sex reversal of gonad was studied. During its reversal, the transformations of germ cells including cell deformation and cell reformation were observed and drawn down. In 1934, I reported the observation and my viewpoint of such phenomenon at a seminar in the Biology Department of Zhejiang University, where I held a post of professor. But, the report was not published until 1942[1] and 1943[2]. The reason of the delayed publication of the report was multiple. Firstly, under the turbulent circumstances of the Anti-Japanese war, Zhejiang University was wandering from Hangzhou into inland and was moving from place to place many times. Secondly, there was no suitable journal to which the scientific report could be submitted for publication. Until 1942, the report was not formally published on a newly established periodical *Science Record*. These reasons were all the objective facts, and the subjective reason is that I also felt some hesitation in publishing the report to the public because my observation and viewpoint would be a challenge to the traditional theory of cell proliferation. In my two papers[1),2)], I analyzed the deformation and reformation of germ cells during the sex reversal process about all five types of intersexes, descussed what its mechanism might be. I called this phenomenon the reformation instead of new formation because the reformation only means resurgence and the yolk granules possess all raw materials of the cellular constituents. When the cells deformed, the yolk granules were yielded, which in turn provided the reformation of cells with the raw materials. It suggests that when the material basis for cell restitution and a suitable environment exist, the cell may be self-reconstructed not through the way of cell division. But in the circle of biology, it is a traditional view that a cell comes from its par-

1) Pai, S., *Science Record*, **1**(1942), 187.

2) Pai, S., *ibid.*, **2**(1943), 573.

ent cell and the cell division is the only way of cell reproduction and proliferation. Therefore, the idea that the cell can be reproduced and proliferated by the way of cell reformation besides cell division would be considered as a profane conduct against the biological science. Some unfair words such as ridicule, ignorance or arrogance, etc. might be also imposed upon the idea. These doubts and misgivings should be beneath notice for the reports were published after all and did not incur censure. Perhaps somebody thinks that the cell reformation is not easy or frequent to observe if it exists. However, the traditional point of view is always accepted as an infallible law, the influence of which is wide and lasting. So, my research appeared to be an isolated example and was not enough to elucidate a general rule of cell proliferation. Since there was no response, my lonely feeling was hard to avoid and at that time I was busy at other work, so I could only put this research aside.

Time was slipping away fast and more than twenty years had elapsed when the study on cell reformation was started again in 1970. Since then, the research has entered a new period and had a new appearance as compared to that in the 1930s. In the past, the work was done mainly by one person, but now, we have established a research group in the Institute of Biophysics under the Chinese Academy of Sciences; in the past the experimental material was only one kind, i.e. *Chirocephalus nankinensis*, but now we use chicken embryo, mouse bone marrow, *Chlamydia trachomatis* and soy bean nodule bacteria besides *Chirocephalus nankinensis* as the studying materials. Light microscopic observation was the sole way used to study cell reformation in the 1930s, but now we have used many kinds of new techniques and methods such as electron microscopy, time-lapse microcinematography, phase contrast microscopy, radioautography, fluorescence polarization, energy transfer with double fluorescence labels, fluorescence recovery after photobleaching, Raman spectra and many other biochemical methods. On the basis of the past research work, we have acquired new discoveries and understanding about cell reformation. For example, we have found DNA, histones and chromatin in the yolk granules of chicken eggs. A new discovery that the yolk granules of chicken eggs possess chromatin has never been reported before in the biological science. Futhermore, the chromatin of yolk granules and that of nucleus have the same structure and behavior. The shapes of DNA molecules from both origins are similar too. The chromatin is believed, according to the traditional biology, to exist only specifically in nucleus, so the fact that the yolk granules possess chromatin cannot but attract the attention of the biological circle.

In conclusion, we have obtained fairly systematic knowledge on cell reformation through our experimental research. It can be summarized as follows:

1. Cell reformation is a process of self-organization and self-assembly. It is able to take place in organism *in situ* or in cell-free preparations *in vitro* only if there exist a material basis for cell restitution and suitable conditions.

2. Cell reformation exists extensively in the nature. It can be found not only in eukaryotic cells, but also in prokaryotic cells; not only in germ cells, but also in somatic cells of developing and adult animals.

3. The superficial yolk granules beneath the chicken blastoderm contain DNA, histones and chromatin, and can reform cell under suitable environments. It should be pointed out that the chromatin is not a specific substance belonging to nucleus only and the yolk granules are not merely a non-living inclusion of cell.

4. Cell and nucleus can be reformed from cytoplasm. It suggests that there is no strict barrier between nucleus and cytoplasm.

5. Cell reformation is probably the reflection of cell origin on the earth in the present living world. It is an epitome of the long progress of a cell from the simplest living form. The research on cell reformation would help to elucidate the evolution of life.

6. Cell division is a "closed" type of cell reproduction, when cells divide, they are isolated from their surrounding environment by a cellular membrane; while cell reformation is an "open" type of cell reproduction, during the whole process of cell reformation the constituents of cell and the surrounding environment are merged into one. So, if the study of cell division is combined together with that of cell reformation and the simulation of self-assembly is combined together with the induction of self-assembly, then they would provide a new approach of changing the cell structures and properties, selecting good qualities and eliminating harmful factors, controlling directive breeding, i.e. promoting and developing the cell technology and cell engineering.

Twenty-four reports in detailed description of a part of the research results mentioned above are selected into this compilation. Other five papers have already been published in *Scientia Sinica* (Series B) in 1983[1]. Also, more than twenty reports are in preparation, which would be selected into the second compilation.

Some of our researches have been published, some are being prepared for publication and some are in progress. Of course, there is still a lot of work to do in the future. Some researches in the future are expected to gain evidence more extensively, some are expected to explore the essence more deeply and some will be the new topics. We say that the cell reformation is a phenomenon extensively existing in nature. It includes two meanings herein. (i) The phenomenon exists in various species. Although we have used *Chirocephalus*, chicken eggs, mouse, *Chlamydia* and soy bean nodulus bacteria as the experimental materials in our lab which represent invertebrate, vertebrate and microbes, there are only five kinds of

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1) Bei Shizhang et al., *Scientia Sinica* (Series B), **26**(1983), 454; Bei Shizhang et al., *ibid.*, **26**(1983), 592; Bei Shizhang et al., *ibid.*, **26**(1983), 708; Bei Shizhang et al., *ibid.*, **26**(1983), 818; Bei Shizhang et al., *ibid.*, **26**(1983), 822.

organisms. It needs further exploration in a wider extent. (ii) This phenomenon extensively exists in various parts of organisms and happens in various living processes. We have studied the cell reformation of germ cells and somatic cells but it is worthy to note whether the processes of cell proliferation in the way of cell reformation do happen in stem cells of various tissues and during the wound healing, regeneration, metamorphosis, etc.

Actually, the cell self-assembly includes the cell self-synthesis. It is a biological process of synthesis (biosynthesis) and should be able to be simulated under artificial conditions. In the cell self-assembly or self-synthesis, the nucleus is the most important for a cell, and the chromatin and nuclear membrane are the most important for a nucleus. As for the chromatin, we have analyzed and simulated the process of self-assembly of chromatin from DNA and histones, and the phase changes of chromatin to chromosome and their reversibility. However, these studies are far from the systematic simulation of chromatin self-assembly under artificial conditions, that of chromatin change during cell cycles and that of chromatin self-synthesis *in vitro*. As for nuclear membrane, considering that during cell division its disappearance (as in metaphase) and its reformation (as in telophase) depend on the change of microenvironment, we are going to simulate the disappearance and reformation of the nuclear membrane by artificially established microenvironment.

In addition, there is also a problem about the induction of cell reformation (self-assembly). The induction factors may be various. Perhaps they are within the body, i.e. self-induction, or they are the environmental factors, i.e. artificial induction. Currently, we are conducting some researches using some physical factors to induce cell self-assembly. Considering the effect of environment on cells, we have paid attention to the physical factors, especially to the electric field, magnetic field and gravitational field. Take the gravitational field as an example, the effect of weightlessness or microgravity on the cell growth, proliferation and differentiation is great. Gravity effects on the cell sticky to the wall, on the cellular interaction and adhesion between cells, and the adhesion of cells to any back ground are closely related to the reformations of nucleus and cell. These problems have important significance in both theory and practice.

There is still a pile of problems facing us, such as, what is the relationship between cell reformation and cell division? In what conditions does a cell proliferate in the way of cell division and in the way of cell reformation? It is observed that the reformed cells in *Chirocephalus* and chicken embryo conduct cell division, but we wonder if all the reformed cells are able to conduct cell division. Which way of cell proliferation, cell reformation or cell division is more primitive in the evolutional scale? And which one is more advanced? What is the relationship between the origin of cancer cells and cell reformation? All these problems need to be answered.

Therefore, there is a lot of work to do. The amount of work is huge and it covers a extensive scope. The work done is necessary to summarize in time but I regret that this first compilation has been postponed for four years. We hope we would do our best in the future in researching, writing thesis, making manuscripts and reporting the results in time.

The work has been supported by a grant from the Chinese Academy of Sciences. On behalf of the authors of this compilation I wish to express our appreciation to the leaders and colleagues of the Institute of Biophysics, the Chinese Academy of Sciences, especially the colleagues in the Group of Electron Microscopy of this Institute for their kindest support, and we sincerely thank Ying Youmei and Zheng Zhuying who helped us review the drafts.

Bei Shizhang

April 1988, Beijing

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蓝碧霞　韩行采　赵希和　贝时璋

（中国科学院生物物理研究所，北京）

摘　　要

本文对鸡胚早期发育中的细胞重建和重建细胞的自组装作了描述．实验以受精鸡蛋未孵育和孵育不同时间的胚盘和胚下腔下表层卵黄以及布散在邻近各部分的卵黄球为材料，在整体原位上或离体培养后，进行光学和电子显微镜切片观察．实验结果表明，在鸡胚早期发育中，细胞重建现象是广泛存在的．早期重建的细胞，主要是成下层细胞和卵黄囊细胞．

30 年代初，本文作者之一在甲壳类动物南京丰年虫（*Chirocephalus nankinensis*）二倍体中间性的性转变过程中，观察到细胞重建（cell reformation）现象[1,2]．过去从细胞繁殖增生的传统观点出发，人们总是集中研究细胞分裂，尤其是有丝分裂，对于细胞繁殖增生的其它途径，没有更多的注意．

最近十多年来，关于“小细胞”（minicells）、“微细胞”（microcells）的制备和细胞质体（cytoplasts）与核质体（karyoplasts）的融合，以及对于它们的性质、存活力等的研究，开展了大量的工作（Veomett, et al.[3]; Ege, et al.[4,5]; Lucas 和 Kates[6]等）．通过折合的手段产生了重建细胞（reconstructed cells），这与我们提出的重建细胞（reformed cells）含意是不一样的．前者是由原来细胞的一部分，或者部分与部分的融合或“杂交”产生的．我们所说的重建细胞是生物体的一定部位，在一定时期，在具备组成细胞的原料和条件时，一步一步地重新建立起来的细胞．这是生物体内自己组装细胞，自己合成细胞的一个过程，是细胞繁殖增生的另一途径．

近年来，关于自组织、自装配问题，各国学者进行了很多讨论．最近，Forbes 等[7] 和 Newport 等[8] 通过实验发现非洲爪蟾的卵在注射微量噬菌体 DNA 后，卵内的噬菌体 DNA 周围形成了核状结构．他们把爪蟾卵制成无细胞的提汁，在提汁内加入噬菌体 DNA 进行培养，结果在 DNA 周围也重建出核结构．他们称这种自组装现象为“自然形成”（spontaneous formation）、“自然装配”（spontaneous assembly）．

1970 年以来，我们在南京丰年虫生殖细胞重建的研究中[9－12]，曾证实了细胞重建现象的客观存在．本文以鸡胚早期发育中胚下腔下表层卵黄（简称胚下表层卵黄）为主要

对象，观察细胞重建及其自组织、自装配过程，阐明细胞重建现象在胚胎发育的体细胞繁殖增生中也是广泛存在的.

一、材料和方法

1. 实验材料 莱杭鸡蛋，受精未孵育或孵育不同时间. 孵育温度为 37°C.

2. 电子显微镜标本制备 蛋黄固定在 1% 福尔马林中两天以上. 经流水冲洗，用 2.5% 明胶浸透，冰冻，取出所需部位，固定于 1% 四氧化锇. 经乙醇脱水，Epon 812 包埋，醋酸双氧铀和柠檬酸铅双重染色，用 JEM-7 型电子显微镜观察、摄影.

3. 离体培养 未孵育的鸡胚盘及其下表层卵黄，放入 Tc-199 培养液（加 15% 小牛血清、青霉素 100 单位 /ml、链霉素 100μg/ml）中. 在不同时间培养后，作电子显微镜切片或相差显微镜观察.

4. 光学显微镜制片 未孵育或孵育不同时间的鸡胚及其表层卵黄，固定于 Bouin, Clarke, 氯化汞或 Susa 固定液中，石腊包埋切片，切片厚度 5 — 7μm，孚尔根、铁苏木精 - 伊红或番红 - 亮绿等染色.

二、结果和讨论

1. 鸡胚早期发育中的细胞重建

刚产下的受精未孵育鸡蛋，胚盘中的细胞可分为成上层细胞和成下层细胞. 图版 I-1 示未孵育鸡胚盘接近居中的下部分切面，可以看出成下层细胞的来源与胚下表层卵黄的关系. 在胚下表层卵黄中有不少核状结构呈孚尔根阳性反应（小箭所指）. 这些都是分布在卵黄中的裸核. 裸核的形成与卵黄关系密切，我们称它为卵黄的重建核. 用电子显微镜观察未孵育胚盘，也可见裸核和成下层细胞的形成与胚下表层卵黄的关系（图版 II-2, 3）. 图版 II-2 为受精未孵育鸡蛋胚下表层卵黄一个切面，视野中可看到四个发育程度不同的核结构（小箭）. 其中一个（箭头所指）较小，电子密度较浓，这是新形成的裸核，核膜比较模糊，是一个原始的重建核. 图版 II-3 示脱离了胚下表层卵黄（箭头）的成下层细胞（长箭）. 这里原来是一个成下层细胞，已割裂（fragmentated）为两个（小箭）. 细胞核很原始，电子密度很浓，核膜隐约可见（长箭所指）.

未孵育鸡胚的成上层和成下层细胞位置有上下，体积大小不同，核的形态结构也不一样. 成上层细胞核多呈圆形，电子密度较稀（图版 III-4, N），而成下层细胞核多不规则，当其初形成时电子密度较浓（见图版 III-5 a, b 中的 N）. 成上层和成下层细胞都含有较多的大小卵黄颗粒，尤其是成下层细胞. 值得注意的是，当成上层（图版 III-4）和成下层细胞（图版 IV-6）的卵黄颗粒处在演变时，可以看到各种发育阶段. 图版 IV-6 示 7 个成下层细胞通过丝状足（filopodia）相连或直接连在一起. 在图版 IV-7 中可见成下层细胞的表面伸出典型的丝状足（见箭头），但重建核的结构比较原始，核膜仅隐约可见. 从图版 III-5a 和 b 还可以见到成下层细胞也正在发生割裂（小箭所指）. 就这两个切面看，可能将割裂成 3 个（图版 III-5a）和4 个细胞（图版 III-5b）. 由于卵黄颗粒多，胞质稠密度大，通个割裂形成新的质膜可能是细胞重建的重要方法.