SCIENCE

Vol. LVII   May 11, 1923   No. 1480

SCIENCE: A Weekly Journal devoted to the Advancement of Science, publishing the official notices and proceedings of the American Association for the Advancement of Science, edited by J. McKeen Cattell and published every Friday by

THE SCIENCE PRESS

100 Liberty St., Utica, N. Y.   Garrison, N. Y.
New York City: Grand Central Terminal

Annual Subscription, $6.00.   Single Copies, 15 Cts.

Entered as second-class matter January 21, 1922, at the Post Office at Utica, N. Y., Under the Act of March 3, 1879.

DYSTROPHIC MORPHOLOGY AND ITS SIGNIFICANCE[1]

Among the environmental factors which influence the structure and functions of the living organism, nutrition is of primary importance. One of the most fruitful methods of studying the process of nutrition is that of inanition. By withholding or decreasing the normal diet (total inanition) or merely one or more of the essential nutritional elements (partial inanition), we may observe effects which throw much light upon the normal process of nutrition from the standpoint of physiology, of pathology or of normal morphology. It is with the morphological aspect of the problem that we, as anatomists, are primarily concerned. We desire to learn the significance of the form and structure of the living organism and the factors concerned in its morphogenesis.

Experimental work by many investigators in this field during the past century has resulted in a large number of widely scattered data concerning the effects of inanition upon the growth and structure in numerous species. These effects of inanition have been extensively and carefully studied, not only in the vertebrates, but also among the lower organisms, the invertebrates and the plants. It may therefore be profitable to review briefly some of the principal results of inanition in these lower forms, partly because they are less well known to anatomists in general and partly because certain aspects of the problem are more clearly revealed in these simpler organisms. In general, only those phases will be considered which appear of most significance in comparison with the results in the higher animals, including man.

EFFECTS OF INANITION IN PLANTS

Plants in general, much more than animals, appear susceptible to modification by various

[1] Presidential address, American Association of Anatomists, Chicago, March 29, 1923.

external factors, including the food supply. It is difficult to summarize briefly the principal morphological effects of inanition upon plants on account of the wide range in the character of these organisms and the great differences in their mode of nutrition. In general, however, it is clear that the effect of inanition is to restrict or inhibit their growth during the developmental period, often resulting in premature development with the production of marked abnormalities of form and structure. In the poppy (*Papaver*) an inheritance of some of the experimentally produced variations is claimed (De Vries, Hoffman, Rignano). In later stages the plants are usually less susceptible; but sooner or later a deprivation of nutriment will usually produce protoplasmic atrophy and progressively degenerative changes in the cells and tissues, finally resulting in the death of the organism. Of the cell constituents, the formed storage products (starch, oil, etc.) are usually consumed first; then the cytoplasmic structures are attacked; lastly the nucleus, which is the most resistant.

These effects are produced not only by general or total inanition (either complete or incomplete) but also often in a strikingly characteristic manner by partial inanition, when there is a marked deficiency of only one (or a few) of the numerous essential factors of plant nutriment. Lack of any one of these factors—water, calcium, potassium, magnesium, iron, phosphorus, sulphur, manganese, nitrogen, carbohydrates and possibly vitamins—will cause stunting of growth with variable degenerative cell-changes. These are expressed by morphological and physiological derangements, often resulting ultimately in the death of the organism. The effects are apparently most severe in the case of phosphorus or nitrogen deficiency.

In addition to the deleterious effects more or less common to all these partial deficiencies, there are in each case certain peculiarities due to the special functions which each of the food-elements normally performs. These peculiarities appear also to vary considerably in different classes of plants.

Thus water deficiency is usually expressed promptly by characteristic changes in form and structure of plants on account of its fundamental importance in morphogenesis and vital structure, as well as in transportation. Of the various salts, those of calcium, potassium and magnesium are especially essential for chlorophyll production and starch formation. Phosphorus appears to be more concerned with the transformation than with the origin of carbohydrates. Cellulose formation proceeds in the absence of phosphorus, but is impossible without calcium. Mitosis may occur in the absence of calcium or of magnesium, but not without potassium or phosphorus. The process of inflorescence and the development of the sexual organs in general appear to be unusually susceptible to the effects of malnutrition and in some cases (especially in fern prothallia) a deficiency of calcium or nitrogen may influence sex by inhibiting the development of the female organs (archegonia).

EFFECTS OF INANITION IN PROTOZOA

Some of the more important results of inanition among the protozoa may be indicated briefly in relation to changes in body size, endoplasm and ectoplasm, nucleus (macronucleus and micronucleus), reproduction (cell-division and conjugation) and recovery upon refeeding.

Change in size and form of the body—All the evidence shows a marked reduction in the size of protozoa during inanition. The maintenance of the original size in *Noctiluca* is merely apparent, the increase in peripheral vacuoles masking the decrease in cytoplasm. The recorded data indicate a decrease in length to about one half of the original in *Paramecium,* one fifth in *Stentor* and one tenth in *Dileptus* and *Pleurotrichia.* Thus in these extreme cases the volume may be reduced to less than one per cent. of the original. The rapidity of the loss varies according to temperature. There are also more or less marked and variable changes in form accompanying the diminution in the size of the body.

Changes in the endoplasm—The cytoplasmic changes at first appear chiefly in the endoplasm, which becomes progressively reduced in amount and transparent, on account of the disappearance of the food-vacuoles and similar inclusions. In the later stages of inanition a progressive vacuolation of the endoplasm has been described in various species by all recent observers except Lipska. Such vacuolation of the endoplasm apparently does not occur in *Noctiluca* and *Pleurotrichia,* however, and Lipska's results indicate that even in *Paramecium* it is probably only an indirect effect of inanition, being due primarily to other environmental factors.

Changes in the ectoplasm—In all cases the cell-membrane and associated ectoplasmic structures (cilia, trichocysts, cytopharynx, etc.) appear more resistant than the endoplasm, but in the later stages of inanition they also may be attacked and partially resorbed. Associated with these regressive changes there is a progressive decrease in motility and in other vital phenomena.

Nuclear changes—The nucleus in general is much more resistant than the cytoplasm, but may show changes in form with loss of chromatin content. In forms such as *Paramecium,* with macronucleus and micronucleus, the former shows more distinct changes. In the earlier stages of inanition it frequently elongates and enlarges. Later it usually divides and may show degenerative changes, with granulation, vacuolation, fragmentation and variable extent of resorption. The micronucleus usually persists practically unchanged, although rarely it may divide with reunion of the daughter nuclei. This persistence of the nucleus is a factor of great importance for the survival of the organism during periods of inanition. The less important constituents of the organism are usually consumed first, the most essential apparently survive longest. The persistence of the nucleus during starvation recalls a similar behavior when living cells are engulfed and digested (*e.g.* by *Trichosphaerium,* according to Schaudinn) and in trypsin digestion experiments upon dead cells. This may be of significance as indicating the presence of similar enzymes during the autolysis of cells in starvation.

Effects on reproduction—The relations of inanition to reproduction in protozoa have attracted much attention. Many observers have noted an apparent stimulus to division resulting from a brief period of starvation. R. Hertwig, however, observed that while under certain conditions fasting protozoa may divide more readily than well nourished, as claimed by Jickili and others, this does not occur as a general rule. In *Paramecium,* which has been more extensively studied, divisions occur to a variable degree in the early stages of inanition, but rarely or never in the later stages. According to Hertwig's theory, inanition upsets the cell-equilibrium as expressed by the nucleus-plasma ratio; but the relative increase in the nucleus may be equalized later by a reduction in chromatin, associated with the process of conjugation.

Rolph, who proposed a nutritive theory of sex, claimed that conjugation occurs in protozoa when conditions result in an interference with their nutrition. Thus sex is considered as primitively a form of hunger, which drives the organism to engulf its neighbor ("isophagy"). A similar theory of sex was elaborated by Geddes and Thompson. The studies of Maupas and of numerous more recent investigators, however, have shown that the life cycle of the protozoa, with its phases of sexual and asexual reproduction, is apparently a very complicated process, involving both internal and external factors. Among the latter, inanition is doubtless an important factor, which under certain conditions may induce conjugation. This was observed by Maupas and others in numerous species of Infusoria. Hertwig discovered that when low temperature cultures (which have a relatively large nucleus) are placed at a high temperature and kept without food, an artificial depression is produced which leads to conjugation. This was confirmed by Prandtl for *Didinium,* and by Popoff for *Epistylis.* Conjugation has been observed in the earlier stages of ordinary inanition in *Paramecium* by Kasanzeff, Wallengren and Chainsky; but Calkins and Lipska found inanition very unfavorable to conjugation. It is evident that further research is necessary in order to clear up this fundamental problem.

Recovery upon refeeding—The protozoa show an astonishing capacity for recuperation upon careful refeeding after inanition. Maupas found that an atrophic *Stentor* regained its original size in two days of abundant realimentation, which evidently involved an increase of over one hundred times its reduced volume. Joukowsky observed a similar remarkable capacity for recuperation in *Pleurotrichia.* In *Paramecium* Wallengren found a normal recovery possible, even in the greatly vacuolated condition after fifteen days of inanition. Lipska, however, found recovery in general possible only up to four or five days of inanition. The process of recovery is the inverse of that during inanition, and cell-divisions begin after three to five days of refeeding. Jennings noted that variability in size is increased during refeeding, some individuals recuperating more rapidly than others; but the normal condition is eventually restored.

EFFECTS OF INANITION AMONG THE HIGHER INVERTEBRATES

Although it is impossible to summarize satisfactorily the effects of inanition upon such a large and varied group of organisms as those represented by the metazoan invertebrates, it may be profitable to review briefly some of the principal features involved.

Effects on body weight and size—As pointed out by Pütter, the possible decrease in dimensions during inanition is much less in those forms having a firm skeleton (*e.g.*, Arthropoda). The maximum possible reduction in body weight and size varies greatly among the higher invertebrates, ranging from fifteen or twenty per cent. in some Arthropoda to over ninety per cent. in some coelenterates and planarians. Among coelenterates, *Hydra* is reduced to one seventh or less in length; the jellyfish *Aurelia* to one fourth and *Cassiopea* to one twenty-fifth of the original volume. Planarians (flatworms) may be reduced one twelfth in length and to one three hundredth in volume. In the snail *Helix,* the loss in weight apparently varies from eleven to fifty per cent. or more, according to species and conditions, with much individual variation. Among the Arthropods a loss of seventy-five per cent. in weight is recorded for the water-flea *Daphnia* and of fifteen per cent. for the crayfish *Astacus*. Great variation has also been found among the insects.

There are relatively few data on the loss during inanition in larval stages. The larvae of the sea-urchin *Strongylocentrotus lividus* may decrease to half the diameter of the original ovum. *Chortophaga* nymphs lose twenty to twenty-five per cent. and the tent-caterpillar (*Clisiacampa*) thirty-five per cent. The remarkable reduction (to one six hundredth) in the larva of the beetle *Trogoderma* is apparently exceptional. The loss during the pupal stage in general appears relatively slight.

Effects on the form of the body—During inanition the body is not only reduced in size, but also frequently more or less changed in form. *Hydra,* for example, becomes at first abnormally elongated, later greatly contracted and relatively broader. The water-flea *Daphnia* presents a peculiar modification of body form attributed to malnutrition and said to be hereditary (Woltereck). In the sponges, the coelenterates and the planarians the changes are remarkably great, not only in external form but also in corresponding internal structure. The so-called "reduction" process in these forms more or less resembles a reversal of the developmental process, which will be discussed later. In planarians the involution frequently involves the posterior portion of the body to a greater extent, resulting in a relative enlargement of the head region. This is also true of the nemertine worm *Lineus lacteus,* but not of *Lineus ruber,* which illustrates the differences which may occur between species.

Changes in various organs and tissues—It is a remarkable fact that the various organs and tissues of the invertebrate body differ greatly in their resistance to inanition. Some undergo changes very quickly, others only after longer periods, and still others show a remarkable resistance. There are also differences in the extent of atrophy, as well as the order of sequence.

In the medusa *Cassiopea* the loss is almost entirely at the expense of the gelatinous ground substance; while in sponges, on the contrary, this substance is increased in amount. The ectodermal structures are more resistant but they atrophy to a variable extent in different regions. In planarians the intestinal epithelium, eyes, pigment tissue and sexual duct systems are affected relatively early; the muscles atrophy later, while the gonads and nervous system persist with great tenacity. In *Lineus* the relative resistance of the various tissues is somewhat similar to that in planarians. Although among the higher invertebrates the skeleton is usually unaffected by starvation, in the snail *Helix* the calcareous shell is attacked as well as the soft tissues; while in sponges the results appear variable. Calcium deficiency usually causes involution of the invertebrate calcareous skeleton, both in larval and adult stages. In the reproductive passages of *Helix* the non-glandular parts appear more resistant than the accessory albuminous gland, which undergoes an enormous involution. While the gland cells are greatly reduced, however, the associated "parenchyma" (stroma) nuclei persist and proliferate by amitosis.

Effects on the gonads and sex—The effects of inanition upon the reproductive system and process have aroused much interest and have been carefully observed in various invertebrates as well as in other organisms. In forms where the process of reproduction may be either asexual (by budding, fission or parthenogenesis) or sexual, the tendency of abundant nutrition is to favor asexual reproduction; while inanition or other unfavorable environment usually occasions a change to the sexual form, in many cases especially favoring the development of males. The gonads themselves are usually very resistant to starvation, being (like the nervous system) as a rule among the last of the organs to undergo involution. There are, however, evident variations in different species and individuals.

Among sponges the process of involution during inanition frequently results in the formation of numerous small bodies ('gemmules'), from which new individuals may be reproduced later. In *Hydra* budding is inhibited but the gonads, especially the testes, may mature in spite of the atrophy of the body as a whole. The predominating development of testes in *Hydra* during inanition was emphasized by Nussbaum, Schultz and Berninger, but was denied by Hertwig, Whitney, Hänel, Krapfenbauer and Frischholz.

In planarians asexual reproduction is inhibited by inanition and there is a return to sexual reproduction; but the 'cocoons' are reduced in size and the number of enclosed young markedly diminished. In the nemertine worm *Lineus* the gonads undergo partial involution, but some areas (likewise the ducts) are very persistent.

In the rotifers (wheel-animalcules) Leydig noted that inanition causes prompt atrophy of the ovary and a tendency to production of males. Nussbaum concluded that in the rotifer *Hydatina* underfeeding in the *phase preceding the ripening of the ovum* tends to produce male offspring. This was confirmed by Lennsen but opposed by Whitney. Shull concluded that sex in *Hydatina* is determined by both internal and external factors, but that the production of males during inanition is probably only an indirect effect.

The relation of nutrition to sex has also been studied extensively in the crustacean water-fleas by Leydig and others. The change from parthenogenetic to sexual mode of reproduction under unfavorable conditions (especially inanition) in this group was noted by Kerhervé, Cuenot and Issakowitsch. More recently, the internal factors have been emphasized, although it is admitted that the hereditary tendency may be influenced by external factors, such as malnutrition, especially during the labile period of the ovum. Green recently concluded that in *Simocephalus* the sex is probably predetermined in the ovary, but is also subject to environmental influence, though probably not through starvation.

Among the insects the relations of nutrition to sex have been noted especially in the aphids (plant-lice), the Lepidoptera and the Hymenoptera. The appearance of winged male forms in aphids as a result of underfeeding was noted by Kyber (1813), Leydig and others. The same phenomenon in the grape-louse *Phylloxera* was found by Keller and Behr. Thus apparently all observers admit the effect of unfavorable environment, especially underfeeding, in causing the cessation of parthenogenesis and the appearance of males and sexual reproduction among the aphids. The conditions in this group therefore form strong evidence supporting the theory of nutritional sex-determination.

In the Lepidoptera, Treat observed a preponderance of males as a result of underfeeding the larvae of certain butterflies. This was not confirmed by Poulton, although he admitted that a lesser resistance to inanition in the female larvae might result in a selective mortality with survival of a relatively larger number of males. This, of course, is not strictly a process of sex-determination, but rather of sex-survival. In the underfeeding experiments by Kellogg and Bell on the silkworm *Bombyx* and by Guyénot and Loeb and Northrup on the fruit-fly *Drosophila,* no effect on the sex-ratio was observed.

Among the termites and Hymenoptera the sex is known to be determined by fertilization, the unfertilized eggs producing the males. The diet, however, determines the development of the female reproductive tract, which in the few larvæ well-fed (with "royal diet") becomes functionally developed, producing the "queens"; while in the less richly nourished larvæ the reproductive tract remains rudimentary, producing the "workers" of which there may be different kinds, depending upon the amount of food available. There is some evidence, however, indicating that in wasps (and possibly other Hymenoptera) the sex-ratio may be affected by nutrition, but this is somewhat uncertain.

Among the invertebrates in general we may therefore conclude from the available evidence that malnutrition tends to favor the sexual, rather than the asexual, mode of reproduction. Furthermore, especially in Hydra, rotifers, daphnids and aphids the sex-ratio is at least to some extent subject to environmental influence, inanition tending to produce a preponderance of males. Wilson concluded that nutrition is one factor which may determine sex. Schultze reached this conclusion for Hydra and Hydatina, but felt less certain regarding the daphnids and aphids. How this influence becomes effective, however, is still a matter of uncertainty. The whole question requires further investigation, especially in the light of the recent theory of sex-determination by the accessory chromosome.

Effects on cell structure—We have noted that the effect of inanition is to produce a variable decrease in the size of the body as a whole, which is found to involve a variable reduction in the various parts, organs and tissues. This, of course, depends ultimately upon the changes in the underlying units, the component cells of the organism. Some cells are destroyed and absorbed, others persist more or less changed. From his study of the histological changes in *Hydra* and planarians during the involution process of inanition, Schultz inclined to attribute the marked decrease in size of the body to a decrease in the number of cells, those persisting being practically unchanged in size. The preponderance of evidence is against this view, however. Especially in the adult organism, all the cells of the body during inanition tend to undergo more or less atrophy. The extent and character of this atrophy vary in the different tissues and in different cells of the same tissue. The decrease in the size of the body is therefore due partly to the complete disappearance of cells and partly to an atrophy of those persisting.

During the process of atrophy the cytoplasm of the starving cells undergoes in general a series of characteristic changes, first losing its stored food material, pigment, mitochondria and various inclusions. Later the cytoplasm of the cells often fuses into a syncytium. Vacuolation usually appears, with progressive decrease in amount of the cytoplasm, and terminal disintegration with complete absorption in the case of some of the cells. There is usually an earlier stage of reduction in size (simple atrophy) and a later stage of degeneration.

The nucleus is usually more resistant than the cytoplasm, giving a higher nucleus-plasma ratio. At first the nucleus may even enlarge, but later it tends to shrink (pycnosis) with perhaps ultimate fragmentation, karyolysis and final absorption. The reduction in cytoplasm and relative increase in nuclear size frequently gives the atrophic tissue an embryonal appearance.

Some further special features in the atrophic cell changes may be reviewed briefly. As noted by Terroine from the chemical viewpoint the fat changes show great variation among species and individuals. While fat in general is quickly absorbed during inanition, in the vitelline gland cells of planarians it is tenaciously retained, disappearing only when the cells undergo final necrosis. In planarians and molluscs the nerve cells may show certain degenerative changes, although the nervous tissue as a whole is remarkably resistant. It may be noted that apparently the final absorption of the degenerated cells in the various tissues is usually accomplished by simple solution in the interstitial tissue fluids; although phagocytosis has been noted in sponges, sea-urchin larvae and especially in the case of the nemertine worm *Lineus*. The process of phagocytosis is said to occur also in the metamorphosis of insects.

Some specific changes in cell-structure are noted during various forms of partial inanition. Thus calcium deficiency may loosen the intercellular attachments but it does not affect the ciliary mechanism and apparently permits mitosis to continue in the embryonic tissues of various invertebrates. Phosphorus and potassium, however, are evidently necessary for mitosis, as in plants. In addition to the mineral salts, certain proteins, fats or carbohydrates, water, etc., are doubtless essential to life, but we have as yet little data upon the morphological effects of their deficiencies among the higher invertebrates.

Effects on the developing organism—The effects of inanition upon the developing invertebrate organism, especially during the earlier embryonal stages in many respects often differ markedly from those previously described for the adult. The embryonal cells have a characteristic tendency to growth and differentiation which may enable certain organs and tissues not only to persist but even to enlarge and develop at the expense of the remainder of the starving organism. This is true for general inanition and is also especially evident during various forms of partial inanition. Thus in many cases it is evident that a deficiency in one limiting factor does not necessarily altogether inhibit the development of the invertebrate organism when that factor is exhausted, but occasions instead a disproportionate, abnormal growth, the extent and character of which will vary according to circumstances.

On the other hand, in many cases the developing embryo or larva (in some species even the adult organism) tends to undergo during inanition a series of retrogressive changes more or less reversing the normal order of development. This process (technically called 'reduction') was apparently first described by Lillie (1900) in *Planaria maculata*. It is often well marked in sponges, coelenterates and planarians, though apparently rare in the more highly organized invertebrates. Even in the lower invertebrates, however, there is some question as to whether the (often remarkable) resemblance of the atrophic organism to the earlier embryonic stages may not be more apparent than real. But in many cases these atrophic remnants are actually able, under proper conditions of nutrition, to regenerate the normal structure of the organism. Child concludes that starvation results in morphological rejuvenation, followed by physiological regeneration upon refeeding.

The relatively great resistance to inanition usually offered by the gonads has already been mentioned for adults. This applies also in some cases to the developing organism, so that sexual maturity may occur in undersized bodies as a result of underfeeding (*e.g.,* silkworm and certain bees). But in others (starfish) sexual maturity is reached only upon the attainment of a certain body size, or the development of the gonads may even be entirely inhibited by inanition (fruitfly).

The sex of the offspring, as already mentioned, may also be influenced through the effect of inanition upon the germ cells in the larval stages, particularly at certain critical periods (rotifers, daphnids, aphids, etc.). In some insects sexual maturity appears to be determined entirely by larval nutrition, in others chiefly by the adult nutrition.

Underfeeding during the larval period may also result in undersized adults (various insects) and also sometimes in marked structural modifications (pigmentation, etc.). In some cases these acquired characters appear hereditary, at least for a few generations (as found by Woltereck, Pictet, Kellogg and Bell); although ultimately upon adequate diet there is an evident tendency to return to the original condition.

The experiments with media or diets variously deficient have shown that compounds of P, K, Na, Ca, Mg, Fe, S and Cl appear necessary for development, growth being inhibited or variously perverted when the amount stored in the ovum is exhausted, unless a supply from without is available. Remarkable results in this field have been obtained by Herbst, Loeb and others. The marvelous effect of fat upon the development of the reproductive tract in the female Hymenoptera also illustrates the morphogenetic potency of a single dietary factor. As to other forms of partial inanition, Baumberger holds that protein is in general the limiting factor in the growth of insects. The fruitfly *Drosophila* apparently requires yeast as well as sugar for growth and other insects living on fermenting substrata of low protein content usually feed on the micro-organisms present. Little or nothing is known concerning the possible requirement of vitamins by the invertebrates in general.

Regeneration during inanition—In many of the invertebrates indications of regenerative activity may be observed in certain cells or regions during the degenerative process of involution. Driesch noted that the reserve materials of the body which are consumed during starvation may be used to build up other parts of the organism. Thus in daphnids, crustacea and insects repeated ecdysis (moulting) with regeneration of a new exoskeleton and appendages may occur during total inanition. This regenerative process occurs notably in the lower invertebrates such as the sponges and coelenterates and has been studied especially in planarians by Morgan, Schultz and others. Here the starving organism exhibits the remarkable capacity to regenerate large portions of the body, such as the head, with all its parts, pharynx, nerve ganglia, musculature and excretory system. Thus even during starvation regeneration may restore a complete normal individual of much smaller size. In this process there is an extensive involution of the older tissues to furnish material for the regenerated parts.

Recovery upon refeeding—In general it is possible for the starving invertebrates to recover their normal size and structure upon appropriate refeeding if the process of involution has not proceeded too far in degeneration. This applies also to partial inanition. In sponges, for example, the skeleton is reformed upon restoring calcium carbonate to the medium. In planarians regeneration of the gonads is possible even when they have nearly disappeared after three or four months of inanition. In the gland cells of the snail *Helix* starved five months, evidences of recuperation were found by Krahelska even after only two days of refeeding. *Drosophila* (fruitfly) larvae are capable of normal development even after long periods of retardation on inadequate diet; and in this form, as likewise in the larvae of the beetles *Trogoderma* and *Tribolim,* the normal period of life may be greatly extended by retarding the developmental process through alternate periods of fasting and refeeding. Underfed larvae of the moths *Acronyeta* and *Bombyx* produce smaller pupae and adults, the effect in the case of *Bombyx* being carried over to the second and third generations.

COMPARISON WITH VERTEBRATES

Comparison of the results of inanition among plants and invertebrates with those found in vertebrates reveals many differences. Especially in the degree of change the vertebrates appear in general less plastic and more resistant to inanition, as to environmental influences in general. Thus while many invertebrates may survive a loss of ninety per cent. or more in weight, vertebrates usually perish when the loss reaches forty per cent. Likewise there are found among vertebrates no such radical and profound changes of structure as may occur during inanition among plants and many invertebrates, especially in those which undergo the remarkable process of "reduction."

On the other hand, amidst the diversity of phenomena resulting from inanition in the various plants and invertebrates we find certain features in essential agreement with those occurring among vertebrates, indicating a fundamental resemblance in the reactions of all living organisms. This applies not only to the general atrophy of the whole body, but also to the variable extent and character of change in different parts and organs. Thus the nervous system and (usually) the skeleton are relatively resistant to inanition in both vertebrates and invertebrates. The variable losses in the different parts of the body lead to marked abnormalities of form which differ greatly according to circumstances.

During the development in both animals and plants, inanition (especially of the chronic type) frequently results not merely in a retardation or cessation of growth, but in an abnormal, disproportionate growth, which differs greatly according to the species, stage of development, type of inanition and other factors. Some parts may show persistent growth at the expense of others, even during total inanition with continued loss in body weight. This applies likewise to various types of partial inanition. The abnormal growth occurring in the absence of certain dietary elements necessary for normal nutrition is contrary to Liebig's "law of the minimum or limiting factor" according to which (as narrowly interpreted by some authors) growth should cease when any factor essential for normal growth is exhausted. Whatever may be the influence correlating the relative growth of the various organs and parts this correlation may be markedly changed during total or partial inanition and the process of morphogenesis is accordingly subject to experimental control.

The possibility of regeneration and recuperation upon refeeding after inanition, although more strikingly evident in the lower forms, is characteristic of all living organisms. Although the effects of inanition vary widely in different cases, up to a certain stage of severity perfect recovery is possible; beyond this only partial recovery (or none at all) is possible, resulting in permanently dwarfed and stunted forms. The age at the time of inanition is very important, there being critical periods at which the various organs are most susceptible to change through inanition and other environmental factors. This is strikingly illustrated in the case of the effects upon the sex glands and possibly sex determination.

These various changes observed in the dystrophic organism are associated with changes in the constituent cells. The relative loss in cytoplasm and the resistance of the nucleus during inanition are characteristic in all plants and animals. The general result is to reduce the cell to a more embryonal type of structure with a modified nucleus-plasma ratio, which may perhaps in part explain many of the curious resultant changes in form during dystrophic growth. While mitosis is usually inhibited during inanition, it may persist with great tenacity in those organs in which growth continues.

While the cells during inanition are reduced to an embryonal condition, from which recovery is possible upon refeeding, they do not so remain permanently. Sooner or later, in all living organisms, they pass from a stage of simple atrophy to a condition of degeneration. The cytoplasm typically undergoes cloudy swelling, with subsequent fatty or vacuolar degeneration. The nucleus, though relatively more resistant, also later undergoes progressive degeneration, usually with pycnosis and finally karyorrhexis or karyolysis. It is apparent that the above mentioned possibilities of recovery depend chiefly upon the degree of cell injury which has been sustained. Cells which have undergone extensive cytoplasmic and especially nuclear degeneration are obviously unable to recuperate. There are always great individual differences, however, even among cells of the same organ, so that some may remain capable of regeneration even though others have degenerated beyond the stage of possible recovery.

The question as to why certain cells or organs have a greater resistance to inanition has received various answers. Roux has long held that during inanition those cells persist which require less food in the struggle for existence. This theory was opposed by Schultz and others who claimed that the order of disappearance of the (invertebrate) organs reverses the order of their appearance during ontogenetic and phylogenetic development. Another view widely held is the teleologic explanation that those organs persist longest which are most valuable to the organism or species. All such theories, however, appear inadequate to explain the facts observed. Runnström (for sea-urchin larvae) proposed a more rational theory, explaining the morphological changes upon the basis of the varying physico-chemical conditions in the starving organism. Future investigation along this line will probably give better comprehension of the phenomena involved.

The question may also be raised as to why the degenerative changes in the various cells during inanition are so similar, not only in the various types of total and partial inanition, but likewise in many other abnormal conditions, such as extremes of temperature, fatigue, toxic or electrical stimuli, etc. Various answers to this question are possible, but the most probable would appear to be that the effects are similar because these all represent conditions which obstruct the normal cell metabolism, thereby causing the same degenerative cell changes. The fundamental similarity in the cellular results of such varied conditions recalls the dictum of Cuénot that "la plupart des influences de milieu se ramènent en somme à des différences de nutrition."

Nutrition therefore becomes a factor of primary importance for morphology as well as for physiology. The form and structure of all living organisms are clearly dependent in large measure upon the quantity and quality of their nutriment. The effects of inanition of various types apparently account for many of the variations observed among living organisms, under both normal and abnormal conditions. A knowledge of these effects gives a deeper insight into the process of morphogenesis and a means whereby it may be experimentally controlled to a degree hitherto generally unrealized. Furthermore, even though it be contrary to the generally accepted biological doctrine, there is another possibility which must be considered. Not only the somatoplasm, but under certain circumstances even the germ plasm may perhaps likewise be modified by nutritional conditions, a possibility of fundamental significance for heredity and evolution.

CLARENCE M. JACKSON

A RESEARCH CAREER IN ASTRONOMY

WIDELY different types of investigation are now included in astronomy, and only the most general remarks would apply to all of them. For the student who is considering a professional career in astronomical research it may be useful to outline the various branches from the standpoint of the personal aptitudes of the investigator.

THEORETICAL ASTRONOMY

For the mathematically inclined there is the great field of theoretical astronomy. The theoretical astronomer is a mathematician who uses the principles of mechanics, for example, together with calculus, infinite series, etc., to achieve his purposes, as a carpenter uses hammer and nails. If the tools and materials are not properly handled the structure either never rises at all, or collapses the first time its strength is tested. Hence a thorough apprenticeship is essential. Typical problems with which the theoretical astronomer deals are the computation of orbits of comets, planets, satellites, meteors and double stars; the more general problems of celestial mechanics, such as the formation of stars and stellar systems, or the stability of rotating bodies; statistical inquiries concerning the structure of the universe; and, of growing importance, the application of theoretical physics and chemistry to celestial bodies.

The theoretical astronomer can get along without a telescope, but he needs a library and the assistance of computers. His usual position, therefore, is that of professor of astronomy at a college or university. He will ordinarily be expected to conduct classes, but at many institutions some research will be possible if he is sufficiently eager and persistent. The American student who is looking forward to work of this character should prepare to teach, as there are few theoretical astronomers in the United States who do not have duties of instruction.

OBSERVATIONAL ASTRONOMY

Astrophysics—For one whose interest is along the lines of physics and chemistry there is the expanding realm of astrophysics. This science is concerned with deriving all possible information from a study of the quality and intensity of the light received from the heavenly bodies. The observational goal of astrophysics is a complete knowledge of the spectral energy curves (including state of polarization) of the light radiated from every celestial source. The heart of the matter lies in the interpretation of these curves and here astronomy and physics blend. The three main divisions are spectroscopy, photometry, and radiometry.

Spectroscopy is the study of spectral details, *i.e.*, lines and bands, without special reference to the absolute intensities. This line of work has undergone a remarkably extensive development since the pioneer days of Secchi and Huggins. The chief subjects of research are chemical identifications, physical conditions, radial velocities, and intrinsic stellar luminosities (which when combined with apparent luminosities give distances). There are, of course, many special problems of great importance, in particular, those referring to the disk of the sun. It would take too much space even to outline the contents and value of the branches of astronomical spectroscopy, but nearly every school library contains a few books describing them. Miss Clerke's "Problems in astrophysics" and "The