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REGENERATION STUDIES IN INDIA

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Regeneration is a challenging area for studies in developmental biology. Although this phenomenon in animals was discovered more than 200 years ago the active interest of biologists in this field dates back to only the last decade of the 19th century. In India the interest in regeneration as in other areas of developmental biology is even more recent. Active research in this field has been carried out at different laboratories for about the last 25 years mainly on regeneration in *Hydra*, lizards and anuran amphibians. The aim of this brief review is to indicate the broad lines of such studies in these animals and the major findings.

HYDRA

Research on *Hydra* regeneration was initiated by Professor Sivatosh Mookerjee in the late 1950s at the Department of Zoology of Presidency College, Calcutta. On his moving to Delhi in the early 1970s the centre of these studies shifted to the School of Life Sciences of Jawaharlal Nehru University, New Delhi. The studies have been concerned mainly with the role of various cell types, nucleic acids, polarity determination during regeneration of *Hydra* and the relationship between the size of the body fragment and the resultant regenerate. Regeneration in *Hydra vulgaris orientalis* is observed to involve primarily reorientation of cells in the already available cellular material and hence largely morphallaxis instead of mitosis and cell migration; endoderm is found to be the main source of the cells and it plays the major role in restitution at both hypostomal and basal disc ends (Sanyal, 1962, 1967; Mookerjee & Bhattacharjee, 1966; Sanyal & Mookerjee 1967; Mookerjee, Chakraborty & Sinha, 1979).

It was noted by Mookerjee (1962) that the regeneration in *Hydra* was interlinked with cell mass available. Further studies clearly demonstrated this relationship. When the hypostomal region was isolated and its tentacles cut away the isolate could regenerate them even after their repeated removal; but repeated cutting and regeneration diminished the size of the isolate and reduced the number of tentacles restored. Each time about half of the total volume of the isolate was transformed into tentacles and no mitosis was involved (Sanyal & Mookerjee, 1967). From an annular midgastric piece of the body the entire *Hydra* can be restituted. However, whether the regenerate will be only structurally complete but unable to feed and grow or whether it will be both structurally and functionally complete depends upon the size of the midgastric annulus. Presence of a sufficient number of endodermal cells is essential for the regenerate to attain a functional level (Mookerjee et al., 1979).

According to experimental studies of Sinha (1966) using auto-transplantation methods, polarity determination during regeneration in *Hydra* is the result of not only interaction between the opposing hydranth and basal disc forming tendencies but is also related to quantitative aspects of these two opposing tendencies.

Recently, actinomycin D has been employed to study the role of RNAs during regeneration. It was found that regeneration at the hypostomal end was more dependent on fresh RNA synthesis than at the basal disc end (Datta & Chakraborty, 1970; Venugopal, 1978; Venugopal & Mookerjee, 1980). The effect of actinomycin D is dose dependent. With 30μg dose structural regeneration could occur but the functional level was not attained. Wound healing and conversion of endodermal to ectodermal cells were not affected by this antibiotic but later phases of regeneration required fresh synthesis of new RNAs (Nangia & Mookerjee, 1982). A mutant hydra produced by treatment with the carcinogen, dimethyl sulphate, is found to need more fresh RNAs for regeneration at both hypostomal and basal disc ends than the wild type (Rattan & Mookerjee, 1979).

LIZARDS

The Department of Zoology of M. S. University, Baroda, has been an active centre of research on tail regeneration in lizards for about two decades. Here Professor R. V. Shah and his associates have been studying this phenomenon in the gekkonid house lizard, *Hemidactylus flaviviridis*, the scincid *Mabuya carinata* and the agamid *Calotes versicolor*. Earlier, perhaps only two papers on tail regeneration in lizards had been published from India, one on *Hemidactylus* (Woodland, 1920) and the other on *Mabuya* (Sibtain, 1938). Shah and Chakko (1968) have published a detailed account of histological sequence of events during regeneration of the tail in the house lizard. The broad lines of investigations followed at Baroda have been the metabolic pattern with special reference to oxidative enzymes during the various phases of regeneration, the role of hormones and the physiological effects on various body organs and tissues following tail amputation and its subsequent regeneration.

Studies on glycogen and phosphorylases (Shah & Chakko, 1967) have shown that their content in the broken tissues of the tail stump is depleted during wound healing, remains rather low in the blastemic phase but progressively increases during differentiation and growth. Thus different levels of glycogen utilization during the sequential phases of tail regeneration are indicated. During tail regeneration in the house lizard the concentration of RNA was found to be high in the epidermis and blastema cells, increasing further in the latter in the course of differentiation; but on completion of this phase its level in all tissues came down to normal (Shah & Chakko, 1972). Acid phosphatase activity has been shown to be high in different tissues during wound healing and dedifferentiation as well as during the early period of redifferentiation in the regenerate (Shah & Chakko, 1966).

A number of studies have been made on various enzymes during different phases of tail regeneration in lizards including lactate and malate dehydrogenases (Shah & Ramchandran, 1970; Shah, Swamy & Ramchandran, 1982), aldolase (Shah & Ramchandran, 1972), glucose-6-phosphate dehydrogenase and malic enzyme (Shah & Ramchandran, 1973), diphorases (Shah & Ramchandran, 1974) and cytochrome oxidases (Ramchandran, Radhakrishnan & Shah, 1975). Localizations of α-glycerophosphate, β-hydroxy butyrate, succinate and isocitrate dehydrogenases have been histochemically observed in different phases of regenerating tails of *Mabuya* (Shah & Ramchandran, 1975; Swamy, Ramchandran & Shah, 1982). These studies indicate increased anaerobiosis during wound healing but blastemic and early differentiation phases are marked by an aerobic pattern of metabolic processes (Shah et al., 1982). The activity of all enzymes (G-6-PDH and malic enzyme, aldolase, LDH, SDH and ICDH) increases during the blastema stage when the lipid content of cells and nucleic acid and protein requirements of the blastema increase also and glycogen is depleted. It is suggested that in the regenerating tail a short pyruvate-centered metabolic cycle is operative and that increased malic enzyme during blastemic and early differentiation phases could aid in lipid biosynthesis by supplying $NADPH_2$ (Shah & Ramchandran, 1973). Aldolase was found to be active in all stages of regeneration with an above usual level during the differentiation phase. It has been suggested that during the entire course of regeneration there is an uninterrupted glycolytic activity. During the blastemic phase the cells have little or no glycogen but presence of high aldolase means that the blastema cells perhaps depend upon blood glucose for glycolysis. With commencement of the growth phase aldolase comes down to normal levels (Shah & Ramchandran, 1972).

Histological changes have been observed in the thyroid glands of lizards with depletion of follicular colloid during tail regeneration (Ramchandran, Kinariwala & Shah, 1981). Males of the house lizard are observed to regenerate their tail faster than females; and this difference is attributed to greater anabolic effects of testosterone in the former sex (Kothari, Hiradhar & Shah, 1979). Role of hypophysis in lizard tail regeneration has also been studied. (Shah, Varughese & Hiradhar, 1981).

Evidence has been obtained that tail amputation and subsequent regeneration produces changes in the levels of certain metabolites such as glucose, glycogen, lipids, cholesterol, LDH, SDH, etc. in blood, liver, muscle, kidneys and adipose tissue (Kinariwala, Shah & Ramchandran, 1978; Shah, Varughese & Hiradhar, 1979). Lymphocyte population in circulating blood increases greatly during early phases of tail regeneration in the gekkonid. This is correlated with significant enlargement of the white pulp area of the spleen and enhancement of the weight of this organ which thus is involved in regeneration by producing a greater number of lymphocytes. Splenectomy delays wound healing but does not affect subsequent phases (Shah, Kothari & Hiradhar, 1978; Shah

Kinariwala & Ramchandran, 1980). The regenerating tail also obtains its ascorbic acid requirements from hepatic and renal sources (Shah, Hiradhar & Magon, 1971; Shah, Kothari & Hiradhar, 1976). These studies indicate that in the lizards physiological homeostasis of the body is considerably altered following tail autotomy so as to contribute towards extra energy and material demands for repair and regeneration.

ANURAN AMPHIBIANS

At the Department of Zoology of University of Rajasthan, Jaipur, research on tail and limb regeneration of frogs and toads has been in progress since the later half of the 1960s. Five species, *Bufo andersonii*, *Bufo melanostictus*, *Rana tigerina*, *Rana breviceps* and *Rana cyanophlyctis* have been employed in these studies. The broad aims have been to find answers to the following questions: a) Do various anuran species lose regenerative ability according to the same pattern and at the same developmental stage during their larval life or do they differ among themselves in these respects? (b) Is thyroid hormone involved in any way in the loss of this power in anurans ? (c) How does vitamin A affect developmental processes during regeneration ? (d) Is it possible to reverse the process of decline of limb regenerative ability in tadpoles or revive it to any extent in advanced tadpoles and post metamorphic anurans ? The major findings are briefly described under separate sub-headings.

Pattern and rate of decline and loss of limb regenerative capacity

Comparison of some recent studies (Dent, 1962; Fry 1966; Michael & El Malkh, 1969) indicated that anuran species differ with regard to the rate of loss of the ability to regenerate the limb along its proximodistal axis. This is confirmed by results of systematic studies of hind limb regeneration after amputation through thigh, shank and ankle in tadpoles of *Bufo andersonii* (Shivpal, 1976), *Rana tigerina* (Agarwal & Niazi, 1980), *Bufo melanostictus* (Alam & Niazi, 1980) and *Rana breviceps* (Niazi & Sharma, 1980) of a series of morphologically equivalent developmental stages. The pattern of decline and loss of regeneration capacity is similar in all species. It is manifested in a decreasing number of perfect pentadactylous regenerates, increasing oligodactyly and defects among them and ultimately amputation resulting in simple healing of the stump. This occurs proximodistally along the limb axis as tadpoles grow towards metamorphosis. However, in some species this process is slow and in others relatively more rapid and steep (Table 1). Compared to tadoples of *Rana tigerina*, those of *Bufo andersonii* lose this ability much more rapidly and earlier during larval life along the entire length of the limb. In even the youngest tadpoles of the latter species not all regenerates resulting from amputation at any limb level are perfect with 5 toes. These differences appear to be related to shorter larval life and quicker and earlier development of thyroid activity in the tadpoles of *Bufo* than of the *Rana* species (Shivpal, 1976; Agarwal & Niazi, 1979).

Table 1. *Percentage of pentadactylous limbs among all regenerates resulting from limb amputation in Bufo andersonii (Ba) and Rana tigerina (Rt) tadpoles.*

(Adapted from Shivpal, 1976 and Agrawal & Niazi, 1980)

Stage at amputation	LEVEL OF AMPUTATION					
	Thigh		Shank		Ankle	
	Ba	Rt	Ba	Rt	Ba	Rt
V	44	100	—	—	—	—
VI	33	100	79	100	—	—
VII	22	80	44	90	64	95
VIII	16	78	40	90	45	90
IX	9	75	14	77	15	84
X	6	67	12	68	9	70
XI	0	21	0	40	5	45
XV	0	0	0	0	0	26

Stages according to Shivpal & Niazi (1979)

Thyroid hormone and limb regeneration

It has been often suggested that thyroid hormone may be implicated in the loss of limb regeneration ability in anuran tadoples. That this may be true was demonstrated in studies of hind limb regeneration in *Bufo andersonii* tadpoles of a series of developmental stages made hypothyroid by rearing them in potassium perchlorate solution (Shivpal, 1976; Shivpal & Niazi, 1978). This treatment significantly improved the incidence of regeneration and its morphological quality at both thigh and shank levels; but in a decreasing degree as the experiments started with more and more advanced tadpoles possessing a progressively reduced ability to regenerate (Table 2). It appears that limbs progressively lose this power as their tissues differentiate and once they have reached a certain degree of maturity reduction in thyroid activity alone cannot revive this power to any significant extent.

Table 2. *Effect of immersion of Bufo andersonii tadpoles in 0·2% potassium perchlorate solution for 15 days following thigh level amputation at various developmental stages on morphological quality of limb regenerates.*

(Adapted from Shivpal, 1976)

Group	Percentage of pentadactylous limbs among all regenerates. (Developmental stages)						
	V	VI	VII	VIII	IX	X	XI
Control	44	33	22	16	9	6	0
Treated	69	54	32	22	17	7	0

Developmental stages according to Shivpal & Niazi (1979)

Results of treating young *Bufo* tadpoles with 10^{-6} and 10^{-7} concentrations of DL-thyroxine (T_4) before and/or after amputation through the shank demonstrated that this hormone does affect the process of regeneration adversely (Jangir, 1980). This treatment resulted in a drastic reduction in the percentage of perfect 5-toe regenerates, increased oligodactyly and other defects or even completely suppressed regeneration. These effects were particularly severe when tadpoles were exposed to T_4 before amputation or during the period of blastema formation (first 3 days post-amputation). The effects were also dose dependent (Table 3). It was observed that T_4 interferes with the temporal pace of regenerative processes, rapidly induces redifferentiation of cells emerging from stump tissues and consequently distorts the morphogenesis of the blastema. In extreme cases blastema cells redifferentiate into a formless mass of cartilage. Mitosis is enhanced by T_4 but it occurs in differentiating cells and is not an indication of proliferation of dedifferentiated cells for growth of the blastema to a proper size before redifferentiation (Niazi & Jangir, 1979; Jangir, 1980).

Table 3. *Effect of immersion of young Bufo melanostictus tadpoles in 10^{-6} and $^{-7}$ DL–thyroxine (T_4) at and for different periods after shank level amputation on morphological quality of limb regenerates.*

(Adapted from Jangir, 1980)

Treatment during days 1-9 after amputation		Percentage of pentadactylous regenerates	Average no. of toes per regenerate
Nil (Controls)		67	4.6
T_4 : 10^{-7}	Days 1—9	32	4.2
	Days 1—3	25	4.2
	Days 4—9	42	4.4
T_4 : 10^{-6}	Days 1—9	4	2.7
	Days 1—3	0	3.5
	Days 4—9	26	4.0

Effect of Vitamin A palmitate on regeneration

Vitamin A treatment of tadpoles following amputation inhibits regeneration of axial tissues of the tail; the caudal fin regenerates to some extent but its morphogenesis is modified in a strange manner (Niazi & Saxena, 1978). This effect is dependent upon dose, time and duration of treatment. The most adverse effects are seen when tadpoles are exposed to this vitamin during the dedifferentiation phase of tail regeneration (Niazi & Saxena, 1979).

The effects of vitamin A treatment of frog and toad tadpoles on limb regeneration have been found to be most unexpected and remarkable (Jangir & Niazi, 1977 & 1978a; Saxena & Niazi, 1977; Niazi & Saxena, 1978; Jangir, 1980; Sharma, 1982). Immersion of tadpoles in solutions of up to 15 IU/ml vitamin A following limb amputation causes development of blastema in all cases but if this treatment continues beyond this stage the morphogenesis and growth of the regenerate is inhibited so that the blastema persists or its cells become necrotic (Saxena & Niazi, 1977; Jangir & Niazi, 1978a).

Restriction of treatment to 3 days post-amputation (up to blastema formation) or for lesser periods results in the production of the following one, two or all three types of regenerates : (i) Normal type consisting of parts only distal to amputation level, (ii) whole limb type (single or multiple regenerates per stumps) in which the regenerate contains the skeleton of entire limb+girdle irrespective of amputation level; this type of regeneration violates the rule of distal transformation of the blastema (Figs. 1-5), and (iii) persistent blastema type in which redifferentiation and morphogenesis do not occur (Jangir & Niazi, 1978; Sharma, 1982). Proportions of these types among all regenerates depend upon the dose, duration of exposure to vitamin A, developmental stage and species of tadpoles, and also the state of differentiation of the segment of limb through which the amputation is made (Sharma, 1982; Niazi & Alam, 1981a). Very short treatment leads to production of only normal type regenerates but their morphological quality is significantly improved. With increasing duration of treatment up to some optimum duration the frequency of whole-limb type regeneration also increases; but beyond this vitamin A becomes inhibitory (Table 4). Treatment of young *R. breviceps* tadpoles with 15 IU/ml vitamin A for 12 hrs/day for 3 days post-amputation resulted in whole limb type regeneration in 100% cases at thigh and shank as well as ankle levels (Sharma, 1982). *Bufo* tadpoles are more resistant to the action of this vitamin than those of *Rana* (Niazi & Alam, 1981a).

Table 4. *Percentages of different types of regenerates resulting from treatment of young Rana breviceps tadpoles with 15 IU/ml vitamin A palmitate for different periods after limb amputation.*

(Adapted from Sharma, 1982)

Level of amputation	Types of regenerates	Duration of treatment (hrs)					
		1	6	12	24	48	72
Thigh	N	100	85	64	32	7	0
	WL	0	10	23	53	77	31
	PB	0	5	13	15	16	69
Shank	N	100	80	44	5	0	0
	WL	0	20	56	95	40	27
	PB	0	0	0	0	60	73
Ankle	N	100	100	100	97	2	0
	WL	0	0	0	3	73	32
	PB	0	0	0	0	25	68

N = Normal; WL = Whole limb; PB = Persistent blastema

The influence of vitamin A persists for some time even after treatment is withdrawn. Reamputation of previously treated tadpoles without any further exposure to the vitamin still resulted in whole limb type regeneration in a significant percentage of cases (Jangir, Alam & Niazi, 1980).

The blastema produced in vitamin treated tadpoles is capable of differentiating into a whole limb even when isolated and grafted autoplastically into eye orbits (Jangir & Niazi, 1978 b; Jangir, 1980).

Vitamin A treatment of tadpoles delays or inhibits their growth and metamorphosis (Niazi & Saxena, 1972). It causes a great deal of destruction of stump tissues (Jangir & Niazi, 1978a; Sharma 1982), enhances mitotic activity in the differentiated blastema cells (Niazi & Alam, 1981b); increases acid phosphatase activity in the wound epidermis, blastema and injured ends of stump tissues (Sharma & Niazi, 1980a) and delays the onset of redifferentiation in the blastema. These observations suggest that vitamin A increases the morphogenetic potency of the blastema to the level of the original limb bud by intensifying dedifferentiation of blastema cells, radically altering the biochemical conditions in their cytoplasm and in turn probably also affecting the nucleus. Perhaps all the genes responsible for the development of the entire limb pattern are derepressed and reactivated in the nuclei of blastema cells. Vitamin A appears to be a reliable agent which can help in unravelling the biochemical, molecular and genetic nature of dedifferentiation that occurs during tail and limb regeneration in amphibians.

Reversal of decline in, and revival of lost, regenerative power

Vitamin A treatment of tadpoles with declining power to regenerate limbs improves the regenerative capacity. It improves the morphological quality of regenerates. It has also been found to revive this capacity to some extent in advanced frog and toad tadpoles (Sharma, 1982) as well as in postmetamorphic frogs (Niazi, Jangir & Sharma, 1979; Sharma & Niazi, 1979). Exposure of young *Rana breviceps* tadpoles to 3 μA DC current and of advanced tadpoles to 10 μA DC current for 24 hours after amputation improved the morphology of limb regenerates in the former and induced regeneration in nearly 40% cases in the latter (Niazi & Sharma, 1979; Sharma & Niazi, 1980b).

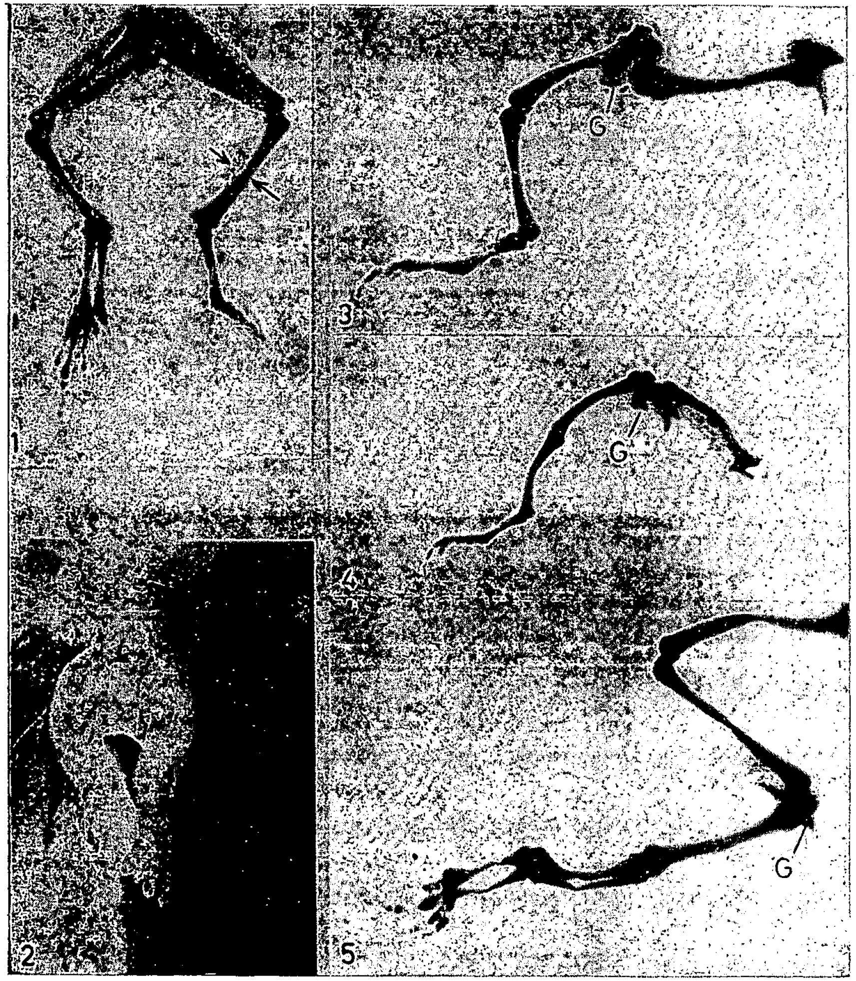

Fig. 1 Normal type regenerate of a *Bufo melanostictus* tadpole resulting from amputation through midshank of left hind limb (arrows.)

Fig. 2 A case of multiple whole limb type regeneration resulting from amputation through thigh in a young *Rana breviceps* tadpole treated with vitamin A.

Figs. 3, 4, 5 Single whole limb regenerates of young *Bufo melanostictus* tadpoles treated with vitamin A after amputation through proximal shank just below knee (Fig. 3), mid-shank (Fig. 4) and proximal tarsal region (Fig. 5). Note regenerates consist of entire limb skeleton plus girdle (G), irrespective of amputation level.

From this brief review it should not be concluded that regeneration studies in India are entirely confined to the few laboratories mentioned and restricted to *Hydra*, lizards and anurans only. Interest in this field is more widespread and there are both published and unpublished reports of recent studies at various other institutions made on regeneration in ciliates, earthworms, appendages of crabs, electric organ of fishes, frog muscles, etc.

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