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Review Article

ENDOCRINOLOGY OF CALCIUM HOMEOSTASIS IN FISHES

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ABSTRACT - Though fish live in aquatic medium from freshwater to environments of varying Ca concentrations, their plasma Ca level is precisely regulated. They possess well-developed ultimobranchial gland (UBG) and corpuscles of Stannius (CS) as well as 25-hydroxyvitamin-D-1α-hydroxylase in their renal tissue. UBG secretes calcitonin (CT) while CS elaborates two forms of stannicalcins - STC1 and SCTC2. The latter is widely distributed in various organs in the phylogeny and its level increases among women with breast cancer. Recently, four stanniocalcin genes have been isolated from CS of teleost and their physiological and phyogetic significance are being studied. Fish do have capacity to metabolize vitamin D with the receptor (VDR) widely distributed in various organs including intestine, gill and kidney. Though fish lack functional parathyroid glands (PTG) found in tetrapods, PTH-like immunoreactivity has been identified in hypothalamus, pituitary and CS. Parathyroid hormone-related peptide (PTHrP) has also been found in elasmobranch and teleosts but its role in normal piscine Ca metabolism has not yet been defined. Recent advances in endocrine regulation of Ca metabolism in fish has been discussed.

Key words : Ultimobranchial gland, calcitonin, Stannius corpuscles, stanniocalcins, Vitamin D, prolactin, somatolactin, Ca homeostasis, fishes.

INTRODUCTION

Placed on the lower rungs of vertebrate hierarchy, fishes offer a special opportunity to study the various endocrine glands involved in calcium (Ca) regulation. The regulation of Ca is a vital feature of all fishes inhabiting extremely varying aquatic conditions. The concentration of Ca^{2+} in plasma of fish is regulated with great precision despite the wide fluctuations in the intake and excretion of Ca. The main Ca regulating endocrine glands are - pituitary, vitamin D-metabolizing system, ultimobranchial glands (UBG) and corpuscles of Stannius (CS). Comparative endocrinology of Ca regulation is very interesting because it provides a most important clue in the mystery of the evolution of the vertebrates (Urist, 1966). Also, the regulatory systems for Ca are very different among vertebrates adapted to different mode of life (Pang and Yee, 1980; Pang *et al*, 1980a, b; Taylor, 1985; Pang and Schreibman, 1989; Pandey, 1991, 1992). Fishes live in the aquatic environment of varying salinity which serves as an inexhaustible reservoir of Ca for them. Even in soft water where the external Ca level is extremely low (0.01-0.40 mM), fish actively extract (transport) this cation from the medium either through integument of the gills, chloride cells, gut, bone or scales (Wendelaar Bonga *et al*, 1983; Ichii and Mugiya, 1983; Ishihara and Mugiya, 1987; Mugiya, 1990; Sundell and Björnsson, 1990; Flik and Rentier-Delrue, 1991), however, gill appears to play major role in hydromineral balance of fishes (Milhaud *et al*, 1977, 1980; Flik *et al*, 1985a, b; Flik and Perry, 1989).

The cyclostomes, chimaeroids and elasmobranchs have only cartilaginous skeleton while many bony fishes have acellular bone which is incapable of remodelling (Copp, 1969). The hagfish maintains serum Ca about half that of SW while the lamprey has concentration almost the same as that of man. These cyclostomes lack all the three important factors present in terrestrial vertebrates (bone, parathyroid and UBG) and apparently regulate body Ca in an open system through controlled transfer across gill membranes (Urist, 1962). The chimaeroids and elasmobranchs also contain no true bones and presumably control Ca through membrane mechanisms (Urist, 1966). However, the UBG first appeared in these fishes and contain calcitonin (Copp *et al*, 1967) which in higher vertebrates control hypercalcemia. Calcitonin can hardly act on bone resorption since there is none but it may possibly facilitate appropriate Ca transport mechanisms and so participates in Ca regulation. This would also apply to teleosts with acellular bones (Copp, 1969).

Though the problem of Ca regulation in submammalian vertebrates has been discussed (Urist, 1976; Dacke, 1979; Oguro and Uchiyama, 1980; Pang *et al*, 1980a; Barlet,1982; Feinblatt, 1982; Clark, 1983;

Taylor, 1985; Wendelaar Bonga and Pang, 1991; Pandey, 1991, 1992; Srivastav *et al*, 1995; Barlet *et al*, 1998: Sasayama, 1999), literature dealing exclusively with the piscine Ca regulation are very few (Urist, 1962, 1964a, b; 1966; Urist and de Putte, 1967; Copp, 1969; Pang *et al*, 1980b; Ma and Copp, 1981, 1982; Wendelaar Bonga and Flik, 1993; Pandey, 1994a; Pandey and Pandey, 2009). An attempt has, therefore, been made to review the recent advances in the field of Ca regulation in fishes.

Pituitary or Hypophysis

The nature of hypercalcemic factor in the teleost pituitary remains to be inconclusive (Olivereau and Lemoine, 1973a, b; Pang *et al*, 1978; Wendelaar Bonga and Greven, 1978; Wendelaar Bonga, 1980). However, the presence of hypercalcemic principles, other than prolactin, in the teleost pituitary can not be excluded (Parsons *et al*, 1978). Somatolactin is a putative pituitary hormone structurally related to both prolactin (PRL) and growth hormone (GH). Immunocytochemical study revealed both cellular and nuclear cross-sectional areas were decreased when rainbow trout was transferred from freshwater (FW) to Ca-FW (10 mM) or to seawater (SW), no change was seen after a transfer from freshwater to FW. The level of somatolactin-mRNA decreased 10 days after transfer to Ca-FW. On the other hand, not only cellular and nuclear areas but also somatolactin-mRNA levels increased after transfer from Ca-FW to FW. The results support a hypercalcemic role for somatolactin (Kakizawa *et al*, 1993). In fish, prolactin cells have been reported to secrete a hypercalcemic principle (Pang *et al*, 1973; Olivereau and Olivereau, 1978; Wendelaar Bonga, 1980; Wendelaar Bonga and van der Meiz, 1980; Wendelaar Banga *et al*, 1981). An ultrstructural study of various endocrine glands of coho salmon has shown that PRL cells appeared active in normal smolts and inactive in SW stunt but GH cells appeared active in all groups. Thyrotropin cell activity was reduced in the stunts. Similarly, the corticotropic (ACTH) cells in the stunt exhibited diminished activity compared with the cells of normal smolts (Nishioka *et al*, 1982).

In intact European eel maintained in SW, ovine PRL treatment induced hypercalcemia as well as stimulated oval type1 cells of the CS. Stimulated CS cells may elaborate stanniocalcin which would compensate for the PRL-induced hypercalcemia. A similar effect, although slightly less intense, was detected in hypophysectomized (HPX)-PRL treated eels in SW (Olivereau and Olivereau, 1978). A gradual transfer of freshwater eels into SW significantly lowered Ca level, HPX has little influence on this response. PRL treatment considerably increased plasma Ca levels in intact or HPX eels (Olivereau and Lemoine, 1973a, b). A maximal hypercalcemia was observed in treated intact eels which was higher after 10 than 6 injections (Olivereau and Olivereau, 1977). HPX juvenile rainbow trout had lower ionized Ca levels indicating that the pituitary plays a significant role in regulation of plasma Ca in this fish (Björnsson and Hansson, 1983). Chan and Woo (1968) and Srivastava and Pickford (1972) have shown that HPX reduced total plasma Ca in the killifish and Japanese eel. It is suggested that HPX unmasks the effects of calcitonin and/or other endogenous hypocalcemic principles thus resulting in hypocalcemia in teleosts. Wagner *et al* (1985) have demonstrated the existence of a cycle for ^{45}Ca uptake in rainbow trout with an average length of 11 days. This cycle does not appear to be temperature-dependent but may be influenced by season as there is a decline in its magnitude with the onset of winter. These changes may be due to variable secretions of PRL which enhances Ca^{2+} uptake (Wendeelar Bonga and Flik, 1982). Swarup (1992) has observed inverse relationship in the seasonal activities of PRL cells and serum Ca levels in common carp. The Indian major carp (*Labeo rohita*) maintained in normal freshwater possessed active prolactin cells with accumulation of secretory granules while those subjected to vitamin D_3-induced hypercalcemia for 15 days depicted the loss of secretory granules and atrophied cells (unpublished observation).

In fish, PRL (Pang *et al*, 1973, 1978, 1980a; Wendelaar Bonga, 1980; Wendelaar Bonga and van der Meiz, 1980; Pang, 1981; Fenwick, 1982; Olivereau and Olivereau, 1983; Flik *et al*, 1984, 1994; Chakraborty and Mukherjee, 1985; Hasegawa *et al*, 1986; Mugiya and Odawara, 1988; Fargher and McKeown, 1989; Flik and Rentier-Delrue, 1991), hypercalcin (Parsons *et al*, 1978; Pang and Yee, 1980; Ball *et al*, 1982; Olivereau and Olivereau, 1982; Olivereau *et al*, 1981, 1985, 1986) and somatocalcin (Kakizawa *et al*, 1993) are the hypercalcemic principles. PRL (slow acting hormone) affects the Ca regulation by two ways - (i) reduces skin Ca loss by diminishing its permeability to this cation and (ii) enhances Ca influx by recruiting the new population of chloride cells with altered high affinity Ca^{2+}-ATPase activity (Flik *et al*, 1984, 1986; Flik and Rentier-Delrue, 1991).

Hypercalcin which immunologically resembles mammalian parathyroid hormone (PTH) is a fast acting hormone (Parsons *et al*, 1978). Pituitary extract of cod induces hypercalcemia in killifish, bullfrog and rat within 2 hours (Pang and Yee, 1980). An immunoreactive PTH-like molecule has been identified in the brain, hypothalamus, pituitary and plasma of different groups of vertebrates (Harvey *et al*, 1987; Kaneko and Pang, 1987; Pang *et al*, 1988; Fraser *et al*, 1991). These studies point

that PTH is present even in the vertebrates which lack encapsulated parathyroid gland and this molecule has been conserved during evolution. It has been suggested that the pituitary hypercalcemic regulation is a primitive mechanism associated with the life in water and the hypophysis has yielded gradually its hypercalcemic function to parathyroid during transition from water to land (Oguro *et al*, 1978; Pang and Yee, 1980; Pang *et al*, 1980a). Clark (1983) has also emphasized the important role of pituitary gland in maintenance of blood Ca in aquatic vertebrates.

Vitamin D-Metabolizing System

Hay and Watson (1976) reported that bony fish have a specific plasma transport protein (α-globulin) for 25-hydroxycholecalciferol (vitamin D_3). Henry and Norman (1975) demonstrated that many species of vertebrates contain 25-hydroxy-vitamin D-1α-hydroxylase in their kidney. The bony fish, similar to that of higher vertebrates, possess a metabolic pathway for vitamin D_3 which results in the production of a metabolite, 1,25-dihydroxycholecalciferol [1,25 $(OH)_2D_3$] (Dacke, 1979; Hayes *et al*, 1985). In higher vertebrates, this substance is considered to be hormonal in nature and released in response to Ca or trophic factors (Lops, 2006). Though low molecular weight calcium-binding protein (CaBP) has been identified in gill, intestine and kidney of freshwater eel, *Anguilla anguilla* (Hearn *et al*, 1978) and zebrafish, *Danio rerio* (Craig *et a*l, 2008), the literature concerning the physiological role of vitamin D_3 and its metabolites in fish is very few (Lopez *et al*, 1977; Dacke, 1979; Srivastav, 1983; Srivastav *et al*, 1985a; Srivastav and Srivastav, 1988; Das *et al*, 1991; Srivastava *et al*, 2011).

Administration of vitamin D_3 in sharks, skates and rays and vitamin D_3 and 25-OH-D_3 to lungfishes does not affect their serum Ca levels (Urist, 1962, 1964b; Urist *et al*, 1972). In marine fishes which live in virtually Ca-saturated environment, vitamin D_3 has apparently no role in Ca homeostasis although it is abundant in their liver (Urist, 1963; Urist and van de Putte, 1967; Urist *et al*, 1972; McIntyre *et al*, 1976). In unfed immature eels, vitamin D_3 and 1,25$(OH)_2D_3$ do not alter serum Ca value (McIntyre *et al*, 1976; Lopez *et al*, 1977; Fenwick *et al*, 1984) whereas in mature eels 1,25 $(OH)_2D_3$ causes hypercalcemia (Lopez *et al*, 1977). Pang *et al* (1978) speculated that vitamin D_3 might be the hypercalcemic factor responsible for the restoration of normocalcemia in HPX killifish suffering from hypocalcemia. Ahmed and Swarup (1979) recorded vitamin D_2 induced hypercalecemia in unfed *Mystus vittatus* maintained in Ca-rich environment. Swarup and Srivatsav (1982a) demonstrated the direct evidence of vitamin D_3 induced hypercalcemia in male unfed catfish, *Clarias batrachus*. Later on, Fenwick (1984) and Fenwick *et al* (1984) have also reported vitamin D and vitamin D_3 induced hypercalcemia in fed goldfish and American eels, however, the unfed specimens remained unaffected to the treatments. On the contrary, vitamin D/vitamin D_3 induced hypercalcemia even though the fish remained unfed during the treatments (Swarup and Ahmed, 1978; Ahmed and Swarup, 1979; Swarup and Srivastav, 1982a; Swarup *et al*, 1984, 1991a; Das *et al*, 1990a, 1991; Srivastava *et al*, 2012) (Table 1). Unfed fish seems to draw Ca from non-dietary sources such as ambient water, soft tissues, bone and scales (Srivastava *et al*, 2012).

Swarup *et al* (1984, 1991a) observed that male unfed *C. batrachus* and common carp (*Cyprinus carpio*) responded even to physiological doses (0.50 IU/100 gm body weight) of vitamin D. Elevation of serum Ca levels is also observed after vitamin D_3 administration in the mud eel, *Amphipnous cuchia* (Srivastav, 1983) and threatened *Notopterus notopterus* (Srivastava *et al*, 2012), however, the response was quick in fishes maintained in Ca-rich medium after treatment (Srivastav, 1983). Dose-dependent gradual hypercalcemia have also been reported following administration of 1,25(OH_2) Vitamin D_3, vitamin D_2 and vitamin D_3 (Swarup *et al*, 1984, 1991a; Srivastav and Srivastav, 1988; Das *et al*, 1991). Das *et al* (1990a) recorded significant increase in the serum Ca level after vitamin D_3 administration only upto 5 days thereafter levels fall possibly due to endogenous secretion of hypocalcemic factors like calcitionin and stanniocalcin. Maintenance of vitamin D_2-injected fish in Ca-rich medium led to the exaggeration of hypercalcemic response (Das *et al*, 1990a). Similar changes have also been observed in *Cyprinus carpio* (Swarup *et al*, 1991b).

Vitamin D_3 administration has been reported to induce osteoclastic resorption and reduce Ca content in bone of fishes (McIntyre *et al*, 1976; Lopez *et al*, 1977, 1980; Wendelaar Bonga *et al*. 1983). However in mature female eel, vitamin D_3 stimulated bone formation and inhibited osteoclastic resorption also (Lopez *et al*, 1980). Chartier-Barduc (1973) and Sundell *et al* (1992) identified Ca-binding protein (CaBP) in the intestine of fishes. Several studies have shown that vitamin D_3 and 1,25$(OH)_2$ D_3 enhaced intestinal Ca resorption in teleosts (Chartier *et al*, 1979; Flik *et al*, 1982; Fenwick, 1984; Fenwick *et al*,1984; Sundell and Bjornsson, 1990) whereas 24,25$(OH)_2$ D_3 does not affect Ca absorption in the gut (Flik *et al*, 1982; Fenwick *et al*, 1984; Sundell and Björnsson, 1990) rather an anti-hypercalcemic role has been suggested for its metabolite in Atlantic cod (Sundell and Bjornsson, 1990). It is pertinent to remark that unlike in mammals where 1,25$(OH)_2$ D_3 is more potent hormone, fish respond more

Table 1 : Effect of vitamin D_3 administration on serum calcium level of threatened *Notopterus notopterus* maintained in freshwater.

	Time					
	6 hr	**1 day**	**2 day**	**3 day**	**5 day**	**9 day**
Control	8.1±0.11	8.2±0.21	8.2±0.21[a]	8.4±0.18[b]	8.4±0.43[b]	8.6±0.22[b]
100 IU	9.3±0.08	9.6±0.23	10.0±0.14[b]	9.8±0.17[b]	9.3±0.19[b]	8.6±0.10[a]
500 IU	9.3±0.07	9.7±0.21	11.2±0.92[b]	10.1±0.56[b]	9.8±0.72[b]	9.1±0.09[a]
1,000 IU	9.4±0.41	9.7±0.27	12.0±0.46[b]	10.3±0.13[a]	9.8±0.17[a]	9.6±0.23[a]

(after Srivastava *et al*, 2012)

strongly to unmodified vitamin D_3 than to its other metabolites (Chartier *et al*, 1979; Fenwick *et al*,1984; Sundell and Bjornsson, 1990). Sundell *et al* (1992) have found significant quantities of $1,25(OH)_2 D_3$ in the plasma, plasma binding protein and localization of specific high affinity receptors for this metabolite in Ca regulatory tissues suggesting a physiological role for this metabolite in the Ca regulation of the marine Atlantic cod.

Ultimobranchial Gland (UBG)

The ultimobranchial glands were the first of the Ca regulating gland to appear in the vertebrates during phylogenetic progression as they are found in all groups of gnathostoms while the encapsulated parathyroids are recorded only in terrestrial vertebrates (amphibians onwards) (Robertson, 1986). The UBG are lacking in cyclostomes (Watzka, 1933) while parathyroid glands have generally been considered absent in fish (Hoar, 1951; Pickford, 1953; Pandey, 1991, 1992). Rasquin and Rosenbloom (1954) suggested that the UBG might have functions analogues to that of parathyroid of tetrapods. These findings were the first to indicate that UBG might be related to Ca metabolism in fishes but the gland remained neglected until calcitonin was extracted from fish UBG (Copp *et al*, 1967, 1972; Pang, 1971; Fenwick 1978). Calcitonin, secreted from the thyroid parafollicular cells in mammals, induces hypocalcemic and hypophosphatemic effects by inhibiting osteoclastic bone resorption and renal tubular phosphate resorption (Barlet *et al*, 1998). Calcitonin immunoreactivity has been demonstrated in UBG of fishes (Tissernand-Jochem *et al*, 1977; Sasayama *et al*, 1984; 1989, 1995, 1999; Shinohara-Ohtani and Sasayama, 1998). Generally, the gland is a paired structure but there are instances of the occurrence of single gland too (Otani *et al*, 1975; Sasayama and Oguro, 1992; Sasayama *et al*, 1994; Shinohara-Ohtani and Sasayama, 1998). Earlier studies concerning administration of calcitonin indicated its failure to induce hypocalcemia in marine fishes (Pang, 1971; Wendelaar Bonga, 1980; Hirano *et al*, 1981). It may be significant that the bone in these fishes is acellular and incapable of normal bone resorption. Subsequently, partially purified mammalian calcitonin was shown to be hypocalcemic (Louw *et al*, 1967; Chan *et al*, 1968). Acid extract homogenate of UBG of perch, catfish and eel produced significant hypocalcemia in rats, however, the same extract failed to induce any change in serum Ca of the same species (Singh, 1988). The UBG of the Indian major carp, *Labeo rohita*, consisted of a number of follicles which may or may not contain eosinophilic-Colloid-like material in their lumina. The epithelial lining cells of the follicles are differentiated into basal (b), secretary (s) and degenerating (d) cells based on their secretary profiles (Fig. 5).

In fishes, there are two endocrine glands which secrete hypocalcemic (anti-hypercalcemic) factors - one is UBG which is similar to other poikilotherms and the other is corpuscles of Stannius (CS) which is unique to ray-finned fishes. Fish calcitonin was first demonstrated in the UBG of dogfish (Copp *et al*, 1967). Hypocalcemic activities were observed in the UBG extracts of sharks (Urist and Schjeide, 1961) and teleosts (Copp 1969). Dacke *et al* (1971) reported an increased plasma calcitonin in fishes injected with $CaCl_2$ solution. Similar increase in plasma calcitonin level/hypertrophy and hyperplasia in the gland were also recorded in fishes kept in hypercalcemic media (Dacke *et al*, 1971; Suryawanshsi and Mahajan, 1976; Swarup and Ahmed, 1978, 1983; Srivastav *et al*, 1985b; Hasan *et al*, 1994). Calcitonin is secreted mainly in response to increased serum Ca level and induces hypocalcemia on exogenous administration (Suryawanshi and Mahajan, 1976; Das *et al*, 1990b; Srivastav and Swarup, 1982b; Srivastav *et al*, 1989; Sasayam *et al*, 1992, 1993). The UBG of the Indian major carp, *Labeo rohita*, gets stimulated on day 7 and 10 of vitamin D_3 administration which is evident by increase in the size (hypertrophy) and number (hyperplasia) of secretory cells as well as formation of secondary follicles in the epithelial lining of the gland (Fig. 6). Biological half-life of fish calcitonin is longer than those found in mammals (Watts, 1973).

The fundamental differences between the SW and FW environment in term of teleost Ca regulatory strategies have been called to attention by several workers (Pang, 1973; Dacke, 1979; Feinblatt, 1982). A review of the literature clearly indicates that studies on Ca homeostasis

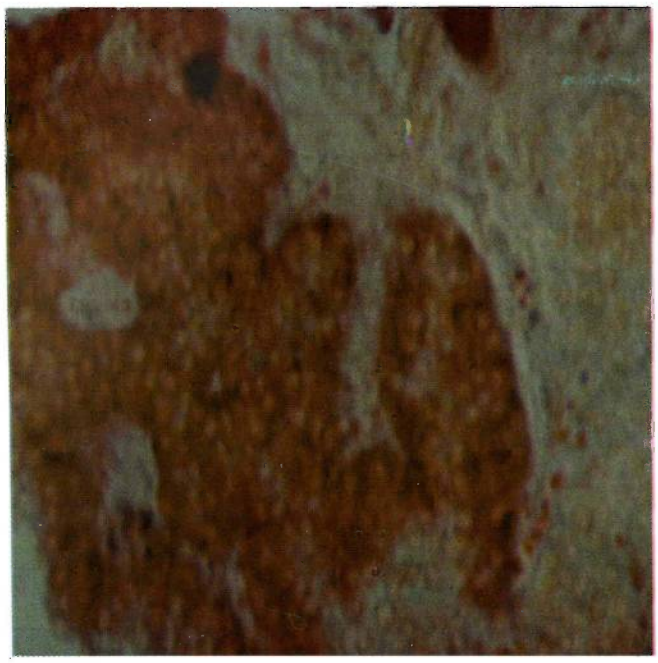

Fig. 1 : Prolactin cells of coastal fish, *Liza parsia*, kept in sea water (32 ppt). x 400.

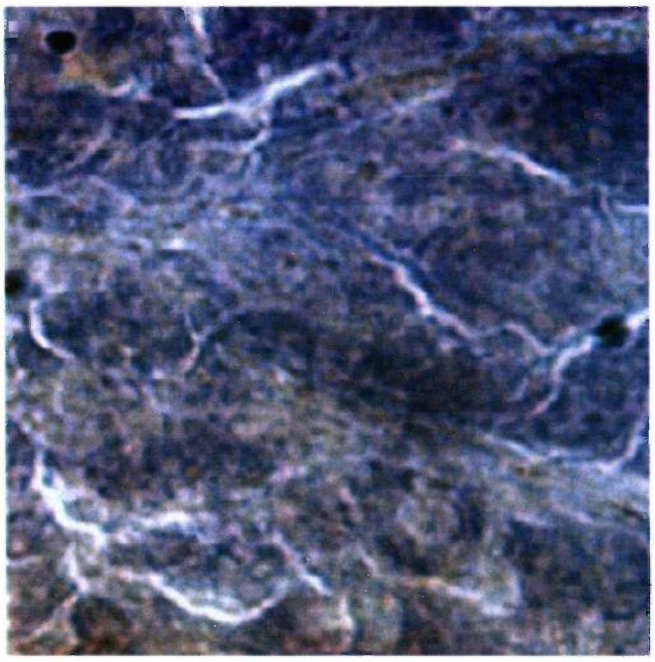

Fig. 2 : Prolactin cells of marine teleost, *Megalaspis cordyla* arranged along the sinusoids. x 800.

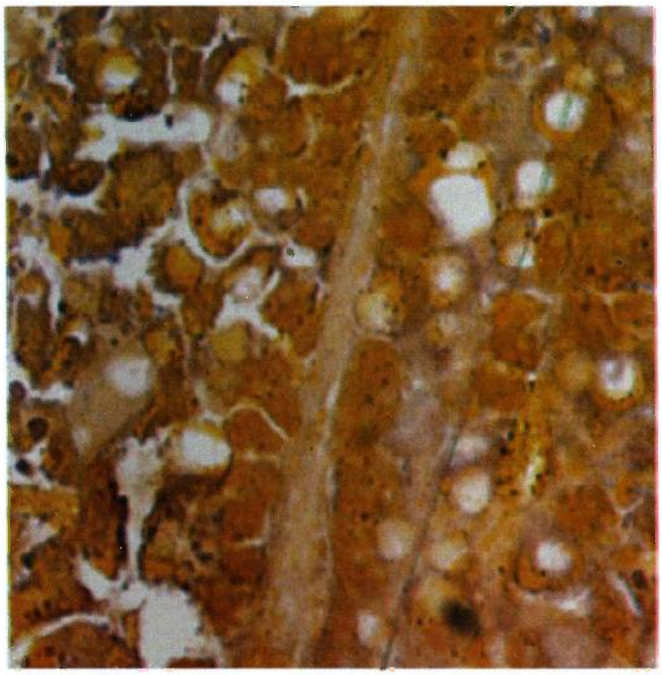

Fig. 3 ; Prolactin (orange G +ve) cells of immature seabass, *Lates calcarifer* arranged along sinusoid. x 800.

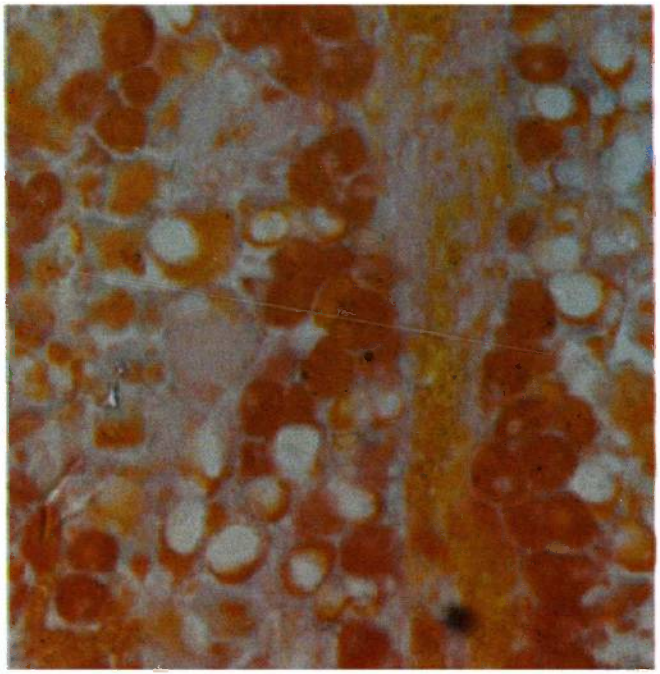

Fig 4 : Prolactin cells (erythrosine +ve) of mature seabass, *Lates calcarifer* loaded with secretory granules. x 800.

literature clearly indicates that studies on Ca homeostasis in SW fish have been neglected and that only a very limited knowledge of Ca regulatory systems of marine fishes is available (Urist and Schjeide, 1961; Copp *et al*, 1967; Dacke 1979; Oguro and Uchiyama, 1980; Feinblatt, 1982; Bjornsson and Nilsson, 1985; Bjornsson *et al,* 1986). Studies concerning the role of calcitonin in plasma Ca regulation of marine teleosts have been restricted to a few living/adapted euryhaline species (Pang, 1971; Wendelaar Bonga, 1980). Björnsson and Nilsson, 1985a; Björnsson and Deftos, 1985; Björnsson *et al,* 1986) observed no hypocalcemic effects of calcitonin treatments while such effects (comparing to

Barrett, 1983). When euryhaline fishes are being studied, care should be taken to judge the validity of SW adaptation, especially when the adaptation period is very short (Peignoux-Deville *et al*, 1975; Wales and Barrett, 1983). Björnsson *et al* (1986) could not observe anti-hypercalcemic effect of calcitonin in marine cod, an effect described in mammals (Talmage *et al.* 1980). Björnsson *et al* (1989) remarked that calcitonin does not play a major role in short-term plasma Ca homeostasis in coho salmon. Unlike mammals, controversy exists regarding the role of calcitonin in fishes - hypocalcemia (Louw *et al*, 1967; Chan *et al*, 1968; Bradshaw and Sutton, 1970; Lopez *et al*, 1971; Peignoux-Deville *et al*, 1978; Suryawanshi and Mahajan, 1976; Mathur, 1979; Srivastav and Swarup,1980; Wendelaar Bonga, 1981; Wales and Gaunt,1987; Das *et al*, 1990b; Srivastav *et al*, 1998a, b;Chakraborty and Mukherjee, 1993; Singh and Srivastav, 1993; Oughterson *et al*, 1995), hypercalcemia (Glowacki *et al*, 1985; Copp and Kline, 1986; Foucherecu-Peron *et al*, 1986, 1987) or without any effect on plasma Ca level (Urist,1967; Pang and Pickerfold 1967; Louw *et al*, 1969; Hayslett *et al*, 1971, 1972; Pang, 1971; Pang *et al*, 1971; Urist *et al*. 1972; Chan, 1972; Chan and Ma, 1972; Orimo *et al*, 1972; Pang and Sawyer, 1974; Milhaud *et al*, 1977; Yamauchi *et al*, 1978a; Ma and Copp, 1978, 1982; Srivastav and Swarup, 1980; Wendelaar Bonga, 1980; Hirano *et al*. 1981; Wales and Gaunt, 1987; Fenwick and Lam, 1988a, b). These inconsistent results led some workers to conclude that calcitonin does not perform any major role in the maintenance of plasma Ca levels in fish (Hirano *et al*, 1981; Feinblatt, 1982; Clark, 1983; Bjornsson and Haux, 1985a; Pang and Pang 1986; Bjornsson *et al*, 1989; Das *et al*, 1990c). Calcitonin has been reported to be the major gill hormone in fishes (Milhaud *et al*, 1977, 1980). Wagner *et al* (1997) found that salmon calcitonin (sCT) inhibits whole body Ca^{2+} uptake in young rainbow trout. The catfishes (*Mustus vittatus* and *Rita rita*), climbing perch (*Anabas testudineus*) and common carp display a well-marked seasonal cycle in the serum Ca level linked with the ovarian maturation and UBG. The highest level of serum Ca is recorded during the spawning phase with enhanced activity of UBG. Throughout the post-spawning and resting phases the serum Ca level continues to decline which is related to the decreased activity of UBG (Ahmed and Swarup, 1988; Singh, 1988; Swarup, 1992). This may be attributed to the fluctuation in the secretion of estrogen. Moreover, female chum salmon, trout and Japanese eel show higher levels of calcitonin than males during spawing period (Deftos *et al*, 1974; Watts *et al*, 1975; Yamauchi *et al*, 1978b; Bjornsson *et al*, 1986, 1989).

Sex-related differences in the structure of UBG have been described in some teleosts. The cells of this gland in mature females display hypertrophy and hyperplasia (Swarup and Alim, 1990). The UBG extracts taken during gonadal peak from female common carp induces more pronounced hypocalcemia in rat than those of conspecific males. This may be due to the higher level of glandular calcitonin content in females during gonadal maturation and spawning phases (Patel and Das, 1994). The UBG recorded increased cytological activity during breeding season in female teleosts (Lopez *et al*, 1968; Deville, 1970; Oguri, 1973; Peignaux-Deville *et al*, 1975; Yamane and Yamada, 1977; Yamane, 1977, 1981; Ahmed and Swarup, 1988). High levels of circulating immunoreactive calcitonin have also been found in female teleosts (Deftos *et al*, 1974; Watts *et al*, 1975; Milhaud *et al*, 1977; Yamauchi *et al*, 1978b; Björnsson *et al*, 1986, 1989; Fouchereau-Peron *et al*, 1990) implicating the involvement of calcitonin in reproduction of female teleosts. Estrogen appears to act on the UBG cells of the goldfish (*Carassius auratus*) to increase the release of calcitonin which, in turn, plays an important role in reproduction directly and/indirectly through Ca (Suzuki *et al*, 2004). Björnsson *et al* (1989) have suggested a role for this hormone in the embryonic development of teleosts too. However, such information is lacking among the elasmobranch fishes. The UBG of stunted salmon generally show diminished activity in comparison to normal fish (Nishioka *et al*, 1982). The timing of plasma calcitonin increase and decrease around the time of ovulation (Bjornsson *et al*, 1989) can be correlated with changes in gonadotropin and estradiol levels in rainbow trouts (Scott and Sumpter, 1983). Artificially induced sexual maturation of female silver eels result in an increased demineralization of bone and this effect can be partially prevented by pretreatment with calcitonin (Lopez *et al*, 1976). It appears that calcitonin in fish, as in mammals, protects the maternal skeleton during the period of increased Ca demand (Lopez *et al*, 1976; Bjornsson *et al*, 1986, 1989). However, some fundamental differences between the function of calcitonin in teleosts and mammals exist as indicated by the lack of direct feedback regulation Ca and calcitonin levels in teleosts. Regulation of calcitonin secretion seems not to be directly related to free plasma Ca levels and it is suggested that ovarian estradiol/or gonadotropins are involved (Bjornsson *et al*, 1986).

Corpuscles of Stannius (CS)

The CS are unique endocrine gland found exclusively in Holosteii and Teleosteii. They are encapsulated epithelial structures associated with the kidney of teleosts. Embryologically, these cells are derived from the kidney tubules and coalesce during development to form two or

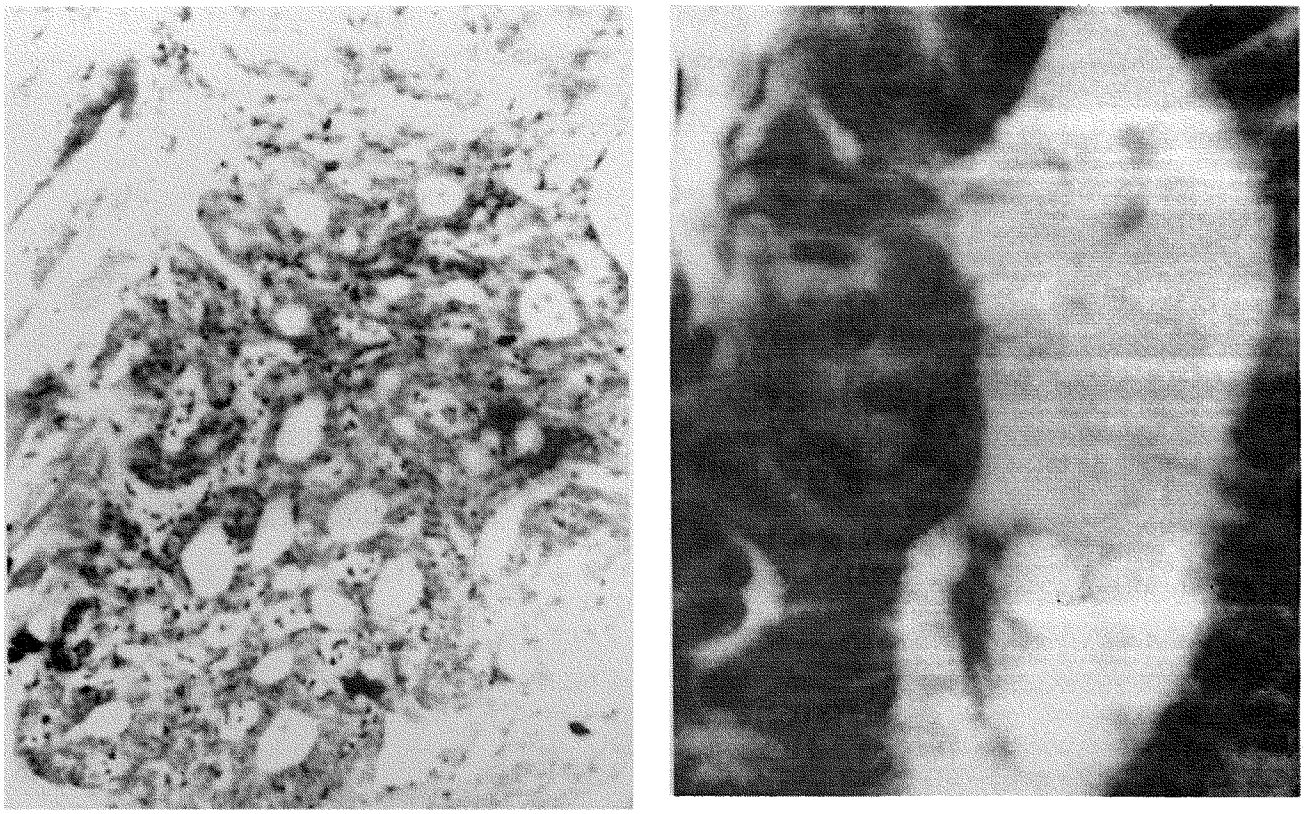

Fig. 5 : UBG of *Labeo rohita* comprising follicles (F) with central lumen. x 240 (left). Maginified view of single follicle with different types of epithelial cells. x 1,000.

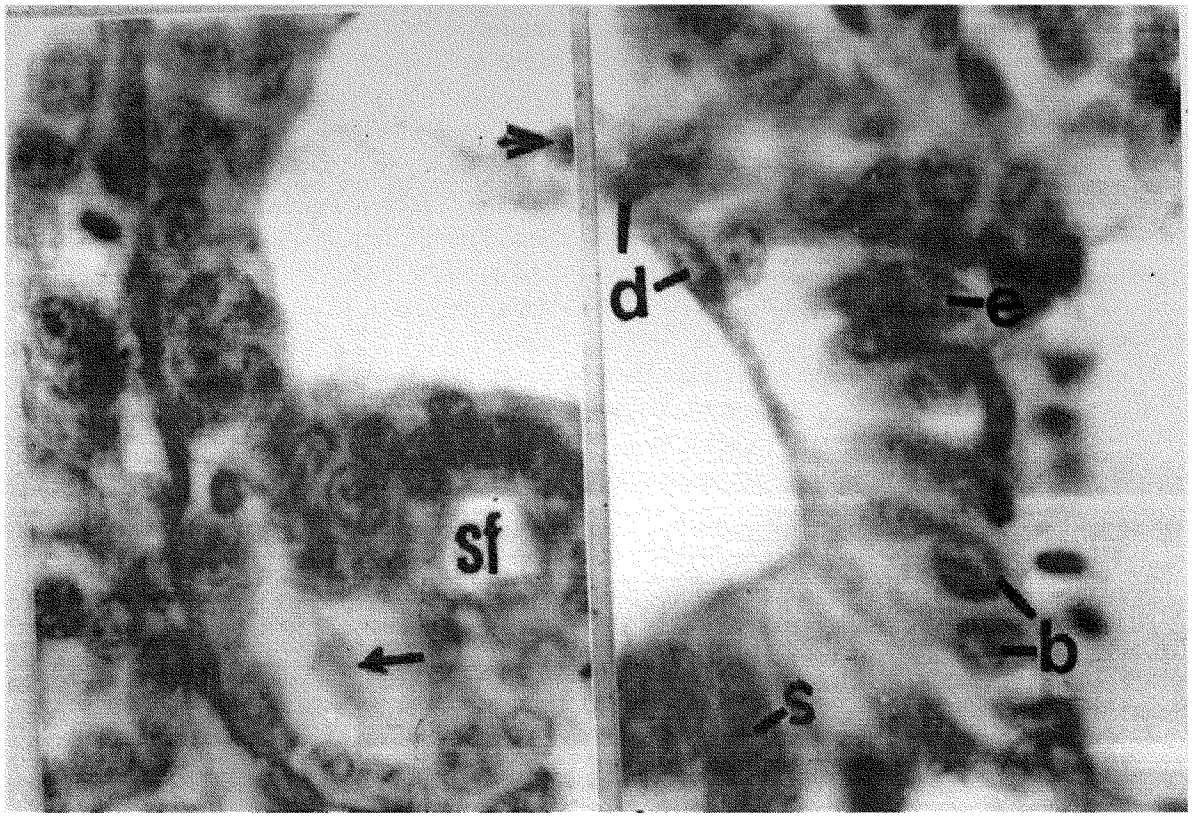

Fig. 6 : UBG of the major carp on day 7 of vitamin D_3 administration showing secondary follicle (Sf), colloid-like material (arrow) as well as few degenerating cells (arrow head) (left). On day 10 depicting pseudostratifed epithelium with increased number of daughter (b) and early maturing (e) cells and decreased number of mature secretory (S) and degenerating (d) cells (right). x 800.

more glands which lie on or within the kidney of the bony fish. Individual differences with regards to number, position and size of the gland varies greatly even in closely-related species (Krishnamurthy, 1976; Fenwick, 1978; Pandey, 1988a; Ahmed *et al*, 2002). The hypocalcemic factor from CS is named as teleocalcin/stanniocalcin (Copp and Ma, 1981; Gellersen *et al*, 1988; Lafeber *et al*, 1988a, b, c; Wagner *et al*, 1989; Wagner and Frissen, 1989; Verbost *et al*, 1993a, b) which is known for regulatory effects on calcium/phosphate transport by gills, gut and kidney (Lafeber and Perry 1988, Lafeber *et al*, 1988b; Hirano, 1989; Wendelaar Bonga and Pang, 1991; Wagner *et al*, 1992; Pandey, 1994a, b; Amemiya and Youson, 2004; Wagner and Dimattia, 2006). Youson *et al* (1991) and Marra *et al* (1992) demonstrated stanniocalcin-like immunoreactivity in corpuscles of Stannius of the bowfin (*Amia calva*) while Sterba *et al* (1993) showed the stanniocalcin gene expression distributed uniformly throughout the gland of sockeye salmon (*Oncorhynchus nerka*) by *in situ* hybridization. Two types of stanniocalcins - stannicalcin 1 (STC1) and stanniocalcin 2 (STC2) have been identified in the CS of fishes (Hang and Balment, 2005; Shin and Sohn, 2008, 2009). Shin and Sohn (2008) demonstrated that in *Paralichyhus olivaceus* STC 1 cDNA (1331 bp) encodes a preprohormone (251 amino acids) with a signal protein of 17 aa and a pro-sequence peptide of 15 aa followed by mature protein of 219 aa. Lowered environmental salinity resulted in decrease in STC 1 mRNA expression *in vivo* in gills, kidney, intestine and CS while extracellular Ca^{2+} increased STC 1 mRNA levels in these organs of the Japanese flounder suggesting that synthesis of the hormone in CS is responsive to the environmental salinity and extracellular Ca^{2+} level. The involvement of CS in Ca regulation was first recorded by Fontaine (1964) following post-operational hypercalcemia in stanniectomized (SCX) eels. Similar changes were also observed in SCX fishes (Ogawa, 1968; Chan 1969; Butler, 1969; Fenwick and Forster, 1972; Pang *et al*, 1974, 1975; Fenwick, 1974; Schreibman and Pang, 1975; So and Fenwick, 1977, 1979; Kenyon *et al*, 1980; Takagi *et al*, 1985; Wendelaar Bonga *et al*, 1986; Perry *et al*, 1989). This hypercalcemia can be reduced by injection of CS homogenate. Administration of CS extract has been shown to produce hypocalcemia in hypercalcemic fishes (Dubewar and Suryawanshi, 1978; Meats, 1978; Swarup and Srivastav, 1982b; Wendelaar Bonga *et al*, 1986; Swarup *et al*, 1992). Mingqi *et al* (1994) demonstrated that stanniocalcin stimulates phosphate reabsorption from proximal convulated renal tubules of the flounder (*Pleuronectes americanus*). The stanniectomy (SCX) causes even more marked hypercalcemia than after UBGX in eels. This was associated with increased basophilia of the UBG cells resulting from increased RNA synthesis. SCX eels no longer respond to porcine calcitonin injections which might be due to presence of excess amount of endogenous hormone (Chan, 1969). Hypercalcemia correlated with enhanced CS activity have been recorded in fish after treatment with vitamin D_2, vtamin D_3, $1,25(OH)_2$ D_3 and/or 0.5% solution of $CaCl_2$ (Ahmed and Swarup, 1979; Srivastav, 1984; Srivastav and Srivastav, 1988, Srivastav *et al*, 1998c). CS epithelial cells of *Labeo rohita* depicted lobular arrangement and get stimulated under hypercalcemic stress induced by vitamin D_3 administration (unpublished observation). Ukawa and Sasayama (1993) reported that serum Ca of goldfish administrated with homogenate of the CS taken from 1/3 SW-acclimatized goldfish was significantly lower than that of the control fish. It has been found that Ca is an equipotent stimulator of stanniocalcin (STC) secretion in freshwater as well as seawater-adapted salmon (Wagner and Jaworski, 1994; Wagner *et al*, 1998a, b). The CS of fish maintained in deionized water appears inactive and shows accumulation of secretory granules. In contrast, the CS of fish kept in SW or Ca/Na-rich water shows depletion of these granules indicating a response to the demand of stanniocalcin in higher Ca medium (Cohen *et al*. 1975; Wendelaar Bonga *et al*, 1976; Pandey and Haider, 1982). The CS from fish kept in Ca-rich water contains more stanniocalcin than those from Ca-deficient water (Pang and Pang, 1974; Urasa and Wendelaar Bonga, 1987; Hanssen *et al*. 1991; Ukawa and Sasayama, 1993; Pandey, 1994b). As evident by histological features, the CS of *Boliophthalamus dentatus* appears to be actively secreting during low saline period while in the high saline phase, they become degranulated - a secretory cycle that follows tidal rhythms (Patel and Desai, 1976).

Treatment with $CaCl_2$ and NaCl produces hypercalcemia and hypertrophy in CS cells of *Heteropneustes fossilis*, *Notopeterus notopterus* and *Cyprinus carpio* (Suryawanshi and Mahajan, 1976; Swarup and Ahmed, 1979; Hasan *et al*, 1994). In common carp injected with the homologous CS extract, the hypercalcemia following maintenance in Ca-rich medium or its injection is not only checked but the level registered hypocalcemia. Ultrastructure of the CS of coho salmon showed signs of appreciable activity during abnormal smoltification. It is possible that the stunt spend considerable energy to reduce Ca levels in SW further hindering its ability to thrive and grow (Aida *et al*, 1980a; Nishioka *et al*, 1982). Prolactin (PRL)- induced stimulation of CS cells and hypercalcemia in SW-adapted eel have been recorded (Olivereau and Olivereau, 1978). Activated

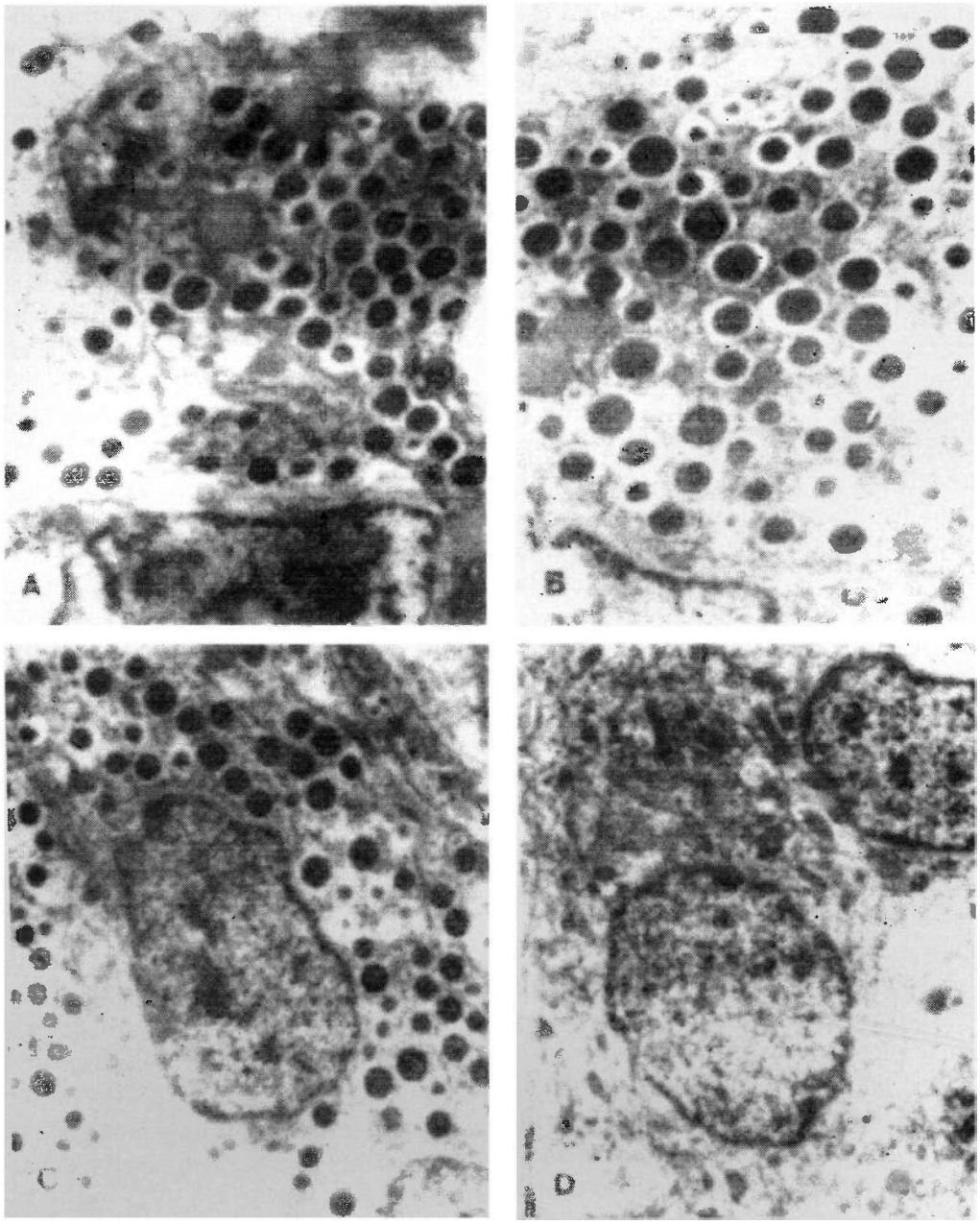

Fig. 7 : Electron micrographs of eel CS after incubation in media containing 0.1μM (A), 0.0 mM (B) and 1.25 mM (C) Ca^{2+} show CS cells with many secretory granules. Incubation in 3.75 mM (D) Ca^{2+} exhibits degranulated cells. x 15,000. (after Hanssen *et al*, 1991; Courtesy: Prof. P. K. T. Pang & Academic Press, Orlando, USA).

eel CS cells may elaborate stanniocalcin which would compensate for prolactin-induced hypercalcemia. The increased activity of CS in response to vitamin D_2-induced hypercalcemia maintained in Ca-rich media has been observed (Ahmed and Swarup, 1979). Concentration of stanniocalcin is enhanced seven-folds in Ca-overloaded eels with very high plasma Ca level (Milet *et al*, 1980). Organ culture and fluorescent as well as ultrastructural studies indicate that the secretory activity of CS cells is directly affected by plasma ions, especially Ca (Aida *et al*, 1980b; Lopez *et al*, 1984). Hanssen *et al* (1991) observed accumulation of secretory granules in the CS cells of eels maintained in freshwater or low Ca-water whereas progressive degranulation was noticed when the fish were transferred in media with Ca^{2+} concentrations of 1.25 mM and 3.75 mM (Fig. 7). True parathyroid are absent in fishes (Roth and Schiller, 1976; Oguro *et al*, 1978; Pang *et al*, 1980a; Clark *et al*, 1986; Pandey, 1991, 1992; Sasayama, 1999). However, the presence of PTH-like substance has been observed in the plasma (Orimo *et al*, 1982), pituitary gland (Parsons *et al*, 1978; Kaneko and Pang 1987; Harvey *et al*, 1987; Pang *et al*, 1988)

and the CS of teleosts (Milet *et al*, 1979a, 1982, 1984a, b, 1985; Lopez *et al*, 1981, 1984; Pang *et al*, 1988; Hirano, 1989). Immunoreactivity for stanniocalcin has also been observed in the CS cells of some teleosts (Tissernand-Jochem *et al*, 1987; Kaneko *et al*, 1988; Wendelaar Bonga *et al*, 1989a; Wagner *et al*, 1986, 1988a). Moreover, exogenous administration of high doses of PTH in FW teleosts and marine cartilaginous fishes did not produce hypercalcemia (Budde, 1958; Clark and Fleming, 1963; Moss, 1964; Urist, 1964a, b; Simmon, 1971). Also in the eel having osteoclastic cells, mammalian PTH has no hypercalcemic response (Lopez, 1971). Even in the FW lungfish, PTH administration has no appreciable effect on the plasma Ca level (Urist *et al*, 1972). The CS extract injection into rat led to hypercalcemia and osteoclastic resorption of the femoral periosteal area (Milet *et al*, 1979a) and such a PTH-like effect of the CS extract on embryonic mouse bone culture has been confirmed (Lafeber *et al*, 1986). Injections of bPTH and CS homogenate produce hypocalcemia in fishes adapted to Ca-deficient SW or FW, respectively (Wendelaar Bonga *et al*, 1986). The CSX induces a decrease in gut alkaline phosphatase activity in fish and CS extract administration increase this enzyme activity *in vitro* (Milet *et al*, 1985). These results can be taken as examples of the resemblance between the biological effects of the PTH (hypercalcemic hormone of terrestrial vertebrates) and the stanniocalcin (hypocalcemic hormone of the CS) (Milet *et al*, 1985; Wendelaar Bonga *et al*, 1986). In contrast, administration of bPTH causes hypocalcemia in teleosts (Milet *et al*, 1985; Wendelaar Bonga *et al*, 1986; Lafeber *et al*, 1988c). The mechanism of such action is not yet known but it is believed that PTH does not regulate gill membrane permeability in the FW teleosts (Urist *et al*, 1972; Urist, 1976). Uma Devi (1977) reported the accumulation of radiolabelled calcium in kidney and bone of PTH-treated *Heteropneustes fossilis* and suggested these organs as sites of the hormone action in the catfish. Apart from the reported decreased gut Ca transport after SCX (Chartier *et al*, 1983), stimulation of resorption of mammalian bone *in vitro* have also been observed (Milet *et al*, 1979b; Lafeber *et al*, 1986). The PTH and stanniocalcin have in common the ability to stimulate ^{45}Ca influx in an isolated eel gill preparation (Milet *et al*, 1985). Furthermore, in mouse calvarial bone, both the PTH and stanniocalcin probably act via the same receptor (Lafeber *et al*, 1986). A rainbow trout fry bioassay based on ^{45}Ca uptake has been used to compare the effects of pure coho salmon stanniocalcin and several synthetic peptide fragments of the hormone. The N-terminal 1-20 amino acid peptides of both eel and salmon stanniocalcin (STC) significantly inhibit Ca intake, the effective doses of the peptides on a molar basis were 20-200 times that of the intact molecule. In contrast, the C-terminal fragments of the eel stanniocalcin (amino acids 202-231) did not have inhibitory effect on Ca uptake instead it significantly enhanced ^{45}Ca uptake (upto 6 folds) (Milliken *et al*, 1990). Stanniocalcin concentrations in FW and SW eels do not differ by the hormone secretion and metabolic clearance rates in SW are 70-75% higher than in FW. Increased hormonal distribution space and receptor density have also been observed in SW eels. Hormone has higher hypocalcemic potency in SW than in FW eels suggesting that SW fish requires more hormonal control over transcelluar influx of Ca than FW fish (Hanssen *et al*, 1993).

The CS extract from female carps have been shown to induce more pronounced hypocalcemia as compared to male common carps (Patel and Das, 1994). Enhanced cytological activities in CS of Atlantic salmon (*Salmo salar*) have been observed during spawning migration (Heyl, 1970). Subedhar and Rao (1979) observed seasonal variations in histology of the CS of *Heteropneustes fossilis* in relation to gonadal maturation and recorded heightened activity in the gland of female catfish during breeding peak. In common carp, there exists corresponding changes in the activity of CS, gonadal maturation and serum Ca levels (Swarup, 1992). The increased correlated activity of CS and UBG during gonadal maturation perhaps be to protect Ca pools during the period of high Ca demand, especially in females owing to increase in Ca-bound vitellogenin. In tilapia, CS cells are activated in high-calcium FW or during ovarian maturation, the conditions associated with hypercalcemia (Urasa and Wendelaar Bonga, 1985). A corresponding change in the activity of corpuscular cells in relation to ovarian maturation and seasonal changes in Ca levels has also been observed (Ahmed and Swarup 1990; Swarup, 1992).

Gill Permeability

The use of ^{45}Ca in eel *in toto* demonstrates that the positive net flux of Ca and above all the influx increase is confirmed by perfusion with CS extract of isolated gills (Fenwick and So, 1974). Perfusion of an isolated head of the same species given more precise results - net influx is negative in controls, after SCX Ca^{2+} influx increases and efflux is reduced the small net flux becomes positive. This net influx tends to be similar to that of intact eels when isolated heads are perfused with CS extract (Milet *et al*, 1975). The SCX reduces an increase of the branchial Ca^{2+}-ATPase activity as the total protein concentration of the extracted enzyme preparation is higher, a *de novo* synthesis of more branchial Ca^{2+}-ATPase activity is suggested (Fenwick, 1976). Killifish Ca^{2+}-ATPase in gills is more

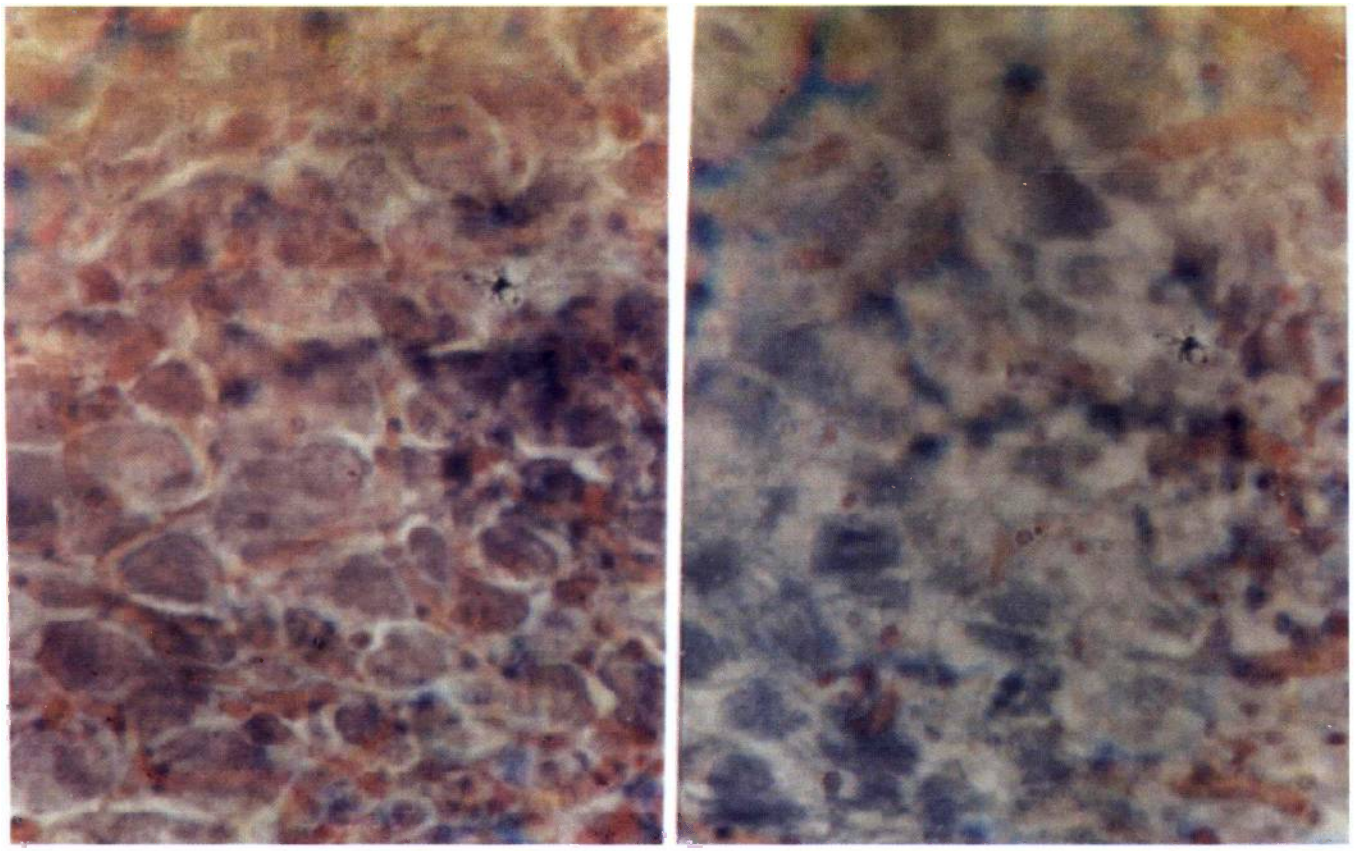

Fig. 8 : Nucleus preopticus (NPO) *Tor putitora* which may depict PTH-immunoractivity.. x 1,000.

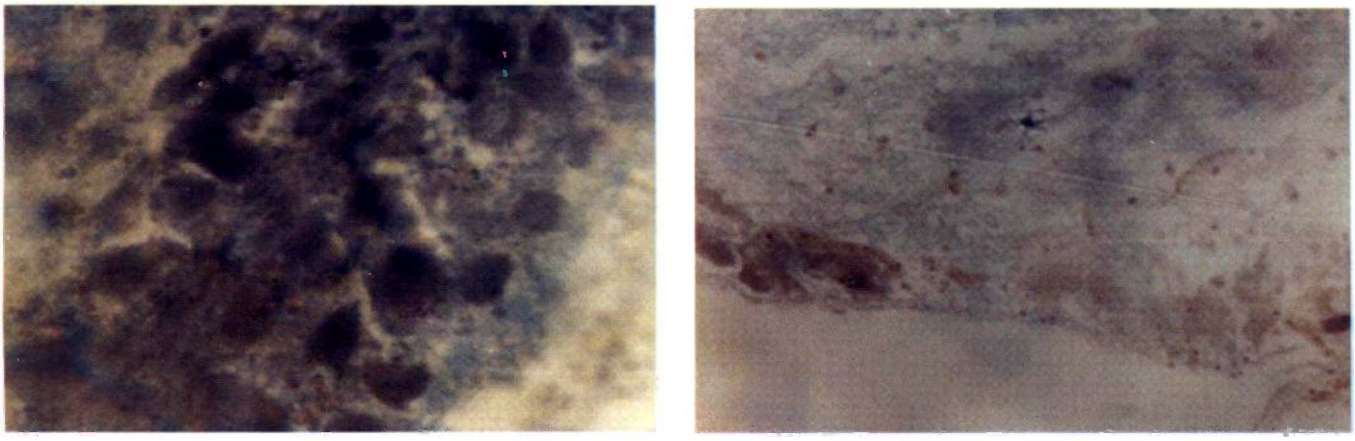

Fig. 9 : Nucleus laterlis tuberis (NLT) of *Tor putitora* which may exhibit PTH- immunoractivity. x 1,000.

(Fenwick, 1976). Killifish Ca^{2+}-ATPase in gills is more active in SW than in FW and Ca^{2+}-ATPase in kidney shows the converse activity. This enzyme is inhibited by the administration of CS extracts (So and Fenwick, 1979). In an isolated gill preparation, the CS and PTH have in common the ability to stimulate ^{45}Ca influx and inhibit ^{45}Ca efflux (Milet *et al*, 1985). Acid labile stanniocalcin of eel exerts its effect on Ca homeostasis by directly attenuating the role of branchial Ca influx. The SCX eels develop hypercalcemia and a greater rate of branchial ^{45}Ca influx than the controls. This can be prevented by post-operative injection of CS extracts (So and Fenwick, 1977, 1979).Ca uptake from water takes places mainly through the gills. The effect of SCX has been ascribed specifically to the absence of stanniocalcin which is an inhibitor of gill Ca transport (Wagner *et al*, 1986,1988b; Lafeber *et al*, 1988c; Hanssen *et al*, 1989). Pandey (1994b) showed that CS of the catfish, *Ompok pabda*, produces stanniocalcin which is active in the natural FW environment (0.4 mM) while its potency is enhanced under

medium. The CS cells of the ovariectomized catfish get inactivated and the total plasma Ca titres are significantly lowered. Converse changes have been observed in the cells and Ca levels following administration of estradiol (Pandey, 1993).

Estrogen

An ovarian-CS axis has been proposed in the fish (Pandey, 1988b). Initially, Bailey (1957) observed that estradiol administration in goldfish results in the enhancement of total plasma Ca levels. Similar observations have also been recorded in other fishes (Pang, 1973; Bjornsson and Haux, 1985). Although estradiol administration to teleosts increased the total plasma Ca (Pandey, 1993) by inducing the synthesis female-specific vitellogenin in liver (de Vlaming *et al*, 1980), free plasma Ca levels essentially remained unchanged (Björnsson and Haux, 1985; de Vlaming *et al*, 1980). The estrogen seems to alter the serum Ca level which, in turn, would affect the CS activity (Aida *et al*, 1980 a, b). Furthermore, Pandey (1988b) showed that bilateral ovariectomy (OVX) induced inactivation of CS cells and estradiol administration led to hyperactivity of these cells. The physiological demands for Ca during reproduction are entirely different in mammals and non-mammalian vertebrates. In fish, large amount of Ca is needed for its deposition in the yolk of eggs (Simkiss, 1974; Bentley, 1982; Björnsson and Haux, 1985; Dacke, 1989). Estrogen administration has been shown to induce hypocalcaemia in kelp bass whereas similar treatment is ineffective in hagfish and sharks (Urist, 1964). Hypercalcemic as well as insignificant effects of estrogen have also been reported in lamprey (Pickering, 1976) and shark (Woodhead, 1969). High levels of Ca have been observed in females during breeding season (Pora, 1935, 1936; Woodhead 1968; Oguri and Takada, 1967; Fontaine *et al*, 1969). Administration of estradiol has been shown to induce hypercalcemia in both the sexes of teleosts (Bailey, 1957; Ho and Vanstone, 1961; Fleming *et al*, 1964; Chan and Chester Jones, 1968; Woodhead, 1968; Balbontin *et al*, 1978; Pang and Balbontin 1978; Mugiya, 1982; Björnsson *et al*, 1989; Pandey, 1993). Though the mechanism of such action is not properly understood (Mugiya, 1982; Pandey, 1988b, 1993; Persson *et al*, 1991) but there are indications that minerals from scales and bones are involved in this process (Mugiya, 1982, 1990; Mugiya and Odawara, 1988; Hermann-Erlee and Flik, 1989).

Other Hormones

Glucagon has been reported to evoke hypocalcemia in cuchia eel (Srivastav and Dixit, 1981; Srivastava *et al*, 1995, 1986). In this fish, exogenous administration of glucagon activates the prolactin cells as is evident from the increase in their nuclear size and release of secretory granules. The increased secretion of hypercalcemic factor from PRL cells gradually minimize the hypocalcemic effect of glucagon to the extent that after day 3 following the treatment, the serum Ca shows a progressive rise resulting in normalization. The PRL cells tend to degenerate after day 10 possibly due to continued hyperactivity, secretion and exhaustion (Srivastav *et al*, 1986).

Evolutionary Aspects

Salmon calcitonin-like immunoreactivity as well as calcitonin receptors (CTRs) have been localized in central nervous system (CNS) of vertebrates suggesting its role as neurotransmitter in mammals (Barlet *et al*, 1998). Though CS is present only in ray-finned fishes, is it effective in controlling plasma Ca in tetrapods or not? Ma and Copp (1978) and Ukawa and Sasayama (1993) reported ineffectiveness of the CS extract in rats. Furthermore, CS extract of bullhead failed to induce hypocalcemia in rats although the CS extract from eel produced hypocalcemia in rats (Leung and Fenwick, 1978). In contrast, the CS extract injections have induced hypocalcemia in birds, amphibians and snakes (Pandey *et al*, 1982; Ma and Copp, 1982; Swarup and Srivastav 1982b; Srivastav and Swarup, 1982; Hasen *et al*, 1987) while Milet *et al* (1984) reported hypercalcemia in the anuran, *Xenophus laevis*, following administration of the CS homogenate. Recently, four stanniocalcin genes have been isolated from CS of the teleost but their physiological as well as phylogenetic significance is not yet clear (Schein *et al*, 2012) It is interesting to note that stanniocalcin and STC analogues have also been identified in ancient invertebrates and human too (Gerritsen and Wagner, 2005). Though encapsulated parathyroids have not been reported in fish but there exists reports for the physiological action of parathyroid hormone in the teleost (Uma Devi, 1977). Though immunohistochemical studies have revealed the presence of hypocalcin and mammalian PTH-like factors in pond snail, the functional significance of such association has not yet been explored (Wendelaar Bonga *et al*, 1989b). Interestingly, parathyroid hormone-related protein (PTHrP) has been identified in the brain of teleostean as well as elasmobranch fishes but its role in piscine calcium regulation is yet to be ascertained (Danks *et al*, 1993; Ingleton *et al*, 1995; Ingleton and Danks, 1996; Flanagan *et al*, 2000). RT-PCR analysis revealed that gene for STC-2 is expressed in a number of tissues like pituitary, brain, heart, gills, stomach, spleen, skin, dorsal fin, skeletal muscle, liver, CS, intestine, ovary and testis of Japanese flounder (*Paralichyhus olivaceus*) (Shin and Sohn, 2009). Immunoreactivity for stannuiocalcin 2 (STC2) has also

been observed from invertebrates (annelids) to mammals (Olsen *et al*, 1996; Ishibashi and Imai, 2002; Roch and Sherwood, 2010; Tanega *et al*, 2012; Yeung *et al*, 2012) and enhanced level is observed in women with breast cancer (Chang *et al*, 2003). With recent advances in cellular and molecular biotechnology, more work should be undertaken in these directions involving different representative classes to understand the phylectic evolution hypercalcemic in the animal kingdom.

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