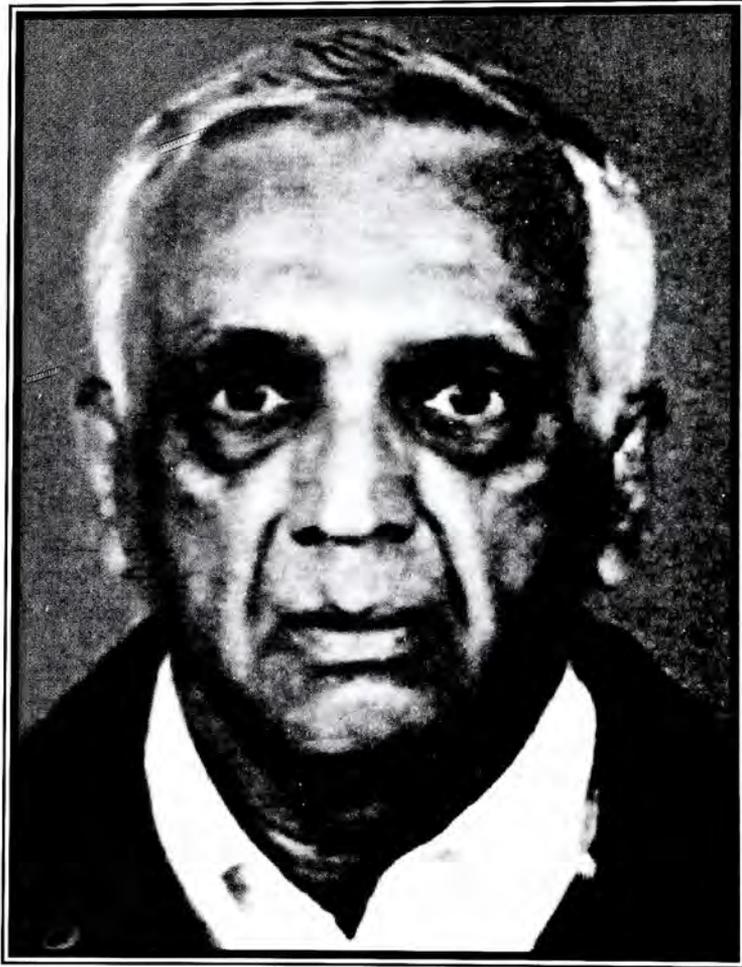


NUGGEHALLI RAGHUVeer MOUDGAL

(4 March 1931 - 8 May 2011)

Biog. Mem. Fell. INSA, New Delhi **40** (2013) 57-74





N. R. Hari Singh



NUGGEHALLI RAGHUVeer MOUDGAL

(1931-2011)

Elected Fellow 1978

PERSONAL LIFE

NUGGEHALLI RAGHUVeer MOUDGAL was born on 4th March, 1931 in Mysore, Karnataka in an upper middle class family. His father, N Narasimha Moudgal was the Chief Electrical Engineer, Mysore State Electricity Board and was largely responsible for the electrification of the state. His mother, Vaidehi Moudgal was a home maker and had tremendous influence on her children as she was artistic and very tidy and organized in her daily activities. He belonged to a community called 'Hebbar Iyengars' who speak at home a dialect which is a mixture of Kannada and Tamil. NR Moudgal was the youngest of five children—three boys and two girls. He adored his two elder brothers, N Shyam Prasad and N Ram Prasad. His two sisters, Prabha Devi Anantram and Harini Madhava Rao were close to him. The latter got him interested in reading classic English literature at an early age and he completed High School in 1946 in Seshadripuram High School, Bengaluru. He stayed with Prabha Devi's family at Bhavnagar and Kolhapur during his college days. This led to a B.Sc degree in 1950 from the University of Bombay. Moudgal, like other young people of his generation went to Madras to obtain his MSc by research in 1954, working on biochemistry of thyroid hormones. He married Prapulla nee Biligiri Rao on 20th May, 1957. His wife Prapulla passed away on December 10, 2008. He is survived by his two sons (Pradeep and Madan), daughter (Priya), two daughters-in-law (Chandrika and Sumana) and son-in-law, Raghav Iyengar and grandchildren, Anita, Divya, Anusha Ashwin, Rohit and Aishwarya.

Raghu, as he was fondly called by his friends and seniors, was a tall man of robust health. In nineteen seventies, he fell ill once seriously with salmonella infection after a trip to Kolkata but recovered luckily. In his last days, which he spent in USA with his children and relatives, he battled with Cancer and ultimately passed away on 8th May, 2011 leaving behind a large group of admirers to whom he was a giant in science, internationally well known and a role model of a dedicated scientist. He was an extremely dynamic person in personal and professional life. He was one of the most creative scientific minds of his generation. To some of us who have watched him take his family to a temple but not enter the temple himself but patiently wait for their return, he may appear to be an agnostic, but in his personal belief he effortlessly managed to bridge his rationalist thinking with his spiritual self. During a Guha Research Conference held at Pachmarhi, Bhopal in 1985, we



eager to go down a cave to see an ancient Shiva-lingam but Moudgal refused to enter. But I have never heard him speak harsh words about any one. He was a multi-faceted good human being. Whether it was his science (controls, more controls, and physiological relevance) or the younger generation, no matter what their line of interest or work, his willingness to help a variety of people in many different ways and his generosity were legendary among a wide circle of friends and relatives. He gave unconditionally and set a high bar of excellence to emulate for all -students, colleagues, friends and relatives who have had the privilege to know him. At the end of a distinguished career at the Indian Institute of Science, Bangalore, he retired from active service in 2006. He never sought positions of power and remained wedded to his science till the last breath. His nephew, Praveen said, "He enjoyed the simple pleasures of life, a good cup of coffee, a fine meal; a nice drink would always perk him up". We could not agree more. Reproductive Biology fraternity has lost a great scientist of truly global dimension. His scientific work in India attracted attention globally and indeed influenced, for a change, westerners in USA and Europe and some in Australia who followed his work, extending it in many ways. The School of Reproductive Immunology that he established and nurtured in Bangalore was indeed one of the distinguished schools of science in India which influenced global level science. Moudgal was a no-nonsense person who did not suffer fools. He was always in a hurry to complete his mission.

ACADEMIC CAREER

NR Moudgal completed his PhD from Madras University in 1957 under the supervision of Professor PS Sarma who was a pioneer biochemist of India. Professor PS Sarma had worked with Elvehjem at Wisconsin, USA and was a Watumul Foundation Fellow. PS Sarma had started his work at the Nutrition Research Laboratories then at Coonoor and later headed the Department of Biochemistry at the University of Madras (AC College of Technology). He was invited by Professor Satish Dhawan to come and take over the Department of Biochemistry at IISc which he successfully built as the foremost department in the country and one of the best in the world. Some of Moudgal's contemporaries at Madras were V Srinivasan, KSV Sampathkumar, LK Ramachandran and PR Adiga. Incidentally PR Adiga also did his PhD under PS Sarma but worked on neurolathyrism. Adiga started his PhD work at Madras but completed at Bangalore, Later in 1970s he became Moudgal's colleague and contemporary at IISc K Sivarama Sastry, another scientist from PS Sarma's research group was also Moudgal's contemporary. It is interesting that LK Ramachandran and Sivarama Sastry went and established a flourishing Department of Biochemistry at Osmania University in early sixties. Moudgal, after his Ph.D., went to work with Professor CH Li at UC, Berkeley and later at San Francisco (1958-61). CH Li, a student of Herbert Evans (Vitamin E and Reproduction) and a contemporary of Fraenkel Conrat (who later joined the Virus Research laboratory of



WM Stanley), established and nurtured the most famous Hormone Research Laboratory. This laboratory of Li was a Mecca for Biochemistry and is known to have made significant contributions to Protein Science, Peptide Chemistry, Hormone Research, and Immunochemistry to name a few areas. Moudgal was one of the most famous scientists from this laboratory.

Majority of Li's post-docs went on to become eminent professors in more than ten countries including India. The laboratory had at that time many future heroes like J Ramachandran, H Papkoff, I Geschwind, and E Hayashida among others. Moudgal's work established that pituitary gonadotropins are immunogenic, notwithstanding their major physiological role in an essential process like reproduction. This was a pioneering observation. Using techniques like quantitative precipitin test which Heidelberger had developed it was unequivocally established that one can raise antibodies to pituitary protein hormones in heterologous species. Moudgal continued his association with Li and Papkoff till the end of his official career. On his way back from USA, Moudgal worked as a Wellcome Research Fellow in the laboratory of RR Porter at St Mary's Hospital Medical School, London (1961-62) working on PAB-Cellulose as a carrier for immobilization of antibodies. Porter later moved to Oxford and went on to become a Nobel Laureate for his work on the gross structure of Immunoglobulins. Moudgal's future work was greatly helped by his experience in these two laboratories. Professor PS Sarma selected Moudgal for the post of Assistant Professor at IISc. Moudgal began his independent career with the help of generous grant from Ford Foundation and the collaboration of his first three brilliant PhD students *i.e.* Sairam, Madhwaraj and AJ Rao. He started work on urinary gonadotropins from macaques. Surprisingly, this work led to the discovery of an inhibitor of FSH. It turned out later to be a Sialidase from kidney. Primates are known to biosynthesize N-acetyl Neuraminic acid as one of the ten types of sialic acids. As sialic acid (NANA, N-acetyl Neuraminic Acid) was essential for plasma life and hence for *in vivo* biopotency (in primates), the Sialidase of kidney origin by its ability to remove sialic acid, was acting as an inhibitor of FSH *in vivo*.

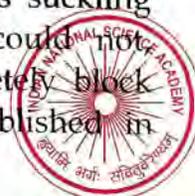
In mid sixties, Moudgal's group made the significant observations that neutralization of circulatory Luteinizing Hormone (LH) results in blockade of reproductive processes like ovulation, implantation, and gestational progress etc. This was the biggest breakthrough in reproductive biology. Not only did it provide a vastly superior substitute technique for hypophysectomy to establish the role of a pituitary hormone in any physiological process, it enabled Moudgal to use such characterized antibodies as fine probes to study hormone action in great detail in later years. The significance of these observations, made in rodents, in the development of immunocontraceptive technology, was not missed. Indeed RO Greep of Harvard invited Moudgal to spend time in his laboratory to extend these observations, if possible, to new world monkeys and sub-human primates. Between 1969 and 1971 Moudgal supervised work at Harvard University (Prof Roy Greep's



group) leading to more than a dozen path breaking papers. Reproductive Immunology was firmly established and Moudgal's laboratory was a pioneer in this. While at Harvard, in collaboration with WR Moyle, Moudgal also gave evidence, for the first time, for the presence of LH specific receptors on testicular tumor cells. These cells were being used as a simpler model to dissect the Hormone-Receptor interactions and their translation into cellular responses like cAMP production and steroidogenesis. On his return to IISc in 1971, Moudgal initiated a long range programme on deciphering molecular aspects of LH-Receptor interaction.. Over the next ten years, a large number of publications from his group described the details of this hormone-receptor interaction. The added impetus for this type of work was of course, the announcement of the Nobel Prize to EW Sutherland for his discovery of cAMP as a second messenger for a majority of hormones whose receptors are on the plasma membrane of the host target cells. Moudgal's group demonstrated the degrees of coupling between hormone binding to receptors and response in terms of cAMP production and steroid output.

Another significant observation made by him was that immuno-neutralization of circulating FSH in bonnet monkeys (*Mecaca radiata*) resulted in oligozoospermia and even azoospermia. This led to his continued interest in developing a vaccine for the purposes of immunocontraception in the male human subjects. His interest in immunocontraception and the concerns expressed by educated society at large stimulated him to look for male immuno-contraceptive vaccine candidate. His own observations in rodents and bonnet monkeys (*Macaca radiata*) convinced him that FSH is the answer. It is important to remember that all the known contraceptive methods for the human males affect his libido to varying degrees. Immunization with FSH is the only contraceptive method which does not affect libido. It went through Phase I clinical trials also. Rules of the game had changed by then and any protein based pharmaceutical had to be made through recombinant DNA techniques. Good Laboratory Practices (GLP) demanded that recombinant antigens be used. At this time Moudgal retired from active service and hence the vaccine was not realized completely. However, this work enabled him to look at other related reproductive phenomena like regulation of follicular maturation and atresia in the female, spermatogenesis in the male, role of estrogen in spermatogenesis, primate reproduction and lactational amenorrhea.

Moudgal's group had demonstrated the hormonal mechanism of ovarian quiescence during lactation in rodents and primates. For the first time in the world, it was demonstrated that prolactin could mimic the action in inhibiting the action of LHRH on pituitaries provided minimal suckling stimulus is maintained. For example in the case of the lactating pregnant rat model, while 8 pups suckling intensity could block implantation and 2 pups suckling intensity could not, administration of prolactin to the 2 pup suckling group could completely block LHRH action and implantation. This significant observation was published in



Endocrinology, the mouth piece of American Endocrine Society and a highly rated journal. The parallel observations made in monkeys were published in the prestigious journal *Nature* (London).

In 1973 Moudgal organized an International Symposium to take stock of the field of Gonadotropins and to resolve some problems in their structure, mechanism of action, and immuno-contraceptive potential. Majority of the good scientists in the area of reproductive endocrinology in the world attended this symposium and shared their data. This included RK Meyer, H Papkoff, C Channing, MR Sairam, G Hennen, Paul Licht, RMG Nair, MRN Prasad, S Duraiswami,, JF Kennedy, SM McCann, AR Sheth, GP Talwar, GS Greenwald, N Schwartz, SS Guraya, K Yoshinaga, F Labrie, HR Behrman, DT Armstrong, AP Labhsetwar, K Ahren, PF Hall, AR Midgeley, RJ Ryan, OP Bahl, SS Koide, AR Means, JH Dorrington and HG Burger among others. It was an unforgettable and inspiring feast of ideas and personnel to young research students. Moudgal's laboratory was firmly established as one of the major players in this field in the world. Those were not the days of internet.

It is at this point in the history of Indian research in Biology in general and biomedical area in particular, that everybody realized the total absence of, any supporting industry to supply quality biochemicals, service facilities for sequencing and synthesis of biomacromolecules, production and supply of quality native hormones or expertise in recombinant DNA techniques in cloning and large scale expression of biologically active glycoprotein hormones. An additional feature was the increasing hostility of Animal Ethics Committees towards animal houses in general and primate houses in particular. All these took their toll on the Contraceptive Vaccines programme of the country as a whole and in particular the Bangalore programme. I cannot help saying that this research story on reproductive vaccines is a reflection on funding policies, the health of the peer-review system in our country in terms of both competence and honesty and the absence of scientific temper in many policy makers. Science by then had become an enterprise and we had and continue to have all kinds of players-good, bad and the indifferent. Science has to be practiced and administered by people with conviction in science and in fair play. Moudgal by this time had come to the end of his formal career. Some of his former students are taking this and related work to greater heights most admirably.

Moudgal rose through ranks starting as Assistant Professor in 1965 and became a full Professor in nineteen seventies. He served with distinction as the Chairman of the Department of Biochemistry, IISc and also as the Dean of Faculty of Science at IISc, Bengaluru. Moudgal was one of the most dynamic and creative scientists of our country. He was always bubbling with ideas. His passion for science was infectious. He set always global standards in science and professional ethics. He was always the leading researcher in his field. At the International organizational level,



was a prominent scientist and much sought after for many matters. His contributions in this regard to the field of Inhibin, the FSH release inhibitory polypeptide, are well acknowledged.

ACADEMIC HONOURS, AWARDS AND SERVICES

Moudgal's group published over 250 papers and reviews and numerous chapters in books. He has published in some of the most prestigious journals like Nature, Endocrinology, Biology of Reproduction, Current Opinion in Immunology, Biochemical Journal, Journal of Biological Chemistry, Journal of Reproduction and Fertility, Journal of Endocrinology, Fertility and Sterility etc. Moudgal's laboratory was recognized as a UGC Centre of Advanced Studies in Reproductive Endocrinology. Though he began his career in the department of biochemistry, his group size and productivity justified the creation of a separate Centre for Reproductive Biology and Molecular Endocrinology (CRBME) which later was upgraded as a Department of Molecular Reproduction and Developmental Genetics (MRDG). He also established and ran the largest primate house in the country as Primate Research Laboratory (PRL). This was one of the best in the world, housing at one point in history, more than 400 monkeys with pedigree and health record. Many veterinarians joined Moudgal and obtained their PhDs. He has served as Editor of the Indian Academy publication, *Journal of Bioscience* in its inception. He was on the editorial board of *Molecular and Cellular Endocrinology*, the European journal. Moudgal mentored 18 PhD students and 14 post-doctoral Fellows. He was a member the Society of Biological Chemists (India), Endocrine Society (USA) and the Society for the study of Reproduction (USA). He was an elected Fellow of both the Indian Academy of Sciences, Bangalore and the Indian National Science Academy, New Delhi. Moudgal received the BC Guha Award (1975), SS Bhatnagar Award (1976), Sreenivasayya Memorial Award of SBC (I), Sanjay Gandhi Award for Science & Technology (1984) and the Yellapragada Subbarow Birth Centenary Lecture Award of INSA (1996). Moudgal was a Homi Bhabha Fellow (1978). Moudgal was and will remain an inspiring leader whose commitment to science, laboratory and his way of doing science and mentoring younger colleagues is unmatched. He was peerless when it comes to focus and single minded devotion to research. He had less than contempt for science administrators and managers. He was a complete laboratory bench scientist leader and not a lazy arm chair philosopher who manages publications from younger colleagues.

MY PERSONAL REMINISCENCES

I first heard of Moudgal during the annual meeting of the Society for Biological Chemists (I) held at Osmania University by the Department of Chemistry (Biochemistry) in 1968. In our MSc classes also both my teachers Professors LK Ramachandran and K Sivarama Sastry used to mention Moudgal's name in the



context of discussions on proteins, hormones and antibodies. In the summer of 1969, I had the opportunity to spend a month and a half in his laboratory as part of an orientation course. I had made up my mind then that if I do a PhD it should be in his laboratory. Madhwaraj and AJ Rao taught me few immunochemical techniques and OAAD assay for Luteinizing hormone activity measurement. The interviews were held in June/July of 1969 and I was fortunately selected for admission into PhD. Unfortunately my University was closed since December of 1968 for political reasons without holding the annual terminal examinations. Hence I was asked to go back to Hyderabad, get my MSc and come back to join. I could do this by March, 1970. Prof PS Sarma came as practical examiner for our batch in February of 1970. He reiterated my admission and asked me to come and join IISc. When I went to join, PS Sarma told me that Moudgal is on sabbatical at Harvard and whether I would like to join any other laboratory. I said I will work only in Moudgal's laboratory. For the next one year or so I worked with the help of my seniors like AJ Rao, Madhwaraj, TSA Samy and Ms Prema Rao. When Moudgal returned in 1971, he asked me to work on cAMP for my PhD instead of immobilized antibodies. I read the relevant literature thoroughly and chose to look at LH-Receptor interactions and coupling of binding of hormone to the receptors and cAMP generation. I received ample guidance from him. He was always enthusiastic and encouraging us immensely during periods of depression when experiments were failing. Every week during lab seminars he would come up with dozens of new ideas. His creative energy and passion for research was simply impressive and infectious. I had the best of my life in science during those days. After I finished my PhD, I had gone home to look for a job. He called me one day and said I should appear for interview for the post of Assistant Research officer in an ICMR sponsored project in his laboratory. I was duly selected and I worked for another year and a half. A former colleague of Moudgal at Harvard and a visiting professor from Florida State University at Tallahassee, Prof Lipner was also in the committee which selected me.

I moved to the newly formed University of Hyderabad (UH) as a Lecturer in Biochemistry but in the School of Life Sciences, but kept in touch with Moudgal. After my marriage when I visited Bangalore, he was extremely warm to us taking us home for a dinner. He visited UH during the tenure of Prof Ramakrishna as Vice-Chancellor. One day he wrote me a big letter advising me to join Prof OP Bahl at SUNY, Buffalo. I went with my wife and joined the laboratory of OP Bahl in May 1979. Moudgal visited us the next year at Buffalo. I kept in touch with him even after I moved to Delhi University upon invitation from Prof Gurubaksh Singh, the then Vice-Chancellor of DU. I met Moudgal several times during this period. During the 1994 IUBMB Congress held in Delhi at Hotel Ashoka, he and KSV Sampathkumar met me in the corridors and were very happy and congratulated me on my election to INSA. I cherish these moments. During a get together at IISc council Hall on the eve of his retirement, I met Mrs. Moudgal and expressed our deep sense of gratitude



to her for sparing Moudgal only for his students. Moudgal spent more time in the laboratory than with his family. The last I met him with his wife was when he was on his way to USA sometime in 1999. Later I had met him several occasions but only officially. After Mrs Moudgal passed away, he visited Delhi for a brief stay with his niece at NOIDA. We went and spent some time with him. Loss of his wife was hurting him and I could notice his sense of loneliness. He started spending more time abroad with his children than in India. Suddenly one day sometime in February, 2011 Rajan Dighe informed me that Moudgal was very sick and has been hospitalized in USA. I sent messages of speedy recovery to Mrinalini, his illustrious niece who is a professor at U. Illinois and whom I had met last in Moudgal's lab during my PhD days in 1971. All of his students and friends were deeply worried about his state of health. Finally when Rajan Dighe telephoned me about Moudgal's demise, I could not believe. AJ Rao confirmed it the next day on telephone. My wife and I can never forget his enthusiasm for science and all the mentoring he has done to me. In a society which is pedigree conscious, I am very proud and privileged to have been his student.

ACKNOWLEDGEMENT

I am grateful to many friends who corrected the draft and helped remove some inaccuracies. Among them I particularly like to thank Prof AJ Rao, Rajaramanna Fellow and an emeritus scientist of INSA at IISc, Bengaluru and Prof Mrinalini Rao, University of Illinois, Chicago, Illinois, a distinguished scientist and Moudgal's niece.

KAMBADUR MURALIDHAR, FNA,
Department of Zoology,
University of Delhi, Delhi-110007
E-mail: kambadur@hotmail.com

BIBLIOGRAPHY

- 1955 (With SRINIVASAN V and SARMA PS) Influence of thyroxin and thyroglobulin on rice moth larva. *Science* **122**: 644-645.
- 1956 (With SARMA PS and SUNDARAM TK) Influence of thyroid hormone on nicotinamide metabolism in the rat. *Biochim Biophys Acta* **20**: 413-414.
- 1957 (With SRINIVASAN V and SARMA PS) Studies on goitrogenic agents in food. II. Goitrogenic action of arachidoside. *J Nutr* **61**: 97-101.
- (With SRINIVASAN V and SARMA PS) Studies on goitrogenic agents in food. I. Goitrogenic action of groundnut. *J Nutr* **61**: 87-95.
- 1958 (With RAGHUPATHY E, SARMA PS) Influence of thyroid status on creatine synthesis in rat liver. *Biochim Biophys Acta* **26**: 651-652.
- (With RAGHUPATHY E and SARMA PS) Studies on goitrogenic agents in food. III. Goitrogenic action of some glycosides isolated from edible nuts. *J Nutr* **66**: 291-303.



- 1958 (With RAGHUPATHY E and SARMA PS) Influence of some iodoaminoacids and iodoproteins on the growth of *Corcyra cephalonica* St. *Nature* **181**: 1655-1656.
- (With RAGHUPATHY E and SARMA PS) Studies on the enzymic digestion of some proteins and their iododerivatives. *Enzymologia* **19**: 303-309.
- 1959 (With RAGHUPATHY E and SARMA PS) Effect of thyroid imbalance on the detoxication of benzoic acid in the rat. *Endocrinology* **64**: 326-332.
- 1960 (With LI CH and PAPKOFF H) Immunochemical investigations of human pituitary growth hormone. *J Biol Chem* **235**: 1038-1042.
- 1961 (With LI CH) Production of antibodies to human pituitary growth hormone in the rat. *Endocrinology* **68**: 704-709.
- (With LI CH) An immunochemical study of sheep pituitary interstitial cell-stimulating hormone. *Arch Biochem Biophys* **95**: 93-98.
- (With LI CH) An immunological study of a human pituitary interstitial cell-stimulating hormone. *Nature* **191**: 192-193.
- (With LI CH) Immunochemical studies of bovine and ovine pituitary growth hormone. *Arch Biochem Biophys* **93**: 122-127.
- (With TRENKLE A, SADRIKK, LICH) Complement-fixing antibodies to human growth hormone and sheep interstitial cell stimulating hormone. *Nature* **192**: 260-261.
- 1962 (With PORTER RR) Immunochemical investigation of a biologically active core obtained from chymotryptic digestion of bovine growth hormone. *Gen Comp Endocrinol* **2**: 236-239.
- 1963 (With TRENKLE A and LI CH) The use of antigen-cellulose suspensions for the isolation of specific antibodies. *Biochim Biophys Acta* **71**: 185-187.
- Studies on pituitary lactogenic hormone. XXI. Immunochemical studies of the sheep hormone. *Arch Biochem Biophys* **100**: 255-259.
- 1965 (With SAMY TS, RAJ HG and CAMA HR) Immunochemical characterization of sheep plasma glycoprotein. *Indian J Biochem* **2**: 250-252.
- 1966 (With SAIRAM MR and MADHWA HG) Presence of a gonadotropin inhibitor in the urine of the bonnet monkey, *Macaca radiata*. *Endocrinology* **78**: 923-928.
- 1967 (With RAJ HG and SAIRAM MR) Role of gonadotropins in implantation: a study using specific antigonadotropins. *Indian J Exp Biol* **5**: 123-124.
- 1968 (With RAJ HG and SAIRAM MR) Involvement of luteinizing hormone in the implantation process of the rat. *J Reprod Fertil* **17**: 335-341.
- (With SAIRAM MR and RAJ HG) Purification and properties of the follicle-stimulating hormone inhibitor obtained from the urine of the bonnet monkey. *J Endocrinol* **40**: 165-173.
- 1969 (With JUNEJA HS and GANGULY J) Studies on metabolism of vitamin A. The effect of hormones on gestation in retinoate-fed female rats. *Biochem J.* **111**: 97-105.
- Effect of ICSH on early pregnancy in hypophysectomized pregnant rats. *NATURE* **222**: 286-287.
- (With MADHWA RAJ HG, JAGANNADHA RAO A and SAIRAM MR) Need of luteinizing hormone for maintaining early pregnancy. *Indian J Exp Biol* **7**: 45-46.



- 1970 (With RAJ HG) Effect of anti-luteinizing hormone serum on the ovulation of rats. *Nature* **227**: 1344-1345.
- (With RAJ HG) Hormonal control of gestation in the intact rat. *Endocrinology* **86**: 874-889.
- (With RAO AJ) An immunochemical study of ovine pituitary follicle-stimulating hormone (FSH). *Arch Biochem Biophys* **138**: 189-198.
- (With RAO AJ and RAJ HG) Need of luteinizing hormone for early pregnancy in the golden hamster (*Mesocricetus auratus*). *J Reprod Fertil* **23**: 353-355.
- (With RAO AJ, SAIRAM MR and RAJ HG) The effect of human urinary luteinizing hormone (LH) inhibitor on implantation and pregnancy in the rat. *Proc Soc Exp Biol Med* **134**: 496-498.
- 1971 (With MACDONALD GJ and GREEP RO) Effect of HCG antiserum on ovulation and corpus luteum formation in the monkey (*Macaca fascicularis*). *J Clin Endocrinol Metab* **32**: 579-581.
- (With MOYLE WR, GREEP RO) Specific binding of Luteinizing hormone to Leydig tumor cells. *J Biol Chem* **246**: 4983-4986.
- (With MOYLE WR and GREEP RO) Cessation of steroidogenesis in Leydig cell tumors after removal of Luteinizing hormone and adenosine cyclic 3',5'-monophosphate. *J Biol Chem* **246**: 4978-4982.
- (With RAJ HG) A comparative immunochemical study of Luteinizing hormone derived from ovine, murine, equine & human species. *Indian J Biochem* **8**: 314-320.
- (With RAJ HG) Hormonal control of gestation in the intact rat. Studies using specific antigonadotropins. *J Reprod Fertil* **27**: 309.
- (With RAO AJ) An immunochemical study of ovine pituitary follicle-stimulating hormone. *J Reprod Fertil* **27**: 310.
- (With SAIRAM MR) On the mechanism of action of the monkey urinary follicle stimulating hormone inhibitor—its sialidase activity. *Indian J Biochem* **8**: 141-146.
- (With YOSHINAGA K and GREEP RO) Progesterin secretion by the ovary in lactating rats: effect of LH-antiserum, LH and prolactin. *Endocrinology* **88**: 1126-1130.
- 1972 (With BEHRMAN HR and GREEP RO) Studies with antisera to Luteinizing hormone *in vivo* and *in vitro* on luteal steroidogenesis and enzyme regulation of cholesteryl ester turnover in rats. *J. Endocrinol* **52**: 419-426.
- (With BEHRMAN HR and GREEP RO) Effect of luteinizing hormone antiserum on progesterone and 20 -dihydroprogesterone secretion in the pregnant rat. *J Endocrinol* **52**: 413-418.
- (With MACDONALD GJ and GREEP RO) Role of endogenous primate LH in maintaining corpus luteum function in the monkey. *J Clin Endocrinol Metab* **35**: 113-116.
- (With RAO AJ and RAJ HG) Effect of LH, FSH and their antisera on gestation in the hamster (*Mesocricetus auratus*). *J Reprod Fertil* **29**: 239-249.
- 1973 (With MACDONALD GJ, RAJ HG and GREEP RO) Maintenance of progesterone secretion by ovine prolactin or pituitary autografts in the absence of endogenous LH. *Proc Soc Exp Biol Med* **144**: 923-926.
- (With MANECKJEE R) Differential threshold of progesterone required for maintenance of diestrus smear, pseudopregnancy and pregnancy in rats. *Proc Soc Exp Biol Med* **143**: 692-695.
- (With MANECKJEE R and RAJ HG) Comparative effects of antiserum to Luteinizing hormone on pseudo pregnancy and pregnancy induced in the same rat. *Biol Reprod* **8**: 43-47.



- 1974 (With GUPTA G, RAJALAKSHMI M and PRASAD MR) Effect of antiserum to Luteinizing hormone (LHA/S) on the physiology of the epididymis and accessory glands in the albino rat. *Contraception* **10**: 491-504.
- (With GUPTA G, RAJALAKSHMI M and PRASAD MR) Alteration of epididymal function and its relation to maturation of spermatozoa. *Andrologia* **6**: 35-44.
- (With LIPNER H, HIRSCH MA, MACDONALD GJ, YING SY and GREEP RO) Ovulating-inducing activity of FSH in the rat. *Endocrinology* **94**: 1351-1358.
- (With JAGANNADHA RAO A, MANECKJEE R, MURALIDHAR K, MUKKU V and SHEELA RANI CS) Gonadotropins and their antibodies. *Rec Progr Horm Res* **30**: 47-77.
- (With RAO AJ, RAJ HG, LIPNER H and GREEP RO) The role of FSH and LH in the initiation of ovulation in rats and hamsters: a study using rabbit antisera to ovine FSH and LH. *J Reprod Fertil* **37**: 323-330.
- 1975 (With BOSE TK and PRASAD MRN) Changing patterns of sialic acid in the spermatozoa & luminal plasma of the epididymis & vas deferens of the hamster *Mesocricetus auratus* (Waterhouse). *Indian J. Exp. Biol.* **13**: 8-11.
- (With MANECKJEE R) The onset of oestrus and ovulation in lactating rats. *J. Reprod Fertil* **44**: 313-315
- (With MANECKJEE R) Induction and inhibition of implantation in lactating rats. *J. Reprod Fertil* **43**: 33-40.
- (With MUKKU V) Studies on luteolysis: effect of antiserum to luteinizing hormone on sterols and steroid levels in pregnant hamsters. *Endocrinology* **97**: 1455-1459.
- (With PRAHALADA S, VENKATRAMAIAH M and RAO AJ) Termination of pregnancy in macaques (*Macaca radiata*) using monkey antiserum to ovine luteinizing hormone. *Contraception* **12**: 137-147.
- 1976 (With MANECKJEE R and SRINATH BR) Prolactin suppresses release of luteinising hormone during lactation in the monkey. *Nature* **262**: 507-508.
- (With MUKKU V) Relative sensitivity of the corpus luteum of different days of pregnancy to LH-deprivation in the rat and hamster. *Mol Cell Endocrinol* **6**: 71-80.
- (With MUKKU V and PRAHALADA S) Effect of constant light on nycthemeral variations in serum testosterone in male *Macaca radiata*. *Nature* **260**: 778-780.
- (With MURALIDHAR K) Studies on rat ovarian receptors for lutropin (luteinizing hormone). Interaction with beta-subunit of sheep lutropin. *Biochem J* **160**: 615-619.
- (With MURALIDHAR K) Studies on rat ovarian receptors for lutropin (luteinizing hormone). Factors influencing binding and response. *Biochem J* **160**: 607-613.
- (With MURALIDHAR K) Studies on rat ovarian receptors for lutropin (luteinizing hormone). Applicability of radioimmunoassay to measure lutropin bound to receptors. *Biochem J* **160**: 603-606.
- (With NANDINI SG and LIPNER H) A model system for studying inhibin. *Endocrinology* **98**: 1460-1465.
- (With RAJALAKSHMI M, ARORA R, BOSE TK, DINAKAR N, GUPTA G, THAMMANAN TN, PRASAD MR and ANAND KUMAR TC) Physiology of the epididymis and induction of functional sterility in the male. *J Reprod Fertil Suppl*: 71-94.



- 1977 (With MURALIDHAR K and MANECKJEE R) Inhibition of in vivo pituitary release of luteinizing hormone in lactating rats by exogenous prolactin. *Endocrinology* **100**: 1137-1142.
- (With RANI CS) Examination of the role of FSH in periovulatory events in the hamster. *J Reprod Fertil* **50**: 37-45.
- (With SHEELA RANI CS and MOUDGAL NR) Role of the proestrous surge of gonadotropins in the initiation of follicular maturation in the cyclic hamster: a study using antisera to follicle stimulating hormone and luteinizing hormone. *Endocrinology* **101**: 1484-1494.
- (With SIVASHANKAR S, PRASAD MR, THAMPAN TN and RANI CS) Effects of a highly purified antiserum to FSH on testicular function in immature rats. *Indian J Exp Biol* **15**: 845-851.
- (With ZACHARIAH E) Enzymic changes in the cervix of the rat and hamster during the oestrous cycle and the effect of steroids. *J Endocrinol* **72**: 153-161.
- 1978 Hypothalamic-pituitary axis is disturbed during lactation. *Fertil Steril* **29**: 222-223.
- (With PRASAD MS, MURALIDHAR K and ADIGA PR) Effect of human chorionic gonadotrophin and ovine luteinizing hormone on rat ovarian macromolecular metabolism. *J Endocrinol* **76**: 283-292.
- (With RANI CS) Examination of the role of follicle stimulating hormone in estrogen biosynthesis in vivo and in vitro in the ovary of the cyclic hamster. *Steroids* **32**: 435-451.
- (With SHARMA KR and MURALIDHAR K) Heterologous radioimmunoassay systems for measurement of follicle stimulating hormone (Follitropin) & Luteinizing hormone (Lutropin) in the bonnet monkey *Macaca radiata*. *Indian J Exp Biol* **16**: 153-156.
- (With SHEELA RANI CS and MOUDGAL NR) Measurement of FSH in the ovarian tissue by radioimmunoassay: correlation to serum FSH levels and follicular development in the hamster. *Mol Cell Endocrinol* **11**: 293-307.
- 1979 (With DIGHE RR and MURALIDHAR K) Ability of human chorionic gonadotropin beta-subunit to inhibit the steroidogenic response to lutropin. *Biochem J.* **180**: 573-578.
- (With MURTHY HM and RAMASHARMA K) Studies on purification and characterization of sheep testicular inhibin. *J Reprod Fertil Suppl*: 61-70.
- (With MURTY GS, RANI CS and PRASAD MR) Effect of passive immunization with specific antiserum to FSH on the spermatogenic process and fertility of adult male bonnet monkeys (*Macaca radiata*). *J Reprod Fertil Suppl*: 147-163.
- (With RAMASHARMA K and MURTHY HM) A rapid bioassay for measuring inhibin activity. *Biol Reprod* **20**: 831-835.
- (With RANI CS and SUSHEELA AK) Effect of neutralization of endogenous follicle stimulating hormone (FSH) or luteinizing hormone (LH) on ovarian lipids in the hamster: a histochemical and biochemical evaluation. *Biol Reprod* **21**: 117-123.
- (With SHEELA RANI CS) Effect of follicle-stimulating hormone and its antiserum on the activity of ornithine decarboxylase in the ovary of rat and hamster. *Endocrinology* **104**: 1480-1483.
- 1981 A need for FSH in maintaining fertility of adult male subhuman primates. *Arch Androl* **1**: 117-125.



- 1981 (With MUKKU VR, MURTY GS, SRINATH BR, RAMASHARMA K and KOTAGI SG) Regulation of testosterone rhythmicity by gonadotropins in bonnet monkeys (*Macaca radiata*). *Biol Reprod* 24: 814-819.
- (With VIDYASHANKAR N) Studies on the mechanism of follitropin action at the cellular level. *Arch Biochem Biophys* 209: 241-248.
- 1982 (With Li CH) Beta subunits of human choriogonadotropin and ovine lutropin are biologically active. *Proc Natl Acad Sci USA* 79: 2500-2503.
- (With PAPKOFF H) Equine luteinizing hormone possesses follicle-stimulating hormone activity in hypophysectomized female rats. *Biol Reprod* 26: 935-942.
- 1983 (With DHANASEKARAN N and SHEELA RANI CS) Studies on follicular atresia: lysosomal enzyme activity and gonadotropin receptors of granulosa cells following administration or withdrawal of gonadotropins in the rat. *Mol Cell Endocrinol* 33: 97-112.
- (With DIGHE RR) Use of alpha- and beta-subunit specific antibodies in studying interaction of hCG with Leydig cell receptors. *Arch Biochem Biophys* 225: 490-499.
- 1984 Corpus luteum of the nonhuman primate. *Adv Vet Sci Comp Med* 28: 343-366.
- (With RAO AJ and KOTAGI SG) Serum concentrations of chorionic gonadotrophin, oestradiol-17 beta and progesterone during early pregnancy in the south Indian bonnet monkey (*Macaca radiata*). *J Reprod Fertil* 70: 449-455.
- (With VIDYASHANKAR N) Effect of pregnant mare serum gonadotropin on the induction and degradation of FSH and LH receptors in the granulosa cell of the immature rat. *Mol Cell Endocrinol* 37: 215-222.
- 1985 (With JAGANNADHA RAO A, CHAKRABORTI R, KOTAGI SG and RAVINDRANATH N) Effect of LHRH agonists and antagonists in male and female bonnet monkeys (*Macaca radiata*). *J Steroid Biochem* 23: 807-809.
- (With SAIRAM MR and MAHONEY J) On the immunogenicity of the beta subunit of ovine luteinizing hormone (oLH beta) and equine chorionic gonadotropin (eCG) in the chimpanzee (*Pan troglodytes*): effect of antiserum on monkey cycle and early pregnancy. *Am J Reprod Immunol Microbiol* 8: 120-124.
- (With RANI CS) Differences in the behavior of luteinizing hormones of various species at the rat gonadal cell receptor site. *Endocrinology* 116: 597-603.
- 1986 (With DHANASEKARAN N) Studies on follicular atresia: role of tropic hormone and steroids in regulating cathepsin-D activity of preantral follicles of the immature rat. *Mol Cell Endocrinol* 44: 77-84.
- (With DHANASEKARAN N) Gonadotropin regulation of rat ovarian lysosomes: existence of a hormone specific dual control mechanism. *Biosci Rep* 8: 279-285.
- 1987 (With RAVINDRANATH N) Use of tamoxifen, an antioestrogen, in establishing a need for oestrogen in early pregnancy in the bonnet monkey (*Macaca radiata*). *J Reprod Fertil* 81: 327-336.
- 1989 (With Bhat PJ) Isolation and characterization of a gonadotropin receptor binding inhibitor from porcine follicular fluid. *Int J Pept Protein Res* 33: 59-66.
- (With DHANASEKARAN N) Biochemical and histological validation of a model to study follicular atresia in rats. *Endocrinol Exp* 23: 155-166.



- 1989 (With DHANASEKARAN N) Studies on follicular atresia: role of gonadotropins and gonadal steroids in regulating cathepsin-D activity of preovulatory follicles in the rat. *Mol Cell Endocrinol* **63**: 133-142.
- The immunobiology of follicle-stimulating hormone and inhibin: prospects for a contraceptive vaccine. *Curr Opin Immunol* **2**: 736-742.
- (With RAVINDRANATH N) Requirement for estrogen in implantation and post implantation survival of blastocyst in the bonnet monkey. *Prog Clin Biol Res* **294**: 277-288.
- (With RAVINDRANATH N, SHEELA RANI CS and MARTIN F) Effect of FSH deprivation at specific times on follicular maturation in the bonnet monkey (*Macaca radiata*). *J Reprod Fertil* **87**: 231-241.
- 1990 (With ARAVINDAN GR, RAVINDRANATH N and GOPALAKRISHNAN K) DNA flow-cytometric analysis of testicular germ cell populations of the bonnet monkey (*Macaca radiata*) as a function of sexual maturity. *J Reprod Fertil* **89**: 397-406.
- (With DIGHE RR, MURTHY GS and KURKALLI BS) Conformation of the alpha-subunit of glycoprotein hormones: a study using polyclonal and monoclonal antibodies. *Mol Cell Endocrinol* **72**: 63-70.
- (With DIGHE RR and MURTHY GS) Two simple and rapid methods to detect monoclonal antibodies with identical epitope specificities in a large population of monoclonal antibodies. *J Immunol Methods* **131**: 229-236.
- (With RAO AJ, RANI CS and RAVINDRANATH N) Effect of modulating endogenous prolactin secretion on testosterone production in the adult male bonnet monkey (*Macaca radiata*). *Andrologia* **22**: 251-259.
- (With RAVINDRANATH N) Luteal-phase defect induced by deprivation of FSH at a specific period of the follicular phase prevents pregnancy in the bonnet monkey (*Macaca radiata*). *J Reprod Fertil* **88**: 25-30.
- 1991 (With VAISHNAV MY) Effect of specific FSH or LH deprivation on testicular function of the adult rat. *Indian J Biochem Biophys* **28**: 513-520.
- 1992 (With RAVINDRANATH N, MURTHY GS, DIGHE RR, ARAVINDAN GR and MARTIN F) Long-term contraceptive efficacy of vaccine of ovine follicle-stimulating hormone in male bonnet monkeys (*Macaca radiata*). *J Reprod Fertil* **96**: 91-102.
- (With PRAKASH N, NARAYANA K, MURTHY GS and HONNEGOWDA) The effect of malathion, an organophosphate, on the plasma FSH, 17 beta-estradiol and progesterone concentrations and acetylcholinesterase activity and conception in dairy cattle. *Vet Hum Toxicol* **34**: 116-119.
- (With RAVINDRANATH N, SRILATHA NS and SAIRAM MR) Ability of deglycosylated human chorionic gonadotropin (dghCG) to block luteal function and establishment of pregnancy in bonnet monkeys (*Macaca radiata*). *Indian J Exp Biol* **30**: 982-986.
- (With BHAT PJ) Effect of 80 kDa protein of porcine follicular fluid on gonadotropin stimulated progesterone production in rat granulosa cells *in vitro*. *Regul Pept* **38**: 231-238.
- 1993 (With ARAVINDAN GR, GOPALAKRISHNAN K and RAVINDRANATH N) Effect of altering endogenous gonadotrophin concentrations on the kinetics of testicular germ cell turnover in the bonnet monkey (*Macaca radiata*). *J. Endocrinol* **137**: 485-495.



- 1993 (With MEDHAMURTHY R and ARAVINDAN GR) Hemiorchidectomy leads to dramatic and immediate alterations in pituitary follicle-stimulating hormone secretion and the functional activity of the remaining testis in the adult male bonnet monkey (*Macaca radiata*). *Biol Reprod* **49**: 743-749.
- (With SELVARAJ N and MOUDGAL NR) Development of an LH receptor assay capable of measuring serum LH/CG in a wide variety of species. *J Reprod Fertil* **98**: 611-616.
- 1994 (With SELVARAJ N) *In vivo* and *in vitro* studies on the differential role of luteinizing hormone and follicle-stimulating hormone in regulating follicular function in the bonnet monkey (*Macaca radiata*) using specific gonadotropin antibodies. *Biol Reprod* **51**: 246-253.
- (With SELVARAJ N, SHETTY G, VIJAYALAKSHMI K and BHATNAGAR AS) Effect of blocking oestrogen synthesis with a new generation aromatase inhibitor CGS 16949A on follicular maturation induced by pregnant mare serum gonadotrophin in the immature rat. *J Endocrinol* **142**: 563-570.
- (With VAISHNAV M) Role of FSH in regulating testicular germ cell transformations in the rat: a study using DNA flow cytometry. *Andrologia* **26**: 111-117.
- 1995 (With ARAVINDAN GR and KRISHNAMURTHY H) Rat epididymal sperm exhibit on dithiothreitol treatment in vitro quantifiable differences in patterns of light scatter, uptake of ¹⁴C-iodoacetamide and binding of ethidium bromide to DNA. *Indian J Exp Biol* **33**: 899-910.
- (With JEYAKUMAR M, SURESH R and KRISHNAMURTHY HN) Changes in testicular function following specific deprivation of LH in the adult male rabbit. *J Endocrinol* **147**: 111-120.
- (With MEDHAMURTHY R, SURESH R and PAUL SS) Evidence for follicle-stimulating hormone mediation in the hemiorchidectomy-induced compensatory increase in the function of the remaining testis of the adult male bonnet monkey (*Macaca radiata*). *Biol Reprod* **53**: 525-531.
- (With SELVARAJ N and BHATNAGAR AS) Is there a role for estrogen in follicular maturation in the primate? *Endocrine* **3**: 245-249.
- (With SHETTY G and BHATNAGAR AS) Blockade of estrogen synthesis with an aromatase inhibitor affects luteal function of the pseudopregnant rat. *J Steroid Biochem Mol Biol* **55**: 347-353.
- (With SURESH R and MEDHAMURTHY R) Comparative studies on the effects of specific immunoneutralization of endogenous FSH or LH on testicular germ cell transformations in the adult bonnet monkey (*Macaca radiata*). *Am J Reprod Immunol* **34**: 35-43.
- (With SURESH R) A role for nocturnal serum testosterone surge in regulating spermatogenesis in the adult non-human primate. *Endocrine* **3**: 487-492.
- 1996 (With JEYAKUMAR M) Immunization of male rabbits with sheep luteal receptor to LH results in production of antibodies exhibiting hormone-agonistic and antagonistic activities. *J Endocrinol* **150**: 431-443.
- (With SHETTY G, SELVARAJ N and BHATNAGAR AS) Use of a specific aromatase inhibitor for determining whether there is a role for oestrogen in follicle/oocyte maturation, ovulation and preimplantation embryo development. *J Reprod Fertil Suppl* **50**: 69-81.



- 1997 (With ARAVINDAN GR and KRISHNAMURTHY H) Enhanced susceptibility of follicle-stimulating-hormone-deprived infertile bonnet monkey (*Macaca radiata*) spermatozoa to Dithiothreitol-induced DNA decondensation in situ. *J Androl* **18**: 688-697.
- (With JEYAKUMAR M, KRISHNAMURTHY HN and DIGHE RR) Demonstration of complementarity between monoclonal antibodies (MAbs) to human chorionic gonadotropin (hCG) and polyclonal antibodies to Luteinizing hormone/hCG receptor (LH-R) and their use in better understanding hormone-receptor interaction. *Recept Signal Transduct* **7**: 299-310.
- (With MOUDGAL NR, JEYAKUMAR M, KRISHNAMURTHY HN, SRIDHAR S, KRISHNAMURTHY H and MARTIN F) Development of male contraceptive vaccine—a perspective. *Hum Reprod Update* **3**: 335-346.
- (With MURTHY GS, PRASANNA KUMAR KM, MARTIN F, SURESH R, MEDHAMURTHY R, PATIL S, SEHGAL S and SAXENA BN) Responsiveness of human male volunteers to immunization with ovine follicle stimulating hormone vaccine: results of a pilot study. *Hum Reprod* **12**: 457-463.
- (With SAIRAM MR, KRISHNAMURTHY HN, SRIDHAR S, KRISHNAMURTHY H and KHAN H) Immunization of male bonnet monkeys (*M. radiata*) with a recombinant FSH receptor preparation affects testicular function and fertility. *Endocrinology* **138**: 3065-3068.
- (With RAO AJ, RAMESH V, RAMACHANDRA SG, KRISHNAMURTHY HN and RAVINDRANATH N) Breeding of bonnet monkeys (*Macaca radiata*) in captivity. *Lab Anim Sci* **47**: 180-183.
- (With SHETTY G, KRISHNAMURTHY H, KRISHNAMURTHY HN and RAMACHANDRA SG) Use of norethisterone and estradiol in mini doses as a contraceptive in the male. Efficacy studies in the adult male bonnet monkey (*Macaca radiata*). *Contraception* **56**: 257-265.
- 1998 (With ARAVINDAN GR) Susceptibility of sperm chromatin to acid denaturation in situ: a study in endogenous FSH-deprived adult male bonnet monkeys (*Macaca radiata*). *Arch Androl* **40**: 29-41.
- (With SAIRAM MR) Is there a true requirement for follicle stimulating hormone in promoting spermatogenesis and fertility in primates? *Hum Reprod* **13**: 916-919.
- (With SHETTY G, KRISHNAMURTHY H, KRISHNAMURTHY HN and BHATNAGAR AS) Effect of long-term treatment with aromatase inhibitor on testicular function of adult male bonnet monkeys (*M. radiata*). *Steroids* **63**: 414-420.
- 2001 KRISHNAMURTHY HN, SUREKHA S, KRISHNAMURTHY H, DHOPLE VM, NAGARAJ R and SAIRAM MR) Immunobiology of a synthetic luteinizing hormone receptor peptide 21-41. *J Androl* **22**: 992-998.
- 2007 (With RAO AJ, RAMACHANDRA SG, RAMESH V, KRISHNAMURTHY HN and RAVINDRANATH N) Establishment of the need for oestrogen during implantation in non-human primates. *Reprod Biomed Online* **14**: 563-571.

