Pollination biology in India — surveying the past

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In this article, we review the development of science in general and that of pollination biology in particular, in India through ancient to post-independent period. We examine several upheavels in these areas in the light of the changing priorities and interests of the various periods.

In this article we intend to survey the contributions from India to the subject of pollination biology. We attempt to present the social, cultural and historical contexts in which contributions to this subject have been made in the past. For convenience, we discuss these factors separately for three periods, viz. i) ancient India, ii) the colonial British India and, iii) the resurgent period of Indian biology.

Ancient India

There are several excellent reviews tracing the knowledge of biology in general and to the study of plant sciences in particular in ancient India (see ref. 1 and references therein). All of these suggest that ancient India had a rich tradition of life sciences. But the references to the events associated with the pollination biology indicating the awareness of this subject among the ancient Indians are sparse. Nevertheless, the occasional references available from ancient texts do suggest that they were at least aware of the important processes of sexuality, pollination and fertilization leading to seed production.

One probable reason for such scanty references to specific events of pollination could be the pre-occupation of ancient Indians with specific areas of plant life. As Haraprasad Chaudhuri traces, the study of plants in ancient India '*developed along two natural channels of practical utility namely botany of medicinal plants and botany of agricultural plants*'. Nevertheless studying plants and animals merely for the sake of knowledge is not unknown. For instance it is recorded that more than 2500 years ago, in Taksasila University, Jivaka was assigned the job of collecting, identifying and describing all plants within a radius of four yojanas (≃eight miles) around Taksasila (Sen cf. Haraprasad Chaudhuri[1]). Further, in the ancient texts of Charaka and Bramhanas, a description of '*What parental characters are transmitted to the offspring and how*' is also provided (Seal cf. Haraprasad Chaudhuri[1]).

The early records of plants and agricultural practices are found in Vrikshayurveda chapter of *Agnipurana*. In this book, regarded as a popular encyclopaedia of all kinds of knowledge, information on sexuality and reproduction in plants, recipe for treating bareness of fruit trees and for promoting inflorescence is available (Ray cf. Haraprasad Chaudhuri[1]).

While reviewing the contributions from ancient India, there has often been a highly ridiculed syndrome of glorifying the past often beyond limits and mis- or over-interpreting to suggest the pre-empting about anything that is new in science. We were wary of repeating such an error while reviewing the cultural and historical background. However despite such caution, it is clear that during the vedic period spanning three to four thousand years, Indian saints have indulged in an active exploration of several aspects of life. Unfortunately, this grand pursuit of knowledge that was deeply ingrained in the life of vedic period, took a downward plunge along with the decline of Buddhism. During the 1000 years or so that followed '*with the decay of Hindu and Buddhistic culture, an intellectual torpor took possession of Indian mind, and the spirit of inquiry after truth rapidly declined. Authority of Shastras took the place of reason which was inimical to the study of science, which accepts things not on trust, but on verifications*' (Haraprasad Chaudhuri[1]).

The colonial period

The most significant contribution after this long period of lull came 'in tow with the Europeans' whose primary interest was in geography and botany to help in their obvious pursuit of harvesting the resources of the Indian subcontinent[2,3]. The beginning of the British era in botany is obviously crowded with Europeans such as John Gerard Koenig (1768), a student of Linnaeus who started a society called 'the United Brothers' to study plants, Lieut. Colonel Robert Kydd (1787) who was instrumental in starting the Royal Botanic Garden in Calcutta, Sir Joseph Hooker (1848) and others. Understandably most of their work was guided by the commercial interests of the colonial powers and hence was restricted to cataloguing and collecting plants with an emphasis on their economic importance[2].

The British also brought with them the new

methodology of science. The Indian mind which for ages depended so much on faith and trust and almost little or none on verification was suddenly exposed to a diabolically opposite method of approaching nature. Befuddled with the new methodology Indians were not used to, their inquiring facet was further numbed and went into another period of dormancy. Added to this, they were trained systematically by an education that aimed at '*nothing higher than candidates for service in the subordinate ranks and persons who would be just good enough to act as interpreters between the rulers (the British) and the ruled (the Indian mass)*'[4]. Consequently, during most of the colonial period, biology research in general was exclusively by Britishers. Probably because of all such inhibitions, 'botany meant little more than the collection, description and classification of plants' to Indians and most doubted 'that botany can progress ever beyond this stage of being an observational science'[4]. It was not realized however for long that it is because of the suppression that the creative facet was not sensitized among Indians. This unfortunately lead to the propagation of the belief 'by interested persons and accepted by their dupes that Indians lack the capacity for original research work'[4]. However during the thirties a few did realize the disastrous influence of such a mental lid and blew it out from inside.

The resurgence period

Gradually breaking out of this apprenticeship and mental slavery, Indian biologist truly started to appear on the scene a few decades before independence. Though late to arrive on the scene, a few workers during this period became the world leaders in areas of embryology and cytology. The unrelenting contribution in the area of plant embryology initiated by Panchanan Maheshwari and his group[5] culminated in the monumental publication of '*Introduction to embryology of angiosperms*', well known as the 'Delhi book'. The importance of the book was immediately realized as evident from the review on its first edition by Corner[6] '(This) is an extraordinarily useful and coherent account of those key points in the life cycle which had become too recondite in modern research for the general botanist. A great deal of this research has been carried out in India by the author and his school, and it is noteworthy that in the midst of this maze of specific, generic and family detail in sporogenesis, embryo sac, endosperm and embryogeny, which is coming to light, he has seen so clearly as to give a well-written and concise account useful at once to the lecturer, the undergraduate and the research worker. One emerges from the armchair with the feeling that the author has entirely appreciated, and deftly exemplified the subject from the historical sketch, beginning on page one, to the experimental and theoretical considerations at the end.... How strong must have been the temptation to publish a compendious and unreadable reference book and how much more satisfactory is this introduction!'.

Either directly training or indirectly inspiring the embryologists,' Maheshwari built a strong *Vriksha* of embryologists whose buds and flowers spread all over India. For a 'modern biologist' (in the sense of true 'classic biologist', as Chandrashekaran[7] refers to), who is generally exalted by the conceptualization of the biological phenomena, the relentless work by this strong group might appear merely to be an act of building a tome of dry data. But it is beyond doubt that all of them did enjoy their way of doing science as much as or may be even more than any modern biologist. Because, unlike what frequently drives the present-day biologist (extending the list of publications or submitting the annual reports to the funding agency and occasionally an award), the spirit that mobilized their work was pure pleasure of innovation. In fact their work has often been viewed as mostly descriptive without any perspective. But Maheshwari[8] retorts: 'This is far from true in my opinion. We need more of such investigations and will continue to do so for a long time to come....' He had prophesied that with such descriptive and copy book like work, 'we may be able to prepare in this country a new "Comparative embryology of Angiosperms"'. This vision, of their work serving as a basis for updating the systematics has been realized recently with the publication of the two volumes on this subject[9,10].

It is true that they also had a very clear perspective of their work. Maheshwari[8] writes: '*As someone once said, plant breeder puts the pollen on the stigma and "prays" for results in the ovary! For a scientific explanation of his successes and failures and for finding the ways and means of increasing the former and remedying the latter he must turn to the cytologist and the embryologist*'.

Besides such monolithic contributions, it is not uncommon to find Indian biologist of pre-independent India indulging in authoritative discourses on philosophical issues of evolution and adaptation. As early as 1931, Parija[11], in his presidential address to the Annual Meeting of the Indian Botanical Society at Nagpur, stressed the need to resist the teleological arguments then prevalent in support of the evolutionary theories. Deliberating on his 'Law of Modification' defined by him as 'If an organism, an organ or a cell is subjected to a stress, physical or chemical, the organism, the organ or the cell changes in such a way that the effect of the imposed stress is nullified', he cautioned the dangers involved in grouping together all the responses of the organisms to the environmental stimuli as adaptive.

Even amidst the turbulence of the Independence movement, Indian biologist seem to have insulated specifically his academic life and gained time to stay with the crest of the moving ideas of biology as evident from Parija's concluding statement of his address, '*Form and function are so intimately related to each other that the study of one cannot be complete without the study of the other*'—a reflection of their interest on the on-going debate on D'Arcy Thompson's book *On Growth and Form*[12]. During this period, Indian biologist also started exhibiting strong confidence and excelled in new frontiers of research; they laid the foundation of a few areas. For example, there used to be a session exclusively devoted to electricity and agriculture in the Indian Science Congress during the thirties[13].

Much of the work of botanists of this period has emerged not as an ensemble of any mega project with a planned and highly funded national agenda, a practice of the present-day science. More often their contributions emerged as a dove-tail of their personal urge with their persuasive attitude; while their desire to know more, fixed their attention immediately to any deviant biological process they observed, their persuasion brought them the results. Probably the first ever report of parthenocarpy in andro-gyno-monoecious *Dodonea viscosa* by Joshi[14] is one such instance. He observed that the only female plant of this species that survived in his backyard after a dry spell started flowering and fruiting though there was no source of pollen in the neighbourhood. Surprised by this observation, he bagged a couple of flowers (females) and found them still fruiting but with aborted ovules and concluded 'carpels of some plants have inherent nature to grow to their full stature without any regard to pollination and development of seeds'. He also conjectured this as a relic feature of the pteridophytes where the 'sporophylls grow to the full size by the time of spore formation'.

Such tendency to relate queer observations to evolution and systematics was very much in the thinking current of the then botanist. It is this attitude and alertness that led to probably, the first ever discovery of the deposition and germination of pollen grains in the stylar canal and in the intra-carpellary cavities of an angiosperm, *Butomopsis*[15]. In gymnosperms, pollen grains land directly on the nucellus and pollen tubes have to grow only a short distance to the archegonium; in contrast in the angiosperms, where the carpels are covered, pollen grains are deposited on the stigma or style from where they need to grow a great deal to reach the female gametophyte. In this context, it is impossible to explain Johri's results 'except on the assumption that they were drawn in by a sort of suction mechanism like that of "stigma drop" of gymnosperm, stylar canal functioning like a micropyle'[16].

As Sahni[16] wrote on this discovery '*the whole question is intriguing.... Johri deserves thanks for bringing to notice what can be only regarded as a relic of gymnospermy in a confirmed and unquestionable angiosperm*'. This work obviously helped in bridging the pollination mechanisms of angiosperms with that of gymnosperms. Following Johri's discovery, such intra-carpellary pollen grain deposition and their germination was observed in a few other species by the Indian botanists[8].

There used to be not much distinction between the science for fun as a hobby and science for science sake during this period. Singh[17], for example, reports of his observations on sphingid moths and sunbirds visiting the flowers in his backyard and discusses their role in pollination. Nevertheless observations during this period were very meticulous and analytical. For example, while reporting on sunbirds, Singh[18] also distinguished the visits that end up in pollination from those that end up as an act of stealing the nectar. In the latter, the birds were found sucking nectar by making holes at the bottom of the corolla tube such that they avoid contact with pollen grains. Such a 'short cut method' of stealing nectar by pollinators (and a few non-pollinators also) has been frequently observed by others.

It is not uncommon in science that certain important data are generated much in advance of the development of the concepts it supports. Consequently, such data are often neglected. The study by Iyengar[19] on histological and genetic aspects of fertilization events in cotton is one such work that probably would have gained the significance and importance it deserved had it been published in recent years when the theory of sexual selection is extended to plants. He showed that in a situation where gametophytic competition exists on the stigma (i.e. when genetically different pollen grains are on the stigma), the genotypes differ in their ability to sire seeds in the fruit. He also offered evidence that suggests female choice over pollen genotypes at the level of fertilization. (He found that seeds are not polyspermy despite several pollen grains found entering the ovules.) Further, he identified several levels of competition among the pollen genotypes (components of male gametophytic competition) from the stage of pollen grain germination to fertilization. In fact, with the extension of the concept of sexual selection to plants, plant reproductive biologists have been intensely involved in generating such data in the past few years[20–23].

Work in biology in general and in pollination biology in particular, in the post-independent India obviously was in an uninhibited atmosphere and there were a few luminaries such as J. B. S. Haldane and C. V. Raman (floral colours) who not only inspired several groups but also expanded the areas of biology. Consequently, several important contributions emerged

in the areas of pollination biology such as reproductive isolation and differential pollinator visitation[24], origin of floral colours[25], experimental embryology and *in vitro* techniques of pollination[5]. These studies besides contributing substantially to the area of pollination biology have served a tangential but an equally or even more important purpose of instilling confidence among the young generation of workers. They have demonstrated that the logistic difficulties faced by the workers in countries such as India shall never be a hindrance; especially in the areas such as pollination ecology that requires the biological diversity as an important resource which our country is abound with.

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Plant–pollinator interactions

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In this article we review studies by Indian workers on plant–pollinator interactions and discuss the evolution of floral traits in relation to pollination and the foraging behaviour of pollinators. In the process, we identify the contributions of these studies to several conceptual issues in pollination biology.

POLLINATION biology in India started mostly as a descriptive science aiming at understanding plant morphology and anatomy in relation to pollination. Most of the early work was restricted to documenting the kind, number and time of floral visitors on various plant species. Consequently a few investigators have studied plant–pollinator interactions with a right emphasis on the mutual adaptations of the two partners and interactions between them.

In this article we have attempted to sketch a few important discoveries regarding plant–pollinator interactions in the Indian context. In the process, we have also attempted to identify the Indian contribution to the conceptual issues in the area of pollination biology. In the first part, we trace the early works emphasizing anatomical and morphological basis of pollination, and in the second we review studies aimed at identifying floral rewards and attractants as factors molding the foraging activity of pollinators. The third and final part focuses on environmental parameters influencing pollinator activity.

Floral anatomy and morphology in relation to pollination

Among the early workers, Rao[1], Parija and Samal[2], and Narayana[3] studied the anatomical features in relation to pollination. Rao[1] described modification of epidermis as extrafloral nectaries in *Spathodea stipulata* Wall. and found that these nectaries were abundant on the abaxial side of all the floral and foliar parts. The