A TRIBUTE TO ERNST MAYR

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Ernst Mayr, the great evolutionist and systematist of the 20th century, celebrated his 100th birthday in July 2004, and breathed his last in February 2005. He remained academically active throughout his long life, and authored nearly 700 papers and 25 books, the last book appearing in 2004. Commenting on his mental vigour and scientific

temper Coyne (2005) has written, "As he approached the century mark, Mayr retained his critical faculties and productivity, publishing prolifically long after many scientists have retired to devote themselves to reconciling science and religion". In view of his outstanding contributions to evolutionary biology, E.M. has been called by some authors "the Darwin of the 20th century" (Bradt, 2005; Coyne, 2005).

E.M. was born on 5th July 1904 in a small town in Bavaria, Germany. He was awarded Ph.D. in Ornithology in 1926 by the University of Berlin. Then he took several expeditions to New Guinea and to the Solomon Islands. Starting from 1932, for 21 years he was Curator at the American Museum of Natural History, New York. In 1953 he moved to the Harvard University to join as Alexander Agassiz Professor of Zoology, and remained in this position up to 1975. He was also the Director of the Museum of Comparative Zoology, Harvard University from 1961 to 1970. Retiring at the age of 70, he continued to work as Professor Emeritus at Harvard. He received many major awards.

E.M.'s areas of interest included Ornithology, Evolutionary Biology, Systematics, and History and Philosophy of Biology. "…Mayr remained an avid ornithologist throughout his life, writing field guides, checklists, and describing more species of birds (26) than any other living person" (Coyne, 2005).

E.M. was an ardent believer in the Darwinian theory of organic evolution. During his recent (on May 15, 2004) conversation with Steve Mirsky and Claudio Angelo (Mirsky & Angelo, 2004), E.M. fondly quoted the following statement of Dobzhansky: "Nothing in the living world makes sense except in the light of evolution".

Studies, made in the post-Darwinian period, specially those in the first half of the 20th century, created need to supplement the Darwinian theory with results and inferences from such studies. A sort of a synthesis of the Darwin's concept of selection and more recent results in the areas of genetics, population studies and field observations was brought about, and thus resulted the modern theory of evolution, which has been referred to as "the Evolutionary Synthesis" or "the Synthetic Theory of Evolution". This modern theory is built around the Darwinian theory. Progress in the later half of the 20th century has only strengthened the Synthetic Theory.

The synthetic theory has developed through contributions from a number of biologists, but E.M. has been one of the chief architects of this theory. Other names in this context are of Julian Huxley and Th. Dobzhansky. Four books have greatly helped educating biologists, working in different fields, about the evolutionary synthesis, namely Julian Huxley's *Evolution, the Modern Synthesis* (1942), Dobzhansky's *Genetics and Origin of Species* (1951), E. Mayr's *Systematics and Origin of Species* (1942), and E. Mayr's *Animal Species and Evolution* (1963). Mary Jane West-Eberhard, Douglas Futuyama, and Stephen J. Gould, all major evolutionists in the second half of the 20th century, were deeply influenced by E.M.'s 1963 book, *Animal Species and Evolution* (Pray, 2005).

Darwin in his theory almost eluded discussing origin of biodiversity, that is a species breaking up into two or more species. This lacuna in the evolutionary theory was filled by E. Mayr. He pointed out that allopatry or geographic isolation between two similar populations was the main factor responsible for origin of biodiversity. Observations by the young E.M. in New guinea on mollusc and bird populations in isolated areas, developing features of incipient species, inspired him to make further observations and assert the significance of allopatry in speciation.

Jared Diamond wrote the Foreword for E.M.'s book *What Evolution Is* (2001). In that he pointed out the need of Darwin again writing a book on evolution at the close of the 20th century to incorporate what more

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had been discovered in this field, as he (Darwin) was a "clear and forceful writer". But that could not be, as Darwin had died in the 19th century itself. That E.M. was writing a book on evolution was "the next best thing", as he was also a "clear and forceful writer" (Based on Jared Diamond's paragraph, reproduced by Holldobler, 2004).

E.M.'s various books on Systematics (Mayr, 1940, 1942, 1963, 1969; Mayr & Ashlock, 1991) have greatly helped in providing a firm evolutionary basis to the science of classification of organisms.

A major contribution from E.M. in the field of taxonomy has been developing the biological species concept. He gave a clear definition of a biological species. He pointed out that species was the unit of evolution. He precisely described such infraspecific categories as varieties, subspecies, races etc. He has emphasized the role of arbitrariness involved in making out categories above the species level in the Linnaean Hierarchy. Taxa, above the family level, are, however better defined, being separated by definite gaps. Mayr and Ashlock (1991) have stated, "There is hardly a higher taxon that is not ranked higher by some specialists and lower by others". Clear realization of these views may avoid much of the bickering among taxonomists.

In recent years, those workers who are dabbling with molecular biology often ignore the biological definition of species, which is creating quite some confusion in the field of classification (Harris & Froufe, 2004).

E.M. advocated a polythetic approach in classification, i.e. consideration of a number of shared characters in making out a natural taxon, and not just a few diagnostic characters. Moreover, to achieve a natural or phylogenetic classification it is not enough to take into account only morphological features; characters from other sources should also be used. He particularly emphasized the importance of ecological characteristics. Mayr and Ashlock (1991) say, "Like the genus, but perhaps to an even greater degree, the family tends to be distinguished by certain adaptive characters that fit it for a particular adaptive zone, e.g., the woodpeckers or the family Picidae, the leaf beetles or the family Chrysomelidae. The more distinct the adaptive zone, the wider the gap from other families".

E.M. has helped broadening and rationalizing the meaning of the term "monophyly", a term often used in systematics. Originally, after the term had been suggested by Haeckel in 1866, it was used for more than 70 years in the meaning of "descent from a common ancestor". Subsequently taxonomists tried to make the definition of monophyly more precise; "common ancestor" was replaced with "the most recent common ancestor", so that the common ancestry of beetles and fishes may not be traced back to the common metazoan ancestor, stretching the meaning of monophyly to cover the two groups. To make the "common ancestor" more precise it was replaced with "the most recent common ancestral species". But futility of such a pointed definition in actual taxonomic working became obvious. Birds are a natural group, but it has not been possible, and it does not seem likely to be so in foreseeable future to pin point an ornithischian reptile species as the common ancestor of all birds. Moreover, it could be theoretically visualized, and also realized in practical working, that members of a recognised natural group arose along more than one line from different members of a common ancestral stock, and showed parallel evolution of similar features, due to inheritance of a common genotype and common genetic propensities. Simpson (1961) noted that, among the reptilian order Therapsida, mammalian features appeared several times separately. He also inferred that the horse *Marychippus* evolved from more than one species of *Parahippus*. Simpson held that such parallel descent from a common ancestral stock or parallelophyly has been a frequent event in the evolutionary history. Simpson has suggested that the definition of monophyly sould be extended to include close polyphyly from a common ancestral stock or parallelophyly. Monophyly, as defined by Simpson (1961): "Monophyly is derivation of a taxon through one or more lineages from immediately ancestral taxon of the same or lower rank". While Simpson was criticized by some for his views, E.M. stoutly defended him.

Hennig (1966) introduced a new approach in Systematics, "Cladistics". E.M. has described this approach as "a good method for analysing phylogeny of a group". But at the same time he has pointed out certain limitations of this taxonomic method. Application of this method yields a branching pattern or cladogram, which suggests phylogeny, but does not permit inferences about taxonomic ranking of the members of the group, studied this way. A theory on ranking of taxa from a cladogram has not been outlined in the literature on cladistics. However, it has been said by Hennig (1966) that sister groups have to be of the same rank. By sister groups he meant the groups, which have resulted from phylogenetic dichotomy from the nearest ancestor. E.M. has pointed out impracticality of this cladistic principle. He (with his coauthor) says, "Although birds and crocodilians share a number of synapomorphies that originated in the archosaurian lineage after it had branched off from other reptilian lines, crocodilians are on the whole still very similar to other reptiles because of their joint possession of numerous ancestral characters. Birds, by contrast, in connection with their shift to aerial living, have acquired a vast array of new autapomorphic characters". Obviously there is little justification for regarding crocodilians and birds, which are sister groups, as having the same category rank. E.M. has pointed out that some cladists, with little taxonomic experience, have used cladograms for assigning category ranking to groups, often resulting in unacceptable classification. He recommends considering a cladogram and relevant evolutionary classification together to achieve a natural classification.

In the year, in which he completed a hundred years of his life, he came out with a new book (Mayr, 2004). This one is on philosophy of Biology. He has "incubated" this philosophy all these years after his New Guinea experiences in 1920s. His philosophy is based on the concept of evolution, and centers around the Darwinian theory. He has held that Biology is different from physical sciences, as it deals with the immense variability presented by the organic world. He brings home his point by stating that, while an electron is an electron for a physicist, of earth's six billion humans no two are identical (Claubrecht, 2004). Rationalising and making out order in the huge variability among organisms, and discovering the processes involved in the production of the immense diversity are the central problems in Biology, and that is how Biology stands apart from physical sciences. E.M. describes Biology as an autonomous science. Physical sciences may help developing concepts in Biology, but formulation of the concepts requires a biological training and perception. One important contribution of molecular studies is the demonstration that the same genetic code is for all organisms, from which situation E.M. as a biologist infers that life must have originated on the Earth only a single time. E.M. has opined that spending millions and millions of dollars in search of extra-terrestrial intelligent life is a waste. He was not optimistic about the success of this venture. He believed that resources might be better used for exploring further life on our planet and extending further frontiers of the evolutionary theory. He has stated in his new book that in the field of evolutionary biology "there is still plenty to be discovered".

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