J. Indian Inst. Sci.
A Multidisciplinary Reviews Journal
ISSN: 0970-4140 Coden-JIISAD

GUEST EDITORIAL

An Indian Tribute to William Morton Wheeler

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Abstract | William Morton Wheeler (1865–1937) was among the greatest experts on ants and his influence on the field of sociobiology, along with that of his academic grandson E.O. Wilson, is second to none. In 1923, Wheeler published his landmark book "*Social Life Among the Insects*" (Wheeler in Social Life among the Insects, Haracourt, Brace, New York, 1923), which marked the beginning of the modern study of insect societies. In this centenary year of its publication, we are honoured and proud to pay tribute to William Morton Wheeler.

In March 2021, I received the following message from the editor of the Journal of Indian Institute of Science:

> *"In the Editorial Board meeting of the Journal of IISc, we tried to see if there is anything special about 2023--like a centenary of some important discovery. This is to choose a theme for the Journal… It was pointed out that 2023 may be a centenary of the acceptance of social behaviour of insects. The internet sources are somewhat confusing. So, I am writing to you as you are an expert on this subject. If so, would you be willing to guest-edit an issue of the Journal in 2023 with invited review articles written by experts from around the world?"*

It was obvious that we should celebrate the 1923-Wheeler-book centenary, but it seemed to me that there was probably a better way to do so. Getting 'experts from around the world' to write review articles would be easy and something of a repetition—experts around the world keep writing, and people around the world keep reading them all the time. On the other hand, some excellent work on social insects is being done in India, which is hardly known worldwide. I am glad I convinced the editor that it would be a more glorious tribute to William Morton Wheeler if we wrote about our work than if we merely read about the work of experts around the world. Thus, was born the idea of *An Indian Tribute to William Morton Wheeler*. I must confess that my motivation to pay tribute in this manner received a further boost, if one was needed, when I realised that I am very nearly Wheeler's academic great-great-grandson! My most significant mentor has been Madhav Gadgil[2], who was a student of E.O. Wilson[3], who was a student of F. M. Carpenter[4] who in turn was a student of William Morton Wheeler. And while I was working on this, my son Vikram told me that he heartily approved of my effort as he was a recent recipient of the William Morton Wheeler Family Founders' Scholarship to attend the Methods in Computational Neuroscience course at the Marine Biological Laboratory at Woods Hole.

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Springer IISc PRESS

[William MortonWheeler (1865-1937). This image is in the public domain. Source: http://www.antwiki.org/wiki/File:Wm-wheeler.jpg]

In preparation for editing this special issue, I had the great pleasure of reading Wheeler's writings in several genres. But my even greater debt is to Mary Alice and Howard E Evans' skilled and erudite biography of William Morton Wheeler[5]. Howard Evans (1919–2002) himself was an outstanding wasp researcher and superb communicator[6]; perhaps his best-known book (among many brilliant titles) is *Life on a Little Known Planet*[7]. His wife, Mary Alice, has been a teacher, an educationist, and an entomologist specialising in dragonflies and damselflies (Odonata), while also co-authoring several books with her husband. Their message was loud and clear. William Morton Wheeler was a quintessential zoologist, one of the most famous zoologists of his time, and, without doubt, the most renowned ant researcher of his time. Not surprisingly, Wheeler had very broad interests in philosophy and human affairs. And, of course, he also had his own rather charming little foibles; not surprisingly, his most famous book was titled *Foibles of Insects and Men*[8]. Before presenting our tribute to this remarkable man, I would like to recall some aspects of his life and work.

1 A Quintessential Zoologist

William Morton Wheeler was born in Milwaukee in the State of Wisconsin in the USA on March 19th, 1865. Most people with distinguished careers in natural history and organismal biology often attribute their interest to some early childhood experience with nature. In Wheeler's case, it was his chance observation of a spider capturing a moth and his uncle's explanation of the phenomenon. That pull towards natural history remained and was regularly reinforced throughout his life. Whether in India or the USA, whether now or then, our straight-jacketed, one size fits all, schooling system usually fails to cater to gifted children. Wheeler 'confessed' that his "persistently bad behavior" in school led to his transfer to a German Academy known for its "extreme severity of discipline". But it is also true that gifted children often make the best of a bad situation. During his time in the German Academy and the following German school to which he was sent, Wheeler mastered several languages, including German, French, Greek and Latin, which put him in a unique position to read and translate zoological literature from around the world. At this time, he also volunteered to help unpack, identify, and organize specimens for the local municipal natural history museum.

2 How Wheeler Came to Study Ants

Before becoming a world-famous myrmecologist, Wheeler became an outstanding insect and worm embryologist. Indeed, he did not publish on ants until 1900[9] when he moved to the University of Texas at Austin. His biographers say: "*That Wheeler would soon abandon this area and achieve fame in wholly different aspects of biology could not have been suspected by anyone who observed the young Ph.D. who had effectively mastered so difficult and disputatious a subject as insect embryology*"[5]. Therefore, how did Wheeler become interested in the study of ants? Therein lies a charming story described in a memorable passage by his biographers Howard and Mary Alice Evans:

> *"In 1899, Wheeler left Chicago, after several years of teaching there, to direct the department of zoology at the University of Texas at Austin. After the years of rich academic associations and atmosphere, Texas seemed virtually a frontier. There were few books and little laboratory equipment available in the University, and Wheeler was faced with the formidable task of not only teaching the beginning course in zoology, but also most of the advanced ones. Discouraged at the prospect of so much to do and so little with which to do it, Wheeler took his lunch one day and went out to eat it in a*

dry stream bed near the campus. Passing near him in steady procession were long lines of ants carrying leaves. He watched them with puzzled fascination for a while, and then said to himself: these are worth a lifetime of study! Wheeler went on to become a world authority on ants, the most abundant of all animals on earth, as Wheeler himself often pointed out."

As someone trying to spread the message that we can do cutting-edge research even with little or no money or access to sophisticated laboratory facilities[10], this story warmed my heart like no other in Wheeler's remarkable life story. If the University of Texas at Austin had good facilities for Wheeler to continue his interest in embryology and histology, the world's ants and myrmecologists might have been deprived of one of their most illustrious champions of all time. Wheeler's story also illustrates the value of reading biographies and autobiographies of scientists.

3 In Search of the Big Picture

Wheeler described hundreds of ant species from America and around the world, including the invasive species *Tryglyphothrix striaditens* from India[11]. But, as his student, W.S. Creighton remarked[12]:

"…the most valuable contribution which Wheeler made to the taxonomy of our ants was not in the large number of new species which he described. It was rather that Wheeler carried his taxonomy into the field and amplified structural distinctions with others relating to habits, distribution and ecology…It is Wheeler's singular distinction that by his indefatigable efforts he made our ant taxonomy the living thing it is today."

In the preface to his provocative book *Randomness in Evolution*[13,14] John Bonner says:

"Many biologists … live two lives at the same time. In one they work with organisms from day to day in the laboratory, or in the field. This is what keeps them in touch with their subjects—the real world that they find so fascinating. The other life is a concern for the big picture: how it all fits together"

William Morton Wheeler fits Bonner's description admirably. And it is Wheeler's brand of 'living taxonomy' that permitted him to see the big picture. A mere ten years after he first started studying ants, Wheeler published his 663-page *Ants—Their Structure, Development and Behavior* (1910)[15] of which a reviewer said[16]:

"Here we have morphology, anatomy, embryology, psychology, physiology, sociology, paleontology, zoogeography, taxonomy, and even philosophy dealt with in an illuminating manner. The ant is presented to us as the hub of the universe, and if there is any biological subject which may not be suggested by the study of myrmecology, it is probably of small consequence"

Continuing to describe new species of ants every year, Wheeler aimed for the big picture, going from ants to all social insects. He was invited to deliver a set of six lectures at the Lowell Institute in Boston, which were published as *Social Life Among the Insects* (1923)[1], the volume whose centenary we are now celebrating. Two years later, he gave the same lectures in French at the University of Paris, which were published as *Les Sociétés d'Insectes, leur Origine, leur Evolution* (1926)[17]. Because the French edition was more technical and an update of his 1923 book, it was translated into English and published as *The Social Insects, their Origin and Evolution* (1928)[18]. These three volumes, along with his 1910 *The Ants,* made Wheeler the foremost authority on social insects for several decades to come, to be superseded perhaps only in 1971 when his academic grandson, E. O. Wilson, also at Harvard University, published *The Insect Societies*[19].

Wheeler's insatiable curiosity and inexhaustible energy led him to seek yet bigger pictures.

4 The Origins of Ethology

Wheeler's contribution to the science of ethology is next only to his role in ushering in the modern study of social insects. Indeed, Wheeler's biographers, Mary Alice and Howard Evans, make a strong case for shifting at least some of the credit for the birth of the science of ethology to the United States chiefly on account of William Morton Wheeler. Starting from rooting for the term 'ethology' as the best way to describe the study of animal behaviour to the development of methods for doing comparative ethology and understanding the role of ethology in evolution, Wheeler was one of the earliest spokespersons for making behaviour central to the study of zoology.

As early as 1904, Wheeler wrote a perpetually relevant paper entitled *The Obligations of the*

Student of Animal Behavior[20] in *The Auk*, an influential journal published uninterrupted since 1884 and now renamed *Ornithology*. The paper was borne out of his frustration concerning sloppy observations and fantastic interpretations of the behaviour of animals and a tendency to attribute human-like qualities to animals uncritically. The situation has improved somewhat, but not enough. Thus, many of Wheeler's statements in this paper, written in his characteristically powerful and forthright prose, are worth reading and re-reading even today and should be made part of the training of every student of animal behaviour. I will quote a small sample below:

> *"It is well known that every common or conspicuous animal, like every eminent human personage, is destined sooner or later to become the nucleus of a myth-nimbus… This nimbus of myth is not entirely the work of the ignorant and child-like observer. The savant himself, from the days of Aristotle and Pliny down to the present era of abounding 'nature-books', has contributed not a little to the hero-worship of animals…in view of these conditions, the student of any science of animal behavior or comparative psychology worthy of the name, has a two-fold duty to perform. This is both destructive and constructive; destructive, in so far as he is compelled to submit traditions concerning animals to searching and depurative criticism; constructive, in so far as he is obliged to rebuild our knowledge of animal behavior on the securer foundations of careful observation and experiment…the constructive work of the student of animal behavior is not completed with the accumulation of knowledge in conformity with true criteria. He may be expected to present the truths thus acquired in clear and attractive form for the purpose of encouraging others to continue the great work in this limitless field of observation and experiment."*

Wheeler's lifetime work is replete with evidence of his performing both the destructive and constructive duties he describes so clearly, not to mention his even greater compliance with the duty of presenting his work to a broad audience. Because many have heeded Wheeler's advice for decades, we can now begin to explore possible examples of intelligence, consciousness and the mind of animals, adhering to his admonition of applying Occam's razor [21–24].

In 1905, Wheeler went so far as to claim that:

> *"It is, indeed, not only conceivable, but very desirable, that a taxonomy should be developed in which the ethological will receive ample consideration, if they do not actually take precedence of the morphological characters. It is certainly quite as rational to classify organisms as much by what they do as by the number of their spines and joints, the color of their hairs and feathers, the course of their wing nervures, etc.*[25]"

5 Wheeler the Pioneer

Wheeler was a pioneer in many ways, but I will mention some examples I admire most.

In claiming that:

> *"…the honeycomb is as much a part of the bee as is her chitinous investment, and the nest is as much a part of the bird as her feathers, and every organism, as a living and acting being, fills a much greater sphere than that which is bounded by its integument."*

Wheeler thus foresaw the concept of the extended phenotype brilliantly developed by Richard Dawkins as recently as 1982[26].

While the German-born Zoologist, Botanist, and Naturalist Karl August Gustav Fiebrig, Director of the Museum of Natural History, Botanical Garden and Zoo in Paraguay, had described insect sleep in 1912[27], Wheeler drew attention to this phenomenon in his inimitable style in 1920 in an essay entitled *On Instincts*[28]:

> *"Insects undoubtedly sleep. Do they dream? If they do, what a pity that we shall never be able to apply the Freudian analysis to the dreams of that symbol of sexual repression and sublimation, the worker ant!"*

In a 1900 paper on Ponerine ants of Texas[29], Wheeler described the unusual mandibles and the remarkable mechanism of the predatory behaviour of *Odontomachus* species in the words:

> *"The touching of a living insect or of any unfamiliar object with these [mandibles] calls forth a peculiar response, which seems to be largely of a reflex nature. The ant darts forward and suddenly closes its mandibles with a very audible click. The signal for closing the*

mandibles seems to be given the moment the long sense hairs touch the object. The mandibles are brought together with such force that if they strike a solid object the ant is thrown backwards – often to a distance of three or four inches – occasionally even to a distance of 10 to 12 inches."

In a 1993 paper, Gronenberg, Tautz and Hölldobler [30] showed that the trap-jaw response described by Wheeler lasts only 0.33 to 1 ms and that the long sense hairs described by Wheeler are each associated with sensory cells whose sensory axons are among the largest neurons known (15–20 mm in diameter) making possible rapid information transfer facilitation by the rapid snapping of the jaws. Wheeler would have loved this result. Interest in the biomechanics of ultrafast trap jaws of ants continues today and is being used to understand the co-evolution of form and function [31]

In *The Superorganism: the beauty, elegance, and strangeness of insect societies,* Hölldobler and Wilson[32] point out that it was William Morton Wheeler who first applied the (the previously existing) concept of the superorganism to social insects in his 1911 article *The Ant as an Organism*[33] and the first to use the term superorganism in his 1928 book *The Social Insects: Their Origin and Evolution*[18].

In a 1926 paper entitled *Emergent Evolution and the Social*[34], Wheeler reviewed a great deal of the most interesting older literature and made many of his own remarks that bear an uncanny resemblance to our current concepts of self-organization, collective behaviour and emergent phenomena in biology.

6 Wheeler on Natural History, Amateurs, and The Practice of Science

Wheeler lectured widely to diverse audiences and wrote extensively in many genres, which allowed him to not only inform his audience but also to espouse his strongly held opinions and philosophical positions on a variety of issues. Because of his enormous fame and high stature, coupled with his facility with several languages, Wheeler was invited to review and comment on nearly every important book or encyclopedia published during his time. He often used these as opportunities to espouse his pet ideas and opinions. Many of Wheeler's pet themes are so dear to my heart and worthy of appreciation today that I cannot resist recounting at least some of them in his own words.

One of them concerns Wheeler's love of Natural History[5].

"What was formerly called natural history is the perennial foundation of the biological sciences. It has given rise to all the theoretical branches and will no doubt give rise to others in the future, and all the practical applications of biology have their roots in ecology"
"Unlike the "pure scientist" who is devoted to simplicity, the naturalist like the artist, feels at home in the profusion, multiplicity and diversity of natural phenomena"
"Certainly the pursuit of any branch of natural history may be recommended as an avocation to our youth, to convalescents, to our tired business men, or in fact to anyone who craves a hobby, a surcease from the nerve-racking routine of our city life, or a valid excuse for remaining as many hours as possible in the open air of the woods and fields."[35]

Another has to do with his admiration for the amateur and his critique of academia. Wheeler minced no words, as revealed by the title and contents of his essay *The Dry-Rot of our Academic Biology*[36]

"We have all known amateurs who could make an enthusiastic naturalist out of an indifferent lad in the course of an afternoon's ramble and, alas, professors who could destroy a dozen budding naturalists in the course of an hour's lecture…The typical professor has about the same liking for the amateur that the devil has for holy water, and the amateur habitually thinks of the professor in terms which I should not care to repeat…The truth is that the amateur naturalist radiates interest and enthusiasm as easily and copiously as the professor radiates dry-rot."

My third example concerns the practice of science, what we today call 'best practices [5]:

"There can be little doubt that scientific investigation is often impeded rather than furthered by too much attention to the "literature of the subject." Many a piece of zoological research may be perverted from the outset by an incessant appeal to what has been written . . . Investigation and publication are, however, two very different matters. One may investigate a thousand things, experience all the thrills of first discovery . . . But whenever one does decide to publish, it is necessary to reckon with the great "paper memory of mankind,"

the conserved experience of other workers who have loved and investigated the same things. It then becomes a duty to study the "literature of the subject," if only for the purpose of bringing the new work into intelligible, organic relation with the old. Failure to do this may be justly interpreted as carelessness, sloth, ignorance or conceit."

7 Administration and Institution Building

We have already seen Wheeler's impatience with, and even disdain for, the stuffy academic Professor. He held administration with equal contempt, although he shouldered his fair share of it, especially after he moved from The American Museum of Natural History to the Bussey Institution of Harvard University[37], first as Professor and later as Dean, to reorganize what was an undergraduate school of agriculture into a graduate school in applied biology. But he remarked to his friend that:

"I must say that with the somewhat more intimate knowledge of the trials of the university president, acquired since I have become Dean, that my former antagonism to university presidents in general has somewhat softened. You see how far I have degenerated, but this is all due to the fact that I, like yourself, have come to realize that the academic mind, as developed by most faculty members in the university, is pretty nearly as bad as the ecclesiastical mind." [5]

I was pleasantly surprised to learn that Wheeler had a big hand in setting up the Barro Colorado Island (BCI) research station. Now run by the Smithsonian Tropical Research Institute (STRI) in Panama and celebrating its centenary this year, BCI was initially founded by William Morton Wheeler. His biographers Mary Alice and Howard Evans[5] quote the following passage from Wheeler's letter of March 21, 1923, to Thomas Barbour:

"Yesterday Zetek, Johannsen, Dr. Strong and I spent an hour on the island which is reached by launch in 20 min from Frijoles on the railroad, not far from Colon. In a small clearing, less than an acre in area, I took 19 species of ants, Zetek took 10 species of termites (1 new species) and both of us took a dozen species of myrmecophiles and termitophiles (2 new genera, one a beetle, very remarkable!). The vegetation is extraordinarily diverse. It is an ideal place for a lab. in every way...The ground is dry and rises in hills, one of which ("Gigante") is about 500 ft. above the level of Gatun Lake. A small bungalow with screened verandah for a lab., a good launch, a resident director (Zetek would be just the man), a cook and one or two competent negroes as assistants, the development of a few good trails across the island, and we should have an ideal zoological and botanical paradise."

And his biographers go on to add that:

"The site was available, but money was not forthcoming from government sources, and apparently neither was organization. So, Wheeler appealed to his friends and associates for both…Wheeler, Fairchild, and Barbour not only contributed considerable amounts of their own cash to the enterprise, but persuaded many others to do likewise"

Having spent three months on Barro Colorado Island in 1980/81 and studied *Polistes versicolor* wasps there, this was a revelation to me—another connection for me to William Morton Wheeler!

8 Wheeler on Genetics

One of Wheeler's little foibles, I mentioned earlier, concerned his skepticism about genetics. It is unlikely that he actually did not see the importance of genetics. It is more likely that he was worried that most people would sit inside the laboratory and work on a small number of model organisms and neglect natural history and field-based and biodiversity-enriched organismal biology, a worry that I share even today. We must also remember that the importance of genetics was not really all that clear in the early part of the twentieth century. Wheeler's biographers graciously speculate that "*Perhaps, had genetics dealt in its early days with a hymenopterous insect instead of "that stupid little saprophyte" (his description of Drosophila as expressed to his students), he might have been convinced of the validity of Mendelism*" [5].

9 A Man of Letters

Sadly, finding a scientist who may be described as a 'A Man or Woman of Letters' has become rare. But William Morton Wheeler was undoubtedly a most distinguished 'Man of Letters'. His written contributions have been estimated to be as many as 467[38] titles, a large proportion of them being essays, transcripts of lectures, book reviews, opinions and commentaries, the very genres that are

today discouraged and expunged on account of not showing up as peer-reviewed papers in the ISI list of journals! Backed up by an enviable breadth and depth of scholarship, Wheeler employed many interesting literary devices to capture the attention and sustain the interest of his audience.

Wheeler's writing could be acerbic but was always couched in wit and sarcasm that bought a smile on the faces of his readers, at least those that were not the butt of his comments. He once described an author's unsubstantiated opinions as "*tenuous and fanciful creations for which one could have wished that euthanasia, that silent death so becoming to pet speculations when they have ceased to afford either amusement to their originators or edification to their readers*" [5].

Probably my most favourite among Wheeler's prolific productions is his lecture at a Symposium of The American Society of Naturalists in Princeton on Dec. 30th, 1919. The lecture was subsequently printed in *The Scientific Monthly,* published by the American Association for the Advancement of Science between 1915 and 1957 and which was later absorbed into what we today know as *Science*[39]. Here, Wheeler memorably describes the termite society and compares it with the human society from the point of view of a termite! It is really charming and worth reading in the original. Taking a swipe at people who attribute super-human qualities to animals (such as the *Clever Hans* phenomenon), Wheeler tells us that he decided to write a letter to the queen of the West African *Termes bellicosus*. He does not tell us what he wrote but reproduces the reply he got in full. The reply begins as follows:

> *"Dear Sir: Your communication addressed to my most gloriously physogastric consort, was duly received. Her majesty, being extremely busy with oviposition—she has laid an egg every three minutes for the past four years—and fearing that an interruption of even twenty minutes might seriously upset the exquisitely balanced routine of the termitarium, has requested me to acknowledge your expression of anxiety concerning the condition of the society in which you are living and to answer your query as to how we termites, to quote your own words, "managed to organize a society which, if we accept Professor Barrell's recent estimates of geological time, based on the decomposition of radium, has not only existed but flourished for a period of at least a hundred million years."*

And, after some 5000 words brimming with clever metaphors, many witticisms and abundant sarcasm, the letter ends as follows:

> *"It is my opinion, therefore, that if you will only increase your biological investigators a 100-fold, put them in positions of trust and responsibility much more often and before they are too old, and pay them at least as well as you are paying your plumbers and bricklayers, you may look forward to making as much social progress in the next three centuries as you have made since the Pleistocene. That some such opinion may also be entertained by some of your statesmen sometime before the end of the present geological age, is the sincere wish of Yours truly, WEE-WEE, 43rd Neotenic King, of the 8429th Dynasty of the Bellicose Termites."*

I will (almost) leave it at that and let you read it in full—it is easily available in the public domain. However, I simply cannot resist one more quote. People often ask me what humans can learn from social insects. My answer is always that we should not attempt to imitate insect societies but learn all about them as they can hold a mirror to help us understand ourselves better. I was so pleased to see the bellicose termite king said pretty much the same:

> *"If I extol the splendid solutions of sociological problems by my remote ancestors, I refrain from suggesting that your society would do well to imitate them too closely. This, indeed, would be impossible. I believe, nevertheless, that you may be interested in my remarks, for, though larger and more versatile, you and your fellow human beings are after all only animals like myself."*

10 Wheeler's Intellectual Legacy

An important measure of an academic's success is the success of their students, and by extension, the measure of their students is the success of their students, ad infinitum. The Germans have charmingly codified this tradition by referring to one's PhD mentor as '*Doctor-Father*'. Wheeler mentored a large number of students. If I were to single out two names from his academic lineage, one would surely be his academic grandson E.O. Wilson[40], whose accomplishments rivalled Wheeler both as myrmecological extraordinaire as well as in his reach for the big picture. My other choice would be Alfred Kinsey (1894–1956), who

was unique in being a distinguished zoologist and entomologist while also becoming the best known sexologist. Despite all the controversy, Kinsey has been etched in popular memory for his pioneering, if scandalous, study of the *Sexual Behavior of the Human Male*[41] and *Female*[42]. But it is not so widely known that Alfred Kinsey was a keen naturalist fond of watching birds and collecting insects, especially gall wasps, and writing such books as *Edible Wild Plants of Eastern North America*[43] and popular high school textbooks such as *An Introduction to Biology*, *Field and Laboratory Manual in Biology* and *Methods in Biology*[44].

11 Wheeler on Wheeler

I am always interested in knowing what famous people think about themselves and how it compares with what the world thinks of them. Which movie does a director think is their best, which book an author thinks is their best, and which piece of art does the artist think is their best? And it is especially interesting if their choices are at odds with what the world and their friends and fans believe are their best productions. I tell my students that they are not ready to be independent scientists until they have an opinion of themselves that is independent of the world's opinion. Not surprisingly, I was keen to know what Wheeler thought about his work. And I found that Wheeler's case is particularly interesting. As we have seen, Wheeler spent his entire career dividing his time between his work on ants—collecting and describing new species from around the world on the one hand and looking for the bigger picture not only in the world of insect societies but in history, philosophy art and literature, on the other.

Wheeler himself (as his friends testified[5]) felt that his taxonomic work, which his wife called "his knitting", was his more important contribution than everything else he did. His biographers, Mary Alice and Howard Evans, disagree. They write:

> *"In retrospect, it appears that Wheeler was wrong in rating his taxonomic work of more permanent value than his essays. It was in taxonomy, especially, that his work suffered from undue devotion to the past, for it was his admiration for Emery and Forel, in particular, that led him to cling to outmoded terms and to describe many trivial variants as varieties and subspecies."*

Their argument seems to rest on the observation that:

> *"the many hundreds of ants described by Wheeler have had various fates: some are now regarded as species, others as subspecies, and a rather considerable number are no longer used at all, but simply cited as synonyms of other forms."*

I beg to disagree. My primary argument is that, while naming and classifying species is an ever-changing enterprise, it is Wheeler's discovery and description of hundreds of species—and no one has claimed that his descriptions were shoddy—was, therefore, more important rather than what names he gave them, and whether he considered them species, sub-species, or varieties. Mine is admittedly the view of a non-taxonomist, but we cannot deny that most people in the world, even those who (should) read and admire William Morton Wheeler, are non-taxonomists. My second argument is more personal. I value the opinion of great people about themselves much more than other peoples' opinion of them. It is not for nothing that his friends regarded Wheeler as *"one of the world's foremost biologists, the greatest American zoologist since Agassiz, and so forth"*[5], *"an outstanding example of one who fulfilled every requirement of scientist, investigator, naturalist and literary master."*[45], and that they knew of no one *"who would have been both worthy and able to sustain a conversation with Aristotle"*[38]. Let us give Wheeler the right to opine about himself!

12 An Indian Tribute

Our Indian tribute to William Morton Wheeler consists of 12 articles describing some of the best research on social insects carried out in India, whether by Indian citizens or foreigners.

We begin with the article *Suzanne Wellington Tubby Batra: A life dedicated to pollen bees*[46] by Miriam H. Richards of the Department of Biological Sciences, Brock University, Canada and Francisco J. Posada-Florez and Jay D. Evans of the USDA-ARS Bee Research Laboratory, Maryland, USA. Their article is a fitting opening piece both because it describes the oldest research on social insects in India (considering the research described in all the remaining articles) and because its theme is of fundamental importance. Social insects display many levels of sociality of varying degrees of complexity. The term *Eusocial*, meaning truly social, has become ingrained in the social insect lexicon to denote the highest level

of social complexity. E.O. Wilson made the term famous in his 1971 book *The Insect Societies*[19].

However, it was young Suzanne Batra who originally coined the term eusocial while studying pollen bees in India. Suzanne was unhappy that the bees (which we today call primitively eusocial) she studied were called 'primitively social', because she did not accept the implication that her bees were in any way more primitive as compared to honey bees, ants and termites, which were called 'social' without the 'primitive' prefix. To her great disappointment, Michener[47] and Wilson[19] expanded the scope of eusocial to include ants, honey bees, termites, as well as her kind of 'primitively' social bees. As a simple extension, ants, bees, and termites came to be labelled as 'highly eusocial', and Batra's bees and many species of social wasps and bees were ironically re-labelled as 'primitively eusocial! Richards et al. tell the story in great detail, in addition to telling us about the exquisite research that Suzanne Batra carried out on pollen bees in India and about how she came to work on the bees of India in the first place.

The second article in our tribute is *Comparative psychophysics of colour preferences and colour learning in bees with special focus on Asian social bees*[48] by Hema Somanathan and G.S. Balamurali of the Indian Institute of Science Education and Research Thiruvananthapuram, Kerala, India. Somanathan and Balamurali focus on Asian honey bees and stingless bees, the latter being primitively eusocial, or just eusocial, as Suzanne Batra would have liked them to be called. They summarize a decade of their ongoing research on the sensory ecology of bees-flower coevolution. They study the bees' colour detection abilities, innate preferences, learning abilities, and nocturnal colour vision. These studies are a necessary first step towards understanding how the sensory ecology of bees interacts with floral colour diversity in diverse and complex tropical habitats to create or disrupt pollination networks. As the authors point out, we must conduct similar research on other sensory modalities, especially olfaction, to factor in multimodal sensory interactions and gain a more realistic picture of flower-bee mutualism. Studies like those of Somanathan and Balamurali show how little we know and how much more can be relatively easily accomplished in a country like India.

The third article *How India changed my ideas about honey bees*[49] by Axel Brockmann of the National Centre for Biological Sciences, Bangalore, is a welcome outlier in how science generally happens in India. After a distinguished career studying the European honey bee *Apis mellifera* in Europe and the USA, Axel Brockmann took the bold step of permanently relocating to India to study Asian honey bees, of which there are several species, in contrast to the single species in Europe and America. It must be said that Axel Brockmann's bold step was matched by the equally bold step of the National Centre for Biological Sciences to hire a foreign national on their faculty, which is very unusual in India. The happy coincidence of two complementary bold steps resulted in a unique 10-year study of Asian bees by a researcher well-trained in researching honey bees. Add to this yet another happy coincidence that the European honey bee *Apis mellifera,* having been introduced into India, for better or worse, became available to Axel Brockmann to conduct a unique comparative study of Asian and European honey bees. Here, Brockmann describes the fruits of his decade-long sojourn in the land of bee diversity and also tells us how India changed his very ideas about honey bees. He ends his article, however, on a sombre note that the Indian (urban) public needs to better appreciate the importance of honey bees and learn to coexist with them.

We have yet another article on honey bees, but this one is on beekeeping: *Beekeeping for Sustainable Economic Development of India: Challenges and Opportunities*[50] by DP Abrol. Working at the Sher-e-Kashmir University under challenging circumstances, Abrol, a dear friend for many decades, has done an extraordinary amount of outstanding work on pest management, beekeeping and pollination biology in India. Abrol has done all his life's work with the goal of providing better income for the ordinary people of India while at the same time promoting sustainable development through beekeeping. In this special issue in honour of William Morton Wheeler, Abrol demonstrates the potential for achieving his life's goal while at the same time clearly spelling out the challenges we must face along the way. He says, for example, that "only 10% of the existing potential for beekeeping has been utilized in the country and there is … potential of over 200 million bee colonies as against 3.4 million colonies at present which can provide employment to over 6 million rural families."

Following these four articles on bees, we have three on wasps. In honour of Wheeler, we begin with the article on wasp taxonomy. This article is by Thresiamma Varghese, the only real entomologist in my research group at the Centre for

Ecological Sciences, Indian Institute of Science, Bangalore, and P. Girish Kumar of the Western Ghats Regional Centre of the Zoological Survey of India, and currently India's best expert on the taxonomy of wasps and who has the distinction of describing 123 species of wasps (not necessarily social) new to science. They provide an excellent compilation of the Taxonomy, Biology and Distribution of the Social Wasps (Hymenoptera: Vespidae) of the Indian Subcontinent[51]. They cover India, Pakistan, Bangladesh, Nepal, Sri Lanka, Bhutan, and the Maldives. They report that this region has at least 104 species of social wasps out of a world total of 1100 species. It may come as a surprise that the largest genus of social wasps in this region is *Polistes,* which is very poorly studied, although that is slowly changing (see below). The genus with the next rank in the number of species is *Ropalidia,* and even here, there is a significant amount of information only for a couple of species (see below). I would like to believe that such a compilation of taxonomy, biology and distribution of our 104 species of social wasps will shine a light on the extent of our ignorance and, therefore, on the great opportunities waiting to be exploited by our young researchers.

The following article on social wasps by Deepak Nain and Ruchira Sen begins to remedy the sorry state of our knowledge of the genus *Polistes*. Its title, *A Review of Our Meagre Knowledge of Asian Polistes, and a Call for More Studies*[52] says it all. Ruchira Sen obtained her PhD working with me on the social Wasp *Ropalidia marginata*, went to The University of Texas at Austin to study the molecular ecology of leaf-cutter ants and then to Purdue University to study the metagenomics of termite guts. However, the most laudable entry in her CV is that she returned to India to work, despite challenging circumstances, in an undergraduate college, Sri Guru Gobind Singh College, Chandigarh, toward increasing our knowledge of Indian social wasps. She has done well in choosing to work on *Polistes*, which is different from her PhD model system and even less known than *Ropalidia*. Her co-author, Deepak Nain, is her student working in the nearby Punjab University in Chandigarh. Reviewing the scant information available on *Polistes* in our regions, they lament that even "The speculation that *Polistes* originated in oriental regions can neither be confirmed nor refuted due to the lack of knowledge on Asian *Polistes*." I hope that their clarion call to study our local fauna will be heeded by the hundreds of young scientists in India and the neighbouring regions looking for ways of doing original research despite access to little or no funds or laboratory facilities.

The final article on wasps is about the genus *Ropalidia*. My research group has focused on *Ropalidia marginata* and, to a lesser extent, *Ropalidia cyathiformis* over four decades, with the aim of understanding everything possible about the social life of these fascinating wasps. Our focus has been deliberately biased towards behaviour and ecology from an organismal biology perspective. Throughout this period, I have often reviewed the findings of our group for a broader audience[10, 53, 54, 54–57]. On this occasion, I wanted to do something different. I therefore invited two of my brightest (former) students, Sujata Deshpande and Anindita Bhadra, to write about our work on *Ropalidia* from their perspective. Sujata Deshpande bravely chose to do her PhD on *R. cyathiformis* because I had found and warned her that *R. cyathiformis* was very difficult to study. Sujata has returned to her passion for teaching undergraduates at St. Xavier's College in Mumbai. For her PhD, Anindita Bhadra studied the power relations between queens and their successors in *R. marginata,* showing, among other things, that even though we could not (at that time) predict the queen's successors, the wasps themselves behaved as if they know the identity of their queen's successor. Now, she has become well known for her pioneering studies of the behavioural ecology of free-ranging dogs[58]. In their joint article *A tale of two wasps and why we should listen to it*[59], Sujata and Anindita present our group's journey into the social lives of these wasps. Their engaging narrative also offers a glimpse into the process of our science.

Compared to the social Hymenoptera (ants, bees and wasps), termites, another major group of social insects, have received less attention worldwide and in India, too. Luckily, my colleague at the Centre for Ecological Sciences, IISc, Renee Borges, has been studying a locally available termite species. The first thing that comes to mind when we think of termites is their mounds, which are true marvels of architecture. Not surprisingly, her focus has been on their nest-building behaviour, and she has done the smart thing of collaborating with civil engineers. For our volume, Renee Borges and Tejas G. Murthy (of the Department of Civil Engineering of the Indian Institute of Science) have written a fascinating review of their joint work in an article appropriately entitled *Building Castles on the Ground: Conversations Between Ecologists and Engineers*[60].

The final section of our tribute will feature four articles on the Ants so dear to William Morton Wheeler. The first is a remarkable study in the Himalayas of the equally impressive species of ants belonging to the genus *Myrmica.* In their article, *Surviving in the Himalayas: A Story of Endurance in Ants*[61] Himender Bharti and Meenakshi Bharti of the Punjab University in Patiala and Abirami Meenath of the Indian Institute of Science Education and Research, in the temple town of Tirupathi in south India, present a fascinating account of the natural history of Himalayan *Myrmica* species. Their study reveals, "*The odyssey from egg to queen in Myrmica species takes about 1.5 years as these species must over-winter twice to complete its journey*." Despite having to deal with the harsh climate of the Himalayas, or perhaps because of it, these species also raid each other's nests to steal pupae and have them work for their own colonies, adding an additional biotic burden to the already severe abiotic burden of the environment—such is the drama of life.

The following ant paper deals with the fascinating phenomenon of house hunting in ants that do not lay chemical trails, but instead, leaders walk their nestmates to a new location. After studying reproductive conflicts, or the lack thereof, in *R. marginata* for her PhD in my lab, Sumana set up her own research group at the Indian Institute of Science, Education and Research in Kolkata. In a decade of intensive work with many enthusiastic students, Sumana has uncovered some of the most intricate details of how and when the queenless ponerine ant species *Diacamma indicum* relocate their nests. I am so pleased that many of my students have followed my example of giving as much importance to conveying the process of science as we do to convey its products. Here, Sumana Annagiri and her student Eshika Haldar take us through their journey in the article *Marching with Ants to a New Nest: Colony Composition and Relocation Dynamics of Diacamma indicum*[62]. Their very title, '*Marching with Ants,* ' invites us to march with them and promises to reveal as much about the researchers as about the ants. That their "*journey has brought to light answers to several questions but has also opened up several more avenues for exploration*" is a mark of good science, and their promise that "*With time and dedicated minds, we hope to continue on this route*" is a mark of great researchers.

Our third serving on ants is an *Evolutionary exploration of the recruitment strategies and foraging strategies of ants*[63] by K.N. Ganeshaiah. Ganeshaiah has spent all of his career at the Department of Plant Genetics and Breeding at the University of Agricultural Sciences in Bangalore, conducting pioneering research in the broad area of evolutionary biology, focusing mainly on plant reproductive biology. Along with his colleague R. Uma Shaankar, he pioneered the study of 'plant behaviour' and demonstrated that although plants "*can neither sing nor dance*", they do show complex behavioural strategies such as parent–offspring conflict and sibling rivalry. Ganeshaiah has also conducted exciting research on how ants scour their environment in search of food when alone and how they organize their foraging parties when they do so in groups, often in collaboration with his late wife and collaborator T. Veena. Here, Ganeshaiah reviews many decades of this work in the broader context of recruitment and foraging strategies in different ant species and explores the evolutionary forces that shape these diverse strategies.

Our final offering on ants and the last item in this special issue is in a different genre. We have presented a set of eleven excellent articles showcasing some outstanding research on social insects carried out on Indian soil. But these pale compared to what could have been done given our rich biodiversity and our vast supply of young researchers. We need to make much more effort to spread the word that our social insect fauna presents unlimited opportunities to study these magnificent creatures and their sophisticated societies, rivalling those of our own. In this context, science outreach is as important as doing science itself. Therefore, we must provide opportunities and social prestige to those dedicated science communicators who help to multiply the efforts of researchers. With this in mind, we end this special issue with a fine example of science outreach. In the article *Engaging citizens in watching ants*[64] Sunil Kumar, now Senior Science and Innovation Adviser to the British High Commission in India, presents a first-person account of his decades of effort in spreading the knowledge of and interests in ants in the Indian context.

I sincerely hope that this special issue of the Journal of the Indian Institute of Science showcasing the meagre but high-quality work on social insects in India will stimulate others to undertake similar and ever-better research on our diverse fauna. I like to think that William Morton Wheeler would have appreciated our little effort and taken pride in the fact that he has inspired us.

I thank Sanjay Sane for reading this article prior to publication and offering helpful comments.

Publisher's Note

Data availability

There are no data asscociated with this article.

Published: 18 December 2023

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