

The secret society of the paper wasp

Raghavendra Gadagkar, India's preeminent biologist, speaks on a lifetime of research on the insect society, and the state of science education the country.

By Akshai Jain



aghavendra Gadagkar, 65, one of India's most accomplished scientists, is a maverick. He has spent the better part of the last four decades studying the social structure of the paper wasp, *Ropalidia marginata*, found so commonly in cities and forests across India that it was completely ignored by everyone else. He has done what few contemporary scientists do—let the subject do the talking. Over years of painstaking observation and analysis, wasp society has revealed some of its secrets to him: how are tasks shared among wasps in a colony? How does this impact social structure and caste hierarchy? What happens when the queen wasp dies? By his own admission though he has only scraped the surface, things are just beginning to get interesting.

He is now an honorary professor at the Indian Institute of Science in Bengaluru, having spent almost his entire career there. He is also a fellow at the Institute for Advanced Study in Berlin. Akshai Jain spoke to him about his life in science.

You've been researching *Ropalidia marginata* for nearly four decades now. Haven't you been tempted to move to another species?

Yes, I have had the great pleasure of studying the primi-

tively eusocial Indian paper wasp *Ropalidia marginata* for over 40 years, 45 years if you count the hobby period and 50 years if you count the staring in awe as a layman. There are several reasons why I have not moved on to other species (with one minor exception, more about that later). The first is that *R. marginata* is incredibly fascinating, ideally suited for observation and experimentation and really beautiful. The second is that even after 40 years, it is clear that I have barely scratched the surface and there is so much more to understand, making it completely unreasonable to switch to another species. The third reason has to do with my style of research.

In our field some people study many species simultaneously and use what we call the comparative method to draw conclusions. One problem with this approach is that your understanding of each species is 1/N if you are studying N species. If 40 years is not enough for one species, 1/N would be too little for any value of N greater than 1. My style is to go as deep as I can and understand everything humanly possible about this species. If there are other passionate people who similarly study other species in depth, we can then do a comparative study as a community effort.

There are many questions that you have answered but as you've said a few times there are more to be answered about this species. What are some of the questions that you would like to answer next?

The questions that remain to be answered are endless. Indeed, we do not even know the existence of many questions which will only become apparent when we begin to answer some questions. Answering every question inevitably



We know that queens are periodically replaced by their workers who become future queens. We have tried very hard but failed so far to predict the identity of the successor even before the death of the previous queen. leads to one or more new questions. That is why I say that as knowledge increases linearly, our ignorance increases exponentially. Considering what we have already discovered about *R. marginata*, perhaps the most interesting unanswered question is how the successor to the queen of a colony is chosen.

We know that queens are periodically replaced by their workers who become future queens. We have tried very hard but failed so far to predict the identity of the successor even before the death of the previous queen. What makes this situation even more intriguing, and in some ways, ironical, is that we now have good evidence that the wasps themselves seem to know the identity of

their next successor. At a more general level, an important unanswered question is how the wasps manage to lead an apparently harmonious social life with very little overt conflict, even during the most crucial period of queen succession.

Another problem with simultaneously studying many species is that we tend to pick the low-hanging fruit, i.e., answer the easy questions. Staying with one species forces us to ask deeper, difficult questions.

It's very rare to find someone who has devoted most of their career to a single species. What are the advantages of this? Isn't one of the drawbacks the fact that your findings may not be widely applicable/ open to generalisation?

I have already referred to the several advantages of in-depth study of a single species. I have also pointed out that the main disadvantage of lack of generalisability can be overcome if other scientists similarly study other species in-depth. In my opinion, there is an advantage to each scientist studying one or a small number of species in depth, compared to everybody trying to study every species. Another problem with simultaneously studying many species is that we tend to pick the low-hanging fruit, i.e., answer the easy questions. Staying with one species forces us to ask deeper, difficult questions. By allotting one or two species per scientist, each of us will have the opportunity of starting with easy questions and then going on to difficult, more difficult and almost impossible questions.

How did you first decide to start studying *R. marginata*? And at what point did you decide that you would stick to this species for nearly all your research? Have you ever had any misgivings about this decision?

When I joined the Central College (now Central College University) in the year 1969 to do a BSc (Hons) in Zoology, I encountered a very large number of colonies of this fascinating wasp, on nearly every window of the Zoology and Botany departments. It now amuses me that none of my Zoology teachers had any interest in or knowledge of these fascinating insects in the corridor. They seemed only to be interested in reading books about animals written by Western authors and dissect dead animals.

I became fascinated by these 'real' animals and could not stop watching them for hours together. Five years later, armed with a BSc (Hons) and MSc in Zoology, I joined the Indian Institute of Science and registered for a PhD in Molecular Biology. At the beginning of this five-year period, I met Prof Madhav Gadgil who encouraged me to continue studying *R. marginata* as a hobby. He also introduced me to the writings of E. O. Wilson, W. D. Hamilton, R. L. Trivers, Mary Jane West-Eberhard and his own work. I came across a statement in one of Wilson's books that *Ropalidia* probably holds the key to understanding the evolution of social behavior. The transition from watching the wasps nearly in awe to studying them scientifically and Wilson's statement convinced me that I should continue to study *R. marginata*, at least as a hobby, for the rest of my life. At the end of my PhD, I was equally smitten by molecular biology and sociobiology and could not easily choose between the two. One option was to continue with a career in molecular biology and study the wasps as a hobby. I realised, however, that there is no better place to practice molecular biology than a well-endowed laboratory in the USA or UK. On the other hand, there was no better place to study sociobiology of the wasps than India. I had a clear preference to live and work in India and that is when I decided to switch roles and convert the study of wasps as my profession and molecular biology as my hobby. I have never had any reason to regret this decision.

You have also said that one of your important discoveries has been the caste differentiation in *R. marginata* into sitters, fighters and foragers. This discovery was a long time back. What has been the most interesting discovery since then?

I would still rank the discovery of sitters, fighters and foragers as the most important. This is especially because that discovery has been a starting point of most of the research that we have done subsequently. That discovery raised more questions than we have been able to answer in over 35 years. Another important discovery that I am very fond of is the realisation that the long developmental period of the young wasps and the highly variable life spans of the adults together provide a unique advantage of group living because several adults with short life spans can serially divide the labour of caring for the helpless young. I have called this 'Assured Fitness Returns', meaning that those who live in groups have more assured returns for their investment because, even if they die, someone else can continue their work—all is not lost. In contrast, a solitary individual has to necessarily survive until the end of her job of taking care of the eggs all the way through their larval and pupal stages and become adults no longer requiring the care of adults. If a solitary wasp dies midway through this job, all her investment is lost. I am happy to name a third, equally interesting and fascinating discovery—as already mentioned we know that the wasps know (who their next queen will be).

You've used *R. marginata* to develop a new fitness model (assured fitness returns) for altruism/ evolution of social life in insect societies. Could you tell us a little more about this particular model? What are the results when you apply this to other species?



Raghavendra Gadagkar. Photo: Special arrangement.

This model has not been applied to any other species. Of the few species studied, some have 'assured fitness returns' and some don't. This is not surprising because assured fitness returns are expected for certain unique combinations of long developmental period of the young that require care and relatively short and/or uncertain life expectancies of the adult care givers. The strength of the model is not to be judged on how many species it applies to but on its ability to distinguish between species where it applies and where it does not apply and understand the reasons for this. Much more work needs to be done here.

In a talk you mention-'I have since been able to incorporate various other factors along with assured fitness returns into a unified model for the evolution of eusociality.' Could you tell me a little more about this model?

In the theoretical framework that we use to understand the evolution of sociality, three factors, namely, genetic relatedness, ecological productivity and demographic population structure, interact with each other to make either solitary life or social life more suitable for a given species. Measuring and combining these three factors in *R. marginata*, we were able to construct a theoretical model that predicted that only about 5 per cent of the wasps should opt for solitary life while the remaining should live in social groups even if it means a subordinate, non-reproductive status. Our field research shows that this is approximately how *R. marginata* behaves. This has now placed us in a unique situation where we should be able to increase or decrease the propensity for cooperation in this species by altering one or more of these three factors. As I speak, we have probably seen the first success in experimentally making *R. marginata* less cooperative and more selfish.

Isn't the evolution of eusociality a continuum rather than either/or? In which case would it make sense to have some sort of multidimensional model for classifying eusociality in species? Does such a model exist?

Yes, it is a continuum and my unified model is one example of a multi-dimensional model. Of course there have been many other attempts, too. A major area of research is to find the appropriate dimensions so that we can place different species along the continuum. I personally believe that we should take a sufficiently broad approach so that we can place not only insects but also birds, mammals and even humans on a continuum.

In 2009 you wrote: 'Our interrogation of *R. marginata* suggests that features such as (*i*) nonaggressive, noninteractive queens, (*ii*) pheromonal as opposed to aggression-based regulation of worker reproduction, (*iii*) decentralized, self-organized regulation of the nonreproductive activities



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No, I have not studied other evolutionary lineages. I hope that others will do so, and we will be able to combine knowledge from different research groups on different evolutionary lineages to enhance our

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understanding of the evolution of social life.

There are vast variations in social structure between *R. marginata* and a close species *R. cyathiformis*. What could the reasons for this be?

I would not say that the variations are vast. It appears that *R. cyathiformis* is a more typical primitively eusocial species, known for their aggressive queens and relatively unsophisticated social organisation. *R. marginata* on the other hand, appears to have acquired many features reminiscent of advanced insect societies such as those of honey bees and of ants. It is reasonable to think that this is a natural evolutionary progression and we should expect different species to be at different steps in the evolution from solitary life to advanced sociality. This does not mean that all species will gradually evolve advanced sociality. Many such intermediate steps may be stable evolutionary equilibrium states for which there is a specific ecological niche available.

In a lecture you gave in 2016 you said, 'I often have to *cure* my students of their education before I can nurture them into thinkers and problem solvers.' What does this say about the Indian education system?

I am not convinced that the Indian education system can be singled out as being worse than most other systems around the world. My problem is with education systems around the world including in India. Of course, my experience and thoughts may be more applicable to the natural sciences. Science is taught as a body of knowledge, a large collection of facts, growing in leaps and bounds, bursting at the rim. Students are not taught how to think. In the best scenario, education produces erudite scholars with a vast store of knowledge but with little education in how to make new discoveries. In the worse scenario, the natural in-born curiosity of children is actively suppressed in favour of accepting and memorising previously established facts. Education should guide young minds to rediscover the laws of nature and the world around them by a process similar to how this was done in the first place. Such education will prepare students to discover new laws and learn new facts about nature.

I find that today the 'best' students 'know' everything but are ill-prepared to

discover what is not yet known. It is no exaggeration to say that I have to 'cure' my students of their prior education before I can teach them how to think and solve new problems. Indeed, I have to work very hard to convince them that there are many important unknowns and they are perfectly capable of discovering them, and that knowledge does not grow in text books. This of course is not very easy and takes a great deal of effort. One shortcut I sometimes use is to only discuss such topics with my students about which they have no prior knowledge. This sometimes leads to an amusing situation. I ask a question and call upon only those students who don't know the answer to give me an answer. Those who already 'know' the answer are often incapable of learning how to find the answer *de novo*.

As a follow up to this, given that science has become so specialised that looking/borrowing from other fields—as you have done in the case of using meteorological models to study ants—seems to have become increasingly more difficult. Has it really? Or is this just a lazy excuse?

I advise my students to read as little as possible of what appears to be relevant to their research problem and read as much as possible of what appears irrelevant. No, it has not become more difficult. If anything, it has become easier because knowledge has grown in so many directions. What we need is a change in our mindset. I advise my students to read as little as possible of what appears to be relevant to their research problem and read as much as possible of what appears irrelevant. Such an attitude often makes it possible to approach the same problem from a completely different perspective. Part of the problem is that we demand that students/ researchers rapidly produce large number of results in a time-bound, predictable rate. Research should be a quest for the unknown with no guarantee of success and

certainly no predictability of what the solution might be. If we reward effort and not success, many things currently impossible will become routine.

You've mentioned at different times that E.O. Wilson has been one of your inspirations. Could you tell me a little more about why this is? Who are the other people who have inspired you?

It is difficult to stop talking about E. O. Wilson, if I begin to do so! In 1971, Wilson wrote a book called *The Insect Societies* which really gave birth to the modern study of insect societies. This has been and continues to be a bible for most of us. In 1975, he wrote another book called *Sociobiology* which gave birth to another whole new discipline. Since then, Wilson has written almost one book every year, each one inspirational. Wilson is arguably the greatest

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living biologist today. I must confess that meeting him periodically has hugely added to my admiration of the man. In my work I have also been greatly inspired by people like W. D. Hamilton, C. D. Michener, Mary Jane West-Eberhard and Madhav Gadgil.

You have also talked about the process of doing science—yet this process has changed a lot since you first started out. What is your opinion of the process of science today? Do you think money and the need to publish skews this process even more than it did in the past?

Yes, the process of doing science has changed, for the worse, I must say. This is a rather depressing topic and I try not to talk about it too often. When I began my career, science was driven by curiosity and was a playful activity (not so different from a hobby), without too much expectation of any product or, indeed, even a result. This made the most difficult problems the most attractive ones. The process of science was more important than the result. In the long run, we learnt much more, even then we failed to get what we sought to get.

Today science has become far too institutionalised and corporatised. There is enormous pressure to succeed and less emphasis on the process. Young scientists are under pressure to tackle easily tractable problems and are judged by quantity rather than quality and, worse, by incredibly stupid metrics. This is especially bad for basic science and makes it very difficult to make big discoveries. It is true that this is a worldwide problem. But it is especially unfortunate for a country like India where we have a very large and extremely intelligent manpower reserve and there are many outstanding fundamental problems, especially in biology where we are at an advantage due to the lowcost, low-tech nature of such work and access to amazing biodiversity. And yet we are throwing away our advantages and competing with the West with an enormous handicap. Either our policy makers cannot distinguish between basic science and applied science or they cannot see the value of basic science. Consider the recent circulars requiring vice-chancellors of our universities to ensure that students take up PhD work only in a small number of pre-specified problems of so-called national interest. This makes no sense for basic research.

In a recent interview you've said that *R. marginata* "continues to give you great delight". Having studied this species for over 40 years it must be like living with an old friend. As with all relationships there must be parts that are very familiar, and some that you still don't understand – is that true?

It is true indeed that I have had an almost personal relationship with *R. marginata*. I have known it for exactly the same amount of time as I have known my wife. One example of my deep relationship with *R. marginata* is reflected in a kind of pleasure I get when it still holds secrets that are not easily revealed to me. For example, they know their next queen while I don't! It is true that we understand much about the species so that we sometimes know what to expect when we study a new colony. But this knowledge really refers only to the relatively low hanging fruit that I referred to above.

Perhaps the most profound thing that we don't understand about the wasps is, as I have said above, how they manage their affairs by burying conflict and displaying cooperation. We have good reasons to believe that there is a great deal of potential for conflict, but that conflict is never displayed to us. What



Perhaps the most profound thing that we don't understand about the wasps is, as I have said above, how they manage their affairs by burying conflict and displaying cooperation. We have good reasons to believe that there is a great deal of potential for conflict, but that conflict is never displayed to us. we see is the expression of cooperation following the 'almost private' resolution of conflict.

Would you recommend a similar devotion to a species to scientists today?

I hope very much that a large number of scientists, at least in India, and at least those who study whole organisms, devote their lives to understanding one or a small number of species. There are many species of animals and plants almost unique to India that deserve such lifetime devotion. Moreover, such devotion to local species would do much more to contribute to the world's body of knowledge than trying to work

on model organisms made famous by Western scientists. If I had to start life all over again, and if for some reason, I did not come across *R. marginata*, I would probably devote my life to studying the peacock, the common crow, the stray dog, or one of the common garden birds unique to India.

You have always dug your own furrow. You've said that scientists should take 'what is not a hot area and make it hot'. This seems particularly applicable to science in India, which seems to take its cues from trends abroad. Do you agree?

Yes, I agree completely, both that it is especially important for Indian scien-



A nest of the Ropalidia marginata or the paper wasp. Photo courtsey: Thresiamma Varghese

tists who choose their own problems and that we instead routinely borrow problems from trends abroad. I have written quite often about this.

In my assessment, there are many young Indian scientists who understand this, and I want to be different and indeed, have the great potential of making discoveries. The system of science administration and evaluation is the real culprit which pressures young scientists into following the Western bandwagon. This may appear to be a bit surprising because a good thing about India is that science policy, administration and evaluation is largely in the hands of scientists themselves. I think the problem is that scientists in power are often those who were trained abroad and who have continued to do similar work in India that they did abroad. Often, they are not able to see that we have all the ingredients for making hitherto unfashionable areas into fashionable ones.

In practical terms what does this translate into—what are the kinds of areas that Indian scientists need to be looking at?

There are many unique problems open to us and for many of them we have a unique advantage over scientists from developed countries. Our biodiversity, including human diversity, our diseases of animals, plants and humans, our geology, our human activities that influence biodiversity and climate change are all often unique. But even in these areas, we wait for Western scientists to take the lead and make one or more areas fashionable.

We are often worried that if we study a local problem which has not caught the fancy of Western scientists, we will not be able to publish in high-profile Western journals. Buy why should we demand and judge our work by publications in high-profile western journals? Are we incapable of judging the merit of our own work? Do we still need a stamp of approval from western scientists? Actually, the situation is even worse. We seem to need the approval of western journals which are often not even run by scientists but are for-



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At the talk you gave at the Young Investigators Meet you said that 'I did feel a tinge of jealousy that it was Konrad Lorenz and not I who had discovered imprinting in birds, that it was Karl von Frisch rather than I who deciphered the honey bee dance language, that it was Douglas Spalding and not I that had put little hoods on newborn chicks and showed that their pecking behaviour was instinctive, that it was Niko Tinbergen and not I that had placed a ring of pine cones around the nest of wasps and discovered that

the wasps use landmarks to locate their nests'. Do you still feel that jealousy or do you think you have established your space in this firmament?

Of course, I feel jealous—every day! There is much discussion today about how to evaluate good science. For me there is only one real way. I should feel a tinge of jealousy that I did not do that research myself. The day I stop feeling jealous that I did not do the science that I read about, I will cease to be a good scientist.

You are also a bit of a rebel—you choose to stay back in India to challenge the assumption that it was not possible to succeed as a scientist without training abroad. As a result you had to wait more than twice the normal period before being appointed lecturer. Are you a heretic in every sphere

I find it shocking that scholars in the natural sciences and human sciences have no familiarity with each other's work and instead, are convinced of the demerits of the other side.

of life or just science?

I try my best to be a heretic in every sphere of life. It is by no means easy, but I keep trying!

In 2004 you helped establish the Centre for Contemporary Studies at IISc. This was meant to be a platform for bringing together the natural and social sciences for 'a discourse of mutual benefit'. Could you tell me a little more about this? What nature of discourse did you envision? Why do you think this is important?

I have spent my entire career at the Indian Institute of Science, arguably the best place in India to do science. My only regret was that we closed our doors to any form of social science and humanities. I will collectively use the phrase 'Human Sciences' to refer to all forms of social sciences and humanities including art, literature, cinema and music. I believe that an institution of research and teaching should have the best scholars in the natural sciences and the human sciences. I find it shocking that scholars in the natural sciences and human sciences have no familiarity with each other's work and instead, are convinced of the demerits of the other side. As a small solution to this problem, I established the Centre for Contemporary Studies and opened a window to the human sciences. We brought the best scholars in every possible kind of human sciences to the campus to lecture, teach, discuss, debate and, in some cases, stay in residence and do their work in our midst. We organised periodic courses with the theme of 'Production of Knowledge: A Comparison of Natural and Human Sciences'.

We have developed a rather unique curriculum and taken the responsibility of teaching humanities to undergraduate students majoring in science in our institute. The philosophy of this curriculum is to avoid teaching humanities as another set of disciplines. Instead, we use the humanities courses to create the context in which students learn science. Our three foundational courses in the humanities have the titles 'Ways of Knowing', 'Ways of Seeing', and 'Ways of Doing'. This I believe is a natural way of bridging the gap between science and humanities.

You have only written two books even though you have done so much fas-

cinating work. Why?

This is a matter of style and tradition. Natural scientists report their research in peer-reviewed papers rather than in books, the latter being the style in the humanities and to some extent, in the social sciences. On the rare occasions that natural scientists write books, they do so either for a non-scientific, or at least a non-specialist audience. They occasionally write monographs reviewing a whole field based either on their own work or that of a whole community, but new results are seldom reported first in books.

Most Nobel Prize winning work in the natural sciences is not published in books. The opposite is true in the humanities. Scholars produce and report new research periodically in a series of books. You can only be counted as a scholar after your first book and taken seriously after a second book. This is not true in the natural sciences. There is good reason for this. Discoveries in the natural sciences are usually so specific that they are best reported in short articles. Nevertheless, I feel that natural scientists refrain from publishing books to a fault. We need many more natural scientists writing books for

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Is the situation in India different from what it was when you started out?

Today it is not unusual for scientists to do brilliant work without training abroad. I hope this tribe grows.

Are you religious? What are your thoughts about religion, especially in places where it intersects/ crosses paths with science?

It depends on what we mean by being religious. I do not believe in a personal God who will bend the laws of nature to get me out of a tight spot. I do not feel compelled to follow any religious practices that defy rational thought es-



Why is it necessary to convince people of the worth of what you are doing? I have deliberately designed my research to depend very little on money and other resources, which has given me a great deal of freedom.

pecially if they are harmful to me, to others or to the environment. I certainly enjoy religions and religious festivities as interesting and entertaining cultural phenomena.

When you started out there was almost nobody working on the social biology of insects in India. It must have been difficult convincing people of the worth of what you were doing. Yet you have been able to run this novel research programme for over 30 years-how did you manage that?

Why is it necessary to convince people of the worth of what you are doing? I have deliberately designed my research to depend very little on money and other resources, which has given me a great deal of freedom. Besides, my work is my reward. No recognition from outside can match the satisfaction of doing my work and understanding my wasps. If someone appreciates my work in spite of this, I have no objection.

Your entire approach has been observational-letting the wasps speak for themselves rather than imposing questions (and implicit assumptions) on them. This seems to be one of the truly meaningful ways of interrogating a species-yet few scientists follow this deeply observational method today-it almost seems that this method has gone out of fashion. Why do you think this is the case?

Observation, especially when combined with experimental manipulation, remains a very powerful way of understanding the behaviour of whole organisms. Occasionally it would help to explore the underlying physiology and genetics. I find that today most of the community of organismal biologists are engaged in understanding the molecular and genetic underpinnings of a very small number of already known phenomena, in an even smaller number of model organisms. This has the danger of failing to discover a large number of as yet unknown phenomena and an even larger number of unknown species.

This obsession with genetics and molecular biology is especially unsuited for scientists with limited access to financial and technological resources. Indeed, it is unpardonable if such scientists also have access to a rich biodiversity. Very large numbers of researchers must work to study more and more species and discover more and more phenomena using modest resources and

a small number of researchers should be at the top of the pyramid probing the molecular mechanisms of some phenomena. It is sadly ironical that researchers in developing countries like India are often under pressure to use the meagre resources of their countries to enter into a losing competition with laboratories in advanced countries to study the molecular biology of social behaviour, instead of proudly studying the rich biodiversity in our backyard at a fraction of the cost.

The onus is on our research policy to create an environment where our scientists can undertake with pride the kind of research that we can do best. It is also necessary that we nurture rebels and heretics who will defy existing norms just for the pleasure of doing so.

Which books are you reading right now?



This obsession with genetics and molecular biology is especially unsuited for scientists with limited access to financial and technological resources. Indeed, it is unpardonable if such scientists also have access to a rich biodiversity. At present I am reading Monk in the Garden – The Lost and Found Genius of Gregor Mendel, the father of genetics by Robin Maranti Henig. Some of the books I have read in recent months include The Sixth Extinction: An Unnatural History by Elizabeth Kolbert, Enlightenment Now: The Case for Reason, Science, Humanism, and Progress by Steven Pinker, Improbable Destinies: Fate, Chance, and the Future of Evolution by Jonathan B Losos, Are We Smart Enough to Know How Smart Animals Are? by Frans de Waal, The Story of the Human Body: Evolution, Health and Disease by Daniel Lieberman and Wittgenstein by W. W. Bartley. Of course, I also read fiction,

permitting myself one novel after every non-fiction book!

Science in India seems to also be facing a religion-driven identity crisis. Do you agree? What do you make of it?

I don't think so. Indians are very religious, but it does not seem to affect their science. Some of our best scientists are deeply religious. We even perform 'Yagnas' before launching satellites into space. But I do not think this affects our science. There are, of course, religious bigots but those are everywhere. Religion is also sometimes used by some politicians, but this happened all over the world. I am not particularly worried about Indian science on this account. There are other more serious worries, some of which I have alluded to above.

If you did have the time, which the other species would you like to look at?

It is not the lack of time that has made me stay with R. marginata. If I had

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more time, I would study *R. marginata* even more deeply. Having said this, I must say that from time to time I have turned my attention to a closely related species *Ropalidia cyathiformis*. The reason for this is very clear. I study *R. cyathiformis* in order to better understand *R. marginata*. It turns out that *R. marginata* is quite unusual in many ways-one might say that it has not read the text books. *R. cyathiformis* seems to be a more "normal" species and we want to be sure that even in our own hands, *R. cyathiformis* behaves like a typical species and *R. marginata* as an unusual species. This gives us more confidence in our claims about the unusualness of *R. marginata*. As I have said above, I might study another species in another life but only if I cannot find *R. marginata*!