the major classes and many physical features are still under debate. To polarise arthropod trees, and define the likely morphological characters and developmental mechanisms of the arthropod ancestor, analysis of sister phyla in the Panarthropoda is required. Tardigrada are all very small, likely to have highly modified developmental processes, and have highly idiosyncratic morphology, and so may be of limited use in this regard. Onychophora have provided fertile ground for investigation.

Examination of velvet worm body patterning has shown that the animals have a mix of segmental and non-segmental features. Externally, the obvious segmental arrangement of the limbs is matched by some other structures (such as excretory organs) but not by others (for example, there are no obvious segmental borders in the body wall). Some segmentation genes first identified in insects are implicated in velvet worm segmentation (as they are in annelids), but overall their development is strikingly different from that of arthropods. For example, the arthropod (and tardigrade) post-cephalic nervous system is characterised by paired ventral nerve cords linked by segmental ganglia; in Onychophora, evidence for segmental ganglia is absent — there are paired ventral cords, but no segmental patterning other than that imposed by the presence of the serially repeated legs. The tripartite arthropod brain was thought to have a counterpart in Onychophora, but recent cell-level and developmental analyses have shown that, while the proto- and deuterocerebral regions have neural input from antennae and jaws, no putative third part innervating the slime papillae could be identified. The tritocerebrum thus seems to be an arthropod innovation.

What resources are available for velvet worms? While zoological and developmental studies of velvet worms have a long history, they are challenging to develop into fully-fledged 'model organisms'. They are difficult to keep in captivity, have rarely been bred, have long reproductive cycles, and there are few legal and ethical routes to obtaining live specimens: they are typically highly endemic but live at low population densities. As velvet worms are mostly internal brooders, obtaining early-stage embryos requires sacrifice of the mothers. Thus, most experimental publications involve specimens transported from the wild into the laboratory, alongside rewarding velvet worm field ecology. Consequently, there is no stock centre where one can get strains, no bank of mutants, and, surprisingly, so far, very little genomic or transcriptomic data (GenBank/EMBL only holds ~13,000 records for all Onychophora, and four complete mitochondrial genomes, compared to ~9 million records for arthropods, including 430 mitochondrial and nuclear genomes). While velvet worm expressed sequence tag projects have been used to identify genes for phylogenetic and functional analyses, onychophoran genomes have been estimated to be in the multi-gigabase range (from 1.5 to 2 times that of the human genome) and so full genome sequencing remains a substantial task.

Despite these challenges, because of their key position in the tree of animals and their fascinating biology, in recent years velvet worms have been the focus of some directed molecular and developmental research projects. The increasing ease of data generation and the delightful biology of these 'living fossils' should mean that these are but the first trickles of a flood of new data that will address key questions in understanding the animal diversity and function of our planet.

Where can I find out more?

Encyclopaedia of Life *Onychophora* http://www.eol.org/pages/6927

Georg Mayer's *Onychophora website* http://www.onychophora.com/ hosts an almost complete bibliography of velvet worm literature

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Reinhard, J., and Rowell, D.M. (2005). Social behaviour in an Australian velvet worm, *Euperipatoides rowelli* (Onychophora: Peripatopsidae). J. Zool. *267*, 1–7.

The University of California Museum of Paleontology, Berkeley *Onychophora and the fossil record* http://www.ucmp.berkeley.edu/onychoph/onychophora.html

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Q & A

Tony Hyman

Tony Hyman was born in Haifa Israel, and moved to London as a young boy. He stayed in London for his undergraduate work at UCL and then did his PhD in Cambridge at the Laboratory of Molecular Biology (LMB). After postdoctoral work at UCSF with Tim Mitchison, he moved to a group leader position at EMBL before becoming a founding director of the Max Planck Institute of Cell Biology and Genetics in Dresden. He was awarded the EMBO gold medal in 2003 and elected a Fellow of the Royal Society in 2007 and this year won the Leibnitz prize from the German Research Foundation, DFG.

What turned you on to biology in the first place? I can't say that I ever had a flash of inspiration that I should become a biologist. I was a dreamy child who used to sit in the middle of the classroom, got middle-of-the-road marks and drifted through my school career. I grew up in London and went to St Marylebone grammar school, subsequently closed by the drive to change London schools from a selective to a comprehensive system. As with so many of those grammar schools, St Marylebone had first class committed teachers and a science block full of labs. We were doing physics, chemistry and biology soon after we started; so in a sense I was fully inculcated with science from an early age. Three A levels in science left one very well trained.

What was your first lab experience? After I left school I was not sure what to do, and worked as a lab technician at the UCL department of Zoology. My job was to make up the tissue culture media. At that time, I had to make the filters by putting a 0.2 micron filter in a metal case and autoclaving it. This was the old school way. Then I discovered that you could also get disposable filters, and that some of the younger professors had these. So I started getting in really early in order to use these filters. I knew that, if they found out I was not using the metal holders, I would be in trouble! One morning at about six, I found Terry Preston in his lab, and it turned out he had been there

all night. I was amazed! So I asked him what he was doing, and before I knew what, he had given me an experiment to do — to look at the role of ionic strength in the speed of movement of *Nigleria*. This led me to apply for a university place at UCL.

Why did you leave the UK? For my PhD I was lucky enough to work at the LMB with John White. With Brad Amos, he had developed a confocal microscope for looking at immunofluorescent *Caenorhabditis elegans* embryos. We were asked to show the microscope on *Tomorrow's World,* a popular science program in the UK. Afterwards we went to meet the presenters. I was pretty excited about that — but they spent the whole time talking to two young bankers who were friends of the producer. Somehow this seems to illustrate what was going wrong with the UK at that stage; a shift away from technical education and focus towards finance as a prime driver of the UK economy, with predictable results. This was before the Wellcome Trust came on the scene and revolutionized biomedical funding in the UK. At this point it made sense to me to go off to the US for a postdoc in Tim Mitchison's lab at UCSF.

Why did you come back to Europe? I have always wanted to travel. I like the feeling of being a foreigner. So when the job at EMBL came up, I jumped at the chance. I don't think I ever expected to spend a large fraction of my life in Germany, but I have really come to appreciate the generous and long-term funding of science here, as well as the strong focus on science education in the schools.

Why did you move to Dresden? After a few years at EMBL, Kai Simons came to see me with the proposition to move to Dresden. I liked the sense of adventure of moving to the old East Germany, and it allowed me to be involved in putting into place some ideas I had on organizing science. In particular I have always believed that success in science depends on the architecture of the building. Humans are very tribal and will only have open discussions with those they consider to be in their tribe; the building must reflect this. Essentially, when you build an institute you are trying to make the institute the tribe, rather than the individual lab. Cramped quarters are important, as are common equipment areas and a central common meeting space. Small issues are important, such as making everyone come and go through the same door and no coffee machines in the institute except in the central café.

What did you like about being a biologist? I think I have one of the necessary skills to be a scientist, which is that I am curious. I want to know how things work. I used to disassemble everything I could get my hands on, including my Dad's car. Every day as a scientist you can satisfy your curiosity, either with your own hands, or later by discussions with your students and postdocs. As you get more senior, you can satisfy your curiosity by the hiring of group leaders in interesting areas. Being a biologist allows you to satisfy your curiosity every day.

Why do you work on cell division? While in John White's lab, I became fascinated with the cytoskeleton, because it was small machine inside a cell. I was well prepared for this by my education at UCL, where I had an excellent cell biology course. I remember at the time thinking that I didn't want to work on DNA or other trivial topics. Cell division was full of machines that seemed to me to be a treasure trove of interesting problems.

And why* C. elegans*? I remain fascinated by *C. elegans* embryogenesis, because the reorganization of an oocyte to an embryo is such an amazing process. After about 30 minutes, the relatively undifferentiated cytoplasm of an oocyte reorganizes for a very complex asymmetric cell division. It is also amazingly robust. For instance, I have looked at many embryos in my time, but still find it hard to tell the difference between a division of *C. briggsae* and *C. elegans*, species which are thought to have diverged 100 million years ago.

What was your most exciting moment in science? I remember that when I was a postdoc in San Francisco, I was trying to reconstitute the movement of microtubules on kinetochores using video microscopy. This was in the infancy of video fluorescence microscopy, and we had to program the image processors and develop many new ways to look at microtubules without bleaching. Nothing worked. After a year and a half of work, I worked out how to used caged ATP and took a movie of the microtubules on kinetochores after uncaging. They moved! I had not seen them before when I had simply perfused ATP, because the movement was so quick. I was so excited I ran out of my small microscope room to find someone, but Tim and the other cell biologists were in a seminar. So I grabbed someone in the corridor and dragged him into my room. He made a good show of looking impressed — it turned out to be Stan Prusiner, who later won the Nobel prize for prions.

How has biology changed since you were a student? The biggest change has been the publication system. When I was a student almost all work was written up for the journals that were run by the societies and edited by scientists themselves. New ideas could be written up as letters to *Nature,* but they did not really have a major effect on your career. Cell Press was just getting started and *Nature* had not proliferated. So I think that, in those days, success did not depend so heavily on where you published, but more on what you discovered.

Where has the publication problem come from? The enormous growth in biomedical research has made the system too anonymous. As a result of this, much of the evaluation system for young scientists has been devolved to the journals. This has put a huge amount of pressure on the top journals, because they have to evaluate so many papers, and only accept a small percentage of submission; many of these journals have dealt with this by a strategy of "shock and awe": you can't even begin to think about publishing there without a huge amount of data, which is often beyond the scope of an individual student. The writing process is so complicated that it is harder to leave it to the students. Thus, the training suffers, as does the innovation. And the time frame is so long that it is often outside the time frame of a student's PhD. In an informal survey of my institute, about a third of the time is spent on revising a paper. Can that be a good use of scientist's time?

How would you change publication? The important thing is to return to a situation where publishing papers is not such a huge effort, and where the

trendiness factor is not such an issue. Not to mention the waste of every scientist's time because new rounds of review are needed at every journal. One idea is every journal would have a front end and a back end. Papers would be submitted to the journal and receive a technical review. Then the editorial board would make the decision as to which of these papers would be in the 'front journal' and which in the 'back end' journal. This would be more like a newspaper, where journalists write articles, subeditors check them, and the editors decide where they should go in the newspaper.

You've had conventional success in science: to what do you attribute this? For me, the important things were the mentors that I had during my education. Not only John White and Tim Mitchison, who I have already mentioned, but Eric Karsenti and Kai Simons at EMBL, as well as Nick Crispe and Jim Morgan when I was an undergraduate. These people all took me under their wing at crucial stages in my career, ensuring that I did not fall into the common traps of young scientists, hubris and lack of ambition. I was also lucky to stumble on the field of cell organization just as it was reawakening from its slumber since the 1920s and E.B. Wilson. It is still amazing to think that when I was a PhD student, we did not know of any molecules required for the division of the cell, and now we know most of them.

What next? Well the cataloguing has been a tremendous success, but it has not told us how cells work. The next stage will be to understand how the collective properties of all these molecules give rise to structures that are many orders of magnitude bigger than the molecules themselves. This will involve a component of theory and we are at an exciting stage where physics biologists and mathematicians will have to work together closely to understand these problems. I don't think it will be possible in the future for isolated labs to make major contributions — the skill sets required are too diverse. This suggests teamwork and collaboration — which I can only applaud.

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Primer

Lateral gene transfer

Olga Zhaxybayeva[1] and W. Ford Doolittle[2]

The four disparate images shown in Figure 1 have this in common: each represents a radical adaptation that would not have happened had *lateral gene transfer* (LGT), also known as *horizontal* gene transfer (HGT), not been the powerful evolutionary force we now know it to be. Those who study the phenomenon are still struggling to quantitatively assess LGT as a process or processes and accommodate its implications for how patterns in nature should be represented — such as the existence of definable species or a meaningful universal Tree of Life. But all agree that the exchange of genetic information across species lines — which is how we will define LGT in this primer — is far more pervasive and more radical in its consequences than we could have guessed just a decade ago. Both prokaryotes (bacteria and archaea) and eukaryotes have experienced LGT, though its potential as a source of novel adaptations and as a challenge to phylogenetics are so far more obvious and better understood for prokaryotes, as are the mechanisms by which it is effected.

How we detect and measure LGT

The overwhelmingly dominant pattern of heredity is of course 'vertical descent' — the passage of

Figure 1. Four novel adaptations made possible by LGT.
Upper left: a solar saltern in Eliat, Israel. Upper right: Utagawa Hiroshige's *Bowl of Sushi* (detail of woodcut). Lower left: pepper plant roots infected by root-knot nematode. Lower right: pea aphids (*Acyrthosiphon pisum*) exhibiting green, red and yellow color polymorphisms. See text for details. Image credits: Upper left, R. Thane Papke; upper right, Wikimedia Commons; lower left, Scott Bauer, USDA agricultural research service, bugwood.org; lower right, Charles Hedgcock and Nancy Moran.