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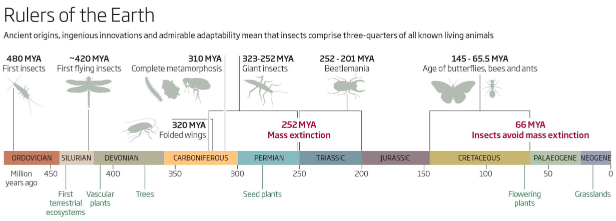
Why insects are the real rulers of the world

They make up three-quarters of all known animal species, yet we are only just starting to understand how insects came to conquer the Earth

BJÖRN VON REUMONT is in search of an oddity. The creature, a blind crustacean, 4 centimetres long and resembling an upside down centipede, is to be found in the watery depths of just a few sinkhole caves around the world – which is why von Reumont is in the ancient Mayan rainforest of the Yucatan in Mexico.

"It's like diving through Vaseline," he says, describing the strange sensation of crossing from the fresh surface water to the saltwater below. Some 25 metres down, he enters a narrow cavern filled with stalactites and sculpted rocks, and it's here, in this dark and alien world, that he spots his quarry. The animal swimming into view in the light of his lamp, searching for prey to impale with its venomous fangs, is a remipede. Although rare, it is not just another curio. Remipedes are the closest living relatives of the most successful creatures on Earth – the insects.

Three-quarters of all known animals are insects, a staggering 1 million species in total with an estimated 4 to 5 million yet to be discovered. By contrast, there are fewer than 70,000 vertebrate species. Harvard University entomologist Edward O. Wilson has suggested there may be as many as 10 quintillion insects alive at any one time – that's 10^{18}, or more than a billion for each person on the planet. They have colonised every continent, including Antarctica. They can live in air, land and water. They even live on us – lice evolved as soon as there was hair and feathers to set up home in. They are the kings of the arthropods – animals with hard exoskeletons – and the most successful group of animals that has ever lived. It's something we have long known, yet we are only now starting to understand how they have come to dominate (see diagram).



Remipedes provide the first clue. Crustaceans are among the earliest arthropods, emerging in the Cambrian period, between 550 and 500 million years ago. The oldest insect fossil is some 410 million years old, but it's an elaborate creature, indicating that insects evolved much earlier. Their ancestors were once thought to be myriapods – land animals including millipedes and centipedes – but von Reumont, an evolutionary biologist from the University of Leipzig in Germany, and others had different ideas. In 2010, he published research suggesting that the closest living relatives of insects are the aquatic remipedes. Similarities in their brains, nervous systems and many of their proteins all point to an ancient common ancestor, he says. That would mean not just that insects evolved in the watery margins between sea and land, but also that they are much older than we thought.

The clincher came a year ago. “Scientists had been debating insect relationships for more than 200 years. It was clear that a new approach was needed,” says Bernhard Misof of the Alexander Koenig Research Museum in Bonn, Germany. So he and a team of more than 100 researchers carried out a huge genetic study of insect evolution and relatedness (*Science*, vol 346, p 763). This confirmed their watery origins. “Insects are terrestrial crustaceans,” says Misof. And they evolved about 480 million years ago, the study suggests, making them among the first things ever to walk on land. Around this time, the first terrestrial plants also evolved, which might have helped insects make the leap.

Whatever the spur, life on land came with formidable challenges, including dealing with dehydration, the effects of gravity, breathing air and daily extremes of temperature and solar radiation. A tough exoskeleton would have helped, but it still probably took millions of years for truly terrestrial insects to evolve. Indeed, some of the most primitive species alive today, the jumping bristletails, still need moist soil to live in. But the land offered big opportunities too. There was plenty to eat and there were fewer predators to deal with than in the sea. Misof’s genetic study indicates that insect evolution really took off around 440 million years ago, with an explosion of species emerging. Then came a development that would take them to another level.

The oldest insect fossil ever found comes from the rolling hills around the village of Rhynie in Aberdeenshire, UK. Those rocks are teeming with tiny centipedes, mites, spiders and stubby plants, all petrified in the silica-rich waters of a volcanic hot spring around 410 million years ago. But in 2004, Michael Engel of the University of Kansas in Lawrence found something else. Examining one of the fossils under the microscope he was gobsmacked to see tiny, perfectly preserved mouthparts of a type only found in insects, and not just any kind of insect. “This was our first peek at a flying insect,” he says. Although its wings were not preserved, all the evidence indicated that *Rhyniognatha hirsti* was a relatively advanced flyer. This would make the origins of flight even earlier, perhaps at the species explosion 440 million years ago. The oldest fossilised insect wing is 324 million years old, so in one fell swoop, flight's evolution has been pushed back more than 80 million years. Misof's study supports the date.

Up, up and away

What got insects into the air? Engel suspects they were climbing the stems of plants bordering swamps to feast on spores, and found it easier to glide back down. Silverfish – primitive flightless insects living today – have a tiny pair of flat lobes extending out of their thorax, which they use for control when falling. And genetic analysis suggests wings evolved by the expansion of such lobes along with the development of hinges derived from the legs to control movement.

Insects were the first to evolve powered flight – and the only ones for 200 million years, until pterosaurs emerged. Wings gave them an enormous boost, helping them find food and mates, colonise new habitats, avoid predators and regulate their body temperature. Winged insects thrived. An astonishing menagerie filled the skies of the late Carboniferous and Permian periods between 323 and 252 million years ago. As tiny plants evolved into massive trees, coal-swamp rainforests spread across equatorial regions. Here, lacy winged palaeodictyopterans sucked the sap from plant stems through elongated beaks and gigantic griffinflies hawked their prey (see "There be giants"). There were also more familiar flyers such as mayflies and dragonflies, but all had wings projecting outwards from their bodies, even at rest, making them vulnerable to damage and limiting the habitats they could colonise.

These "old-winged" insects were about be upstaged, however. Down in the litter on the forest floor were "new winged" insects with hinge mechanisms to fold their wings over their bodies when not in use. This innovation meant they could use hiding places and habitats not available to their forebears. Foremost among them were the ancestral roaches, as successful then as they are today.

Yet the insects were to undergo a further transformation – arguably the most important innovation of all, and its evolution was only pinpointed a couple of years ago. Dazzled by the spectacular creepy crawlies in coal swamps, researchers missed something else going on. "There are dark, coal-rich rocks from 310 million years ago with insects that were only spotted under the microscope," says André Nel of the National Museum of Natural History in Paris. Their small size belies their significance. These are the oldest known insects to undergo complete metamorphosis.

Insects are fundamentally constrained by their inflexible exoskeleton. Until this point, they had grown via a series of nymphal stages, each followed by a moult, allowing miniature forms resembling the adult to get progressively bigger. Complete metamorphosis, by contrast, enabled the insects to divide their life cycle into distinct stages, with the larva specialised for feeding and the adult dedicated to reproducing. The larva, pupa and adult stages of completely metamorphosing insects are thought to be the evolved equivalent of the pronymph, nymph and adult in ancestral insects. This development has proved so successful that more than eight in 10 insect species use it today. Back then, though, Nel's tiny insect fossils, which later evolved into beetles, fleas, wasps, bees and ants, were rarities. "Maybe the ecological niches were occupied by other groups and only after they became vacant could they diversify," he says. This was about to happen.

The most catastrophic mass extinction the world has ever seen came 252 million years ago. Over many millions of years, immense volcanic eruptions, global warming and falling oxygen levels wreaked havoc on Earth's life-support systems, killing off up to 90 per cent of all species on land and in the oceans. This time, unlike earlier mass extinctions, even insects were affected. "There was an enormous shift at the end of the Permian with about 50 out of 110 insect families going extinct," says Peter Mayhew at the University of York, UK, whose team scoured the fossil record to work this out. Gone were the giant griffinflies, the palaeodictyopterans and many other "old wings". But Mayhew's team found one notable exception. This extinction was the making of metamorphosing insects. "They were generating new families and were hardly touched," he says.

How did they succeed where others failed? For a start, they are often smaller, develop more rapidly and have larger populations than other types of insect, all of which allow them to recover quickly following a crisis. But they also had an ace to play. The pupa – the transitional phase between larva and adult – evolved a way to store very high levels of glycerol, helping it withstand freezing and desiccation, so making it very hardy during times of environmental stress.

A recognisably more modern insect fauna ushered in the Triassic. This period, 252 to 201 million years ago, was boom time for beetles. Not only were they small, fecund and able to metamorphose, their forewings had hardened to protect their folded hindwings and conserve moisture and warmth. They were able to colonise a huge range of habitats, from deserts to ponds, and from the Arctic to the tropics. So successful were they that today there are at least 400,000 known beetle species, more than any other type of insect.

For insects, everything was coming up roses. The Cretaceous saw another enormous explosion in insect diversity, with the appearance of flowering plants. This time it was the turn of butterflies, moths, flies, bees and ants. "Flowering plants provided a rich new landscape of resources," says Engel. Like their ancestors before them, these insects took full advantage of the opportunities on offer. "You are getting continued bumps in diversity as each period there are new additions to insects' cocktail of innovations, helping certain groups speciate wildly," he says. When an asteroid impact put an end to the dinosaurs, 66 million years ago, insects breezed through and continued to go from strength to strength.

"There's a long fuse," says Engel. "Insects took this super powerful concoction of traits that built up over hundreds of millions of years, and conquered the world." They have succeeded by longevity, innovation, adaptability and evolutionary exuberance. In today's world they face another challenge, but their diversity and talent for survival will stand them in good stead. As other animals struggle to cope with global climate change, it looks like insects will continue to rule.

(Images: David Liittschwager/National Geographic Creative, Piotr Naskrecki/Minden Pictures/Corbis, Alex Hyde/Naturepl.com, Joel Sartore, National Geographic Photo Ark/National Geographic Creative, The Trustees of the Natural History Museum, London)

There be giants

Meganeuropsis

, or griffinfly, for example, had a wingspan of up to 70 centimetres. *Arthropleura* was a kind of millipede, but longer than a human. How could they grow so big?

One answer is oxygen. Plants had recently evolved the woody compound lignin and, with no decomposing organisms yet present to break it down, trees were being buried rather than recycled. As a result, oxygen levels in the air reached 31 per cent, half as much again as today. Insects breathe through tiny holes in their exoskeleton, which allow oxygen to reach their tissues directly via tracheal tubes. This set-up limits their size because eventually too great a proportion of their body needs to be given over to tubes. But that changes with more oxygen in the air. "Almost all insects develop smaller tracheae," says Jon Harrison of Arizona State University in Tempe, who has tested this in the lab. This allows them to grow bigger.

Gigantism was not to last, however. The maximum size of insects' wings reflected oxygen levels for 180 million years, according to Matthew Clapham of the University of California, Santa Cruz, but then something curious happened. By the time of the Cretaceous, between 145 and 66 million years ago, maximum wingspan had halved, even though oxygen levels rose. And what had evolved by then? Birds. "If birds weren't around, some insects might actually be much bigger today," Clapham says.

Bane or boon?

There are many reasons to dislike insects. They spread some of the world's deadliest diseases including malaria and typhoid. Some destroy crops. Others bore into wood. Stinging insects and parasites can make life a misery. But just one insect in a thousand is a pest – most are harmless and many beneficial.

Insects pollinate four-fifths of the world's crops, amounting to one-third of food production, not to mention our garden plants. We eat their honey, wear their silk and use their dyes and waxes. Where would we be without their pest control, soil fertilisation and ability to clean up by scavenging corpses and waste? They are packed with protein, which could one day feed the world. Fruit flies do sterling work in the lab and together with other insects have been instrumental in medical breakthroughs. And the rate at which some creepy crawlies decompose bodies can even help solve crimes.