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## Viruses and insects

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Living under severe confinement and global state of war imposed by the emergence and worldwide very rapid spreading of the viral epidemic of zoonotic origin—coronavirus SARS-CoV-2, the world is yet again experiencing a weird period. The coronavirus disease 2019 (COVID-19) pandemic is the defining global health crisis of our time and the greatest challenge we have faced since World War II, stressing every one of the countries it touches; it is creating devastating social, economic and political crises that will leave deep scars and will undoubtedly change the way we live and interact with each other. The number of known disease-causing viruses have been increasing in the last few decades and this trend is likely to continue. Therefore, it is legitimate to think about the evolutionary effect of viruses and their influence on the processes of organisms.

In the Recent fauna, insects are the world's most diverse group of animals, making up more than 58 percent of the known global biodiversity. With over one million different species of insects described, and current estimates predicting that another 4 million insect species remain unknown, insects are the most exuberant manifestation of Earth's many and varied life forms (Zhang, 2011; Stork *et al.*, 2015; Footitt & Adler, 2017, 2018; Stork, 2018). The original simple insect body plan has become modified and has survived to produce an enormous variety of species during millions of years of evolution and adaptation to changing environments and other organisms. Insects exploit virtually all terrestrial and freshwater environments on the planet, as well as many brackish waters and even open oceans' surface, where they play major roles in the function and stability of terrestrial and aquatic ecosystems.

Viruses are ubiquitous, obligate intracellular parasites and one of the most abundant biological entities on Earth. Viruses can reproduce only in living cells and, in their simplest form, are composed of a nucleic acid, either DNA or RNA, and a protein shell referred to as the capsid. More complex viruses also contain a lipoprotein envelope (Knipe *et al.*, 2013; Dimmock *et al.*, 2016; Shors, 2017).

The evolutionary history of viruses is difficult to trace because they do not preserve well in the fossil record, being too small and fragile, however the oldest traces of their presence have been found in the Precambrian, Neoproterozoic deposits of the Jiuliqiao Formation in the Huainan region of Anhui Province, China (Lan *et al.*, 2020). Viruses are divided into two broad nontaxonomic categories, the enveloped viruses and the nonenveloped viruses. The formal taxonomic classification of viruses is the responsibility of the International Committee on Taxonomy of Viruses (ICTV) system (ICTV 2019), although the Baltimore classification system (Baltimore, 1971) can be used to place viruses into one of seven groups based on their manner of mRNA synthesis (Shors, 2017; Kuhn, 2020). Specific naming conventions and further classification guidelines are set out by the ICTV.

Interactions between viruses and their insect and other terrestrial arthropod hosts occur at many levels. Since insects play pivotal roles in the biosphere, it can be speculated that insect viruses in general may have radiated through the plant, fungi and animal kingdoms from common insect origins (Thézé *et al.*, 2011). Insects are infected by a diverse medley of viruses – the five most commonly encountered types of insect viruses are iridoviruses, cytoplasmic polyhedrosis viruses, entomopoxviruses, ascoviruses, and baculoviruses (Miller & Ball, 1998; Resh & Cardé, 2009; Asgari & Johnson, 2010). Insects are known as vectors of numerous viral diseases affecting plants, animals and humans. For example, dengue fever, yellow fever, West Nile fever and chikungunya virus are known to be transmitted by the mosquitoes of the genus *Aedes* Meigen, 1818 (Diptera: Culicidae: Anophelinae: Aedini). However, classification of this genus is still not well established (Wilkerson *et al.*, 2015), and only the (sub) genus *Ochlerotatus* Lynch Arribálzaga, 1891 is recorded as an inclusion in Eocene Baltic amber (Pielowska *et al.*, 2018). There is no proof that it was a vector, and further work is required to understand the competence for viruses transmission (Blagrove *et al.*, 2016). Characteristics of mosquitoes as

vectors of viruses and other pathogens still needs to be investigated (Clements, 2012). Spectacular findings, as traces of haemoglobin-derived porphyrins in the Eocene mosquito (Greenwalt *et al.*, 2013) is very important proof of existence of blood-feeding behavior in Culicidae. Culicidae evolution, classification and internal relationships are still subject of debate (Reidenbach *et al.*, 2009; Silva *et al.*, 2019), and fossil records in addition to documenting the existence of extinct species, can often provide information on the behavior and ecology of ancient organisms. The coevolution of viruses with their hosts and vectors depends on the evolution of the hosts and vectors coupled with factors involved in virus evolution. A plant disease is the result of interaction between susceptible host plant, virulent pathogen, and the environment. Insects are the most important vectors of plant viruses and the main or sole means of spread of many plant pathogens. Plant diseases spread by insect vectors can be crucially important to the profitable production of some crops (Resh & Cardé, 2009; Lefeuvre *et al.*, 2019; Takahashi *et al.*, 2019). Insects, belonging mostly to the order Hemiptera, transmit more than 70% of known plant viruses (Hogenhout *et al.*, 2008). The aphids, whiteflies, planthoppers, leafhoppers and treehoppers, as well as some mealybugs, thrips and beetles are vectors of economic importance, identified as being able to transmit plant viruses with extraordinary specificity (Resh & Cardé, 2009; España & López-Moya, 2014; Subramanya Sastry *et al.*, 2019). Hemipterans are particularly well suited to transmitting plant viruses because of their needle-like mouthparts that they use for sucking sap – phloem or xylem and/or the contents of plant cells. The coevolutionary processes of viruses, their host plants and insect vectors seems to be long (Thézé *et al.*, 2011; Possee & King, 2014). The fact that insects are evolutionarily older than angiosperms (also than birds or mammals) suggests that they might have had a preeminent importance in the origin and evolution of several plant (and vertebrates) viruses. Complex interactions are reported: viruses can manipulate plants to encourage vectors to feed for longer periods (Dáder *et al.*, 2017) or discourage potential destructive insects (Safari *et al.*, 2019). The oldest hemipterans are known from the Carboniferous (Nel *et al.*, 2013); however, most of viruses are transmitted by much younger phylogenetically groups (*e.g.*, Aphidini, Delphacidae, Deltocephalinae), often rapidly diverged and differentiated in post-Cretaceous times, when angiosperm plants became dominant (Dohlen & Teulon, 2003; Wu *et al.*, 2008; Zahniser & Dietrich, 2010; Kim *et al.*, 2011; Hull, 2014; Huang *et al.*, 2017). The requirement of optimum conditions for propagation and the presence of host defense mechanisms force viruses to continually coevolve with the host. The majority of viruses have a narrow natural host range, indicating a high degree of adaptation

to the host plant and tight coevolution. In the broader sense, coevolution of viruses and their hosts can be seen as a form of mutualistic symbiosis in that the virus benefits from not compromising the host and the host benefits from not being compromised by the virus (Lovisolo *et al.*, 2003; Gaur *et al.*, 2014; Hull, 2014). As all other organisms, insects are susceptible to many disease-causing viruses. Insects have had to overcome an array of viruses at different points in their life cycle, and viruses have been recorded from a wide range of insects. While there are more than 1,100 reported viruses that infect more than 20 different families of insects, the largest number described to date, over 600, belong to the family Baculoviridae (Schroeder, 2011; Possee & King, 2014; Grzywacz, 2017). Recently, deformed wing virus (DWV) has become the most well-known, widespread, and intensively studied honeybee pathogen in the world—due to the arrival and global spread of a new vector, the ectoparasitic mite *Varroa destructor* Anderson & Trueman, 2000 (Martin & Brettell, 2019). The most spectacular example of relationships between viruses and insects—endoparasitoid wasps (some Ichneumonoidea)—is use of polydnaviruses. The “polydnavirus soups” are produced by the calyx gland, being a modified part of the lateral oviduct, present in some Braconidae and Ichneumonidae (Leobold *et al.*, 2018). Polydnaviruses or virus-like particles play a critical role in suppressing the host (prey) immune response at oviposition, so that successful development of the parasitoid can proceed (Whitfield, 1997; Burke & Strand, 2012; Herniou *et al.*, 2013; Strand & Burke, 2015, 2019). This association of polydnaviruses with parasitoid wasps is about 100 million years old (Murphy *et al.*, 2008; Herniou *et al.*, 2013; Chen & van Achtenberg, 2019); and ‘domesticated viruses’ seems to explain how multidirectional wasp adaptation to different host species. Associations of viruses and insects could be more complicated with endosymbiotic bacteria used as vehicle for transovarial transmission (Jia *et al.*, 2017; Perlmutter & Bordenstein, 2020). Dramatic episodes of viral infections have challenged and shaped animal evolution for hundreds of millions of years. A fraction of paleoviruses have left unmistakable traces—fossilized versions of themselves—now inherited as part of host genomes. Paleovirology, the study of viruses on evolutionary timescales, can exploit information from these endogenous viral elements (EVEs), which are the result of heritable horizontal gene transfer (HGT) from viruses to hosts. Some of these endogenous viruses are derived from ancient relatives of extant viruses, allowing us to better examine ancient viral host range, geographical distribution and transmission routes (Katzourakis & Gifford, 2010; Patel *et al.*, 2011; Aswad & Katzourakis, 2012; Aiewsakun & Katzourakis, 2015). EVEs derived from a strikingly diverse set of viral lineages, both from RNA and DNA

viruses, are scattered throughout the genomes of ants and could be playing an important role in ant genomes (Flynn & Moreau, 2019; Moreau, 2020). Recent data suggest EVEs could represent a deep branch of the insect antiviral defense system (Whitfield *et al.*, 2017; Ballinger & Taylor, 2019). The discovery of numerous and diverse EVE also reinforces the idea that viruses may serve as vectors of horizontal transfer (HT) of genetic material in eukaryotes (Gilbert & Cordeaux, 2017; Husnik & McCutcheon, 2018). Horizontal transfer is the transmission of genetic material between organisms through a mechanism other than reproduction. Over the past hundreds of millions of years, viruses and hosts have been undergoing a continuous co-evolutionary process. Recent evidence suggests that insects have repeatedly acquired genes from symbiotic bacteria that have provided them with key adaptation that has led to their success (Peccoud *et al.*, 2017). The horizontal acquisition of genes for lignocellulose digestion that has led to herbivory in beetles (Wybouw *et al.*, 2016; McKenna *et al.*, 2019). Acquisition of toxin encoding genes that may underlie protection from natural enemies in aphids and vinegar flies (Lynn-Bell *et al.*, 2019; Verster *et al.*, 2019). Several heritable symbionts of insects harbour phage infections, yet the prevalence and roles of phages in heritable symbioses remain poorly understood. A mechanism for gene transfer among various hosts and acquired genes becoming stably inherited elements can have major effects on ecological relationships (Moran *et al.*, 2005; Weldon *et al.*, 2013; Brown *et al.*, 2020).

Insects and their evolutionary tracts have a special role in understanding of viral evolution and how some became pathogens. New viruses that cause diseases often come from animals, as exemplified by the Zika virus transmitted by mosquitoes. Changes in climatic conditions can contribute to the spread of newly introduced viruses and their insect vectors (Ertunc, 2020; Rodríguez *et al.*, 2020). Studies on emergent and reemergent viruses (Ennaji, 2020a, b), evolution and adaptations of their hosts, palaeontomological investigations on phylogeny and evolution of viruses' insect vectors, is now exemplifying research at the cutting-edge, and critical for supporting the long-term survival of humanity.

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