



Symbiotic secrets

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Received: 2 June 2019 / Accepted: 2 June 2019 / Published online: 7 June 2019
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More than half of the known species follow a parasitic strategy, meaning that they are living on or in other organisms, and profit from their so called host. In the very moment that a life form, for the first time, captures a different organism as host, an evolutionary arm race initiates. In many cases, a subtle balance is reached as final state of this arm race, where the host is not exceedingly damaged, and the parasite will restrain itself for the sake of a more sustainable food source. As a rule, evolutionary interactions hide many facets, such that a parasitic interaction, especially if originating from such a co-evolutionary “domestication” process, may not be purely negative for the host. If the host in certain aspects, or under certain conditions, draws some benefit from the parasite, the evolutionary story will make a sharp bend towards symbiosis. With respect to economic and cultural impact, the interaction between the prokaryotic Rhizobia and the pulses (Leguminosa) surely qualifies as the key symbiosis that has shaped humanity. Whether in Middle America, in East Asia or in the Fertile Crescent, it was always the domestication of a pulse along with a cereal that initiated the rapid development of a new civilisation, because it provided humans with a protein source that did not demand a nomadic lifestyle, as impressively documented by the anthropologist Jared Diamond in his book *Guns, Germs, and Steel* (1997).

Despite this impact, many aspects of this curious interaction between two organisms have remained obscure. The crucial difference between balanced parasitism and true symbiosis should be that, as consequence of the encounter, both partners will adjust their physiology in a manner that supports this interaction. This implication can be demonstrated, in fact. Two contributions to the current issue reveal new and surprising secrets from both sides of symbiosis:

The work by Tsyganova et al. (2019) in the current issue investigates changes of cell wall composition in the root nodules after infection by Rhizobia, making use of a panel of monoclonal antibodies that had been developed in the John Innes Institute (Norwich) to map cell-type-dependent surface epitopes in roots (Knox and Roberts 1989). They compare two host species, pea and alfalfa, to identify conserved and variable features of the phenomenon: For instance, they demonstrate that, irrespective of the species, host-cell walls surrounding the infection thread are rich in homogalacturonanes that are only weakly esterified with methyl groups. Likewise, mature endosymbionts are decorated with an arabinogalactan protein recognised by the monoclonal antibody JIM1. However, the authors also detect specificities: the infection-thread walls of pea, but not those of alfalfa, are endowed with galactane side-chains in rhamnogalacturonane I. To get functional insight into those changes, the authors also worked on a pea mutant, *Spring-2Fix-(sym31)*, where the endosymbionts fail to differentiate into viable bacteroids, and find that the JIM1 epitope is absent in these defective endosymbionts. In their previous work (Ivanova et al. 2015), the authors had already used other pea mutants with abortive nodule formation to pinpoint the esterification of homogalacturonanes in the infection thread as a step necessary for symbiosis. The picture emerging from these different facets shows that the host is actively remodelling the interface with the endosymbiont to ensure efficient propagation and encapsulation. This requires complex chemical signalling, because immunity has to be shut down and replaced by a “welcome programme” for the endosymbiont. As part of this “welcome programme”, the host restructures its entire architecture, which means nothing else than that two organisms become functionally integrated into a super-organism.

The work by Rivard et al. (2019) highlights the metabolic side of this symbiotic interaction: the endosymbiont has to encounter a specific chemical environment to adopt its new lifestyle. Since the nitrogenase, able to convert atmospheric nitrogen into ammonium, represents a kind of a historical footprint dating back to a time, where the atmosphere was

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reducing and void of oxygen (which accumulated much later in consequence of photosynthesis), there had been no selective pressure to render nitrogenase oxygen insensitive. On the other hand, nitrogen fixation is energy consuming (the technical version of it, the so called Haber-Bosch process, one of the key innovations for Green Revolution, has to be run at high pressure and high temperature), which means that the mitochondria in the host cells surrounding the endosymbiont need oxygen to generate the ATP required for converting nitrogen into ammonium. Thus, for the functionality of the endosymbiont, it is crucial that the oxygen permeability of the nodule becomes controlled in space. The oxygen conductivity of the nodule cortex is regulated by phosphorus, as well as by sulphur (which is relevant as component of iron-sulphur clusters in those enzymes that participate in nitrogen reduction, but also as component of leghemoglobin, the pigmented complex protecting the nitrogenase from oxidation). The authors use a sophisticated technology, synchrotron micro X-ray fluorescence, to resolve the spatial resolution of sulphur inside of the nodules under different phosphorus regimes. Similar to the work by Tsyganova et al. (2019), they use a comparative approach selecting two Fabacean species, *Vigna unguiculata* and *Vicia faba* that differ in the temporal pattern of nodule formation: In the first species, the nodules are synchronised, which is favourable for statistical quantification, while in the second species, nodules elongate progressively, which allows to track age-dependent changes. The authors succeeded to map the distribution of sulphur with a spatial resolution down to 2 μm . They show clearly that sulphur accumulates in the central cortex of both nodule types. This accumulation is significantly reduced, when the host plants are raised under phosphorus depletion. This achievement extends previous findings (Kanu et al. 2014), where sulphur had been shown to be enriched in rhizobia-infected cells over non-infected root cortex. The refined sulphur map is consistent with a model, where the host plants maintain a defined pattern of oxygen permeability by partitioning sulphur-containing molecules to specific layers of the developing nodule.

Both contributions highlight impressively the degree of sophistication required to establish a successful symbiotic interaction, calling for very specific and precisely regulated signals that have to be exchanged between both partners. This leads to a challenging evolutionary questions—how did this

fine-tuned interaction arise? It is very unlikely that this complexity evolved in a single event, because numerous changes would need to occur in concert. Following Jacob's terminology (Jacob 1977), “tinkering” drawing upon pre-existing functional modules, is more likely. It will, thus, be rewarding to search for other functional contexts for the cell wall modifications occurring in the infection thread, or the molecular events responsible for sulphur accumulation in the central nodule cortex, to acquire a complete picture of this remarkable and impactful phenomenon.

Compliance with ethical standards

Conflict of interest The author declares no conflict of interest.

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