is scope to look at other fossils with new eyes and revisit the different alternative hypotheses through the lens of features predicted by either of the hypotheses. To be sure, in some of the scenarios above[2], the brain in *Stanleycaris* could have been one-segmented, and Moysiuk and Caron[4] would still be correct about how they interpret the nerves coming together in the brain. The idea that the frontal appendage gave rise to both the labrum and the megacheiran great appendage in the serial homologue scenario[11] means that the urge to decide on the affinity of the frontal appendages could be less of a binary choice.

It seems amazing that there still can be so much controversy about arthropod evolution. No other invertebrate group is as well represented in the fossil record, with many exceptionally well-preserved specimens. And, due to their segmented nature and well-defined limbs, there is copious anatomy to mull over, including their nervous system. However, with complex and anatomically rich animals come intricacies and convoluted histories of evolution that need to be picked apart. So, watch this space, this saga is far from over.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Seed dispersal: Hungry hornets are unexpected and effective vectors

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A new study finds that, in the forests of tropical China, hungry hornets are lured to the fruits of *Aquilaria sinensis* by highly volatile compounds structurally similar to volatiles from herbivore-damaged leaves. The hornets disperse the short-lived seeds rapidly to optimal new habitats.

Pollination and seed dispersal are two critical steps in the plant life cycle where the services of highly mobile animal pollinators and seed dispersers are employed. Visual and/or olfactory cues are widely used to advertise the presence of flowers and fruits, with most, but not all, plants subsequently providing food or other rewards in exchange for pollination and dispersal. These plant–animal interactions are thus usually mutualistic. While much is known about the floral volatile signals used by plants to attract pollinators, much less appears to be known about the role of volatile signals to attract animal dispersers. Other major gaps in knowledge about animal dispersal of fruits or seeds include measurements of the rate and extent of dispersal, and whether or not there are optimal rates and optimal dispersal distances to maximise plant reproductive fitness.

Vespicochory, seed dispersal by wasps, is considered to be a rare and unusual insect–plant interaction previously known from just a handful of cases in Asia and North America[1,2]. In this issue of *Current Biology*, Qin, Wen *et al.*[3] report on one fascinating and newly discovered case in which hornets facilitate rapid and long-distance dispersal of the short-lived seeds of agar wood, *Aquilaria sinensis*. They also identify and confirm five of the bioactive semiochemicals involved in hornet attraction by gas chromatography-mass spectrometry (GC-MS), electroantennography (GC-EAD) and field bioassays. A finding of remarkable chemical similarity between the compounds emitted by fruit capsules and herbivore-damaged leaves led the authors to propose the intriguing possibility that this seed dispersal strategy involves an unusual case of plant-defense mimicry.

The Asian rainforest tree genus *Aquilaria* (Thymelaeaceae) has a tropical/subtropical distribution, with many species threatened by human exploitation for their perfume and medicinal properties. All species in the genus produce two-valued capsular fruits that on dehiscence release two diaspores, each consisting of an elaiosome and seed, which hang from a dangling thread, the funicle (Figure 1). Elaiosomes are lipid- and protein-rich appendages attached to seeds that are better known as the food reward in the thousands of cases of seed dispersal by ants (myrmecochory)[1,4].

The process of hornet dispersal of *A. sinensis* seeds in China typically begins within minutes of fruit dehiscence, with arriving hornets 'attacking' the diaspore and rapidly cutting them off at the tip (Figure 1). This active process of excision, taking a median time of just 1 min, is beautifully illustrated in the supplementary video[3]. After removal from the fruit capsule, the diaspores are carried up to 400 m away to the nest tree of the hornet, where the elaiosome is cut from the seed, at or near the nest within the tree canopy, and the seed falls to the ground. One of three *Vespa* species observed dispersing seeds, *Vespa vultina*, was responsible for the dispersal of some 85% of 600 tagged seeds[3].

The highly effective hornet dispersal ensures that the majority of seeds are dropped under the crown of the nest trees, rather than in open areas. To test whether this dispersal to predominantly shaded and moist sites is optimal for seed germination and growth, Qin, Wen *et al.* deployed experiments using differing natural and artificial levels of shade. These experiments revealed that seedling establishment increases with increasing levels of artificial shade, and under natural conditions is higher under the tree canopy than on the canopy edge or adjoining open grassland[3]. In short, the results supported the hypothesis that hornet dispersal does place many seeds in positions optimal for tree establishments.

The rapid attraction of hornets suggests the involvement of olfactory cues. Field bioassays conducted within plantations of agarwood were conducted to test this hypothesis. Choice tests in which fresh capsules were paired with diaspores rendered odorless by solvent extraction, or the converse, odorless capsules and fresh diaspores, were used. The fresh capsules were significantly more attractive than odorless capsules, whereas there was no significant difference in the attractiveness of fresh versus odorless diaspores in the

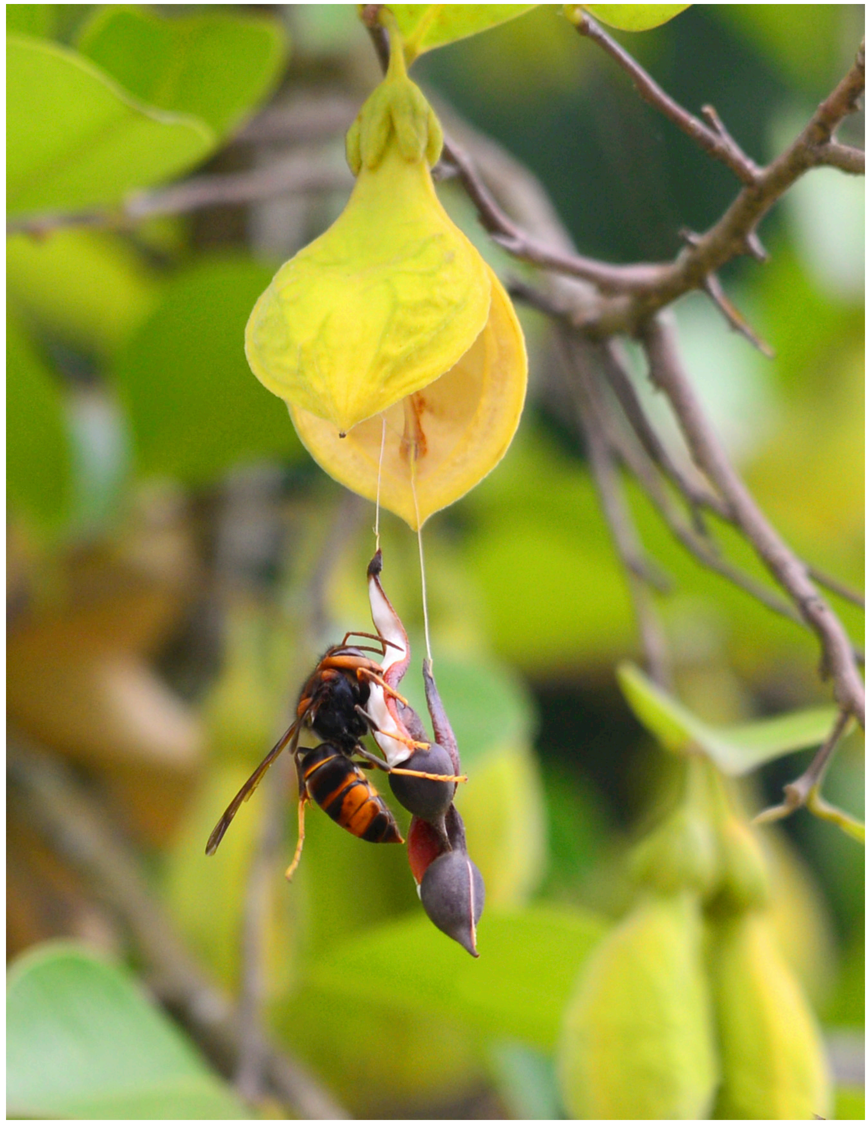

Figure 1. A hungry hornet seed disperser.
A fruit capsule of *Aquilaria sinensis* showing the two diaspores dangling by their funicle, with a *Vespa vultina* hornet about to excise one of the diaspores, consisting of the elaiosome (upper) and the seed (lower). The diaspore will be transported to the nest tree where the elaiosome is cut from the seed and taken to the hornet's nest, while the seed is discarded and falls to the ground. (Photo courtesy of Ren-Bin Zhu, Xishuangbanna Tropical Botanical Garden.)

presence of a fresh capsule. Thus, the fruit capsule, not the diaspores, were revealed as the source of chemical attraction. GC-MS analysis, following solid phase microextraction (SPME) sampling of the headspace of fruit tissues, showed the capsule emitted a more diverse and abundant mixture of volatiles than the diaspores. The chemical profile of volatiles also showed strong similarities to that of the headspace of leaf tissues following caterpillar damage by *Heortia vitessoides*, a specialist pest of *A. sinensis*[3].

The detective work to identify the bioactive compounds underpinning the interaction between hornets and *A. sinensis* fruits employed tools that are widely used in specialised pollination systems[5–8]. One key 'trick of the trade' is GC-EAD, in which volatile compounds first separated in the gas chromatograph are passed over insect antennae mounted in between electrodes to record which compounds are detected by the antennae. Subsequent field bioassays are needed to confirm that GC-EAD activity translates to biological activity[9].

Qin, Wen *et al.*[3] detected 17 candidate compounds emitted by the capsule that were electrophysiologically active at the antenna of *V. vultina*. Fourteen of these 17 compounds were also found in the headspace of damaged leaves. Subsequently, a synthetic blend of five compounds from the capsule (three aliphatic oxygenated hydrocarbons: hexanal, (*Z*)-3-hexen-1-ol, 1-octen-3-ol; and two aromatic: 2-phenylacetaldehyde and 2-phenylethanol) eliciting the antennal signals of highest amplitude was tested in field bioassays. Relative to the control, addition of this synthetic blend to odorless capsules was strongly attractive, while the synthetic blend was equally attractive to fresh capsules, confirming the biological activity of this blend of five compounds for hornet attraction.

It is of interest to compare these chemical findings[3] with two other studies of hornets[5,10]. In addition to its seed dispersal role in *A. sinense*, *V. vultina* (and several other *Vespa* species) also disperses the diaspores of *Stemona tuberosa*[10]. By contrast to *A. sinensis* where the fruit capsule is the source of highly volatile long-range attractants[3], a variety of long chain hydrocarbons of low volatility are emitted from the elaiosome of *S. tuberosa* as short-range attractants. Hydrocarbons are well known on the cuticles of insects, suggesting these elaiosomes may 'smell like prey'[10]. In the orchid *Dendrobium sinense*, which is pollinated by the *Vespa bicolor*, five GC-EAD-active molecules were active in laboratory bioassays (benzyl acetate, benzyl alcohol, octadecan-1-ol, eicosan-1-ol, and (*Z*)-11-eicosen-1-ol)[5]. The latter, not previously known as a floral volatile, is a key constituent of honey bee alarm pheromones and was highly attractive. Thus, in this deceptive orchid, pollination may be secured by alarm pheromone mimicry[5]. A similar set of compounds are involved in pollen and seed dispersal by *Vespula* yellow jacket wasps, closely related to *Vespa*. For example, (*Z*)-3 hexen-1-ol, straight chain aliphatic aldehydes and benzaldehyde are bioactive in the orchid *Epipactis helleborine* pollinated by two *Vespula* species as a plausible case of mimicry of herbivore-damaged plants[6]. (*Z*)-3 Hexen-1-ol is also predicted to play a role in the seed dispersal of *Calycanthus occidentalis* by *Vespula pensylvanica* in California, with tetracosane, nonanal and octan-1-ol confirmed as attractants in field bioassays[2]. A common theme that emerges across these studies of plants utilising hornets and wasps as pollen or seed dispersers is one of chemical resemblance between the plant and chemical cues associated with the food of these wasps as predators. As to whether these cases constituent mimicry, when defined as an adaptive resemblance (see Johnson *et al.*[11]), will require further study.

To most people, hornets will be best known as stinging predators, that when accidently introduced outside of their natural range often become dangerous and highly invasive pests. Yet, this[3] and other mostly recent studies reveal that hornets can play key roles as seed dispersers and pollinators. What is more, given that all members of *Aquilaria* and the sister genus, *Gyrinops*, exhibit the same fruit and diaspore structures, it is predicted that seed dispersal by hornets will span across these two widely distributed forest tree genera[3]. Consequently, this new case of vespicochory is not just a 'one off' example. In fact, it would not be surprising if hornet seed dispersal has not only been overlooked in the diverse forests of Asia, but worldwide.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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