

X-Ray Computed Tomography: a tool to quantify plant reproductive phenotypes.

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The 3D shape of flowers has, until the advent of modern 3D dataset acquisition techniques, remained as elusive as it was thought to be crucially important for pollination. We present here patterns of 3D flower shape variation gained in the study of two systems: the sexually deceptive orchid *Ophrys* and the heterostylous *Primula*. In *Ophrys*, we show that floral shape is more tightly correlated to the shape of the male bee (pollinator) than it is to the shape of the female bee (object of mimicry). We show that the parts involved in pollen transfer belong to well-supported shape modules, both in the bee and the flower. In *Primula*, we present a novel, multidimensional approach to quantify and analyse heterostyly. The best-supported shape module for flowers of both morphs together involves the apex of the stamens and the corolla mouth, both of which restrict the access of pollinators to the floral tube in one morph. Taken together, our analyses of the modularity of flower shape, in two unrelated systems, challenge the established paradigm of a division of flowers into modules of “attraction” vs. “reproduction”, and support a division into a module of parts that are directly in contact with pollinators vs. a module of parts that are not. Our results emphasise the relevance of modularity in flower shape and provide new perspectives into a rapidly expanding field.