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Reprint of "Ranunculacean flower terata: Records, a classification, and some clues about floral developmental genetics and evolution"☆

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ABSTRACT

Teratological organisms originate from developmental anomalies, and exhibit structures and a body organization that deviate from the species standard. In plants, teratological forms are often of horticultural interest. However, besides their aesthetic value, these monsters give essential clues about the formation of the wild-type groundplan. We focus on flower terata, which can be affected in their sterile and/or fertile organs, with special emphasis on the Ranunculaceae. The diversity of perianth shapes and organizations in flowers of this family is huge, and is even increased when anomalies occur during organo- and/or morphogenesis. In order to galvanise research on Ranunculacean flower terata, which has been overlooked since the middle of the 20th century, we provide the necessary material to inspire future studies in this field. We (I) recount the history of the science of flower teratology, (II) review records of flower terata in the buttercup family, (III) propose a system to classify the changes affecting canonical development, (IV) synthesize key studies on the developmental genetics of the flower terata with a focus on Ranunculaceae, and (V) address the issue of their evolutionary potential. We expect Ranunculaceae species to become model organisms in flower teratology studies, focusing on morpho-anatomy as well as on evo-devo or evolutionary ecology.

1. Flower terata through the historical lens: ancient and modern observations

The study of terata had its golden age during the 19th century when reporting and exhibiting human and animal monsters was the object of scientific (and sometimes less scientific) curiosity (Geoffroy Saint-Hilaire, 1826; Geoffroy Saint-Hilaire, 1832). Abnormalities in developing and adult structures have also been widely documented for plants. Concerning flowers, reports of terata are known since the Greek and Roman Antiquity (Aristotle (translated version: Barthélémy-Saint Hilaire, 1887); (Pliny the Elder (translated version: Ajasson de Grandsagne, 1831)). Later on, flower terata have inspired the works of many botanists, ontogeneticists and naturalists, and many of these flower phenotypes have been maintained for horticultural purposes. During the 19th century and in the first half of the 20th century, German, British, and French botanists were leaders in these studies. Some of the very influential botanists who contributed pivotal works to the science of flower teratology (von Jäger, 1814; De Candolle, 1827; Moquin-Tandon, 1841; Brongniart, 1844; Masters, 1869; Penzig, 1890) openly built on the theories of their predecessors (Linnaeus, 1744; von Goethe, 1790). Fig. 1 presents a timeline showing a chronological selection of important contributions to the study of flower terata and of Ranunculacean flower terata in particular. We arbitrarily chose the description of *flore pleno* (filled or full flower) variants of *Aquilegia*, *Consolida*, *Delphinium*, and *Nigella* made by Clusius (1601) as the starting point. The next most important contribution to flower teratology is undoubtedly the description by Linnaeus of a peloric (after the Greek word for monster or wonder) *Linaria* collected in 1742 by one of his students, Magnus Ziöberg (Gustafsson, 1979). The molecular mechanisms responsible for this anomalous flower were elucidated more than two hundred years later (Cubas et al., 1999).

The flower is typically defined as a condensed structure gathering organs differing in their identity (sepal, petal, stamen and carpel), shape and function, organized as concentric whorls or following a tight spiral (Bateman et al., 2006). Flower traits provide

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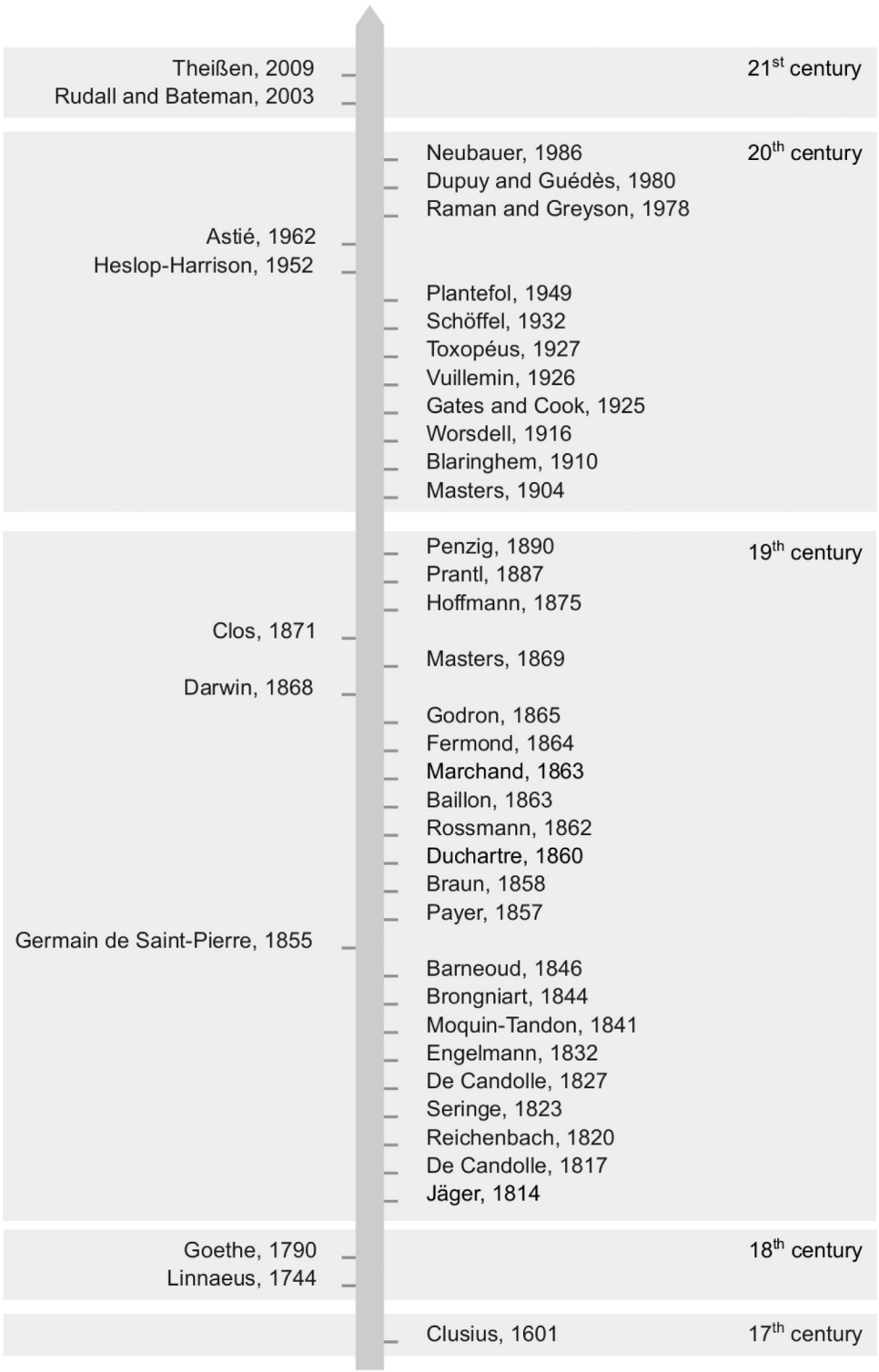

Fig. 1. Timeline presenting studies on Ranunculacean flower terata (right), and some pivotal works dealing, in whole or in part, with flower terata in angiosperms (left). (Blaringhem, 1910; Darwin, 1868; Duchartre, 1860; Engelmann, 1832; Fermond, 1864; Heslop-Harrison, 1952; Hoffmann, 1875; Neubauer, 1986; Rossmann, 1862; Toxopéus, 1927).

criteria of primary importance for plant systematics, because their variability among angiosperms is discontinuous, enabling species typification. Therefore, referring to a species standard is crucial in detecting and describing a teratum. For instance, when a species shows flowers with natural meristic variation as is often the case in flowers with spirally inserted organs (e.g., Lehmann and Sattler, 1994; Kitazawa and Fujimoto, 2014), defining a monster based on the number of floral organs will require a more extensive study than in a species with a fixed merism. Identifying a teratum requires a keen taxonomic expertise, otherwise the temptation to propose a new species name for the specimen with unusual flowers would be strong.

Abnormal flowers deviating from the species standard do not necessarily have to be rare in nature, at least locally. Deviations