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Linnaeus' sexual system and flowering plant phylogeny

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Carl Linnaeus brought order to the knowledge of plants and animals by arranging all known species in encyclopaedic works. He proposed a system of plants, the sexual system, based on the number and arrangement of male and female organs. His artificial sexual system has since long been replaced by 'natural' or phylogenetic systems but there has never been a comprehensive comparison of the sexual system with modern plant classification. The currently most often used classification of flowering plants is the APG-system. It is based on comprehensive phylogenies of flowering plants, reconstructed by analyses of DNA data. The APG-system covers all flowering plants which are classified in 453 families and these are classified in 45 orders. Most of the species were not known at time of Linnaeus. Families and orders in the APG-system are arranged in larger informal groups representing major branches in the flowering plant phylogenetic tree. Three such groups are the monocots, the rosids, and the asterids.

I have examined all genera published in Species plantarum (1753) and classified them according to order and major groups in the APG-system. All classes except one, number 15 Tetradynamia, comprises groups of unrelated plants. Not surprisingly, the sexual system does not display what we know today about plant relationships. As is evident from this analysis, there is little correspondence between the sexual system and the APG-system. This does not mean that the sexual system has been useless or misleading. When it was introduced, it formed the basis for much intensified research and increased knowledge of plants.

This year we celebrate the tercentenary of the birth of Carl Linnaeus. He brought order to the knowledge of plants and animals by arranging all known species in encyclopaedic works. He established a nomenclatural system for plants and animals still in use. He proposed a system of plants, the sexual system, based on the number and arrangement of male and female organs in the flowers. With the anniversary, the life and work of Linnaeus has come into focus. There is a great interest in information as to what extent his classification of plants actually corresponds to what we know today about plant relationships. His sexual system has since long been replaced by 'natural' or phylogenetic systems of flowering plants. There has never been a comprehensive comparison of the sexual system with modern plant classification. Here, I have made such a comparison between the sexual system in Linnaeus principal work Species plantarum (Linnaeus 1753) and the currently used APG-system of flowering plants (APG 2003) (Fig. 1).

Linnaeus' sexual system is an artificial system in the sense that it is constructed by first choosing a number of key characters and then sorting the species according to these key characters. In this case, the key characters comprise the number and arrangement of stamens and pistils in the flowers. Linnaeus observed that these characters are stable and very rarely subject to variation within the species. He was well aware that his system was in some sense artificial. He also presented fragments of a natural system,

where plants similar also in many other characters were classified together, but he never completed it and instead returned to his sexual system.

The sexual system comprises 24 classes, 23 of which contain the flowering plants (Table 1), with stamens and pistils. Most of the classes are defined by the number (1–12 or many) and arrangement of the stamens (1–12 or many, evenly arranged or in groups, equally or unequally long, free or fused). Some classes are also defined by the arrangement of the stamens in relation to the pistils (free or fused with the pistils, in different flowers, on different plants). Some of these stamen and pistil arrangements are very rare, e.g. seven stamens (class Heptandria), and thus comprise very few species, other are common, e.g. five stamens (class Pentandria) which characterise thousands of species.

The currently most used classification of flowering plants is the APG-system, an ordinal classification for the families of flowering plants, proposed by an international group of plant systematists known as the Angiosperm Phylogeny Group (APG 2003). The APG-system is based on comprehensive phylogenies of flowering plants, reconstructed by analysis of extensive DNA sequence data. Due to the increasing amount of sequence data, flowering plant phylogeny is today known in considerable detail and with great certainty. We thus know how flowering plants evolved and how they are related to each other, the basis for what may be called a natural classification.

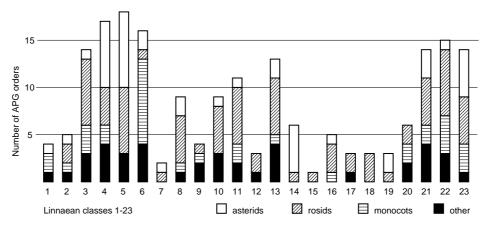


Fig. 1. The number of APG-orders in current classification (y-axis) represented in each of the 23 flowering plant classes of Linnaeus' sexual system (Table 1).

Table 1. The Linnaeus' sexual system, classes 1–23.

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1	Monandria	
2	Diandria	
3	Triandria	
4	Tetrandria	
5	Pentandria	
6	Hexandria	
7	Heptandria	
8	Octandria	
9	Enneandria	
10	Decandria	
11	Dodecandria	
12	Icosandria	
13	Polyandria	
14	Didymania	
15		
16	Monadelphia	
17	Diadelphia	
18	Polyadelphia	
19	Syngenesia	
20	Gynandria	
21	Monoecia	
22	Dioecia	
23	Polygamia	
	70	

About 250 000 species of flowering plants have been described. In the APG-system they are classified in 453 families and these families are classified in 45 orders. Most of the species and many of the families including those of six of the 45 orders were not known at time of Linnaeus. Families and orders in the APG-system are arranged in ten larger informal groups representing major branches in the flowering plant phylogenetic tree. Three such groups are the monocots (e.g. lilies, orchids, grasses, palms), the rosids (e.g. roses, legumes, birches, maples, and numerous other herbaceous and woody plants), and the asterids (e.g. asters, sunflowers, bluebells, primroses, and numerous other mostly herbaceous plants). Each of these three groups comprises between 1/3 and 1/4 of all flowering plants. Magnolias and water lilies are examples of plants that do not belong to any of the three groups. I mention them here because I will use them when comparing Linnaeus' sexual system with the APG-system.

In the mid 18th century, when Linnaeus published Species plantarum (Linnaeus 1753) with a complete list of all known species of flowering plants, about 7000 species were known. Linnaeus classified all these species in over 1000 genera and 23 classes (e.g. sunflower in the genus *Helianthus* in the class Syngenesia). I have examined all these genera and classified them according to order and major group (monocots, rosids, asterids) in the APG-system (2003) (e.g. sunflower in the order Asterales in the asterids).

The figure (Fig. 1) displays the number of APG-orders represented within the classes of the sexual system. Furthermore, for each class it is shown how many of these orders that belong to the monocots, the rosids, and the asterids. The latter three groups represent major branches of the flowering plant phylogenetic tree and hence groups of entirely unrelated plants (except in the sense that they are all flowering plants). All classes except one, number 15 Tetradynamia, comprises groups of unrelated plants. Not surprisingly, the sexual system does not display what we know today about plant interrelationships. The class Tetradynamia is characterised by two short and four long stamens and it comprises what we know today as the family Brassicaceae with cabbage, cauliflower, broccoli, mustard, etc. Class 18 Polyadelphia is characterised by stamens arranged in groups and it comprises only rosids, however several families not closely related to each other.

As is evident from this analysis there is little correspondence between the sexual system and the APG-system. This does not mean that the sexual system has been useless or misleading. As an artificial system, it is well chosen and at the time when it was introduced by Linnaeus, it formed the basis for much intensified research and increased knowledge of plants.

References

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