

SEX AND THE ANGIOSPERMS— ANOTHER PROPOSITION

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When Dr. John W. Thieret published his thoughtful critique of sex and the angiosperms, I found it stimulating. I have always had an active interest in sex. According to Thieret (1973) we are in error to apply sexual terminology to sporophytic structures of flowering plants. Such terms as "male," "female," and "bisexual flower," for example, are inadmissible because they are "misleading," "inconsistent," "inaccurate," and "superfluous." Instead we should use "staminate" for "male," "carpellate" for "female," and "perfect" for "bisexual."

It was my impression that wherever there are structures and functions related to production of sperms or male gametes, we used the term "male," and of eggs or female gametes, the term "female." I am not quite clear as to what is wrong with this procedure as it applies to angiosperms (or, for that matter, any land plants, or fungi or algae) whether the stage involved is sporophytic or gametophytic.

In vernacular the words "male" and "female" have been commonly associated with forcefulness vs. passiveness, hard vs. soft, yin vs. yang, husband vs. wife, leader vs. follower, inflexible vs. willowy, and so on—largely supposed cultural attributes of man and woman, related to certain kinds of family organization and to formerly accepted traditions for behavior, now, fortunately, being more or less eroded away. In biology, however, the words have a more scientific and precise connotation and pertain to the process of sexual reproduction, which comes down to making sperms and making eggs, as well as caring for embryos and juvenile diploid stages. In people the last is baby care; in higher plants, providing seed coats and endosperm. As soon as "syndromes" of structures and (or) functions become differentiated as part of these basic processes, then they become biologically male and female respectively. Below are listed some examples of such differentiation in the land plants, using two taxonomic groups as illustrations:

MALE	FERN	FEMALE
Microsporophyll		Megasporophyll
Microsporangium		Megasporangium
Microspore		Megaspore
Microgametophyte		Megagametophyte
Antheridium		Archegonium
Microgamete		Macrogamete
FLOWERING PLANT		
Staminate tree		Pistillate tree
Staminate flower		Pistillate flower
Stamen		Carpel
Pollen sac		Nucellus
Connective		Ovary wall and style
Pollen tube		Embryo sac
Tube nucleus		Polar nuclei

When one is concerned with functional aspects of biology, precise homology of participating parts is traditionally thrown overboard—in my opinion, wisely—in favor of clear expression of roles. The study of analogous structures is one of the most fascinating phases of modern ecological morphology. Thus we have nouns like arm, beak, eye, grazer, herb, leg, predator, tree—words in constant use in biology in writing and speaking but involving all proportions of homology and analogy. If we rid ourselves of the adjectives “male” and “female” in reference to higher plants, we should also include in our house cleaning such familiar adjectives as cortical, carnivorous, embryonic, glandular, pedicellate, pinnate, sessile, vascular, winged, and the like. Should we delete all the words based upon the sexual roots “andr,” “gam,” “gyn,” and “ov?” Is it better that we use “perfect” from some quaint antiquarian concept, or “pistillate,” derived etymologically from the word for pestle (strong biological meaning here), or “staminate” from the word for hair or thread (ditto)?

Figure 1 is a diagrammatic representation of the evolutionary advancement of sexual differentiation in vascular plants. The most primitive condition is that in which one kind of spore and one kind of gametophyte is produced. From the time it forms in the sporangium, the spore embodies the ability to produce sex cells of both types, and the entire sexual generation is thus hermaphroditic. In heterosporous pteridophytes, on the other hand, the sex organs are borne upon differentiated gametophytes. The spores producing them are different because of divergent processes operating in the micro- and megasporangia, so that the microsporangia produce only male spores and the megasporangia female. In seed plants, the differences become more and more profound and involve more and more structures. Finally, genetic changes arise that change the sporophytes themselves. Now

EVOLUTION OF SEXUALITY IN VASCULAR PLANTS

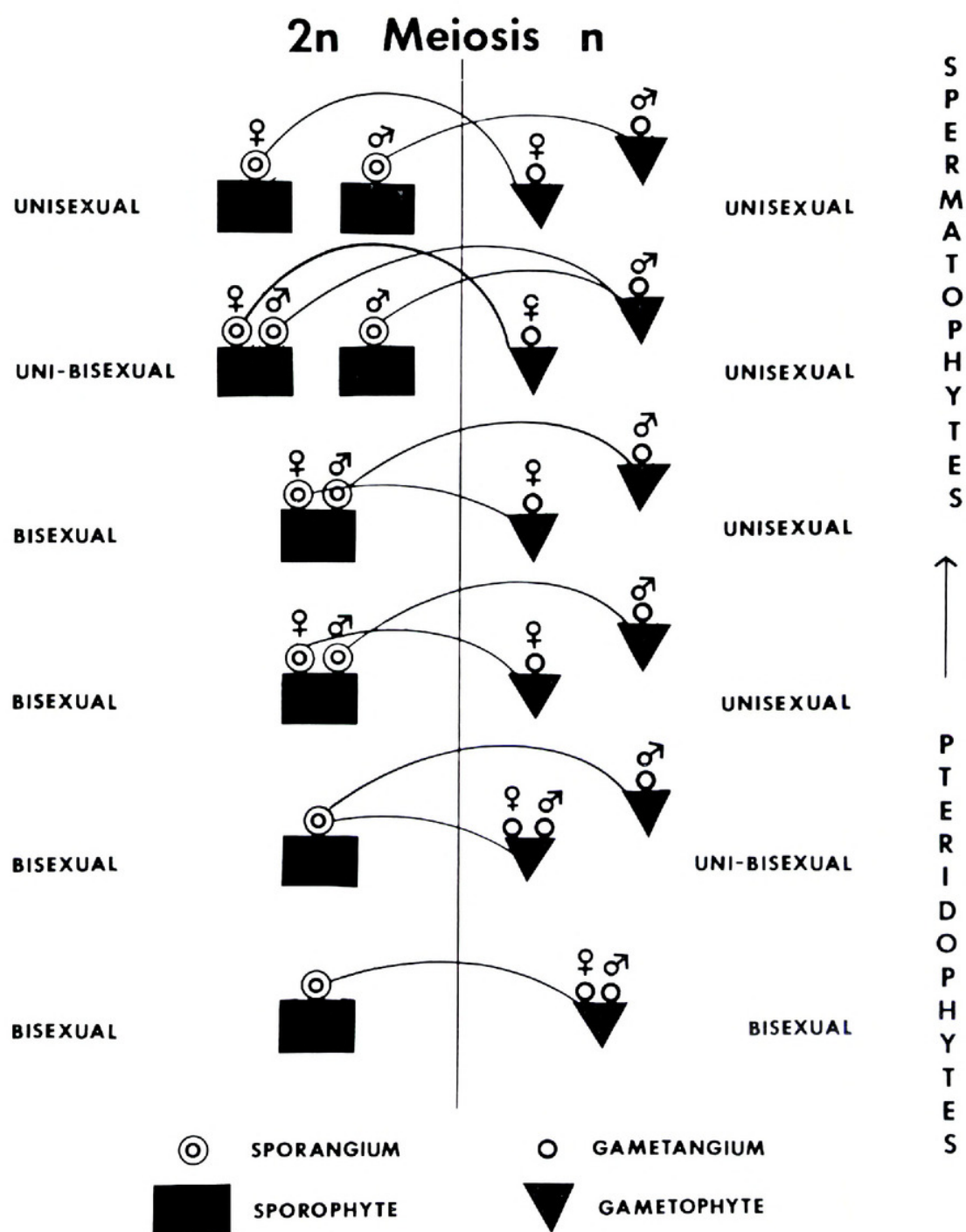


Fig. 1. Diagrammatic representation of the evolutionary advancement of sexual differentiation in vascular plants.

the sexual differentiation has moved into the $2n$ generation, and the staminate plant can produce only sperms and the pistillate only eggs, each utilizing its own now very distinctive structures. In the course of these basic transformations in evolution, we see not only repeated parallels to conditions known in fungi and algae (but surely not homologous, even though they are clearly sexual phenomena), but—what impresses me particularly—beautiful convergences of higher seed plants toward higher animals. It is a remarkable fact that no lower vascular plants are yet known to have evolved sexual differentiation of the sporophytic plant.

In terms of biological strategy, just as the $2n$ scrotum is a male structure, the $2n$ microsporangium is a male structure. Just as ejaculation is a male function in mammals, pollen release is a male function in angiosperms—whether or not the organs involved are homologous. I propose that both words “male” and “female” continue to be used, where appropriate, in connection with vascular plants, and that they be defined as follows:

MALE. Adjective applied to all character-states—diploid or haploid, sporophytic or gametophytic, primary or secondary—adapted to or directly or indirectly correlated with the production and transport of sperms.

FEMALE. Adjective applied to all character-states—diploid or haploid, etc.—adapted to or directly or indirectly correlated with the production and functioning of eggs. Also the structures and functions specifically modified for the protection and nourishment of zygote, embryo, and germling.

As I see them, the advantages of utilizing “male” and “female” in our biological (as opposed to vernacular) terminology are not only in (a) cutting down on polysyllabic verbosity, (b) taking advantage of their obvious meanings, but also—the most important point scientifically—(c) to bring out the remarkable adaptive parallelisms and the universality of “sporophytic” maleness and femaleness, as has evolved separately in higher animals and in higher plants.

To recapitulate, in all probability much of the differentiation into “maleness” and “femaleness” in such diverse groups of organisms as fungi, animals, red algae, and vascular plants constitutes analogy. Nevertheless, the biological functions involved are closely similar in their methods of accomplishment and in their results. Perhaps indeed in some cases the similarities are not so superficial as to some they may seem, for the possibility should be entertained that we are observing homologous genetic potentialities originating in a flagellate common ancestry long since lost in antiquity.

In these terms, a staminate tree of *Salix fragilis*—in spite of its soft and willowy appearance—is just as “male” as a bull, a stallion, or a billy-goat.

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