A COMMENTARY ON THE DEFINITION OF THE ORDER MYRTALES

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ABSTRACT

I concur in the delimitation of the order Myrtales proposed by Dahlgren and Thorne (this symposium), except for the position of the Thymelaeaceae, which they exclude. The Thymelaeaceae are chemically discordant with the Myrtales, but they cannot reasonably be attached to any other order as now constituted. The ancestors of the Thymelaeaceae, at some level, were probably tanniferous as are the modern Myrtales. Thus an evolutionary approach does not require that the Thymelaeaceae be dissociated from the Myrtales because of the chemical differences. Instead we face the question of how best to provide for the admitted differences within the framework of the taxonomic system. I find it more useful to retain the Thymelaeaceae in the Myrtales as a somewhat aberrant group than to establish a satellite order composed of a single family.

It appears that among the participants in this symposium there is substantial agreement on the limits of the Myrtales, with the single exception of the family Thymelaeaceae. The Combretaceae, Crypteroniaceae, Lythraceae, Melastomataceae, Myrtaceae, Oliniaceae, Onagraceae, Penaeaceae, Punicaceae, Sonneratiaceae, and Trapaceae, all of which have traditionally been referred to the Myrtales, are still kept there, although some of us would reduce some of these groups to less than familial status. The Cynomoriaceae, Dialypetalanthaceae, Haloragaceae, Hippuridaceae, Lecythidaceae, Rhizophoraceae, Theligonaceae, and other families that have been included by some authors in the past are properly to be excluded.

My esteemed colleague Academician Takhtajan would add only three families, the Haloragaceae, Lecythidaceae, and Rhizophoraceae, to the list of those included by Dahlgren and Thorne (1984). In his most recent system, Takhtajan (1980) puts each of these three families into a separate suborder, in contrast to the suborder Myrtinae for all the other families. Thus his suborder Myrtinae is functionally equivalent to the order Myrtales as discussed here.

It is interesting and perhaps significant that this degree of agreement has been achieved by several different individuals or groups working more or less independently of each other, although of course not in intellectual isolation. My own treatment was in the hands of the publisher before I saw the manuscript by Dahlgren and Thorne. As new information continues to accumulate, the range of taxonomic schemes that can reasonably be defended is progressively narrowed.

It is also interesting that two of the characters which have played a large role in reshaping the definition of the Myrtales are anatomical: internal phloem, and vestured pits in the vessels. It is only in the last several decades that enough information has become available about the taxonomic distribution of these features both within and without the Myrtales to permit any reliance to be placed on them. We cannot claim to be better taxonomists than our predecessors, but we do have more data to work with.

The position of the Thymelaeaceae remains debatable. On this issue I reluctantly part company with Dahlgren and Thorne. I include this family, somewhat doubtfully, in the Myrtales, whereas they exclude it, also somewhat doubtfully. The necessity to make a choice for purposes of a formal system magnifies the relatively small disagreement between us.

Dahlgren and Thorne (1984) present a considerable list of similarities between the Thymelaeaceae and typical Myrtales, including the usual presence of internal phloem. The vestured pits of the vessels should be added to their list. The evidently pseudomonomerous gynoecium of typical Thymelaeaceae sets the family apart from the rest of the Myrtales, but it does not argue against a relationship. Rather it directs our search for affinities (or at least for a plausible ancestry) to families with a compound pistil rather than to families with simple pistils.

There is a special problem here in that the Elaeagnaceae, with which the Thymelaeaceae

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share some features, appear to have a simple pistil. Yet as Dahlgren and Thorne (1984) point out, there is no inherent reason why the number of carpels could not ultimately be reduced to one in a syncarpous as well as in an apocarpous gynoecium. Indeed that very thing seems to have happened in the Cucurbitaceae. If the Thymelaeaceae were to be associated with the Elaeagnaceae, then it would have to be assumed that the pistil of the Elaeagnaceae became monomerous by reduction. The two families would then have to form an order of their own; collectively they would spoil any other order into which they were put. It is possible that future evidence will support such an association of these two families, but in my opinion the balance is now against it.

The principal argument that Dahlgren and Thorne (1984) adduce against a position of the Thymelaeaceae in the Myrtales is chemical. There is no doubt that the Thymelaeaceae stand apart from the rest of the order in this regard. The question is what evolutionary and taxonomic significance to attach to the difference.

Unlike the other Myrtales, the Thymelaeaceae are not tanniferous, and they characteristically accumulate daphnin and allied compounds, which are simple coumarins. Simple coumarins are widespread among the angiosperms, but apparently not in the Myrtales. Daphnin and its immediate chemical allies are almost entirely restricted to the Thymelaeaceae, so far as present information shows. One species of *Euphorbia* has been reported to contain daphnetin (a daphnin-type compound), but it does not seem reasonable to lay great stress on such a single occurrence in an advanced genus of a family that is chemically so diversified. Furthermore, the Euphorbiaceae, like the Myrtales, are commonly tanniferous, and if this difference can be minimized in assessing a possible relationship to the Euphorbiaceae, it can also be minimized in assessing a possible relationship to the Myrtales. There are several other chemical and morphological features (e.g., phorbol-type diterpenoids, crotonoid pollen) that link some members of the Thymelaeaceae to some members of the Euphorbiaceae, but these similarities are taxonomically scattered rather than being pervasive.

Any attempt to associate the Thymelaeaceae with the Euphorbiaceae must confront the fact that these two families display different sets of advanced features, suggesting only a fairly remote common ancestry. Thus the Thymelaeaceae characteristically have internal phloem, vestured pits, daphnin, wedge-shaped phloem rays, more or less strongly perigynous, mostly perfect flowers, and well developed, often petaloid sepals, all of which are unusual or wanting in the Euphorbiaceae. The Euphorbiaceae, on the other hand, tend to be laticiferous and have mostly unisexual, more or less strongly reduced flowers with an obturator of different nature from that in the Thymelaeaceae. The Euphorbiaceae are so highly diversified, especially in chemical and vegetative features, that individual, ultimately meaningless links to many other families can be found in particular features of particular genera. I don't suppose that anyone wants to use the presence of mustard oils in *Drypetes* to warrant the inclusion of the Euphorbiaceae in the Capparales.

According to a hypothesis of chemical evolution that I proposed in 1977, the subclasses Hamamelidae, Dilleniidae, and Rosidae are all primitively tanniferous, producing ellagic acid and other tannins. Subsequent evolution within these subclasses and in the derived subclass Asteridae led to the substitution of other chemical repellents for tannins in many groups. A similar hypothesis was proposed at about the same time by Gardner (1977), who visualized a "gradual replacement of a defence based on tannins and crystals (primitive Rosidae) by defences based on a variety of toxic and repellent substances (advanced Asteridae)." Under this concept, the ancestors of the Thymelaeaceae, at some level, were tanniferous. Thus the chemical evidence alone does not preclude the origin of the Thymelaeaceae from within the Myrtales. The taxonomic level at which the Thymelaeaceae should be recognized is debatable, but their ultimate attachment to a tanniferous group is inevitable.

In a symposium concerned only with the limits of the Myrtales, I suppose it might be possible to exclude the Thymelaeaceae from the Myrtales as a discordant element. Being concerned with the general taxonomic system, I am not satisfied to exclude the Thymelaeaceae from the Myrtales unless I have a better place to put them. They would be an even more discordant element in any other order as presently constituted (at least in the Cronquist system, which is necessarily my frame of reference). The possibility of a future association with the Elaeagnaceae cannot be entirely discounted, but the Elaeagnaceae are just as strongly tanniferous as the Myrtales. Exclusion of the Thymelaeaceae from the Myrtales on chemical grounds would logically preclude as-

sociation of the Thymelaeaceae with the Elaeagnaceae.

Thus, if the Thymelaeaceae are to be excluded from the Myrtales, they must form an order of their own. I cannot really argue with anyone who chooses that alternative, as Takhtajan (1980) has done. It is a matter of lumping or splitting, in which there is no objective right or wrong. Inclusion of the Thymelaeaceae in the Myrtales does not complicate the distinction of the Myrtales from other orders. Therefore I find it conceptually more useful to tolerate this somewhat discordant family in the Myrtales than to tolerate still another order consisting of a single family.

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