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Parsimony and History

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Sneath (1995) and Edwards (1996) share an interest in the origin of concepts underlying present-day systematic methods. According to Edwards (1996:89):

> Finding arguments for global parsimony in the works of Hennig is an example of that phenomenon well known to the history of science: reading into early writers more than they actually wrote.... One can often discern an ulterior motive in such attributions.

Likewise for the works of Wagner. In Edwards' account, what is now usually called Wagner parsimony arose instead from Edwards and Cavalli-Sforza's (1963) ideas.

Sneath (1995:288) expressed complementary views:

> The earliest work [in quantitative phylogenetic methods] was by Edwards and Cavalli-Sforza (1964) and Camin and Sokal (1965).

He discussed one of the "main conceptual steps":

> It was found necessary to introduce into trees internal nodes that represent putative ancestors (Edwards and Cavalli-Sforza, 1964 ...). This realization led to ... minimum-length trees, and the mathematics of Steiner and Wagner trees.

Both Sneath and Edwards seem to have overlooked relevant literature. Sneath appears to have now forgotten some earlier work that Sokal and Sneath (1963:289) once cited:

> Attention should be drawn to Wagner's method for expressing phylogenetic deductions, which permits quantification of the data. An example can be found in [Mickel, 1962].

Not only did this statement precede 1964, but Wagner's trees already had internal nodes representing ancestors, as indeed did Hennig's (1950) and Darwin's (1859).

Unlike Sneath, Edwards (1996:88) was aware of Wagner's work, but he felt that we misinterpreted Wagner's views:

> [Kluge and Farris, 1969] seem to be reading into Wagner's (1961) method a [parsimony] principle that it does not contain and that Wagner (1980) did not claim.

Edwards did not explain what Wagner (1980:187) would then have meant by

> once taxa are positioned in a distance relationship to the common ancestor, the stage is set for tying lines together parsimoniously,

nor did he say how he thought the method does work, if not by parsimony. In any case (he did not mention), Edwards only repeated an earlier misunderstanding, already discussed by Farris and Kluge (1986: 305):

> It is unnecessary to debate the meaning of Wagner's comments when one may simply ask Wagner himself. When we did so, he assured us that ... his aim was always to achieve a parsimonious tree.

Unless Edwards can produce more direct evidence, the question of Wagner's intent seems settled.

Edwards (1996:88) also felt that we were wrong in suggesting a connection between parsimony and Hennig's ideas, and he advanced three arguments, beginning with

> Duncan and Stuessy (1985:3) stated that "Hennig's original method was modified to include a criterion of parsimony in Farris, Kluge, and Eckardt (1970)."

Edwards did not say just what, on this view, Hennig's original method was supposed to be. Duncan and Stuessy (1985:3) (the introduction to a collection of reprinted papers) simply referred to Duncan (1984). According to Duncan (1984:703),

> Directed character compatibility analysis is equivalent to Hennig's method. Wagner parsimony is distinct from Hennig's method because [with Wagner parsimony] monophyletic groups can be defined by homoplasious characters.

Monophyletic groups can be supported, that is, by derived features that also arise separately in other groups. In compatibility (clique) methods, in contrast, groups may only be defined by features unique within the [more inclusive] group being analyzed, as Duncan (1986) later clarified. But then compatibility can hardly be Hennig's (1981:23–24) method:

> The neoptery of the Neoptera has arisen monophyletically and is one of the constitutive [supporting] characters for this group. It is quite another matter that it has arisen elsewhere as well.

Thus, Hennig (1981) used absence (secondary loss) of compound eyes to support both Diplura (1981:102) and Protura (1981: 104), used larval tracheal gills for both Plecoptera (1981:163) and Megaloptera (1981: 287), and used lack (secondary loss) of ocelli for Embioptera (1981:181), Notoptera (1981:184), and Dermatpera (1981:186). Hennig (1983) used endothermy to support both Aves and Mammalia and used lack (secondary loss) of teeth for both Testudines and Aves. Such examples can easily be multiplied (cf. Churchill et al., 1985; Farris and Kluge, 1986). In each such case, Hennig's analysis shows exactly the characteristic whose lack, according to Duncan, is supposed to distinguish it from Wagner parsimony.

Edwards offered no contrary evidence; the impression that he created, that Dun-

can and Stuessy's (1985) comment reflects a well-substantiated objection to our 1970 paper, rests only on omitting pertinent material. It is much the same with another of Edwards' (1996:88) arguments:

> Felsenstein (1982) described what he called Hennig's dilemma, by which he meant the absence of any procedure in Hennig's proposals for resolving incompatibilities in the data: 'Hennig's method works only as long as there is no internal conflict in the data' (Felsenstein, 1982:381).

Compare Richter and Meier's (1994:216) summary of part of Hennig's (1950:175f) discussion:

> In the case of character conflict, complex similarities overrule even a large number of simple similarities because simple similarities are more easily explained by convergent evolution.

There is more, but this is enough to illustrate that others can see what Edwards (or Felsenstein) insisted is absent.

Other principles from Hennig can be applied to what should evidently be called Felsenstein's Dilemma. One of these, of particular interest here because Edwards discussed it, reads (Hennig, 1966:121; cf. Farris et al., 1970:174)

> The more characters certainly interpretable as apomorphous (not characters in general) that there are present in a number of species, the better founded is the assumption that these species form a monophyletic group.

Characters may be weighted for complexity, as just seen. The application is straightforward: in case of conflict, take the better-founded alternative.

Edwards' (1996:88) remaining argument consists of not considering that application:

> This unexceptionable statement seems to be devoid of operational interpretation. It says that derived (apomorphous) characters common to a group of species are evidence of monophyly, with which all will agree, and of course implicit in this statement is the corollary that the greater the number of derived characters, the stronger the evidence. But how is one to use this idea as a principle for phylogenetic reconstruction?

We use this idea by always selecting the better-founded alternative, which does not seem to us to be hard to understand. Edwards continued:

Hennig might have gone on to suggest that a tree with the minimum number of homoplasies (shared derived steps of independent origin) would possess "well founded" monophyletic groupings . . . but apparently he did not.

This is only a matter of wording. Weights aside, if many apomorphies favor one arrangement and few favor a second, accepting the better-founded arrangement requires postulating homoplasy in the few, not the many.

There is thus an obvious connection between accepting predominant evidence and minimizing hypotheses of homoplasy, but Edwards (1996:88) had one further way of suggesting otherwise:

> Farris et al. (1970:176) correctly observed, "Unfortunately [Hennig's statement] is not sufficiently detailed to allow us to select a unique criterion for choosing a most preferable tree."

We did not analyze that connection fully in 1970, but we later treated the subject in more detail (Farris and Kluge, 1986; cf. Farris, 1986). As we summarized then (Farris and Kluge, 1986:302f):

> In the 1970 paper we were concerned with the possibility that there might be more than one way to evaluate the evidence favoring an entire tree by combining counts of the apomorphies for each of its groups. As our discussion of explanatory ability implies, we now understand that our fears were groundless.

As before, Edwards reached his conclusion by neglecting pertinent material.

This exhausts Edwards' arguments, and we close by addressing two points raised in review. First (anonymous),

> Edwards' acceptance of views by Felsenstein, that have long been overturned, is Edwards' problem more than Felsenstein's.

Felsenstein (pers. comm. to A.G.K.), however, still agrees with Edwards:

> I have not changed my view on "Hennig's Dilemma." I stand by it, rock-solid. I don't think Anthony Edwards was misquoting me or being unfair to me in citing it.

Second (D. Cannatella, in lit.),

> Felsenstein [1984] viewed both (Camin–Sokal) parsimony and compatibility as algorithmic solutions to Hennig's Dilemma.

Those particular algorithmic solutions raise problems. Unlike Wagner parsimony, Camin and Sokal's (1965) method includes no algorithmic provision for concluding reversals and so cannot apply reversals as apomorphies. But Hennig (1966:95) knew that reversals are apomorphies:

> For example, the absence of the wings in fleas is undoubtedly an apomorphous character in comparison with the presence of wings in other holometabolous insects. On the other hand, the possession of wings [in Pterygota] is an apomorphous character in comparison to their absence in the so-called Apterygota.

Several other cases in which Hennig (1981, 1983) applied reversals (secondary losses) as synapomorphies have been listed (cf. Churchill et al., 1985; Farris and Kluge, 1986). The Camin–Sokal procedure is thus inconsistent with Hennig's views, and the same is true of compatibility analysis, as has already been seen. Felsenstein (1984) took none of this into account. It is entirely reasonable to want algorithms, but not just any algorithm can reasonably be considered Hennigian.

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Stingrays, Parasites, and Neotropical Biogeography: A Closer Look at Brooks et al.'s Hypotheses Concerning the Origins of Neotropical Freshwater Rays (Potamotrygonidae)

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The exploration of host/parasite coevolution has been invigorated in recent years, in part by the application of explicit methods of phylogeny estimation to parasitic organisms (Klassen, 1992). A pioneering study in the field was Brooks et al.'s (1981b) investigation of South American stingray biogeography and phylogeny, based on cladograms for helminth parasites (hereinafter referred to as Brooks et al.). The frequent reiteration of the results (e.g., Brooks, 1988, 1992, 1995; Brooks and Deardorff, 1988; Brooks and McLennan, 1991, 1993a, 1993b) has turned this "novel contribution to biogeographic analysis" (Straney, 1982:337) into an "old friend"— a great example to use in teaching (Blair, 1994:296). However, the Brooks et al. analysis has occasionally been questioned. Straney (1982) (and to a lesser extent Simberloff, 1987) voiced concerns about the biogeographic inferences drawn from the presented parasite cladograms. More recently, Caira (1990, 1994) cautioned that several of Brooks et al.'s character data sets and analyses remain unpublished, implying that there may be problems with the parasite data themselves. In this paper, I focus on another aspect of this widely known study, the methods used by Brooks et al. to infer host biogeography and phylogeny from parasite cladograms and distributions.

The exclusively freshwater stingray family Potamotrygonidae ranges throughout the major Atlantic drainages of South