SIMPSON, G. G. 1950b. Orthogenesis. Chamber's Encyclopedia Vol. 10:252.
SIMPSON, G. G. 1970. On randomness and determinism: Discussion. Geol. Soc. Amer. Bull. 81:3185–3186.
SIMPSON, G. G. 1971. The meaning of evolution. Revised edition. Bantham Books, Inc., New York.
SIMPSON, G. G. 1978. Footnote to the discussion of Rosa's theories by Baroni-Urbani. Syst. Zool. 27:346.

CESARE BARONI-URBANI

Natural History Museum of Basle
Augustinergasse 2
Ch-4051 Basel, Switzerland

congruencia
[illegible]
[illegible]

orden jerárquico [illegible]
incongruencias = refutación
rechazadas

Syst. Zool., 28(4), 1979, pp. 624–627

Hierarchy and Reticulation in Systematics

Classification of kinds of things are generally done in a hierarchic manner. Since the beginning of zoology and botany this has also been the method of classifying organisms. Like minerals taxa of animals and plants were considered natural kinds defined by their properties. It was generally the view of systematists that nature's order is indeed hierarchic. Apparently the same view prevails among systematists today and especially cladists tend to refer to the basic hierarchy of nature (Hennig, 1966; Brundin, 1966). Even in recent papers (Platnick, 1979; Platnick and Nelson, 1979) it is taken for granted that if there is an order among organisms, this order is hierarchic.

It is recognized today that kinds of organisms differ basically from kinds of rocks or buttons; the unifying element is continuity of bloodline rather than similarity of features. There is a profound difference between the two ways of looking at kinds of organisms and there is every reason to reconsider whether hierarchy is actually as fundamental as cladists seem to believe.

According to Platnick (1979) a major principle of cladistics is "that nature is ordered in a single specifiable pattern which can be represented by a branching diagram or hierarchical classification." This basic hierarchy among species of organisms is treated as if it were an axiom of systematics. The principle of hierarchy is a straightforward scientific theory, however, and it is as such open to testing. Indeed, it should be tested before we use it or its corollaries as guiding principles in systematics.

As a theory the principle of hierarchy prohibits speciation by hybridization (since this implies a reticulate and not a hierarchic distribution of characters). In botany it has been shown repeatedly, however, that many species of higher plants have evolved by hybridization, especially as a result of processes involving allopolyploidy but also by simple hybridization between sympatric populations. We have tried to show (Bremer and Wanntorp, 1979) that hybridization between geographic populations might be a cause of reticulation also among species of animals. Within a cladistic framework this has been demonstrated among poeciliid fishes (Rosen, 1978, 1979) and it is probably not a rare phenomenon in zoology. Since speciation by hybridization has been shown to occur, the principle of hierarchy is falsified. Order among species of organisms may be networklike as well as hierarchic. Reticulation should be expected in animal as well as plant systematics and it cannot be dismissed as something the botanists (mercy on them) have to grapple with.

Of course, instead of asking, what is the order among species of organisms, we may specifically ask, what is the *hierarchic* order among species of organisms? In the case of reticulation the answer would not tell us much about nature, however. A hierarchic description of a fishing net would be a kind of description indeed but it would certainly be a very poor one.

It may well be that hierarchy is more common than reticulation. This is most probably the case but since the hierarchy principle is falsified, it is not justified to use it or its corollaries to reject evidence of reticulation in systematics.

Whether congruence and hierarchy could or should somehow be retained as principles of cladistics or not is probably worth discussing. If we do retain them we seem to have rejected Popper for Lakatos; as a research program traditional cladistics may still have momentum though its basic hierarchy principle is falsified in a number of instances.

CONGRUENCE OR RECIPROCAL ILLUMINATION

Congruence between characters or reciprocal illumination of characters as a means of character testing is a direct corollary of the principle of hierarchy. Thus under that principle incongruent characters, contradictory to a preconceived hierarchic order, are to be rejected. This would be a doubtful procedure even if the hierarchy principle were not already falsified. As systematists we are trying to find out about order in nature. We may well set out with the hypothesis that order is indeed hierarchic but then this is the hypothesis to be tested and we may not use a corollary of the hypothesis to reject its own possible falsifiers. That is what we do, if we reject characters that are "contradictory" (to hierarchic order) and such a procedure is certainly not compatible with a Popperian methodology of research. Furthermore, since the hierarchy principle is falsified, the use of the congruence principle to reject "conflicting" evidence seems unpermissible.

However, this does not mean that we shall have to return to pre-Hennigian and non-Popperian systematics; testing of characters and groupings is still possible. Though not always hierarchic, there is indeed order in nature and we believe that cladistic methodology including testing of hypotheses can be adjusted to conform with this partly hierarchic, partly reticulate, order.

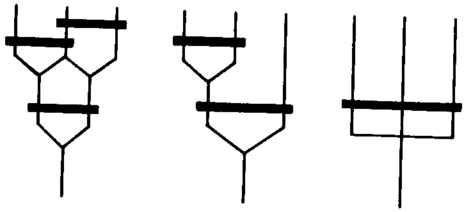

FIG. 1.—Cladograms (see text for explanation).

RETICULATION IN CLADOGRAMS

Platnick (in Harper and Platnick, 1978) contrasts cladogram construction with phylogeny reconstruction, and maintains that, while presenting difficulties in the latter, "hybridization is not a problem for cladistics . . . . Cladistics merely converts reticulations of two taxa (producing a third hybrid taxon) into trichotomies." Nelson (1979) makes the following distinction:

> cladograms are always non-reticulate . . . . In a cladogram, the branch point represents the generality of supposedly true statements ("synapomorphies") that can be made about the terminal taxa. In a phyletic tree, the branch point represents a supposed speciation event. A cladogram is an atemporal concept; a phyletic tree is a cladogram to which the temporal aspect has been added. In short, a cladogram is a synapomorphy scheme; a phyletic tree, a phylogeny.

We agree to the distinction between cladograms and phyletic trees but we disagree with the view of cladograms as principally non-reticulate. Since the evidence of reticulation is at the level of synapomorphies, the problem concerns cladograms—synapomorphy schemes as Nelson has expressed it—as well as phyletic trees. Given adequate, corroborated synapomorphies, indicating reticulation, a cladogram with a reticulate pattern must be accepted. Lack of synapomorphies in one branch (a common instance) will lead to the establishment of a dichotomous cladogram, and only the total lack of synapomorphies in both branches to a trichotomy (Fig. 1).

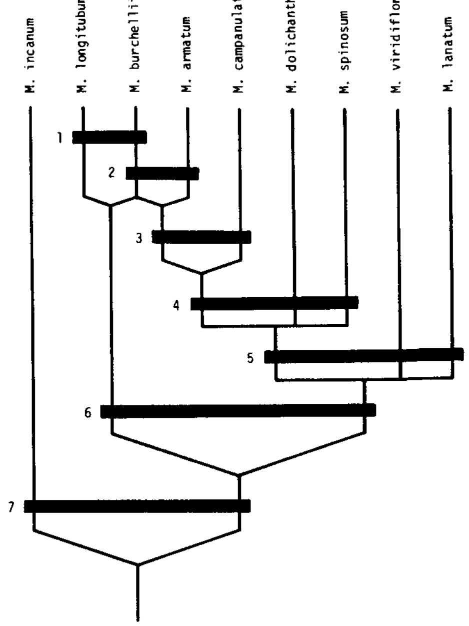

FIG. 2.—Reticulated cladograms of *Microloma* species.

FIG. 3.—Hierarchical cladogram of *Microloma* species redrawn from that of Fig. 2.

In cases of reticulation Platnick advises us to regress to trichotomies, i.e., to avoid using all the "conflicting" characters but this is certainly very rarely done. Instead, the "conflicting" sets of characters will generally be considered of unequal strength. The congruence criterion will then be applied to reject the weaker set in favor of the stronger. Reticulate patterns are thus in normal procedure transformed into trichotomies. In order to arrive at a trichotomy it is necessary that reticulation be accepted as part of the cladogram. If hierarchic constraints are then introduced, as is indeed necessary for classificatory purposes (see below), the reticulation will be rendered into a trichotomy or polytomy.

The insight that reticulations need not involve sister species makes the problem even more intricate. An example where the cladistic relationships have been worked out (Fig. 2; Wanntorp MS) is furnished by the South African genus *Microloma* (Milkweed family, Asclepiadaceae). The hybrid species *M. burchellii* shares unique apomorphies with *M. longitubum* as well as with *M. armatum*, which are several branching points apart in the cladogram. If one, as Platnick advocates, avoids using "conflicting" characters in order to achieve a hierarchic interpretation of the relationships, not only the sets of synapomorphies (1 and 2) joining *M. burchellii* with *M. longitubum* and *M. armatum* but also the sets of synapomorphies (3, 4, and 5) uniting it with the other species down to the common level must be avoided. The resulting hierarchic cladogram (Fig. 3) is not a trichotomy but an octotomy, a polytomy involving eight branches, united only by the basic synapomorphy set (6) for that group, and the cladistic relationships between the eight species cannot be more closely resolved.

In zoology reticulated cladograms similar to that of Fig. 2 were presented for *Heterandria* and *Xiphophorus*, two genera of poeciliid fishes (Rosen, 1978, 1979).

In the case of more complicated combinations of synapomorphies, cladograms sometimes cannot be fully resolved (Fig. 4). In such cases there can be no information in synapomorphies, indicating how the branches below the reticulation should be connected. One might balk at such interpretations but evolutionary processes involving, e.g., hybridization and extinction of parents or fusion of populations and leading to such patterns, are by no means impossible.

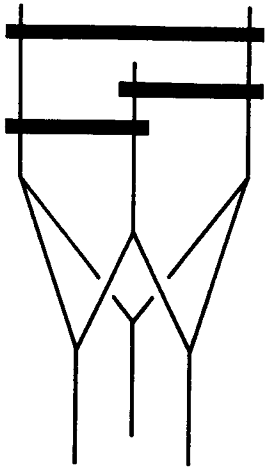

FIG. 4.—Cladogram (see text for explanation).

RETICULATION AND CLASSIFICATION

Biological systems are notoriously hierarchic and thus not really fit to describe reticulate patterns among species of organisms. In a hierarchic system a reduction of reticulations to trichotomies and polytomies is indeed inevitable for classificatory purposes. A classification of the *Microloma* species discussed above would consist of two supraspecific taxa only, indicating the basic dichotomy of Fig. 3. Such a classification is not very informative; the larger taxon containing all of the species except *M. incanum* cannot be subdivided, since we cannot use the conflicting synapomorphies in a hierarchic system.

We conclude that reticulation is a problem in systematics, for classification as well as for cladogram construction. Systematics call ill afford to ignore it.

ACKNOWLEDGMENTS

We are grateful to Norman I. Platnick and Gareth Nelson for stimulating discussions of this issue. The study was supported by travel grants from the Swedish Natural Science Research Council (grant R 3296-101) and the Netzel Fund, University of Stockholm.

REFERENCES

BREMER, K., AND H.-E. WANNTORP. 1979. Geographic populations or biological species in phylogeny reconstruction? Syst. Zool. 28:220–224.

BRUNDIN, L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges. Kungl. Sv. Vetenskapsakad. Handl. (4)11:1–472.

HENNIG, W. 1966. Phylogenetic systematics. University of Illinois Press, Urbana.

HARPER, C. W. JR., AND N. I. PLATNICK. 1978. Phylogenetic and cladistic hypotheses: a debate. Syst. Zool. 27:354–362.

NELSON, G. 1979. Cladistic analysis and synthesis: principles and definitions, with a historical note on Adanson's Famille des Plantes (1763–1764). Syst. Zool. 28:1–21.

PLATNICK, N. I. 1979. Philosophy and the transformation of cladistics. Syst. Zool. 28:537–546.

PLATNICK, N. I., AND G. NELSON. In press. The purposes of biological classification. *In* Asquith, P. D. and I. Hacking (eds.), PSA 1978, Proc. 1978 Biennial Meeting, Philosophy of Science Association, vol. 2.

ROSEN, D. E. 1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool. 27:159–188.

ROSEN, D. E. 1979. Fishes from the uplands and intermontane basins of Guatemala: Revisionary studies and comparative geography. Bull. Amer. Mus. Nat. Hist. 162:267–376.

KÅRE BREMER AND
HANS-ERIK WANNTORP

Institute of Botany
University of Stockholm
S-106 91 Stockholm
Sweden

Syst. Zool., 28(4), 1979, pp. 627–634

Paraphyly of the *Rana boylii* Species Group

Case (1978) presents a novel hypothesis of kinship for several species of the genus *Rana*. According to her, five western North American species—*Rana aurora, boylii, cascadae, muscosa*, and *pretiosa*—comprise a monophyletic group, her *boylii* group. The European *Rana temporaria* is postulated by Case to be the closest relative of her *boylii* group, while the North American *R. sylvatica* is