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Received 10 May 1999; accepted 27 December 1999
Associate Editor: R. Olmstead

Syst. Biol. 50(1):136–141, 2001

Useful Characters in Gastropod Phylogeny: Soft Information or Hard Facts?

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Traditionally, gastropod classification and phylogeny are often based on hardshell structures, although other anatomical characters and molecular characters are increasingly included in systematic studies (Ponder, 1988, and references therein; Bieler, 1992), together with ultrastructural shell characters (Falniowski and Szarowska, 1995). Some authors have expressed a certain scepticism for using shell characters in cladistic analyses (e.g., Kool, 1993; Robertson, 1996; Wise, 1996), whereas others have based their analyses entirely on such characters (e.g., Michaux, 1989), which in turn has been questioned by Emberton (1995). Some authors (e.g., Robertson, 1978, 1996; Davis, 1979; Kool, 1993), however, have stated that shell characters should be avoided, being more prone to selective processes and hence more homoplastic than other characters. According to those authors, selection will increase the risk that an empirically observed similarity is not the result of common ancestry but rather of parallel or convergent evolution, which may lead to erroneous conclusions.

Although shell shape, sculpture, and coloration are the traditional characters in

molluscan systematics (Bieler, 1992), other information has also been used. For example, Cuvier (1797) established the taxa *Gastropoda* and *Cephalopoda* on the basis of how they moved. Lamarck (1799) opposed this by arguing that in most cases only the shell was known and classification should, therefore, be based on conchological characters; indeed, the name *Bivalvia* stems from the emphasis on shell characters. Not until the middle and late nineteenth century (e.g., Lovén, 1840, 1849; Herdman, 1890; Pelseener, 1899) did comparative anatomy of soft parts, histology, and embryology gain acceptance in classification. Milne-Edwards (1848) divided the gastropods into *Prosobranchia*, *Opisthobranchia*, and *Pulmonata* mainly on the basis of the organization of the respiratory system. Spengel (1881) divided the same animals into *Streptoneura* and *Euthyneura*, according to differences in the nervous system. Mörch (1865) argued that different characters were useful at different taxonomic levels; for example, characters of the heart were better for diagnosing higher categories, whereas characters from the reproductive system could be used at lower taxonomic levels. This is a remnant from Cuvier's distinction of important and less important characters (Geoffroy Saint-Hilaire and Cuvier, 1795), in which characters essential for survival were used

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for diagnosing higher taxa and less vital characters were used for lower categories.

Given that gastropod classification at different levels is still often based on shell characters, we ask whether there are reasons a priori to consider these characters less reliable because of their higher degree of homoplasy. Homologous and nonhomologous similarity cannot be distinguished from mere empirical observations but instead have to be recognized in the light of an inferred phylogeny. Such an approach does not give primacy to any single class of data but rather implies that all available information may be useful in reconstruction of the phylogeny, and characters should thus not be dismissed beforehand as less useful. Within this framework, the question as to whether shell characters are more homoplastic than soft-part characters, and hence are less informative in phylogeny reconstruction, must be assessed in the light of phylogenetic hypotheses. Homoplasy is commonly described by the consistency index (CI) (Kluge and Farris, 1969) or the retention index (RI) (Farris, 1989). The CI for a character is m/s , where m is the minimum amount of change possible for a given character (equal to the number of character states minus one), and s is the actual number of changes. Because s exceeds m in the event of homoplasy, CI can be used to measure homoplasy. However, as the number of cladogenetic events increases, a character has more opportunities to undergo evolutionary change. Therefore, the amount of homoplasy is expected to increase with increasing number of taxa, something Sanderson and Donoghue (1989) established empirically (see Hauser and Boyajian [1997] and Givnish and Sytsma [1997] for recent accounts of this problem).

The RI expresses the amount of synapomorphy in the data set for a character by examining the actual amount of homoplasy as a fraction of the maximum possible homoplasy; that is, $RI = (g - s)/(g - m)$, where g is the largest possible number of character-state transitions a character could show on any tree. Because the RI is a fraction of maximum homoplasy, it is supposed to take into account the expected increase in homoplasy levels with increasing number of taxa and should therefore, in theory, be more suitable for comparisons between different data sets. But, as Hauser and Boyajian (1997) show, the RI is weakly correlated with the number of

taxa and strongly correlated with the number of characters that undergo change at each internode of a cladogram.

Because of these correlations, and because taxonomic studies normally differ in both number of taxa and characters, pooled values of CI or RI for shell and soft-part characters cannot be compared. To test whether shell characters are more homoplastic than soft-part characters, we have instead calculated the ratio of average CI (and RI) for shell/other characters *within* each study. If shell characters are consistently more homoplastic, this ratio will be <1 in a statistically significant number of studies. We also tested whether these two sources of phylogenetic evidence demonstrated a statistically significant incongruence by comparing the sum of treelengths obtained by the shell (L_{shell}) and soft-part (L_{soft}) characters with the sum of the lengths obtained by random partitioning ($L_{\text{random/shell}} + L_{\text{random/soft}}$) of the characters within the entire data set (Farris et al., 1995). The test statistic S is the number of repartitions for which:

$$(L_{\text{shell}} + L_{\text{soft}}) < (L_{\text{random/shell}} + L_{\text{random/soft}})$$

The Type I error rate for S is given by $[1 - S/(W + 1)]$, where W is the number of randomly selected partitions; a significant value indicates that the null hypothesis (H_0) of congruence is rejected and hence the two character matrices are incongruent.

RESULTS AND DISCUSSION

We reanalyzed 28 published studies (Table 1) on gastropod phylogeny by taking the published data matrices and reconstructing the phylogeny (unless done in the study cited) by using maximum parsimony. For the reasons given above, we included only studies in which both shell and soft-part characters were used. Phylogenetic analyses were carried out by using PAUP v. 3.1 (Swofford, 1993) on a Macintosh Power PC 8500/150. All the data sets were analyzed with the same options as were used in the original articles (when stated). A time limit of 24 hr was set for practical reasons, and if the analysis was not finished by this time, the next fastest search algorithm was used (i.e., heuristic instead of branch-and-bound). Character

TABLE 1. References for the 28 studies included in our analyses. Number of characters for each category/average consistency index (CI)/average retention index (RI) is listed for each reference. All characters with only one state reported are uninformative and are thus excluded for our analyses. *nd*, no data.

Reference	No. taxa	Shell	Soft	Other	Taxon
Bieler (1988) ^a	13	15/0.87/0.87	12/0.86/0.77	1/0.5/0.80	Architectonicidae
Bieler (1993)	14	10/0.87/0.89	31/0.83/0.78	3/0.61/0.70	Ampulariidae
Boato (1991)	6	8/0.88/0.9	3/0.44/0.44	1/1/1	Chondrinidae
Davis and Rao (1997) ^b	10	3/0.69/0.22	20/0.67/0.49	<i>nd</i>	Pomatiopsidae
Emberton (1995)	51	14/1/1	39/0.98/0.99	<i>nd</i>	Polygyridae
Gosliner (1989)	30	1/0.82/0.82	18/0.52/0.65	1/0.82/0	Cephalaspidea
Hausdorf (1998) ^c	25	3/0.70/0.67	34/0.72/0.63	<i>nd</i>	Limacoidea
Hershler and Frest (1996) ^d	10	2/0.75/0.87	19/0.82/0.88	5/0.68/0.70	Hydrobiidae
Hickman (1996) ^e	11	9/0.73/0.65	19/0.93/0.92	6/0.83/0.88	Turbinidae
Houbrick (1993)	7	5/0.70/0.50	14/0.79/0.59	1/0.50/0.50	Cerithioidea
Jensen (1996a)	36	4/0.88/0.75	46/0.56/0.75	1/0.42/0.7	Sacoglossa
Jensen (1996b)	10	6/0.62/0.46	30/0.73/0.59	<i>nd</i>	Sacoglossa
Jung (1992)	10	12/0.71/0.68	45/0.70/0.60	<i>nd</i>	Planorbidae
Kool (1993)	24	4/0.80/0.89	13/0.94/0.96	1/1/1	Muricidae
McLean and Geiger (1998)	11	13/0.76/0.71	4/0.69/0.58	<i>nd</i>	Fissurellidae
Mikkelsen (1998)	38	4/0.88/0.75	48/0.57/0.79	<i>nd</i>	Sacoglossa
Mordan (1992)	12	4/0.56/0.58	17/0.76/0.74	<i>nd</i>	Enidae
Ponder and Lindberg (1996)	25	6/0.69/0.72	81/0.71/0.76	4/0.88/0.92	Gastropoda
Ponder and Lindberg (1997)	40	9/0.74/0.88	104/0.63/0.80	4/0.88/0.95	Gastropoda
Reid et al. (1996)	22	2/1/1	9/0.94/0.97	2/1/1	Littorina
Rosenberg (1996)	15	14/0.85/0.90	18/0.82/0.80	6/0.94/0.94	Truncatellidae
Roth (1991) ^f	12	3/0.65/0.58	16/0.89/0.82	<i>nd</i>	Haplotrematidae
Roth (1996)	24	6/0.61/0.70	11/0.72/0.82	1/0.33/0.67	Helminthoglyptidae
Schander et al. (1999)	16	12/0.63/0.63	20/0.73/0.79	4/0.53/0.65	Pyramidellidae
Scott (1996)	10	1/0.75/0.50	11/0.65/0.50	<i>nd</i>	Camaenidae
Taylor et al. (1993) ^g	42	8/0.24/0.53	32/0.44/0.57	2/0.37/0.74	Conoidea
Willan (1987) ^h	12	8/0.90/0.76	29/0.75/0.70	<i>nd</i>	Notaspidea
Wise (1996) ⁱ	13	6/0.86/0.91	19/0.80/0.79	2/0.75/0.88	Pyramidellidae

^aAll characters were treated as unordered.

^bMultistate coding was used.

^cCharacter 38 was excluded because of uncertainty of coding.

^dThe data matrix was not published in this study but was obtained from the authors.

^eThis study also contains an analysis of Trochidae, but the phylogeny could not be constructed from the published matrix.

^fThe phylogeny reconstruction in this study is based on character compatibility analysis, but we recoded the characters for parsimony analysis.

^gRecoded as in Mikkelsen (1998); multistate unordered coding was used.

^hPreferences from Rosenberg (1998) were used.

ⁱThe original analysis treated characters as ordered but we have included them as unordered.

homoplasy was calculated as both CI (excluding autapomorphies and invariant characters) and RI. The characters were divided into shell- and soft-part characters. Ecological and behavioral characters, as well as characters of the radula and operculum, are referred to as "other". Molecular data from Rosenberg (1996) and data on diploid chromosome number from Boato (1991) were also included in the latter category. This category of characters was included in the phylogeny reconstruction to make it as reliable as possible (total evidence, in accord with, e.g., Kluge [1989]), but we have not tested this category against shell and soft-part characters because it is such a heterogeneous assemblage of character types. Furthermore, the

question we address, and the one discussed in the malacological literature, is the difference in homoplasy between shell and soft-part characters. The incongruence test was carried out in PAUP* ver. 4 (Swofford, 1998) using the HOMPART command with 1000 replicates.

The average CI and RI values are about the same for the three types of characters, although the CI is slightly higher for shell characters (Table 2). The ri values are more variable for soft-part characters, whereas the ci is much less variable for this category of characters. The frequency distributions of both CI and RI are strongly asymmetric (Fig. 1). When compared within each study, the shell characters do not have

TABLE 2. Descriptive statistics for the three types of characters, shell, soft-part, and others. CI = character consistency index, RI = character retention index, *n* = number of characters.

	Shell		Soft-part		Other	
	CI	RI	CI	RI	CI	RI
Mean	0.77	0.76	0.71	0.75	0.75	0.81
Standard deviation	0.26	0.31	0.28	0.30	0.26	0.23
<i>n</i>	193	192	759	759	45	45
Maximum	1.0	1.0	1.0	1.0	1.0	1.0
Minimum	0.11	0.00	0.09	0.00	0.29	0.00
CV, (%)	34.4	40.8	39.1	39.8	34.5	27.7

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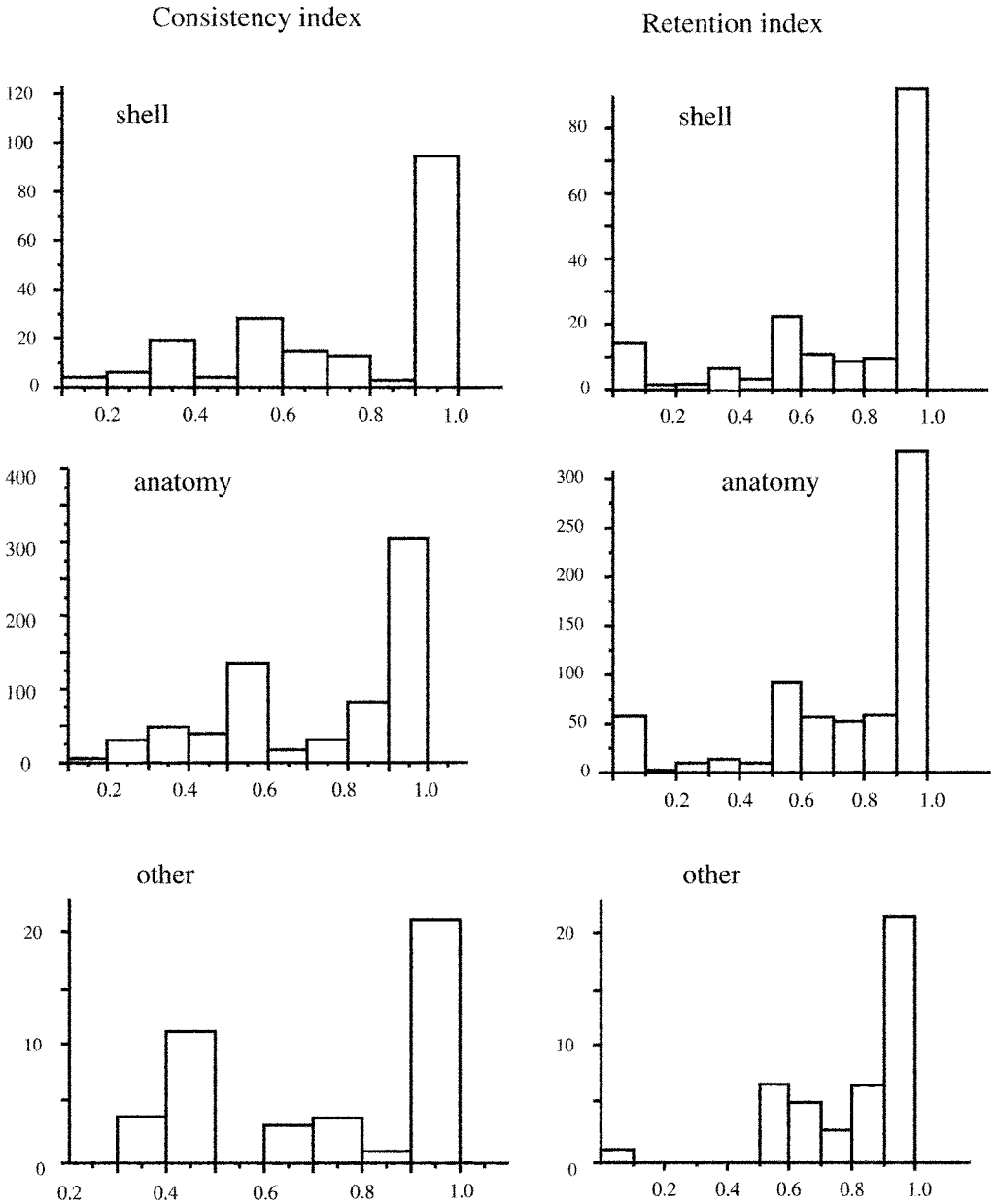


FIGURE 1. Frequency (in absolute numbers) distribution for the consistency and retention indices values for shell, soft-part anatomy, and other characters for all studies combined.

statistically lower *ci* values ($P = 0.71$, two-tailed Wilcoxon matched-pair signed ranks test; H_0 : the median difference between the members of each pair is zero) or *ri* values ($P = 0.78$, two-tailed Wilcoxon matched-pair signed ranks test; H_0 : the median difference between the members of each pair is zero). We therefore conclude that empirical evidence does not support dismissing shell characters in phylogeny reconstruction, or in any discussion about gastropod systematics on a priori grounds. Admittedly, the similar homoplasy values for shell and soft-anatomy characters may be attributable to the authors cited having deliberately excluded characters they considered homoplastic, and therefore already less useful, before the actual analysis. In the absence of evidence for that, however, we conclude that all available information should form the basis for the estimation of the evolutionary history. This interpretation is also supported by the incongruence test, which showed that only 5 of the total 28 character matrices yielded significant (at the 5% level) length differences between trees from soft and shell characters respectively: Boato (1991), Roth (1991, 1996), Jensen (1996b), and Wise (1996).

ACKNOWLEDGMENTS

We thank Kerstin Schander for proofreading the data matrix and Dr. Peter Wagner for useful and constructive suggestions on the statistical treatment. The study was financially supported by the Ax:son Johnson Foundation, Adlerbertska forskningsfonden and Rådman Ernst Collianders Foundation (to C.S.), and the Swedish Natural Research Council (to P.S.). This is contribution number 9946 from Woods Hole Oceanographic Institution.

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Received 20 August 1998; accepted 17 December 1998
Associate Editor: R. Olmstead

Syst. Biol. 50(1):141–149, 2001

Landmark Coordinates Aligned by Procrustes Analysis Do Not Lie in Kendall's Shape Space

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The field of geometric morphometrics is concerned with methods for studying shapes of objects. These methods are increasingly

used to address a broad range of ecological and evolutionary questions. A few recent examples include the study of ontogenetic