Choosing among Poriferan morphological characters
within the cladistic paradigm

by Eduardo HAJDU & Rob W.M. VAN SOEST

Abstract

A protocol is proposed by which certain classes of characters may be selected for use in phylogenetic reconstruction due to their overall better consistency in phylogenies. Alternatively, they could receive additional weight as opposed to classes that show an overall poor consistency and should be down weighted. We recognized 16 classes of characters within previously published data matrices of 17 poriferan phylogenies involving 221 OTUs (Operational Taxonomic Units, = terminal taxa). Only five classes occur in samples of large enough size that can allow discussion of observed trends. The high consistency observed in choanosomal architecture characters is possibly an artefact. Megascleres and microscleres show opposing results and these are discussed with reference to function and adaptation. In general, results are deemed preliminary because sample sizes are too small for the majority of recognized classes of characters, and different classes of characters may perform differently in different taxa, a suspicion which calls for an even larger sample base.

Keywords: cladistics, character selection, Porifera, phylogenetic systematics.

Introduction

The recognition of homologies is a crucial issue in systematics because it is through homologies that relationships among taxa are inferred (e.g. DARWIN, 1859; PINNA, 1991; FOREY et al., 1992; NELSON, 1994; SMITH, 1994). PINNA (1991) stated that homologies sensu lato may actually be classified into primary (those that generate hypotheses of homology) and secondary (those that legitimate hypotheses of homology). Primary homologies are those detected on the basis of similarity alone (e.g. axial condensation in Axinellidae and Raspailiidae), while secondary homologies are the outcome of a pattern-detecting analysis (e.g. acanthostyles of Raspailiidae and remaining poecilosclerids). This interpretation supports PATTERSON’S (1982) equation of homology with synapomorphy.

A phylogenetic analysis may be outlined as a two step procedure then, where the initial assembly of a data matrix (= compilation of a set of conjectures of homology) is followed by parsimony analysis of relationships. The initial conjectures of homology will be either supported, refuted or left undecided. This can be translated in, respectively, scores for the same character state emerging as synapomorphy, homoplasy, or both alternatives being possible in the resulting tree profile. In other words, primary conjectures of homology can be classified, after a phylogenetic analysis, into those which appear to be correct, those which may be wrong and those where no assignment seems possible.

Parsimony has been established as the most powerful and logically sound method to sort among primary conjectures of homology, indicating the status of each - correct, wrong or dubious (FARRIS, 1983; SOBER, 1988; PINNA, 1991; STEWART, 1993), and maximizing those primary conjectures of homology that end up as secondary homology. Since it is the objective of systematists to find the greatest possible number of corroborated primary homologies - otherwise phylogenetic reconstruction would
become a chance method with no objectivity - a procedure indicating which, if any, classes of characters consistently yield more primary homologies that are correct would be welcome. This would allow systematists to focus on those classes of characters where similarities are less misleading, and can thus be more safely translated into true homologies. Phylogenetic systematics made a step forward relative to numerical taxonomy, in recognizing that primitive similarity, plesiomorphy, can be quite misleading for the assessment of relationships among taxa. The use of outgroups is a way of focusing attention onto characters that are derived and thus relevant for the assessment of relationships within a selected ingroup. Nevertheless, even among derived character states there will often be those that are really homologous, those that are homoplastic, and those that must remain undecided after the analysis. Homoplastic characters may also be important in the establishment of tree topology (DAVIS & KLUGE, 1993), but their occurrence should be as few as possible given the assembled data matrix or the obtained tree runs the risk of being not the one that best reflects the original data. Surely, seeking parsimony minimizes the level of homoplasy present in the final cladogram(s), but even so this level frequently remains very high. This may be disappointing in the sense that assembly of a data matrix is quite often an elaborate, time consuming enterprise, and the belief is widespread that low consistency (= high homoplasy) is synonymous with low support [but see GOLDBOFF'S (1991) ideas on decisiveness]. If the assembly of data matrices could somehow be focused on those characters that consistently show less homoplasy, perhaps some optimization of the assembly protocol could be obtained, i.e. some characters could either be ignored, or at least have their assessment postponed to some future analysis.

It is now becoming accepted that total evidence is the best approach to a phylogenetic analysis (e.g. KLUGE, 1989). However, debate goes on as to whether or not independent classes of characters (defined in terms of process partitions; sensu BULL et al., 1993) should be better kept isolated (e.g. KLUGE & WOLF, 1993; MIYAMOTO & FITCH, 1995). A corollary derived from the rational behind this latter approach is that the more characters that are analyzed from each class of characters, and the more concurrence between classes of characters, the more sound the phylogenetic results will be. Nevertheless, systematic practice dictates how 'total', total evidence will be for a particular study. Often, the sole guideline for choosing characters is the author's familiarity with this or that technique (which restricts study to one or a few character environments) - anatomy of hard parts, ultrastructure, cytology, secondary metabolites, isozyme electrophoresis, DNA/RNA sequencing (see NOVACEK & WHEELER, 1992).

With the above in mind, we decided to focus on a procedure for the selection of characters that applies to characters belonging to a single environment. The simple discarding of characters on the basis of personal beliefs on how they perform on phylogenetic analyses is very subjective. We suggest that particular classes of characters within a single character environment might be selected on the basis of their overall better consistency, an idea which paralleled BEGLER'S (1991) scheme for judging the relative usefulness of gain characters as opposed to losses. Another possible use of such an approach could be the establishment of relative levels of confidence on particular classes of characters within a single environment, thus allowing a priori weighting schemes to be adopted.

Materials and methods

CLASSES OF CHARACTERS

Classes were established on the basis of current practice, in parallel with recognized assemblages of characters in the latest glossary of poriferan morphological terms (BOURY-ESNAULT et al., in prep.). There are classes pertaining to more than one character environment, but those approaching reasonable dimensions belong to the domain of the so called 'classical' approach to sponge taxonomy. Other classes were set aside due to their very low number of occurrences within the sampled data sets (Table 1).

METHODS

Seventeen published data matrices for monophyletic groups of poriferan taxa totaling 221 OTUs were used to assess the performance of sixteen classes of characters in terms of their consistency. Data matrices were analyzed with SWOFFORD'S (1993) program PAUP 3.1.1. Shorter trees were searched through the heuristic algorithm following the steps outlined in HAJDU (1995). The performance (p) of each class of characters was calculated according to the following equation:

\[ p = \frac{hc}{n} \times 100\% \]

where \( hc \) is the number of occurrences of characters assigned to a particular class that obtained the highest consistency (c = 1.0) after PAUP's reweighting procedure, and \( n \) is the total number of characters pertaining to the same particular class among the 210 characters sampled in our study.

Table 2 shows the taxa for which data matrices were available, authorship of the compilations, as well as number of OTUs and characters for each of them.

Results

Table 3 shows the five classes of characters that had large enough sample sizes. All of these pertain to classical morphological characters, which include data on the shape of sponges as well as on the anatomy of their hard parts (spongin skeletons included).
Table 1. Number of occurrences of each class of characters within the 17 sampled poriferan data sets (refer to Table 2).

<table>
<thead>
<tr>
<th>Class of Characters</th>
<th>Occurrences</th>
</tr>
</thead>
<tbody>
<tr>
<td>chemistry</td>
<td>3</td>
</tr>
<tr>
<td>choanosomal architecture characters (CA)*</td>
<td>25</td>
</tr>
<tr>
<td>cytology</td>
<td>1</td>
</tr>
<tr>
<td>colour</td>
<td>1</td>
</tr>
<tr>
<td>consistency</td>
<td>2</td>
</tr>
<tr>
<td>ectosomal architecture characters</td>
<td>7</td>
</tr>
<tr>
<td>features of the aquiferous system</td>
<td>1</td>
</tr>
<tr>
<td>habit</td>
<td>13</td>
</tr>
<tr>
<td>habitat</td>
<td>2</td>
</tr>
<tr>
<td>larval morphology</td>
<td>1</td>
</tr>
<tr>
<td>megascleres: present or absent, categories (Mp/a+c)*</td>
<td>23</td>
</tr>
<tr>
<td>megascleres: shape, dimensions (Ms/d)*</td>
<td>29</td>
</tr>
<tr>
<td>microscleres: present or absent, categories (mp/a+c)*</td>
<td>41</td>
</tr>
<tr>
<td>microscleres: shape, dimensions (ms/d)*</td>
<td>51</td>
</tr>
<tr>
<td>reproduction</td>
<td>1</td>
</tr>
<tr>
<td>surface</td>
<td>9</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>210</strong></td>
</tr>
</tbody>
</table>

* abbreviations for character classes used in the text for discussion of observed trends.

Discussion

Our approach is guided by systematic practice among specialists of Porifera - characters most often employed are those related to habit (such as shape, color, surface, consistency) and anatomy of hard parts (spicules, architecture). Whether or not habit should be combined in a single data matrix with data derived from the anatomy of hard parts, and whether all of the anatomy of hard parts belong to a single process in the sense of BULL et al. (1993; cf. MIYAMOTO & FITCH, 1995) are questions beyond the scope of our study.

A more serious concern to us is the fact that some classes of characters are poorly represented within the sampled data sets (e.g. cytology, color, habitat, larvae - Table 1), and accordingly no general picture may be drawn for them until more data is available. Nevertheless, five classes show a reasonable number of occurrences, viz. 23 to 51 times. These were: choanosomal architecture (CA), presence/absence of megascleres (Mp/a+c), shape/dimensions of megascleres (Ms/d), presence/absence of microscleres (mp/a+c), and shape/dimensions of microscleres (ms/d). If we establish above 50 % of scores of c = 1.0 as a minimum requirement for considering a character comparisons (ARCHIE, 1990) will be the same as c, when c = 1.0, and will thus produce no change in our results because only those scores of characters where consistency was maximum (c = 1.0) were selected. Precisely the same reasoning applies to another index proposed by FARRIS (1989a), viz. the rescaled consistency index, rc. A different performance relative to autapomorphies is irrelevant here since these were discarded in the present analyses.

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Table 2.
Seventeen used data matrices*, their source references and number of OTUs.

<table>
<thead>
<tr>
<th>Data matrices:</th>
<th>Numbers of ingroup OTUs : characters</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acarnus</em> (Poecilosclerida)</td>
<td>21 : 19</td>
</tr>
<tr>
<td>(VAN SOEST, HOOPER &amp; HIEMSTRA, 1991)</td>
<td></td>
</tr>
<tr>
<td><em>Ceratopsis/Thrinacophora</em> (Poecilosclerida)</td>
<td>16 : 10</td>
</tr>
<tr>
<td>(HOOPER &amp; LÉVI, 1994)</td>
<td></td>
</tr>
<tr>
<td><em>Clathria procera</em> spp. group (Poecilosclerida)</td>
<td>9 : 7</td>
</tr>
<tr>
<td>(HOOPER &amp; LÉVI, 1994)</td>
<td></td>
</tr>
<tr>
<td><em>Didiscus</em> (Halichondrida)</td>
<td>7 : 11</td>
</tr>
<tr>
<td>(HIEMSTRA &amp; VAN SOEST, 1991; emended**)</td>
<td></td>
</tr>
<tr>
<td><em>Fistulose iophonids</em> (Poecilosclerida)</td>
<td>19 : 14</td>
</tr>
<tr>
<td>(VAN SOEST, ZEA &amp; KIELMAN, 1994)</td>
<td></td>
</tr>
<tr>
<td><em>Halichondrida</em></td>
<td>4 : 4</td>
</tr>
<tr>
<td>(VAN SOEST, DIAZ &amp; POMPONI, 1990)</td>
<td></td>
</tr>
<tr>
<td><em>Halichondriidae</em> (Halichondrida)</td>
<td>12 : 10</td>
</tr>
<tr>
<td>(VAN SOEST, DIAZ &amp; POMPONI, 1990)</td>
<td></td>
</tr>
<tr>
<td><em>Keratosa</em> (Dendroceratida, Dictyoceratida, Verongida)</td>
<td>7 : 8</td>
</tr>
<tr>
<td>(VAN SOEST, 1991)</td>
<td></td>
</tr>
<tr>
<td><em>Mycale</em>, the 'curved-assemblage' (Poecilosclerida)</td>
<td>32 : 27</td>
</tr>
<tr>
<td>(HAJDU, 1995)</td>
<td></td>
</tr>
<tr>
<td><em>Mycalidae + Hamacantha</em> (Poecilosclerida)</td>
<td>10 : 11</td>
</tr>
<tr>
<td>(HAJDU &amp; DESQUEYROUX-FAÜNDEZ, 1994)</td>
<td></td>
</tr>
<tr>
<td><em>Pachastrellidae-I</em> (Astrophorida)</td>
<td>11 : 11</td>
</tr>
<tr>
<td>(MALDONADO, 1994)</td>
<td></td>
</tr>
<tr>
<td><em>Pachastrellidae-IV</em> (Astrophorida)</td>
<td>10 : 10</td>
</tr>
<tr>
<td>(MALDONADO, 1994)</td>
<td></td>
</tr>
<tr>
<td>Poecilosclerid families (Poecilosclerida)</td>
<td>9 : 8</td>
</tr>
<tr>
<td>(DESQUEYROUX-FAÜNDEZ &amp; VAN SOEST, submitted)</td>
<td></td>
</tr>
<tr>
<td><em>Ptiloecaulis/Reniochalina</em> (Halichondrida)</td>
<td>14 : 9</td>
</tr>
<tr>
<td>(HOOPER &amp; LÉVI, 1994)</td>
<td></td>
</tr>
<tr>
<td><em>Rhabderemia</em> (Poecilosclerida)</td>
<td>23 : 20</td>
</tr>
<tr>
<td>(VAN SOEST &amp; HOOPER, 1993)</td>
<td></td>
</tr>
<tr>
<td><em>Tethyidae</em> (Hadromerida)</td>
<td>8 : 18</td>
</tr>
<tr>
<td>(SARÁ &amp; BURLANDO, 1994)</td>
<td></td>
</tr>
<tr>
<td>Tetractinellid-hadromerid-hemiasterellid relations</td>
<td>9 : 13</td>
</tr>
<tr>
<td>(Astrophorida, Desmophorida, Hadromerida, Spirophorida)</td>
<td></td>
</tr>
<tr>
<td>(VAN SOEST, 1991)</td>
<td></td>
</tr>
<tr>
<td>total</td>
<td>221 : 210</td>
</tr>
</tbody>
</table>

* Other phylogenies are available, but they either do not comprise monophyletic assemblages or data matrices were not provided. ** The New Zealand Oamaru fossil species, *D. hindei*, has been added to the data matrix prior to the analysis. Six out of the 16 used characters pertain to the discorhabds and can be scored for the fossil species on the basis of the drawing provided by HINDE & HOLMES (1891).
Table 3.
Relative performance in terms of percent occurrences of \( c = 1.0 \), when \( c \) is tabulated for every single character pertaining to each of five classes of characters, which have a reasonable number of occurrences among the 17 sampled poriferan data matrices (refer to Table 2). Abbreviations according to Table 1.

<table>
<thead>
<tr>
<th>Class</th>
<th>Performance</th>
</tr>
</thead>
<tbody>
<tr>
<td>CA</td>
<td>64% (16/25)</td>
</tr>
<tr>
<td>Mp/a+c</td>
<td>74% (17/23)</td>
</tr>
<tr>
<td>Ms/d</td>
<td>52% (15/29)</td>
</tr>
<tr>
<td>mp/a+c</td>
<td>39% (16/41)</td>
</tr>
<tr>
<td>ms/d</td>
<td>59% (30/51)</td>
</tr>
</tbody>
</table>

The distinctly opposed reliability of megascleres versus microscleres is remarkable. While \( Mp/a+c \) performed better than \( Ms/d \), the opposite trend was observed in microscleres. Megascleres presumably play a more relevant structural role in most sponges due to their prominent occurrence in skeletons (DENDY, 1921) - e.g. coring and/or echinating fibres, supporting ectosomal tangential skeletons. The functional role for microscleres is obscure (cf. RIDLEY & DENDY, 1887; DENDY, I.e.), and even where a particular function has been demonstrated (e.g. VACELET & BOURY-ESNAULT, 1995) it seems unlikely that a similar role could not be performed by a megasclere, or another kind of microsclere. In the case of the *Asbestopluma* reported by VACELET & BOURY-ESNAULT (1995), spines in the megascleres, if they would have been present, would most probably perform the same function as the small anisochelae, viz. trapping of zooplankton. It seems to us then that the evolution of megascleres and microscleres need not be guided by the same factors. WHEELER (1986) quoted the following sentence by DARWIN (1859): "The less any part of the organization is concerned with special habits, the more important it becomes for classification." This is the essence of what is known as Darwin Principle (MAYR, 1979), viz. that characters of low adaptive value are important echoes of underlying genetic similarities.

Extrapolating this idea to the characters under consideration here is not entirely straightforward as will be shown below. The trend observed in megascleres of higher c levels in presence/absence + categories as opposed to shape/dimensions could suggest that changes in shape/dimensions are less decisive for sponge functions and thus more easily achieved independently (i.e. oxeas and styles may have the same function). On the other hand, complete loss of categories seems more problematic in terms of sponge function and thus less likely to happen independently (i.e. megascleres are backbones essential for sponge sustenance, their loss may mean collapse of architecture). These are possible interpretations for adaptively constrained morphological characters. Microscleres, according to RIDLEY & DENDY (1887), DENDY (1921), HAIDU et al. (1994) and others, are most likely non-adaptive characters. As argued above, it is unlikely, in most cases, that microscleres have an unequivocal function in poriferan architecture. If an anisochela is believed to act as a hook, there is no clear reason why such a function could not be performed by a sigma, or by an acanthostyle. Accordingly, \( mp/a+c \) has a generalized low level of c. Why do we observe a high level of c for \( ms/d \) ?

MACBETH (1980) in discussing the concept of irreversibility postulated that evolution never retraces its steps in a big way, but it often reverses one or another change. There is no clear border between irreversibility of the 'big' phenomena and the more
likely reversibility of the 'smaller' ones. LAURENT (1983) compared the former with "the unreeuling of a movie film", and the later with the simpler idea of loss and reappearance of characters (even of complex ones). In our view, the improbability of a big reversion in microscleres can be equated with the relatively high stability of shapes (ms/d : 59 % of c = 1.0). This is so even though some shapes are believed to pertain to a single transformation series. In support of this idea HAIDU et al. (1994) pointed out that only three species are known that may have two distinct cheleae morphotypes. This suggests that although chelae may have evolved in the direction of palmate through arcuate to anchorate, development of a derived morphotype does not imply going through the more primitive ones as in an ontogenetic series. This argument should apply to other forms of microscleres too. In other words, once something new is evolved, information (genetic control) on how to build the former stage once something new is evolved, information are lost. On the other hand, megascleres, shape/dimensions of microscleres perform better (52 and 39 % of c = 1.0, respectively). A much larger data base is needed in order to properly verify these suspicions. A final concern relates to the fact that different characters may perform distinctly well in terms of c within different taxa, i.e. c could be taxon-specific. A much larger data base is needed in order to properly verify these suspicions. An alternative interpretation of the results may be ventilated though, in which, except for the 74 % c = 1.0 obtained by presence/absence + categories of megascleres, results may all suggest high levels of homoplasy, and consequently low confidence levels in most classes of characters. Since the reasonably large classes considered here all pertain to the domain of the anatomy of hard parts, one could be tempted to say: "Let us do chemistry then!". KELLY-BORGES (pers. comm.) commented that she obtained similar consistencies for molecular data. The message may be then that homoplasy is high in different character environments, and that no, or perhaps only a very few classes of characters are more trustworthy than the others. If such a scenario is true, hard labor of the 'blind' systematist is the only tool to extract phylogeny out of it. Additionally, less trustworthy characters, if used in an analysis would need additional care in the scoring of primary conjectures of homology (similar scores for a character state in a data matrix). An alternative use of our protocol is to objectively establish confidence levels on particular classes of characters, an important building block in an a priori weighting scheme. The data base of poriferan characters is still too meager, as a reflection of incipient use of cladistic procedures in day-to-day practice among specialists in Porifera (only 17 phylaenies are available which contain published data matrices). This precludes any firmer conclusions to be drawn for most of the 16 recognized classes of characters. Nevertheless, five classes have sample sizes approaching the reasonable (22-50). Among these, shape/dimensions of megascleres and presence/absence + categories of microscleres perform poorly (52 and 39 % of c = 1.0, respectively). Choanosomal architecture characters, presence/absence + categories of megascleres and shape/dimensions of microscleres perform better (64, 74 and 59 % of c = 1.0, respectively). A much broader data base is needed in order to check whether different classes of characters would perform differentially in distinct taxa.

Conclusions

The method outlined here may help in determining which characters are more trustworthy in terms of phylogenetic signal (congruence with other characters), based on their performance on previously cladistically analyzed data sets. These characters could be the ones selected in the future for new analyses, while less trustworthy characters would have their assessment postponed or simply discarded. Additionally, less trustworthy characters, if

Acknowledgments

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