

Phylogeny of the South Asian Halyini? Comments on Memon et al. (2011): Towards a Better Practice in Pentatomidae Phylogenetic Analysis

Terminal Taxa

TO THE EDITOR:

Recently, Memon et al. (2011) published a article entitled “Phylogeny of the South Asian Halyine Stink Bugs (Hemiptera: Pentatomidae: Halyini) Based on Morphological Characters” (Ann. Entomol. Soc. Am. 104: 1149–1169). The main goal of the authors was to estimate the phylogenetic relationships of the South Asian genera of Halyini based on morphological characters. In our opinion, the authors overlooked some of the basic tenets of a phylogenetic analysis by their: use of an untested a priori hypothesis of relationship, choice of ingroups and outgroups, definition of character and character states, and interpretations of the results. Herein, we do not intend to determine the best practices in phylogenetic analysis but to discuss some points of their analysis that are under-developed and cannot be disregarded.

Ingroup and Outgroup Sampling

According to Memon et al., Halyini is monophyletic, despite the fact that there is no published phylogeny, and its taxonomy and systematic position need revision. The taxon sampling of Memon et al. is restricted to South and Central Asian species; they did not include species from outside the studied area (the tribe is known to include species from North America, Africa, and Australia) or taxa that have been allied to Halyini. Therefore, the absence of outgroups and the restricted ingroup sampling do not allow the authors to investigate their main question or, much less, Halyini monophyly. A group monophyly is tested by the optimal placement of the outgroup terminals outside of the ingroup (Farris 1972). Even without changing ingroup monophyly, outgroup taxa can change their relationships. Furthermore, at least two outgroup terminals are required to test ingroup monophyly. These include one terminal that serves as the root and another that is free to potentially fall inside the ingroup. Memon et al. claim that all analyzed genera belong to Halyini because of basic halyine tribal characters (for such characters see p. 1150), which are used by all the researchers to identify tribe members. In the most comprehensive, although unpublished, phylogeny of Halyini, Wall (2004) described these characters as homoplasious and the tribe as paraphyletic, thereby making it impossible to define the tribe with an exclusive synapomorphy.

Memon et al. adopted the ground plan character coding approach in their analysis. The authors' data matrix has supraspecific taxa as terminals (p. 1151, for a species list see Appendix), but they do not mention the criteria used to manage intra- and interspecific variations nor how they coded the terminals. The ground plan character coding approach consists of a variety of methods that are frequently not specified by the authors and considered to be intuitive (some methodological explanations can be found in Prendini 2001). The main methodological objection to the use of supraspecific taxa as terminals is the assumption of its monophyly, which is particularly dangerous in very diverse taxa such as the Halyini. The exemplar coding approach seems to be superior in this regard because species as terminal taxa are defined on diagnosability criteria rather than monophyly. Therefore, the exemplar approach is preferable for interpreting character polarity because it uses observable and verifiable data, rather than hypothetical states and character combinations (Prendini 2001).

Characters and Character States

The methods of Memon et al. do not adhere to any logical procedure for coding morphological characters. In the same character, is possible to observe information regarding quantitative traits and form as well as the presence or absence of particular characters, such as the character “Shape of Lateral Margins of Pronotum” (p. 1155). Brazeau (2011) analyzed the effects of different coding practices in morphological phylogenetic analysis and suggested that certain practices are undesirable and should be avoided. Particularly, multistate character information may impose congruence artificially by linking more than one character variable to a particular state. Additionally, their character explanations are biased and result in the a priori establishment of the typical character states of a particular taxon, for example, “A dentate lateral margin to the pronotum is a halyine character differentiating genera of the tribe from most others (apart from some Australian genera).” Within a cladistics framework, such a conclusion should be resultant of an analysis and is dependent on the taxa included.

Missing Data

Memon et al. justified the exclusion of some taxa from the analysis on the basis that taxa with large proportions of missing characters decrease the accuracy of phylogenetic inference. However, the level of data completeness alone should not guide the exclusion of taxa, and most studies suggest that it is generally possible to accurately place incomplete taxa in phylogenies if enough informative characters are sampled (Wiens and Morrill 2011). In addition, their matrices

do not have large amounts of missing data, and the authors did not perform tests to ascertain whether such taxa would decrease the accuracy of phylogenetic inference to justify their exclusion.

Phylogenetic Analysis

Although not explicitly stated, the phylogenetic analysis completed by Memon et al. supposedly followed the procedures of successive weighting using the rescaled consistency index with the sole purpose of reducing the number of equally parsimonious trees found. According to Goloboff (1993), some authors still incorrectly advocate weighting as a method only for selecting a tree among the shortest trees under equal weights. In the study by Memon et al., this argument does not apply because the tree determined under successive weighting was not among the equally parsimonious trees found in an analysis with equal weights. Under an equal weights parsimony analysis, the authors found 5,825 equally parsimonious trees for the complete matrix (31 terminal genera) and 52 trees for the reduced matrix (22 terminal genera). This occurred because no collapsing rule was applied during the heuristic search, which was not mentioned. If one uses a collapsing rule, such as "collapsing branches if supported ambiguously" (min. length = 0: PAUP rule 1), 419 and 11 equally parsimonious trees would be determined for the same respective data sets (swapping algorithm = TBR, 3,000 RAS, saving 150 trees per replication).

Final Comments

As challenging as it may be to elect an outgroup taxon for cladistics analysis in Pentatomidae, such difficulty does not justify the exclusion or noninclusion of any taxa. There are some cues to guide such choices, for example, Hasan and Kitching (1993) suggest a monophyletic clade comprising Halyini, Megarrhamphini, Tetrodini, and Phyllocephalini, and Wall (2004) states that Halyini putative genera do not form a monophyletic assemblage in any of his analyses. Moreover, as a first attempt, one can select outgroup taxa based on shared taxonomic history or by the morphological diversity of analyzed characters.

In the last three decades, cladistic analysis has improved with the development of several new procedures. There are current debates concerning relevant practices adopted in cladistic analysis, such as how to describe and encode characters; whether to weight all characters equally or based on some optimization criteria other than the number of steps (e.g., homoplasy); how to choose outgroup taxa and how many are needed; and which measure of branch support is the more appropriate to evaluate the results. Most of these questions are still dependent on the researcher's method-

ological background and theoretical beliefs, but we advocate that whatever method is chosen should be explained and justified.

Aiming toward a better practice of phylogenetic systematics and an improvement on the development and interpretations on the Pentatomidae phylogeny, we suggest the following: 1) the use of broader outgroup samples, allowing more reliable tests of monophyly; 2) the use of more than one species per genus and its individual entry in the data matrix, avoiding the ground plan approach for character coding; 3) encoding of the characters clearly and objectively, making clear the procedure coding type; 4) illustration of the main characters; and 5) clearly explaining all the methodological procedures, allowing for analytic repeatability.

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