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A cladistic re-analysis of the Gadiformes (Teleostei, Paracanthopterygii) using three-item analysis

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Abstract

In the present paper, we describe LisBeth, a newly published phylogenetic program. LisBeth implements the cladistic three-item analysis for systematics and biogeography. We show how LisBeth handles character representation, character analysis, exact search functions, reconstruction of the intersection tree and other features, such as retention index, completeness index, character history and link with other programs such as PAUP*, version 4.0b10, TNT and Xper². Using LisBeth, we reanalyze the phylogeny based on morphological characters of the order Gadiformes (Teleostei, Paracanthopterygii) published by Endo (2002) and compare our results. We also describe the generation of hypotheses of homology following Endo's guidelines versus 3ia representation schemes. We compare the topologies of all results and show the implications of the interpretation of character history.

Key words: Intersection tree, LisBeth, phylogenetic characters, phylogeny, systematics

Introduction

LisBeth v. 1.3, is a computer program that implements phylogenetic and biogeographical analyses (Zaragüeta Bagils *et al.* 2012). In this paper we present a step by step account of how to conduct a systematic analysis using LisBeth. Our analysis is demonstrated using the data from a morphological study of fishes from the order Gadiformes (Teleostei, Paracanthopterygii, *sensu* Nelson 1994).

Gadiforms constitute over one quarter of the world's marine fish catch (Nelson 2006). Their distribution ranges from Arctic to Antarctic waters in all oceans, from the deep-sea benthos to the shore, with both estuarine and fresh waters habitats (Cohen *et al.* 1990). The order displays a great morphological diversity. Despite the general agreement of the monophyly of Gadiforms with its current composition, its classification is still controversial (Endo 2002; Nelson 2006). This demonstration is based on the classification presented by Endo (2002). We have re-examined the relationships among taxa using 23 morphological characters he published (Endo 2002) and we evaluated the effect of theoretical assumptions and methodological choices. Endo (2002) detailed the 23 characters used and provided all the evolutionary assumptions required for their representation in three-item analysis (3ia hereafter) using LisBeth.

LisBeth is the only software to date that implements a hierarchical representation of characters for 3ia. The three-item method was introduced by Nelson & Platnick (1991), as a binary matrix based approach in systematics. Fractional weighting was later introduced by Nelson & Ladiges (1992, 1993) (see also Wilkinson 1994a, Kitching *et al.* 1998; Cao *et al.* 2007; Zaragüeta Bagils & Bourdon 2007; Williams & Ebach 2008; Zaragüeta Bagils *et al.* 2012). The foundations of 3ia are still debated (Harvey 1992; Farris & Kluge 1998; Scotland 2000; Nelson *et al.* 2003; Farris 2012) nonetheless the method has been applied to several studies in systematics (Patterson & Johnson 1995; Udovicic *et al.* 1995; Ladiges *et al.* 1999; Williams 1996; Ebach and McNamara 2002; Bourdon 2006; Cao 2008; Corvez 2012; Grand *et al.* 2013) and in biogeography (Ladiges *et al.* 1992; Morrone & Carpenter 1994;

supported the clade H with 5 synapomorphies (Fig. 3D): two branchiostegal rays on epihyal (9-0), many actinosts (15-1), a posteromedial extension of the median process of the pelvic girdle (16-1), two dorsal supernumerary fin-rays with one pseudospine (18-1) and the reduction of pelvic fins (19-1). The 3ia method of traceability of characters did not retain 15-1 as a synapomorphy for this clade (Fig. 3C). Both of our analyses recovered two branchiostegal rays on epihyal (9-0) and the reduction of pelvic fins (19-1) as synapomorphies (Fig. 3A, B) for the clade H.

Intersection tree. The intersection tree (Cao *et al.* 2009) that we found using LisBeth is a summary tree of greater significance than a consensus tree. The intersection tree summarizes all the information (in terms of relationships) that is common to the optimal trees, and only this information. The intersection tree has the desirable characteristics of consensus trees (Wilkinson 1994b). It is an accurate summary as exemplified by the intersection of Endo's 11 optimal trees (2002). The intersection tree topology is exactly congruent with the strict consensus tree (the clades B, C, D, E, F, G, H are recovered) and even more resolved since it yields the clade A (Fig. 1.D). Since Endo's strict consensus did not yield this clade, Endo (2002) discussed one of the shortest trees presenting the clade A, hence our choice of emphasizing it.

Conclusion

There are fewer differences between our first 3ia analysis and Endo's strict consensus (2002) than between our second 3ia analysis and Endo's strict consensus. This result is not surprising since, for our first analysis, the representation of all of the 23 characters followed Endo's evolutionary assumptions. What is surprising is that the second analysis does not provide a meaningless result, even if 11 of the characters were represented differently (Table 1). For this second analysis, we observed all of the constraints promoted by 3ia. For instance, a "secondarily loss" is not a putative synapomorphy within the character, a state present in a single taxon does not lead to represent such taxon as an internal class by itself in the character hierarchy, taxa for which data are missing are truly absent from the character, taxa for which data are inapplicable are not placed in the less inclusive classes in the character hierarchy.

Researchers who are used to conduct parsimony analyses may have some hesitations to represent constraints such as "secondarily losses are not putative synapomorphies", but we consider it important to remain consistent with the theoretical foundations of each method. Such foundations indicate how to deal with hypotheses and constraints in a proper way, that is, in order to recover the phylogenetic signal. For instance, losses or reversions are not represented as homology hypotheses with 3ia whereas they can be putative synapomorphies with parsimony.

Although losses or reversions are not represented as homology hypotheses with 3ia, 3ia does not forbid hypotheses of loss or reversion in the interpretation of the evolutionary history. The traceability of character history may lead to interpretation of some patterns as secondarily loss events. However, secondarily losses are neither considered synapomorphies nor homoplasies, as in parsimony methods because they are not tested as hypotheses of homologous features. For instance, with our second analysis, the state 4-1 (character 4 being "*Adductor mandibular* A2 covering *levator arcus palatine*") which is "lap partly or entirely covered by A2" characterizes a clade including *Muranolepis*, *Raniceps*, *Meluccius* and the Gadidae. However, Gadinae, Lotinae, *Raniceps* and *Merluccius* do not present such state. Here, this absence can be interpreted as a secondarily loss.

LisBeth's user-friendly interface allows an easy handling of items thanks to a pointing device gesture (i.e., drag-and-drop) (see the Appendix, Fig. 8-10). This intuitive interface makes it easy for both novice and expert users to start and conduct 3ia studies. LisBeth satisfies the long-standing need for a user-friendly and intuitive environment in 3ia.

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APPENDIX

LisBeth: Functions (All figures are screen-shots from LisBeth v.1.3.)

Taxa edition—Under the “Taxa edition” mode, taxon names may be entered, renamed, removed from the list and sorted by name or by code (Fig. 6). For instance, in Fig. 6, Gadinae, Lotinae and Gaidropsarinae have already been entered and Phycinae is being typed. LisBeth generates a text file (with the extension “.3ia”), which stores the list of taxa.

Character edition—Hierarchical characters are named and can be represented as Venn diagrams or rooted trees, both representations being equivalent (use the Tree / Venn diagram button, Fig. 7). Under the Venn diagram representation, included states (i.e., classes of the Venn diagram) are built using <Ctrl-Click> and can be named using <Shift-Click>. Characters are stored in the “Characters” window. In Fig. 7, the “nasal morphology” character has already been stored and the “presence of anterolateral processes on lachrymal” character is being built, displaying one informative state (“present”). Taxa are then dragged in their corresponding class, e.g. *Trachyrincus*, Macrourinae and *Squalogadus* present the anterolateral process on the lachrymal (Fig. 8); all of the other taxa are dragged in the most general class, i.e. the root of the hierarchy (Fig. 9). This hierarchical representation allows for distinguishing missing and inapplicable data (Zaragüeta Bagils & Bourdon 2007). When information is missing, the corresponding taxa are not dragged into the character; when an informative state is irrelevant for a taxon, this taxon is placed in the general class. The rooted tree representation is particularly useful for the modification of taxon connections. For instance, Fig. 10 shows how *Squalogadus* can be dragged from the included class to the inclusive/general one. LisBeth automatically writes characters in the text file.3ia under a given syntax (for more details on the syntax, see LisBeth documentation; the characters of our analysis are provided as supplementary data).

Character analysis—From the list of characters, LisBeth computes their three-item statements (3is) with their fractional weights. A text file (with the extension “.3iz”) is automatically generated.