Xenacoelomorpha flatworms are basal Deuterostome

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Research article

Abstract

Background: Whether position Xenacoelomorpha as an early branch of Bilateria (Protostomes + Deuterostomes) has been intensely debated during last several decades. Considering Darwin's "tree of life", with the "Phylogenetic Species Concept", we choose mitochondrial genome as the subject to predict phylogenetic position of Xenacoelomorpha, by genes genealogy.

Results: Herein, we sequence Heterochaerus australis's mitochondrial genome and infer intrinsic relationships of Metazoan with Xenacoelomorpha. The optimal tree under the popular maximum likelihood (ML) and Bayesian phylogenetic reconstructions are consensus with each other being strongly supported. The relationship between Chordates, Ambulacrarians and Xenoturbella/Acoelomorph is resolved. To avoid previous query about alignment process, the datasets are alignmented and trimmed automatically. Reducing taxon or cutting outgroups can not affect the relationship between Xenacoelomorpha and other Metazoan. Meanwhile, analysis using CAT model and Dayhoff groups also supporting the prediction made by mtZOA, relaxing the restriction of alignment criteria (MAFFT, strategy G−ins−1, BLOSUM 62, 45, 30) introducing potential misleading signals can not challenge the tree topology indicating our auto-alignmented mitochondrial dataset is not artificially restricted one.

Conclusions: Finally, a repeatable prediction of the genes genealogy with reliable statistical support places Xenacoelomorpha as a basal Deuterostome. Let's enjoy the elegent metapher about Tree of LIfe —— "As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation we believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications". (Darwin 1964 [1859], p. 130).

Full Text

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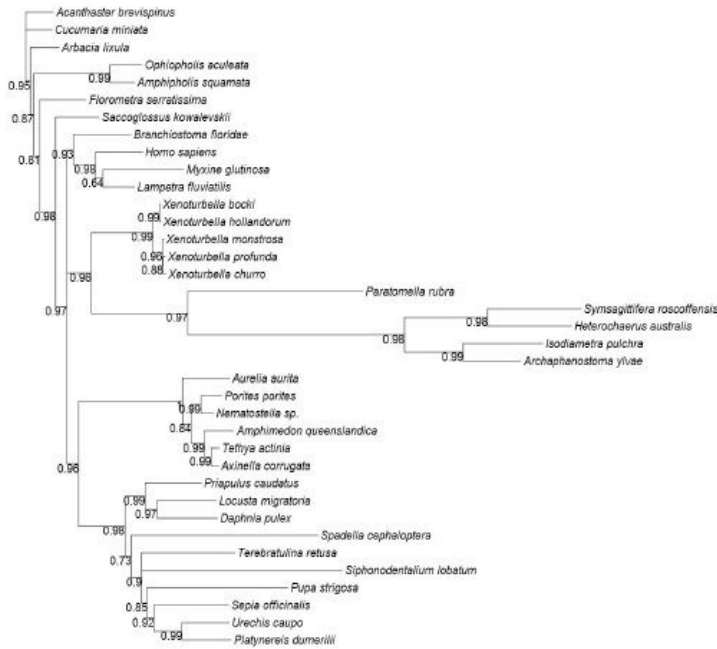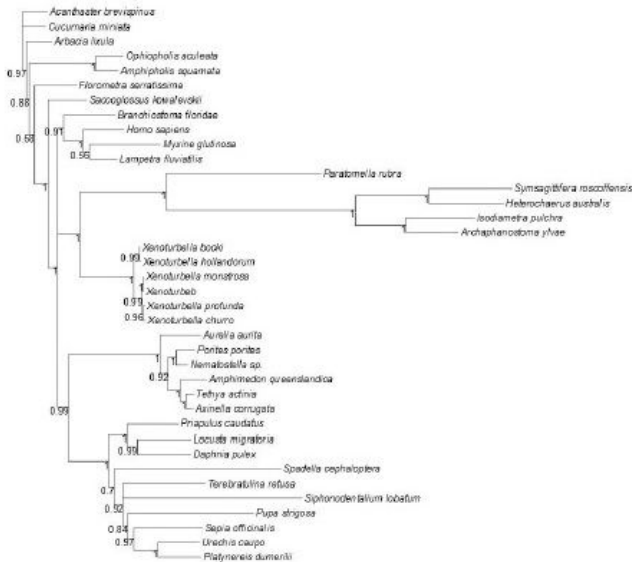# Figures
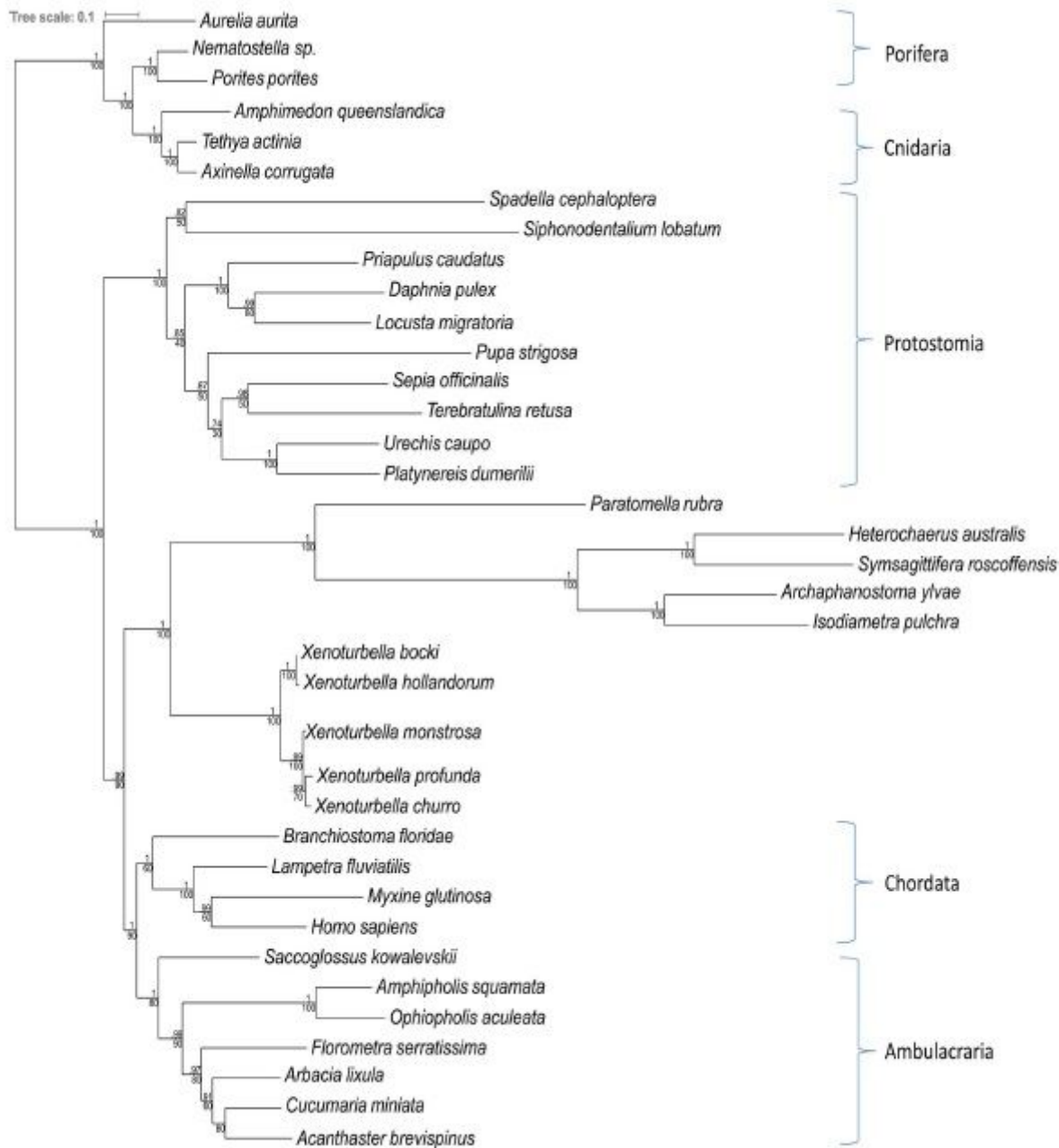
Figure 1

Xenacoelomorpha as a basal Deuterostome. Animal phylogeny based on mitochondrial proteins reconstructed using mtZOA under a Bayesian analyse and mtZOA + I + PROTGAMMA under a Maximum likelihood analyse. Xenoturbella and Acoelomorph consititute a monophyly named Xenacoelomorpha (PP=1 and BP=100), enacoelomorpha as a basal Deuterostome strongly supported (PP=0.99 and BP=90), placing chordates as a sister group of ambulacrarians(PP=1and BP=90) and recovering the monophyly of Deuterostomia (PP=0.99 and BP=90). Topology of both trees is nearly identical. Analysis carried out on auto-trimmed alignments. Scale units are substitutions per site.

Figure 2

Choosing CAT acounts for compositional heterogeneity. (a) Phylogeny of 37 species based on mitochondrial proteins reconstructed using CAT+GTR+Γ12 under a Bayesian analyse, places Xenacoelomorpha as a sistergroup of chordates with dissatisfactory internode support. (b) Phylogeny of 37 species based on mitochondrial proteins reconstructed inferred with CAT + GTR + Γ4 in a Bayesian analyse, problematically groups Xenacoelomorpha with chordates missing node support either. Cross-

validation demonstrates that CAT + GTR + Γ is better fitted model comparing to mtZOA with significantly statistical support (ΔlnL=94±14), but using mtZOA can lead to a prediction strongly supported globally. As a matter of fact, missing internode support can prove nothing but Xenacoelomorpha can be seen as a clade of Deuterostomes (PP=0.97 and PP = 1, respectively. "Xenoturbeb" is "another Xenoturbella monstrosa" illustrated in following section).
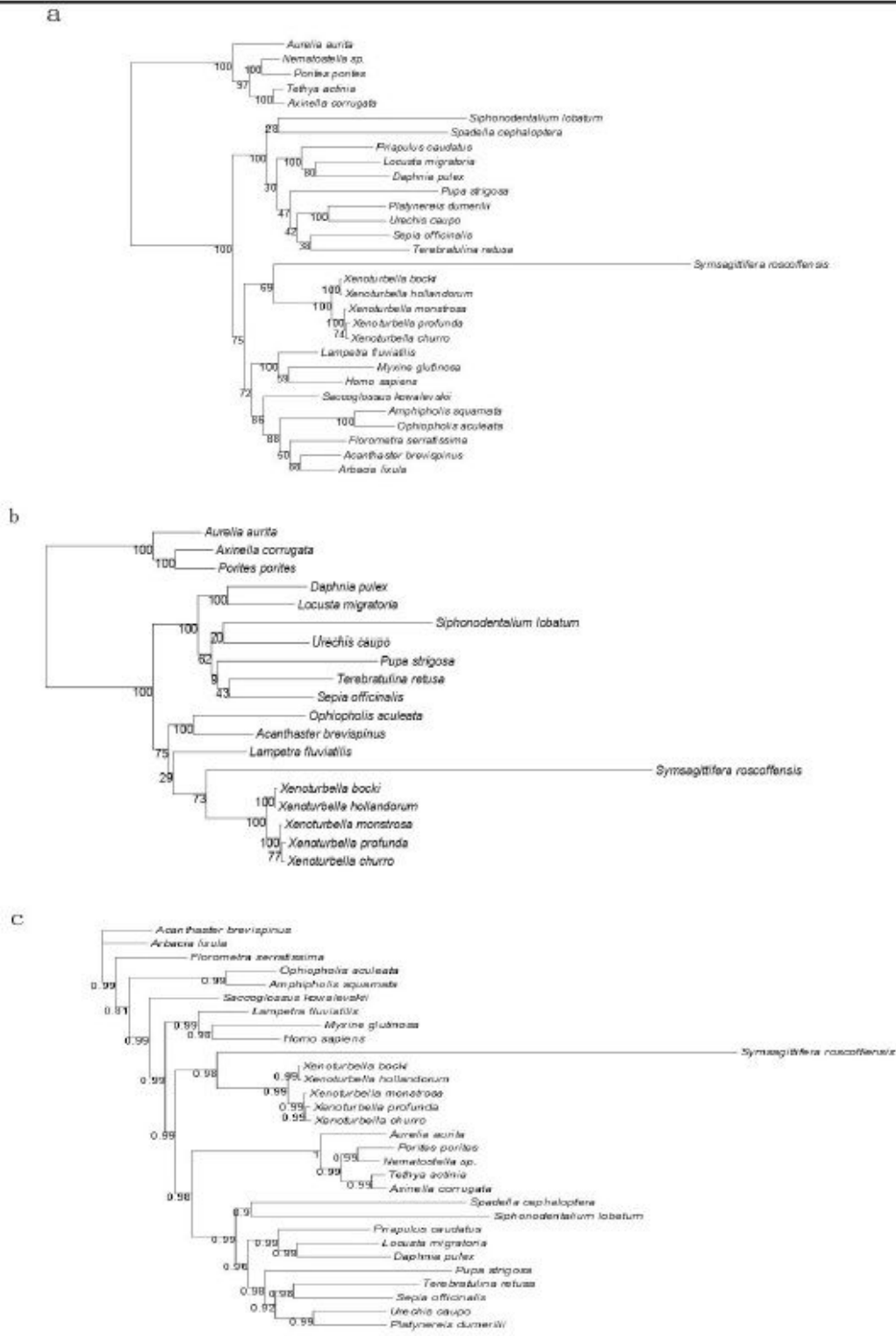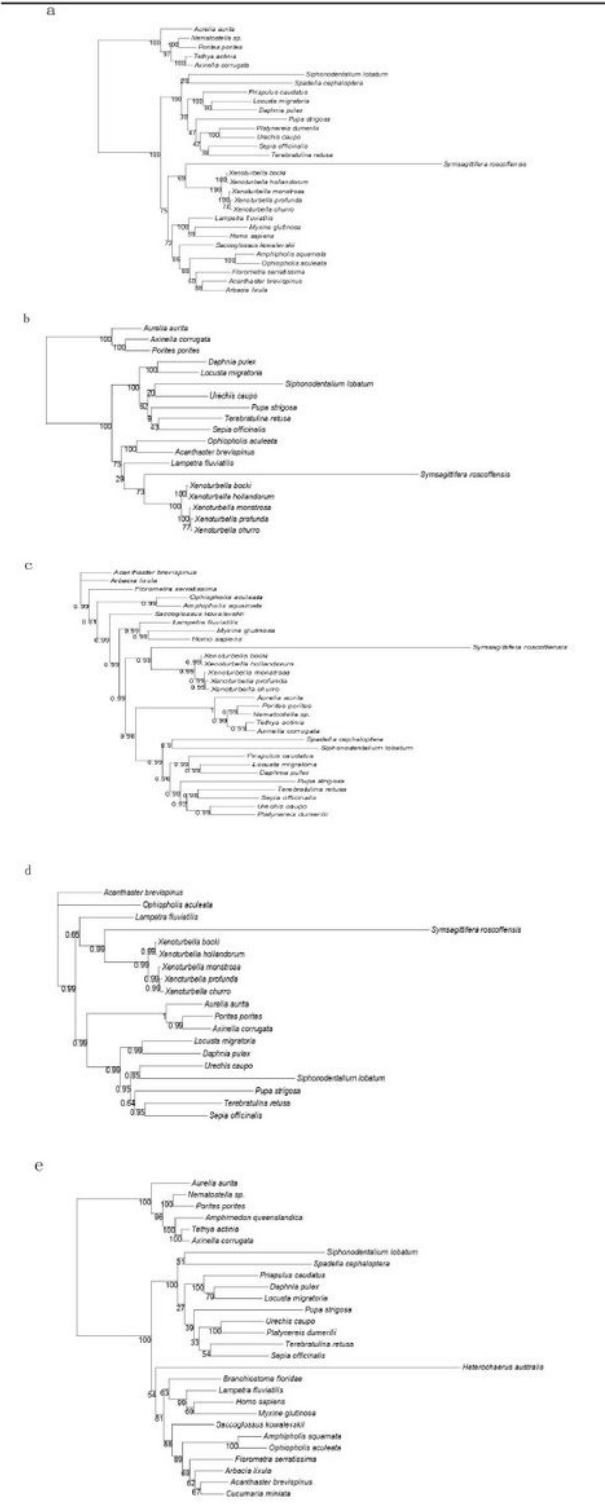

Figure 3

Comparing mtZOA and CAT model with varies aliment strategies. (a,b) Bayesian analyse using mtZOA based on matrixes conducted by alignment parameter BLOSUM30 and BLOSUM45 as the scoring matrix for amino acid sequences, position Xenacoelomorpha as the most basally branching at Deuterostome, respectively (PP=0.8 and PP=0.8). (c,d) ML analyse using mtZOA + I + PROTGAMMA based on matrixes conducted by alignment parameter BLOSUM30 and BLOSUM45, predict Xenacoelomorpha as the sistergroup of all other Deuterostome with weekly supported (BP=88 and BP=86), respectively. (e) Bayesian analyse using CAT+GTR+Γ4 based on matrixes conducted by alignment parameter BLOSUM30, position Xenacoelomorpha as a problematic clade of chordates, missing PP support. (f) Bayesian analyse using CAT+GTR+Γ4 based on matrixes conducted by alignment parameter BLOSUM45, position Xenacoelomorpha as a basal Deuterostome (PP=0.55). (a−f) Monophyly of Xenacoelomorpha haven't been challenged but the support is dissatisfactory (PP=0.84, PP=0.9, BP=59, BP=74, PP=0.73 and PP=0.73). The most enigmatic placing of Schmidtea mediterranea who is anatomically similar to almost all Xenacoelomorpha, probably caused by LBA and show no direct infection to the taxonomic placement of Xenacoelomorpha in our molecular analyse in sharp contrast to other morphological analysis.
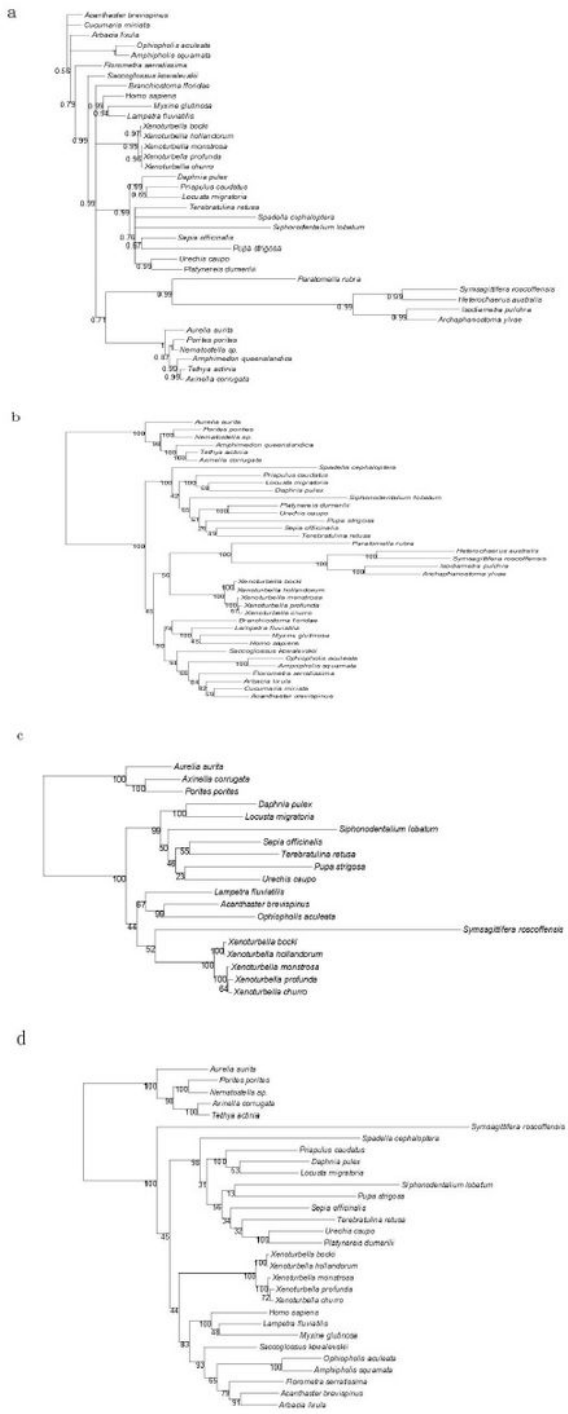
Figure 4

Varies species selection to exaggerate the violation of models. (a) 30 species phylogeny based on mitochondrial proteins reconstructed under a Maximum likelihood analysis with mtZOA + I + PROTOGAMMA, Xenacoelomorpha and five acoel species group together (BP=69) and Xenacoelomorpha within Deuterostome (BP=75) (b) 19 species phylogeny based on mitochondrial proteins reconstructed under a Maximum likelihood analysis using mtZOA + I +PROTOGAMMA, Xenacoelomorpha and five

acoel species group together (BP=73) and Xenacoelomorpha as a monophyly within Deuterostome (BP=75). Weak support can be illustrated by lacking phylogenetic signal in less taxons and the tree topology still consensus with our 37 species results. (c) 30 species phylogeny based on mitochondrial proteins reconstructed under a Bayesian analyse using mtZOA, also groups Xenacoelomorpha and five acoel species together (PP=0.98) as an early branch of Deuterostome (PP=0.99). (d) 19 species phylogeny based on mitochondrial proteins reconstructed using mtZOA under a Bayesian analyse, Xenacoelomorpha and five acoel species group together (PP=0.99), Xenacoelomorpha branching at early Deuterostome (PP=0.99). (e) Using mtZOA + I + PROTOGAMMA under a Maximum likelihood analysis with our acoel included only, demonstrates no significant LBA event.

Figure 5

Reducing the potential influence of compositional heterogeneity on Phylogenomics analyses of our datasets with Dayhoff groups. (a) 37 species phylogeny based on mitochondrial proteins reconstructed using CAT +GTR + Γ50 + Dayhoff6 under a Bayesian analyse places Acoelomorph within outgroups (PP=0.71) (b) 37 species being analyzed using PROTOGAMMA + I + Dayhoff under a ML analyse, places Xenoturbella as a basal Deuterostome but with low support (BP=45) and monopoly of

Xenoacoelomorpha being challenged (BP=56). (c) 19 species analyzed under ML using PROTOGAMMA + I + dahoff , position Xenoacoelomorpha as Deuterostome (BP=44), consititutes Acoelomorph and Xenoturbella as a monophyly (BP=52). (d) The analyse of 30 species under ML, using PROTOGAMMA + I + Dayhoff, places Xenoturbella in Deuterostome (BP=44) but Acoelomorph as a basal bilateria (BP=100).
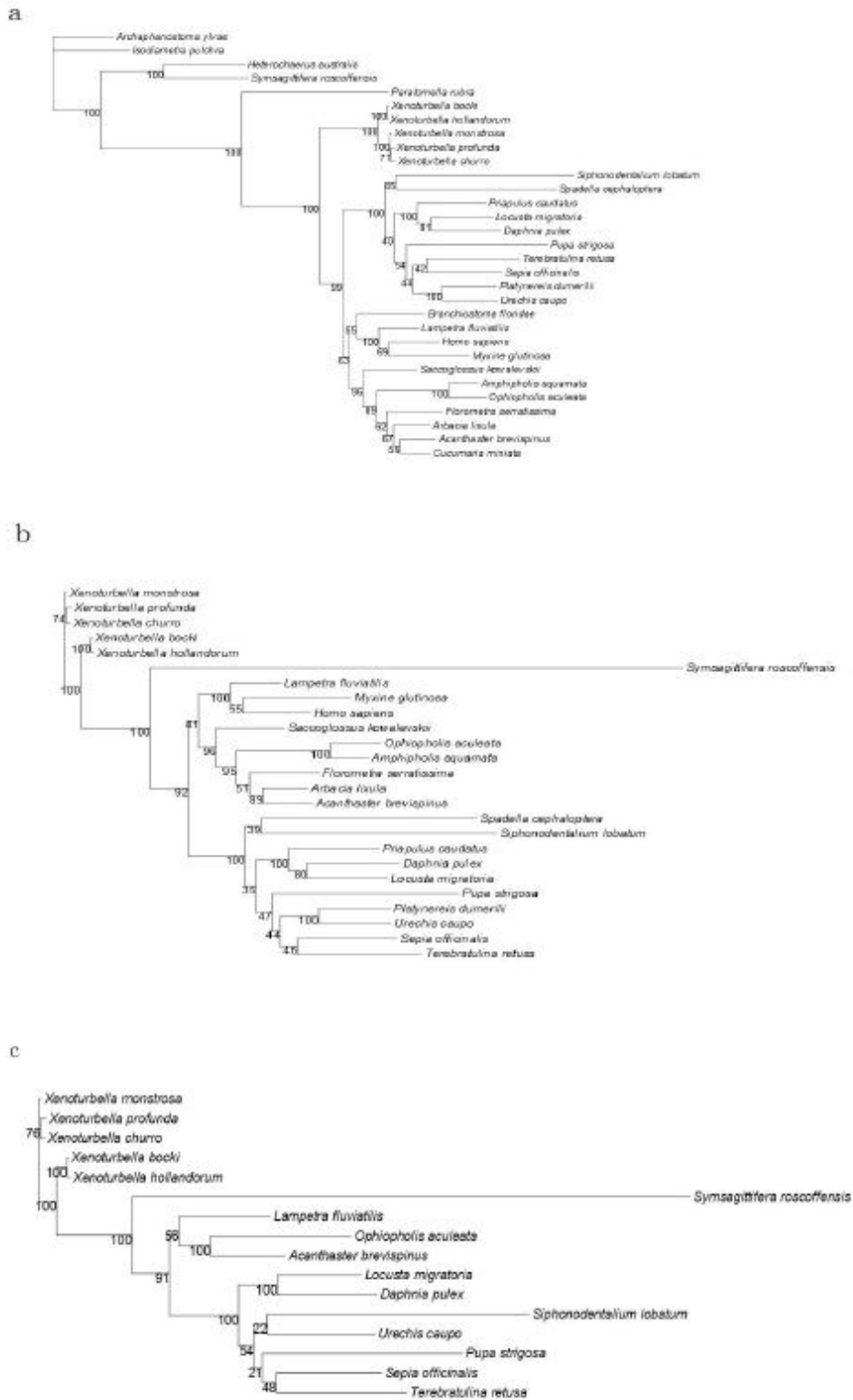

Figure 6

LBA was not the cause of this prediction. (a-c) All three taxons selections (37, 30, 19 species) without outgroups (remaining 31,25 and 16 species, respectively) position Xenoacoelomorpha as a basal Deuterostomes (BP=99,92,91) and consititution of Xenoacoelomorpha being unchallenged (BP=100,100,100), which can be comprehended as logical results after topological cutting.

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