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Genome structures resolve the early diversification of teleost fishes

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35 **Abstract:** Accurate species phylogenies are a prerequisite for evolutionary research. Teleosts are by
36 far the largest and the most diversified group of extant vertebrates, but relationships among the three
37 oldest lineages of extant teleosts remain unresolved. Based on seven high-quality new genome
38 assemblies in Elopomorpha (tarpons, eels), we revisited the topology of the deepest branches of
39 the teleost phylogeny using independent gene sequence and chromosomal rearrangement
40 phylogenomic approaches. These analyses converged to a single scenario that unambiguously places
41 the Elopomorpha and Osteoglossomorpha (bony-tongues) in a monophyletic group sister to all other
42 teleosts, i.e., the Clupeocephala lineage. This finding resolves over 50 years of controversy on the
43 evolutionary relationships of these lineages and highlights the power of combining different levels of
44 genome-wide information to solve complex phylogenies.

45

46 **One-Sentence Summary:** Whole-genome analyses place Elopomorpha (tarpons, eels) and
47 Osteoglossomorpha (bony-tongues) as sister groups at the deepest branching of crown teleosts.

48

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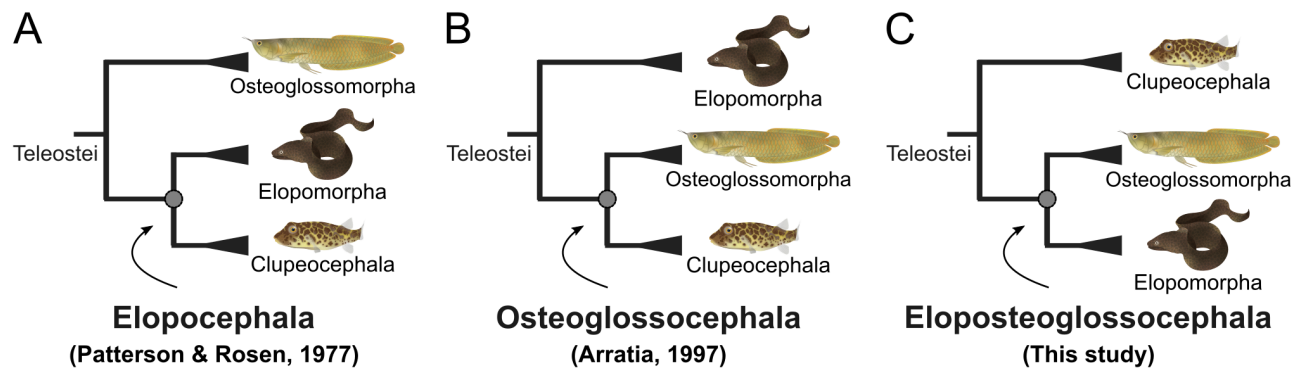
50 **Main Text**

51 Species phylogenies retrace sister-group relationships resulting from evolutionary histories and
52 pathways from common ancestors to descendant species (1). Accurate species phylogenies are
53 important for our understanding and representation of the evolution of life on earth, but they are also
54 a fundamental prerequisite for evolutionary analyses at the developmental, anatomical, genetic, and
55 species levels.

56 With more than 30,000 species, teleost fishes are by far the largest and the most diversified clade of
57 extant vertebrates (2). Understanding their phylogeny has been and is still subject to many disputes
58 at different taxonomic levels (2, 3). Among these debates, a long-standing and unresolved question
59 concerns the topology of the earliest-branching clades of crown teleosts, i.e., the Elopomorpha
60 (named after “*Elops*-like” and including tarpon, bonefish and eels) and the Osteoglossomorpha
61 (named after “bony-tongues” and including goldeye, arapaima, and elephantnose fish) relative to all
62 the other extant teleosts in the Clupeocephala lineage (including for instance zebrafish, a major
63 biomedical species) (3, 4).

64 Based on anatomical and morphological characters, Elopiformes (tarpons and ladyfishes) were first
65 suggested to be the most “primitive living teleosts” nearly 100 years ago ((5) cited in (4)). Since then,
66 Elopomorpha and Osteoglossomorpha have been alternatively placed as the earliest branching clade
67 of teleosts. A first scenario, proposed in 1977 (6), placed the Osteoglossomorpha as the earliest teleost
68 crown group and outgroup to the Elopocephala consisting of Elopomorpha and Clupeocephala. (Fig.
69 1A). This scenario was later challenged in 1997 (7, 8) by the placement of Elopomorpha as the earliest
70 branching clade of teleosts, with Osteoglossomorpha and Clupeocephala composing the
71 Osteoglossocephala clade (Fig. 1B). These early controversies were based on morphological evidence
72 and remained largely unsolved, but the most recent authoritative view still considers the Elopomorpha
73 as the earliest branching clade of crown teleosts (2).

74



75

76 **Figure 1: Alternative phylogenetic hypotheses for the earliest-branching teleost clades.** The Elopocephala (6) (A),
77 Osteoglossocephala (7) (B) and Eloposteoglossocephala (C) hypotheses respectively, propose Clupeocephala and
78 Elopomorpha, Clupeocephala and Osteoglossomorpha or Osteoglossomorpha and Elopomorpha as sister groups (see text
79 for details).

80

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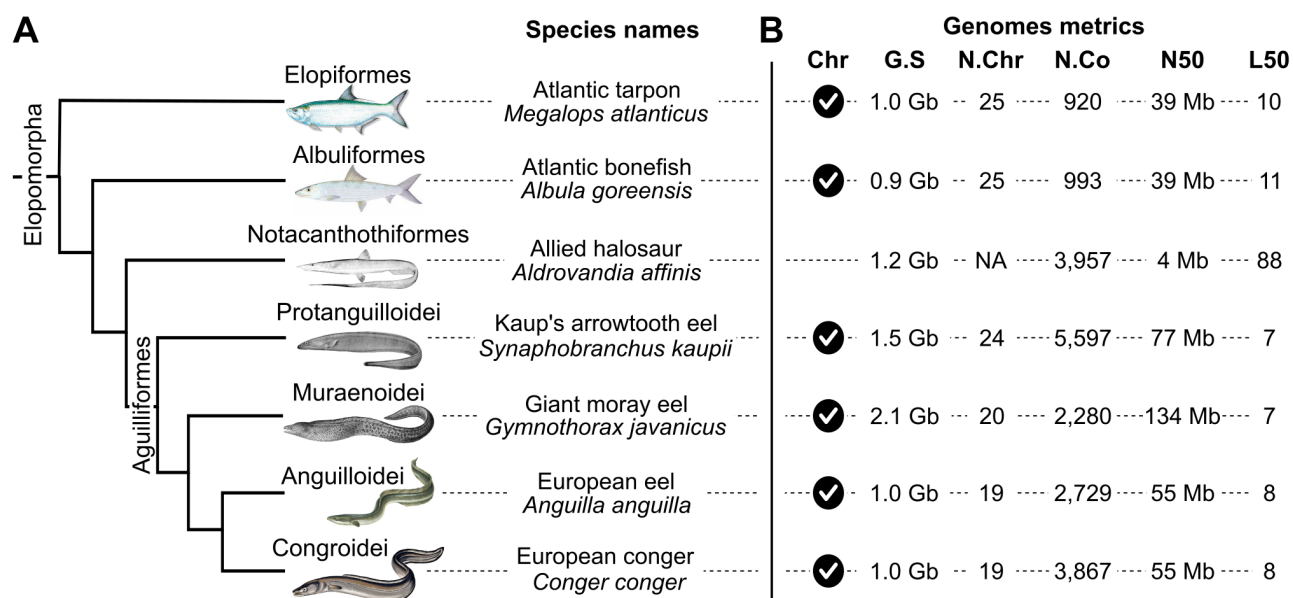
82 With the emergence of molecular phylogenetic approaches in the nineties, this question was
83 extensively revisited using gene sequence phylogeny reconstructions (reviewed in (3, 9)). Despite
84 extensive efforts, including several large-scale multi-locus approaches (10–12), no consensus has,
85 however, been reached in favor of neither the Elopocephala nor the Osteoglossocephala hypothesis.
86 In addition, a third topology placing Elopomorpha and Osteoglossomorpha as sister groups (Fig. 1C)
87 was even suggested in the early nineties (13) and since then supported by a few more recent studies
88 (11, 14–18). This clade, which we tentatively named the Eloposteoglossocephala (Fig. 1C), was never
89 formally retained, probably because this topology was not supported by any morphological evidence
90 (3). The prevailing hypothesis, confirmed by a recent meta-analysis of gene sequence phylogeny
91 studies (9), thus remains the Osteoglossocephala hypothesis that places Elopomorpha as the earliest
92 branching clade of extant teleosts (12)). However, the precise phylogenetic relationships of these
93 major teleost lineages are still debated and have even been recently reviewed by Dornburg and Near
94 (3) as one of the major unresolved questions of the twenty-first century regarding the evolution of
95 actinopterygian fishes. To promote a reexamination of this problem, they provocatively proposed to
96 retain “the unconventional and intriguing possibility of an osteoglossomorph and elopomorph sister
97 group relationship” (3).

98 To resolve the phylogenetic relationships of these early-branching teleost clades, we first sequenced,
99 assembled, and annotated high-quality reference genome sequences of seven species that represent

100 major Elopomorpha orders or families (Fig. 2 and table S1) for which chromosome-level whole-
 101 genome resources were lacking. We combined genome information from these seven Elopomorpha
 102 species with 18 additional publicly available genome assemblies including four Osteoglossomorpha,
 103 10 Clupeocephala and four vertebrate outgroups, including the spotted gar and bowfin non-teleost
 104 fishes, to perform phylogenomic analyses.

105

106



107

108 **Figure 2: Phylogeny of representative Elopomorpha species.** (A) This tree topology is based on ref. (19) and
 109 includes each species for which we provide novel whole-genome assemblies. (B) Six of these seven genomes were
 110 assembled at chromosome scale (Chr) with high-quality genome assembly metrics. G.S = genome size, N.Chr =
 111 haploid chromosome number, N.Co = number of contigs, N50 = sequence length at which half of the genome
 112 assembly is covered by longer sequences, L50 = smallest number of scaffolds needed to sum to half of the predicted
 113 genome size.

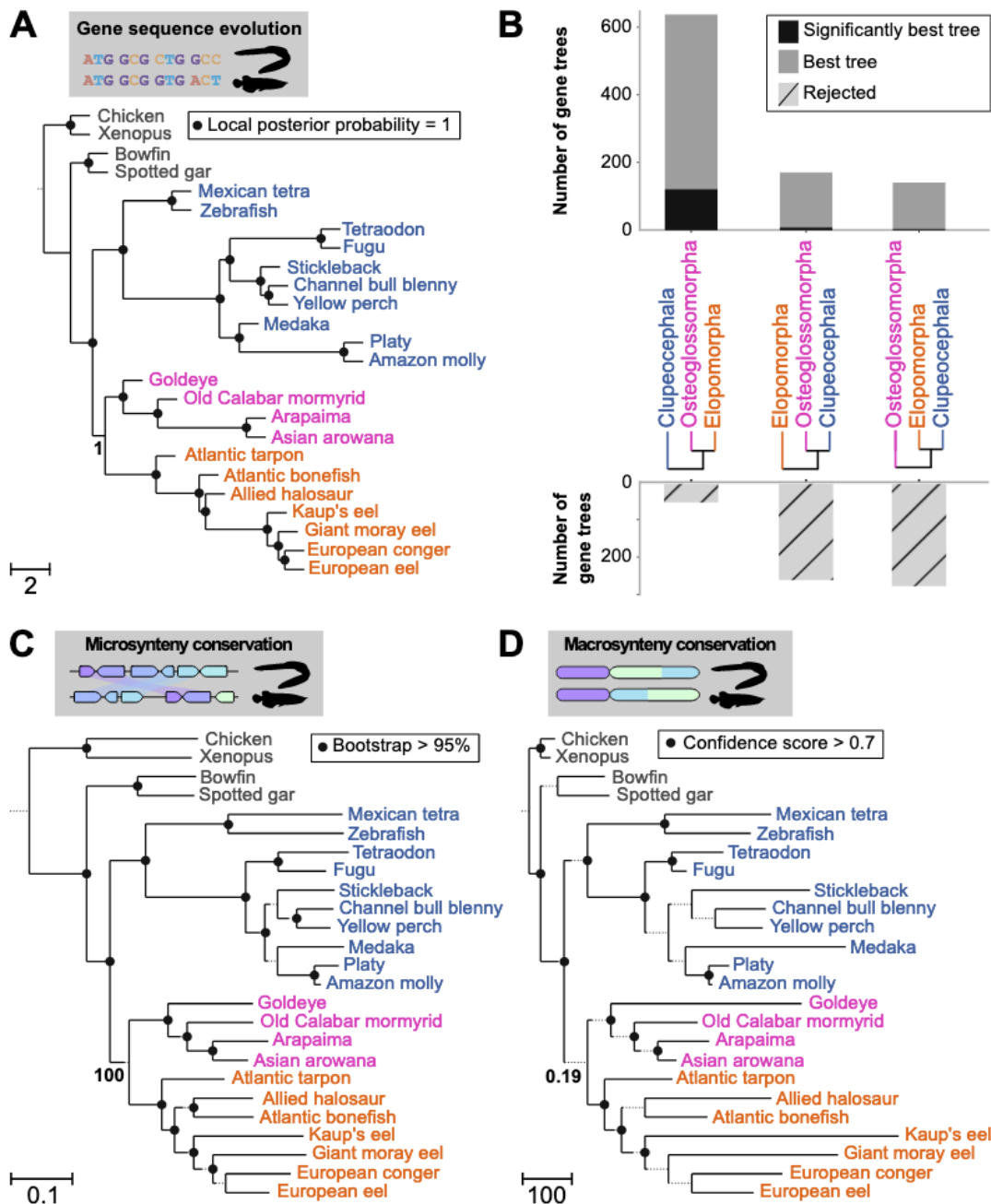
114

115

116 A major challenge for achieving accurate phylogenetic analysis of teleost genomes is their high
 117 number of duplicate (paralogous) gene copies. Many of these paralogs are inherited from a whole
 118 genome duplication (WGD) in their last common ancestor (20), and are known to mislead
 119 phylogenetic reconstructions (11). To mitigate the effect of paralog inclusion, we applied a WGD-
 120 tailored pipeline leveraging gene sequences and synteny conservation (supplementary materials,

121 Methods section) to select 955 high-confidence 1-to-1 orthologous genes across all the 25 genomes
122 we analyzed. This list represents by far the largest molecular dataset considered for teleost phylogeny
123 reconstruction, both in terms of included Elopomorpha genomes and of total alignment size (see fig.
124 S1). We then performed phylogenetic reconstructions of these 955 individual gene trees using
125 summary analyses with ASTRAL (Fig. 3A, and fig. S2 for protein trees), as well as Maximum
126 Likelihood analyses of their concatenated sequences both at the nucleotide and amino-acid levels (fig.
127 S3 and S4). These analyses all provided highly significant support for the Eloposteoglossocephala
128 hypothesis that places Osteoglossomorpha and Elopomorpha as sister groups. Additionally, this
129 Eloposteoglossocephala clade was further supported by gene-genealogy interrogation, which directly
130 compares the likelihood of each of the three evolutionary scenarios based on individual gene sequence
131 alignment (Fig. 3B).

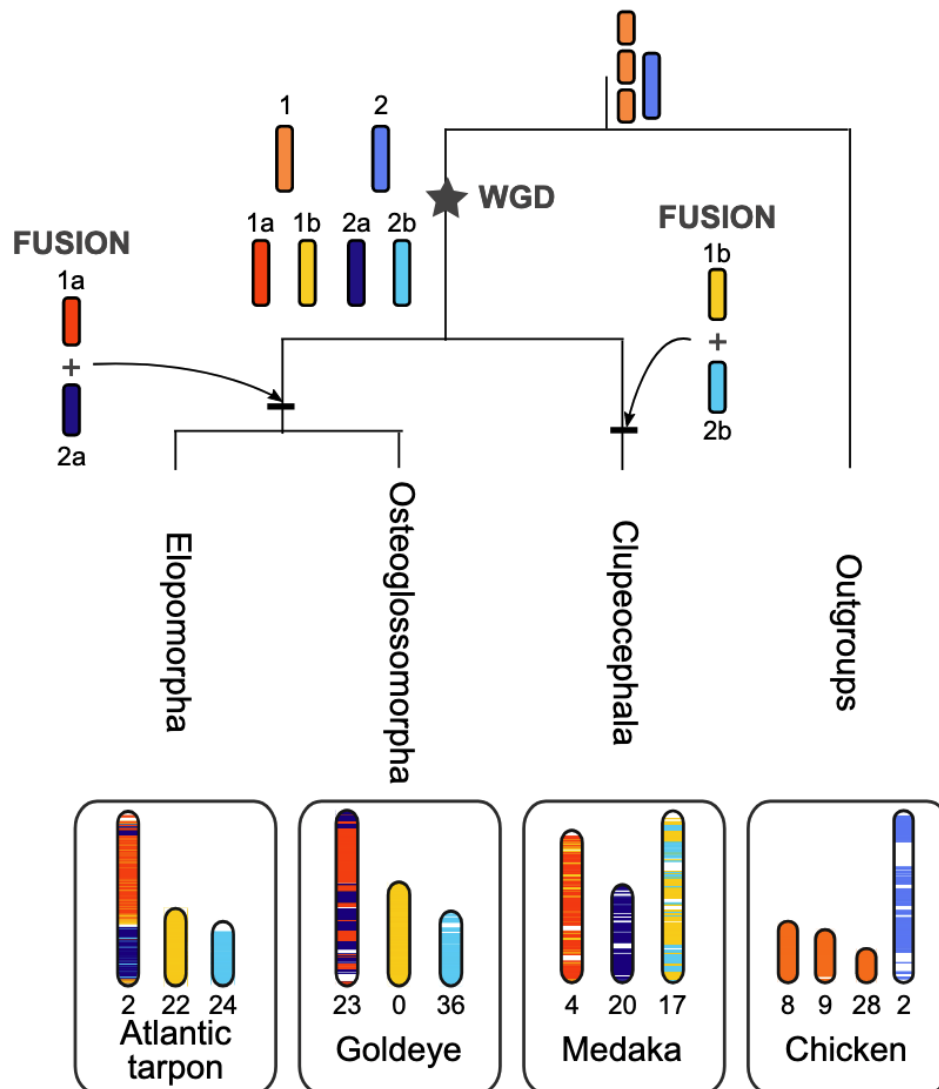
132 However, because previous sequence-based studies have yielded opposing results to resolve the three
133 early diverging teleost branches (9, 11), we also used two novel genome-wide methods to infer
134 species trees based on conservation of genome structures. First, we analyzed the conservation of gene
135 adjacencies between 3,041 orthologous marker genes covering 57-98% of each teleost genome, and
136 inferred a Neighbor-Joining species tree from local microsyntenic conservation (21). Second, we
137 analyzed macrosyntenic evolution by measuring the fraction of shared chromosomal breakpoints
138 between species with PhyChro (22). These two complementary approaches (Figs. 3C-3D, fig. S5)
139 also provided convergent and robust support for the Eloposteoglossocephala scenario, confirming the
140 results from gene sequence phylogenies.



141

142 **Figure 3: Different phylogenomic reconstruction methods converge to support Osteoglossomorpha and**
 143 **Elopomorpha as sister groups.** (A) Species tree inferred under the multispecies coalescent model (23) from 955
 144 single-copy gene trees. This method measures internal branch lengths in coalescent units, while lengths at terminal
 145 branches are represented as equal and arbitrary. Node support is calculated as a local posterior probability. (B)
 146 Molecular gene genealogy interrogation: number of gene trees supporting each hypothesis (top, gray bars),
 147 significantly supporting each hypothesis (top, black bars), and number of significantly rejected gene trees (bottom,
 148 dashed bar). (C) Neighbor-Joining species tree estimated from gene adjacencies between 3,041 marker genes.
 149 Branch lengths represent the proportion of broken adjacencies and nodes are supported by bootstrap values. (D)
 150 Best-supported species tree based on shared synteny breakpoints. Branch lengths are an estimate of the number of
 151 breakpoints. Node supports correspond to the fraction of informative breakpoints that support the clade (22). (A-D)
 152 Broken lines have been added to very short branches, for visualization purposes.

153 Finally, by looking at all potential chromosomal macro-rearrangements we identified a single
 154 chromosomal fusion exclusively shared between karyotypes of Osteoglossomorpha and
 155 Elopomorpha species (Fig. 4, fig. S6). Together with the absence of other rearrangements that would
 156 be consistent with alternative groupings, this identical chromosomal macro-rearrangement further
 157 supports that the two groups descend from a common ancestor, strengthening the phylogenomics
 158 evidence for the Elopsteoglossocephala clade.
 159



160

161 **Figure 4: Chromosomal rearrangement shared within the Elopsteoglossocephala clade.** Inferred
 162 rearrangement scenario for two pairs of duplicated chromosomes (1a-1b and 2a-2b) in teleosts. Osteoglossomorpha
 163 and Elopomorpha share the 1a-2a chromosomal fusion, while Clupeocephala experienced an independent fusion
 164 between 1b and 2b.

165

166 Using a combination of new whole-genome resources for Elopomorpha and an array of
167 complementary phylogenomic reconstruction methods, we unambiguously resolved the long-
168 standing question of the topology of the deepest branches in the phylogeny of extant teleost fishes.
169 This achievement highlights the power of genome-wide methods to resolve complex and ancient
170 phylogenies, especially when these methods consider a variety of informative evolutionary characters
171 in complement to sequence information. Chromosome rearrangements, in particular, are fixed at a
172 low rate and thus are less prone to mutational saturation and character reversal, which can occur in
173 sequence-based phylogenies (24).

174 Our results resolve over 50 years of controversy and demonstrate that Elopomorpha and
175 Osteoglossomorpha constitute a clade for which we propose the name Eloposteoglossocephala
176 (supplementary materials, section 1). This conclusion raises questions about the paucity of anatomical
177 evidence in favor of this hypothesis, despite more than 70 years of extensive research (3, 4). We
178 carefully reexamined the available literature on these anatomical characters in light of our results and
179 we were not able to find a morphological character exclusively and unambiguously shared by
180 Elopomorpha and Osteoglossomorpha (supplementary materials, section 2). However, the fusion of
181 the retroarticular with the angular and/or the articular, a derived character previously considered a
182 synapomorphy of the Elopomorpha (25, 26), has been shown to be shared with at least mormyrids
183 among bony-tongues (26, 27). Even if this character is described as either present (27) or ambiguous
184 in goldeye *Hiodon alosoides*, and absent in two other Osteoglossomorpha (26), we propose this
185 derived state as a morphological synapomorphy of the Eloposteoglossocephala, which was
186 secondarily lost in some Osteoglossomorpha. We anticipate that based on our results, more character
187 mapping and new targeted anatomical and morphological searches will soon provide novel and non-
188 ambiguous synapomorphies shared by the Eloposteoglossocephala.

189

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282 **Author contributions:**

283 Conceptualization: CB, JB, IB, YG, CK, AL, JHP, MRR, HRC

284 Software: CB, AL, EP, HRC

285 Formal analysis: CB, AL, EP, HRC

286 Investigation: CB, OB, CC, AC, CD, RD, CFB, YG, CI, HJ, EJ, CK, GL, JL, AL, JM, EP,

287 HRC, CR, MW, MZ

288 Resources: JB, IB, WJC, RD, YG, CH, HJ, SM, JHP, AT, MW

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291 Funding acquisition: CB, JB, CD, YG, JHP, MRR, HRC

292 Project administration: YG

293 Supervision: CB, YG, HRC

294 Writing – original draft: CB, YG, EP, HRC

295 Writing – review & editing: CB, JB, IB, CC, TD, YG, GL, EP, HRC, CR, MRR

296

297 **Competing interests:** Authors declare that they have no competing interests.

298 **Data and materials availability:** The Whole Genome Shotgun projects for the seven

299 Elopomorpha species are available in the Sequence Read Archive (SRA), under the following

300 BioProject references PRJNA702045 (*Conger conger*), PRJNA692825 (*Albula goreensis*),

301 PRJNA743502 (*Aldrovandia affinis*), PRJNA690086 (*Megalops atlanticus*), PRJNA693699

302 (*Anguilla anguilla*), PRJNA743503 (*Synaphobranchus kaupii*), PRJNA702255 (*Gymnothorax*

303 *javanicus*). All genome assemblies plus their annotations are also available in the omics Dataverse

304 (Open source research data repository) server (<https://doi.org/10.15454/GWL0GP>). All input data

305 (sets of orthologous marker genes, CDS codons alignments, gene coordinates files) and the

306 generated reconstructed species phylogenies have been deposited in Zenodo (doi:

307 10.5281/zenodo.6414307), along with all scripts and environments to reproduce the analyses.